

SELECTION ON THE FERTILITY OF TRANSLOCATION
HETEROZYGOTES IN DROSOPHILA MELANOGASTER. 1.
THE EXTENT OF THE CHANGES PRODUCED BY SELECTION

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ABSTRACT

As part of a study on the suitability of translocations for insect pest control, artificial selection was applied for either higher or lower egg hatchability in each of the reciprocal matings between a translocation heterozygote and a translocation homozygote. In each of four selection lines, there was response to selection but, after 3-4 generations, limits were reached beyond which further selection gave no response. On reversing the directions of selection, the high and low lines rapidly exchanged their levels of egg hatchability and then established new plateaux. Relaxation of selection caused convergence towards the original unselected level. It is concluded that individuals with extremely high or low fertility were disfavoured by natural selection. Populations initiated from two different translocation homozygotes formed a stable polymorphism and after propagation in bottles for 10 generations, small increases were found in the fertility of the double translocation heterozygotes compared with the same genotype newly produced from unselected homozygote stocks. It is concluded that, under the conditions of the bottle cultures, natural selection favoured increase in fertility of the double heterozygotes.

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INTRODUCTION

It is well known that from meiosis in translocation heterozygotes there may segregate gametes with either a normal set of chromosomes, a complete translocated set, or various kinds of duplication-deficiency sets which act as zygote lethals. Hence translocations cause inherited partial sterility and it has been proposed (Serebrovskii, 1940; Laven, 1968; Curtis, 1968) to utilize this property for insect pest control.

In Oenothera (Renner, 1925) and certain Orthoptera (Lewis and John, 1957) translocations exist in natural populations without causing partial sterility, and Lawrence (1963) showed that considerable selection response could be obtained for enhanced fertility of translocation heterozygotes in rye. The question therefore arises whether insect pest populations could evolve so that translocations would lose their power to cause high levels of sterility. We have made a limited study of this question in the Housefly (Hossain and Curtis, in press) and a more intensive study in Drosophila. This paper describes the immediate effects of selection on fertility in Drosophila.

The selection was of two types: (a) artificial selection on egg hatchability between single pair matings of specified genotypes; (b) natural selection in random bred populations in bottles. Robinson (1971) showed that a population of the latter type would continue to segregate for translocation heterozygotes and homozygotes if it was initiated from two translocation homozygotes which could not recombine with each other; conversely, if a translocation homozygote and wild type were mixed, the translocation was rapidly eliminated (Robinson and Curtis, 1973). Thus only the double translocation system was suitable for testing for the effects of prolonged natural selection on translocation heterozygote performance.

METHODS AND MATERIALS

The Oregon R wild type of Drosophila melanogaster and two 2:3 translocation homozygote stocks were obtained from Dr. P. T. Ives, Amherst College, Massachusetts, U. S. A. The translocations are referred to as T_1 and T_2 and their break-points have been located by Robinson and Curtis (1972). The T_1 and T_2 translocations show respectively "smudge" eye and glass eye (Ives, 1965) recessive visible position effects.

Standard Drosophila maintenance methods were used. For measurement of egg hatchability, individual mated females were allowed to lay eggs on charcoal agar for 24 hours, the number of larvae which had hatched after 48 hours was counted and the larvae were then transferred to standard rearing medium.

In order to be able to select repeatedly on matings involving T_1 translocation heterozygotes, the heterozygotes were continually crossed

to $T_1 T_1$ translocation homozygotes (fig. 1). After selecting the four most extreme single pair progenies on the basis of egg hatchability, the offspring were classified as heterozygotes or homozygotes according to whether they had wild type or "smudge" eye and the crosses were repeated, using males and females from different progenies so as to minimise inbreeding. Four selection lines were made: two "male" lines in which male heterozygotes were mated to female homozygotes and two "female" lines in which the reciprocal cross was made. Within each pair of lines, one was selected for high and one for low hatchability. The four lines are referred to as MH, ML, FH and FL.

Two experiments were run in which populations initiated from $T_1 T_1$ and $T_2 T_2$ homozygotes were allowed to breed in standard *Drosophila* bottles, the generations being made discrete by destroying the adults after egg laying and placing a random sample of 200 of the emerging adults into new bottles.

