

## Fitness of third chromosome homozygotes in *Drosophila melanogaster*

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### SUMMARY

A population cage experiment has been carried out to estimate fitness for a sample of fourteen non-lethal third chromosomes in *D. melanogaster*. This measurement, which should take into account all aspects of fitness, gives an estimated mean fitness of chromosome homozygotes of approximately ten percent.

The experiment reported in this paper using the third chromosome of *D. melanogaster* closely parallels an experiment on second chromosome homozygotes reported previously (Sved, 1971). In view of the extremely low homozygote fitnesses obtained in that study (mean of about 15 %), it seemed worthwhile to see whether this finding could be extended to third chromosome homozygotes. As shown below, the estimated fitness of third chromosome homozygotes is if anything lower.

### METHODS AND MATERIALS

The design of the experiment is very similar to that of Sved (1971), and also to Sved & Ayala (1970), Mourão, Ayala & Anderson (1972) and Tracey & Ayala (1974). Basically the experiment consists of setting up population cages using single chromosome lines together with a lethal balancer chromosome. The attainment of an equilibrium indicates a disadvantage of the chromosome homozygote, and the magnitude of the disadvantage is indicated by the frequency of the balancer chromosome at equilibrium.

The balancer chromosome chosen for this experiment, kindly supplied by Dr R. Frankham, was TM2, which is marked with Ubx. The experiment is most appropriately done with a balancer chromosome which does not itself depress fitness to any great extent. While it was hoped that the use of a marker having relatively slight phenotypic effect (anthropomorphically speaking) might achieve this result, it is seen below that this was not the case. It is not clear to what extent the meiotic complications induced by the inversions are responsible for the lowered fitness.

The experiment was originally started with a number of wild-type chromosomes newly extracted from winery populations. Of thirty-eight chromosomes thus extracted, twenty-four were shown to contain lethals. The population cage experiment was carried out using the remaining fourteen chromosomes.

One cage was set up for each chromosome line using Ubx/+ flies. In addition, duplicate cages were set up for six of the fourteen lines (X4, X6, X15, X20, X25, X30) using 90% +/+ and 10% Ubx/+. A further six cages were set up using mixtures of Ubx/+ flies from all thirty-eight chromosome lines, to measure the fitness of the Ubx/+ genotype in comparison to +/+ heterozygotes.

Sampling in the experiment was carried out immediately after the cages were set up, and thereafter at 3-weekly intervals. Flies in the cages were allowed to lay eggs in laying cups for 24 h. Three 4 in. vials were then set up for each cage, each containing an estimated 100–200 eggs. Counts of  $Ubx/+$  and  $+/+$  were made on emergence, usually after 11 and 14 days. The rotation of the six food cups in the cages also followed a 3-weekly cycle.

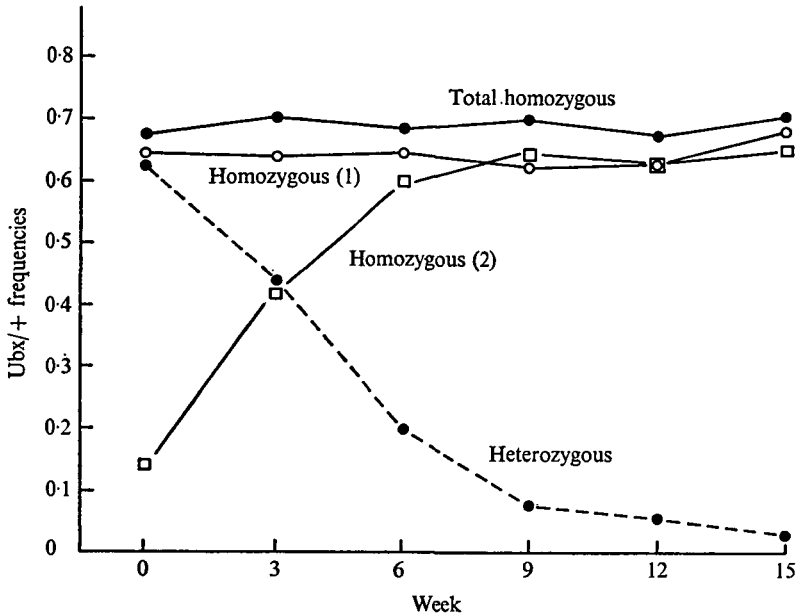


Fig. 1. Averaged  $Ubx/+$  frequencies from cage samples. The closed circles show the overall comparison between homozygous and heterozygous cages. The open circles and squares indicate the comparison of results for a subset of six homozygous lines for which duplicate cages were set up with high and low initial  $Ubx/+$  frequencies, respectively.