RESULTS

The effects of artificial selection

Fig. 2 and 3 show the effects of selection in the four lines. The generation means are based on the means of the percentage hatchability in 24 single pair matings each of which yielded about 40 eggs. The 95% confidence limits were calculated from the standard errors, computed from the 24 hatch observations without transformation. The means of the four matings selected to be the parents of the next generation are indicated in figs. 2 and 3 by stars.

All four lines showed a moderate response to selection for 3-4 generations, after which plateaux were reached despite the continued application of strong selection. The precision of this statement can be somewhat increased by calculation of the realised heritability of egg hatchability (Falconer, 1960). The realised heritabilities were calculated by dividing the total response to selection over the specified generations by the cumulative selection differentials (i.e. the sum of the differences, between the selected parents and their generation means). As shown in Table 1, the realised heritabilities were 10-20% in the first three generations and averaged virtually zero thereafter. At every generation after the second, the high and low selection lines and highly significantly different hatchabilities, as shown by the non-overlap of the 95% confidence limits of the means.

Reversed and relaxed selection

The fact that selection limits were reached might be explained by the exhaustion of relevant genetic variability. This was tested in the female selection lines by reversing the direction of selection after the 18th generation. The result was a very rapid exchange of levels of hatchability

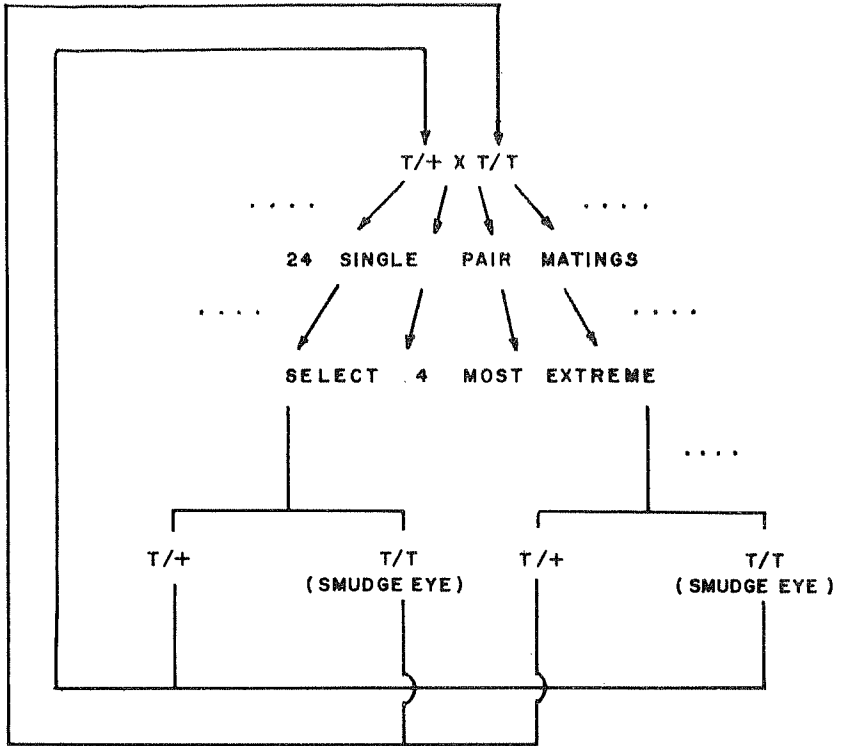


Fig. 1 Diagram of the method of artificial selection $T/+$ = translocation heterozygote, T/T = translocation homozygote, which shows the "smudge" eye recessive position effect.

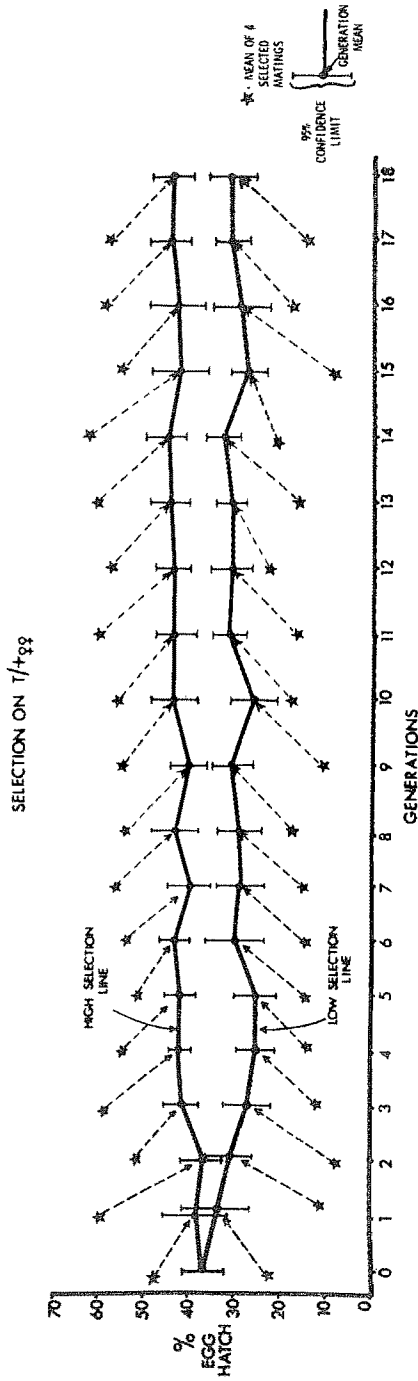


Fig 2 The results of selection in the FH and FL lines. At each generation female translocation heterozygotes were mated to translocation homozygote males.

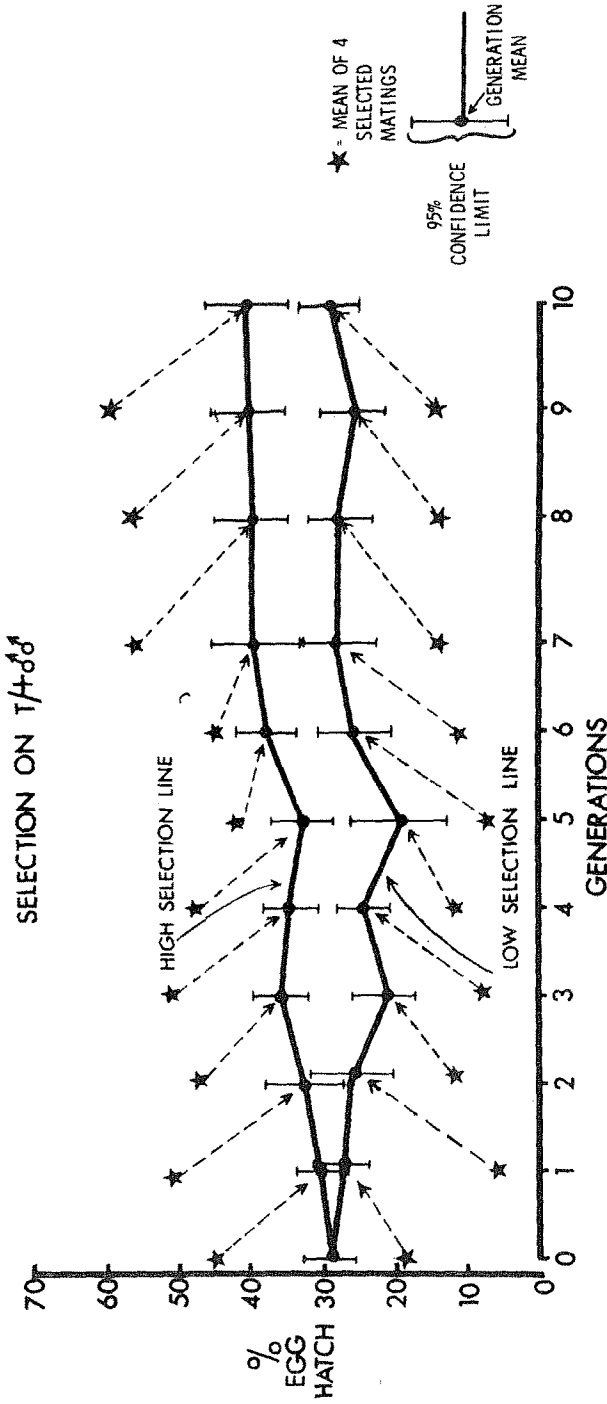


Fig 3 The results of selection in the MH and ML lines. At each generation female translocation homozygotes were mated to male translocation heterozygotes.

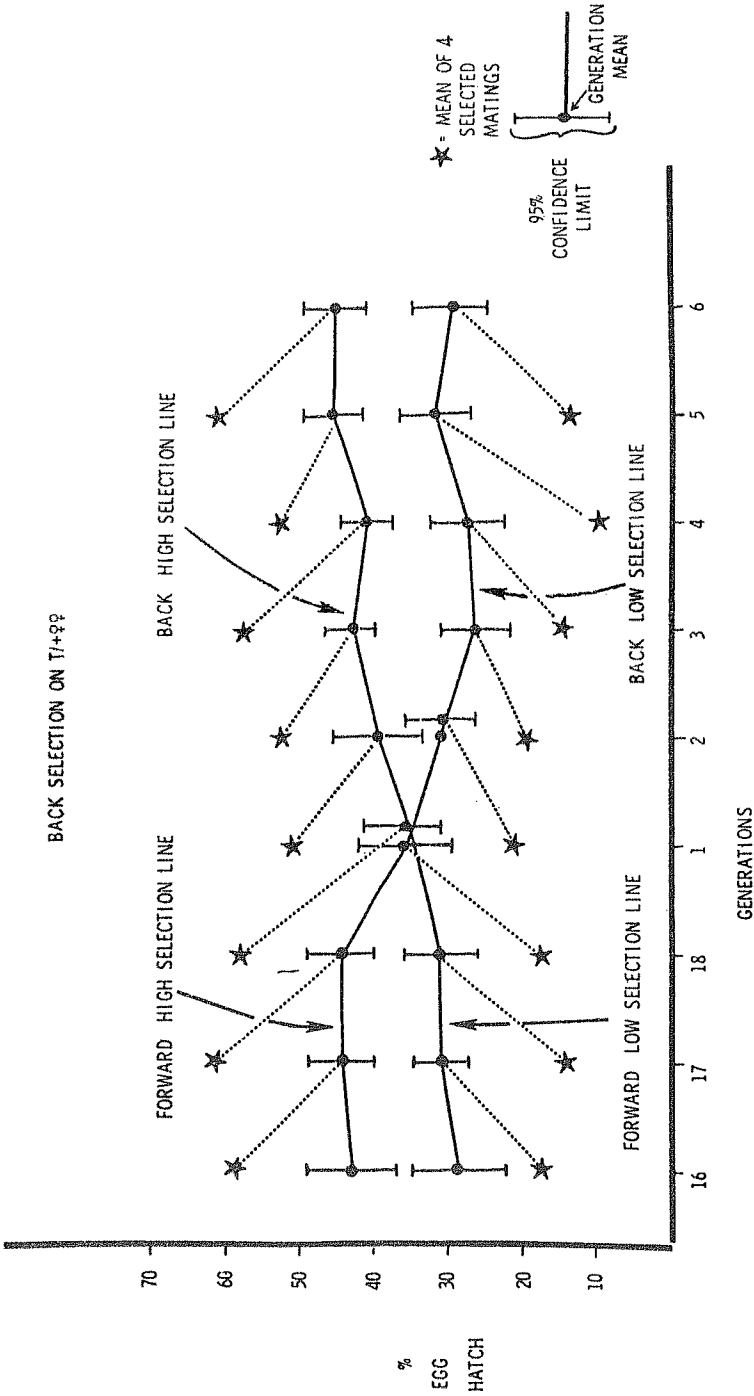


Fig 4 The results of reversal of the direction of selection: downward selection on the FH line and upward selection on the FL line. The horizontal scale shows generations from initiation of forward selection and from the reversal of selection.

by the two lines and the re-establishment of selection limits (fig. 4). The realised heritability during the first three generations of reverse selection was 23-40% (Table 1).

Table 1. Realised heritability in the selection lines

Line	Generations	Response to selection	Cumulative selection differential	Realised heritability (%)
(a) Forward selection				
MH	0-3	6.1	51.0	11.0
MH	3-10	4.0	95.9	4.1
ML	0-3	7.7	44.0	17.9
ML	3-10	-4.6	82.1	-5.5
FH	0-3	5.6	49.0	11.5
FH	3-18	2.3	207.1	1.1
FL	0-3	9.0	59.9	15.1
FL	3-18	-3.3	213.8	-1.6
(b) Reversed selection				
FH	0-3	17.9	40.4	44.3
FL	0-3	12.4	52.3	23.6

These results prove that the original selection limits were not reached because of exhaustion of genetic variability. The most probable alternative hypothesis is that the limits were reached because of a conflict between natural and artificial selection, i. e. lower average fitness of the individuals with more extreme egg hatchabilities. To test this, selection was relaxed in both the FH and FL lines and the lines were inbred for six generations without measuring fertility. Subsequently the hatchability was measured once more and the two lines were found to have converged to 36-37%, i. e. virtually the same as the original unselected level. It is concluded that artificial selection in both directions was being powerfully opposed by natural selection and when the former was removed, the latter rapidly restored the original hatchability level. It is remarkable that in the high lines natural selection was actually favouring individuals with lower fertility.

Egg number and larval survival

One possible source of the natural selection against individuals with extreme egg hatchability rates might have been differences in numbers of eggs produced in 24 hours. Data on this parameter had been collected in the course of obtaining the hatchability scores. The correlation coefficients of egg production and egg hatch were calculated and gave the following results : MH -0.124; ML +0.071 ; FH -0.170 ; FL +0.150. There were 22 degrees of freedom in each case and all four values were non-significant. Thus it appears that fecundity was not the component of fitness which was negatively correlated with extreme hatchability levels, but no further attempt was made to identify the relevant fitness component.

Dr. R. Grell (personal communication) suggested to us that the cause of the changes in hatchability in the selection lines might have been a shift in the average time at which duplication-deficiency zygotes died and that in the high lines an increased proportion of individuals were surviving past the egg hatch stage to die later. On this hypothesis there would have been a lower larval survival in the high lines. In order to obtain a meaningful measure of relative viability of different genotypes of *Drosophila* larvae it is necessary to carry out the tests at densities below that at which competition between the larvae is significant. It was found that, provided input densities of first instar larvae were less than 30 per 8ml of food medium and 15 mg of pasted yeast, there was a linear relationship of output of adults to input of larvae. First instar larvae of the FH and FL lines and from a cross of unselected T_1 homozygotes x heterozygotes were inoculated at a density of 30 per tube. The mean yields of adults (\pm s. e.) from 10 tubes of each were 26.3 ± 0.83 , 25.3 ± 0.84 and 26.0 ± 0.80 . Thus there is no evidence for any difference in rate of lethality in the larval or pupal stages and it is concluded that the differences in egg hatchability between the lines reflect differences in the proportion of zygotes with lethal genotypes.

Effect of natural selection in polymorphic populations

Homozygotes for the T_1 and the T_2 translocations were mixed in either a 4:1 or a 1:4 ratio and allowed to breed in bottles. Within three generations the ratio of flies showing the position effects characteristic of the two types of homozygote and wild type phenotype had reached approximately 15% : 15% : 70% in each bottle population and this ratio was maintained in seven subsequent generations. This confirms the suggestion of Robinson (1971) that this system constitutes a stable polymorphism. Test matings from the 10th generation of breeding of 140 individuals with wild type phenotypes showed that each was partially sterile, i. e. no non-translocation homozygotes had been produced by recombination of the translocations. A sample of 22 of the males with wild type phenotype were mated both to the T_1T_1 and T_2T_2 homozygotes and each gave some T_1T_1 progeny from the first mating and some T_2T_2 progeny from the second, thus proving that the parents were double heterozygotes.

To test the fertility of the double heterozygotes, males and females with wild type phenotype from the 10th generation of breeding of each bottle population were mated individually to unselected $T_1 T_1$ homozygotes, the egg hatchability was counted and the progeny were reared to the adult stage and the eye phenotypes checked. From a few individuals no "smudge" eye $T_1 T_1$ homozygous progeny were found and the hatchability data from these individuals were ignored because of the possibility that they were not double heterozygotes (though, in fact, these individuals showed the same mean level of partial sterility as the rest). Table 2 shows the mean hatchabilities from matings which yielded some $T_1 T_1$ progeny from each bottle population. For comparison, double heterozygotes were made by crossing unselected $T_1 T_1$ and $T_2 T_2$ stocks. As shown in Table 2 both sexes of double heterozygotes from each of the bottle populations showed slightly, but statistically significantly, higher egg hatchability than the controls, indicating that natural selection in the ten generations of rearing had adjusted the double translocation heterozygotes to give enhanced fertility.

Table 2. Comparison of the fertility of $T_1 T_2$ double heterozygotes produced by crossing unselected homozygote stocks and those obtained from the tenth generation of polymorphic populations maintained in bottles.

Sex of double heterozygote	Source	No. of single pair matings	Mean egg hatchability (%)	Standard error	Bottle populations compared with unselected	
					\bar{t}	\bar{p}
Male	Unselected	24	37.91	1.58	-	-
Male	Bottle 1	24	44.60	2.00	2.62	~ 0.01
Male	Bottle 2	22	43.64	1.77	2.42	< 0.025
Female	Unselected	24	36.39	1.04	-	-
Female	Bottle 1	20	42.02	1.34	3.34	< 0.005
Female	Bottle 2	20	42.48	0.79	4.46	< 0.0001

Notes : Bottle populations nos. 1 and 2 were initiated from, respectively, a 4:1 and a 1:4 ratio of the $T_1 T_1$ and $T_2 T_2$ homozygotes. In each case the double heterozygotes were mated to the unselected $T_1 T_1$ stock.

DISCUSSION

All four artificial selection lines showed response to selection, but within 3-4 generations selection limits were reached (figs. 2 & 3). This result is very similar to that obtained with an equal intensity of selection

on matings of Houseflies heterozygous for a translocation (Hossain and Curtis, In press). The results differ from those briefly reported by Erk (1960) which did not show a statistically significant response to selection for fertility of Drosophila translocations.

The evidence from reversal of selection (fig. 4) and relaxation of selection showed that the selection limits were reached because of conflicts between natural and artificial selection. This is a frequent result in artificial selection programmes (Lerner, 1954). It seems paradoxical that natural selection reduced the hatchability when selection was relaxed in the HF line but it produced increases in hatchability in the populations maintained in bottles (Table 2). This may be explained by supposing that the intensive artificial selection and its associated inbreeding left little opportunity for recombination of genes affecting fitness and those affecting hatchability, whereas this recombination could occur in conditions of relatively mild natural selection and the larger breeding populations in the bottle experiments. The latter conditions are more comparable to those that would be experienced in the practical application of translocations to insect control. Krishnamurthy (1974) and Krishnamurthy et al (in preparation) found increases in fertility during laboratory breeding of male-linked heterozygous translocation complexes in Culex fatigans and the increases were somewhat larger than those indicated in Table 2.

When the T_1T_1 and T_2T_2 homozygotes were mixed in either a 4:1 or a 1:4 ratio, the populations rapidly approached the same balanced polymorphic ratio, with adults of the two homozygotes at approximately equal frequencies and adult double heterozygotes at considerably more than the Hardy-Weinberg expectation of 50%. This confirms the conclusion of Robinson (1971) and Robinson and Curtis (1972) that these two translocations do not recombine and, despite their fertility advantage, the net fitness of the homozygotes is considerably less than that of the double heterozygotes. The observed polymorphic ratio indicates approximately equal fitness of the two homozygotes and considerable advantage in fitness of the double heterozygotes at the larval stage. The data in Table 2 indicate only very slightly greater fertility in male double translocation heterozygotes than in females. This contrasts with the much greater sex differences in the data of Robinson and Curtis (1972) on the same genotype. The cause of this discrepancy is unknown.

It is tempting to conclude that the responses to selection for egg hatchability in matings involving translocation heterozygotes were due to changes in the proportions of alternate and adjacent segregation at meiosis, as found in rye by Sun and Rees (1967). However, before this conclusion can be drawn it is necessary to consider other possible effects of selection on genes affecting egg hatchability. Investigation of this requires a comparison of the homozygotes from the selection lines and the results of this and discussion of the nature of the differences between high and low lines will be published separately (Hossain and Curtis, in preparation).

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