During the course of the experiment, egg-to-adult viability was ascertained for each chromosome by use of the ratio viability test. Eggs laid from crosses of the type  $Ubx/+_1 \times Ubx/+_1$  were treated in the same manner as eggs from cage samples. The resultant egg-to-adult viability estimate is needed to correct for the fact that observations in the cage samples are made at the adult stage, rather than at the egg stage as would be required for a valid overall fitness estimate.

Ratio viability tests were in fact carried out before, during, and after the cage experiments. Initial viability estimates were obtained during the screening of the newly extracted chromosomes for lethals. However later viability estimates were also obtained to allow as exact a comparison as possible with cage frequencies towards the end of the experiment. This was done using  $Ubx/+$  flies obtained from the cage samples taken at week 9 and week 15.

## RESULTS

In all twenty cages involving chromosome homozygotes, the frequency of the  $Ubx$  chromosome either remained at or rose to a reasonably high value. Averages for all fourteen cages started with  $Ubx/+$  are given in Fig. 1 ('Total Homozygous'), showing little fall in  $Ubx/+$  frequency over the period of sampling. Averages are also given for the

subset of six chromosomes for which low initial frequency duplicates were made, showing rapid convergence for the two sets. Finally the results from the mixed ('Heterozygous') cages show a steady loss of the Ubx chromosome.

Estimated equilibrium frequencies of Ubx/+ ( $h$ ) are given for each of the fourteen chromosomes in Table 1, column 2. These are based on totals over the last three samples, by which time cages were judged to have reached equilibrium. These values are without exception high.

Table 1. *Fitness estimates for individual chromosomes*

Chromosome	$h$ Ubx/+ freq. in cages	$r$ Ubx/+ freq. in ratio test	$v$ viability (ratio test)	$w$ fitness of +/+ rel. to Ubx/+
X3	0.59	0.78	0.56 (0.50)	0.59
X4	0.59	0.69	0.89 (0.86)	0.35
X6	0.69	0.69	0.90 (0.76)	0.01
X8	0.75	0.77	0.60 (0.50)	0.10
X9	0.63	0.68	0.96 (0.82)	0.18
X15	0.68	0.70	0.86 (0.70)	0.08
X20	0.67	0.71	0.81 (0.84)	0.19
X25	0.62	0.72	0.77 (0.75)	0.38
X26	0.60	0.67	0.99 (1.02)	0.26
X30	0.65	0.65	1.08 (0.71)	0
X38	0.68	0.70	0.85 (0.53)	0.09
X43	0.91	0.88	0.28 (0.51)	-0.47
X45	0.60	0.68	0.93 (0.92)	0.30
X46	0.92	0.97	0.06 (0.12)	0.65
Average	—	—	0.75 (0.68)	0.19 ± 0.07

The average Ubx/+ frequencies from the later two ratio viability tests ( $r$ ) are given in Table 1, column 3. Egg-to-adult viabilities are readily calculated from these using the formula  $v = 2(1-r)/r$  (column 4). The viability estimates given in parentheses are those calculated in the initial viability tests. Finally the estimated homozygous +/+ fitnesses in relation to Ubx/+ are given in column 5. These are obtained using the formula  $w = (r-h)/r(1-h)$  suggested by Dr A. Robertson (personal communication; see Sved (1971) for derivation). The estimated mean fitness over the fourteen chromosomes is around 20%.

Allowance must also be made for the fitness of Ubx/+ in comparison to +/+ heterozygotes. In the heterozygous cages the frequency of Ubx is approximately halved over each 3-week period. Accepting a generation time of 3 weeks, this would indicate a fitness of Ubx/+ relative to +/+ of approximately one-half. The graphical method suggested by Anderson (1969) gives an estimated fitness of 53%. Thus the fitness of +/+ homozygotes relative to Ubx/+ must approximately be halved to give a fitness estimate relative to +/+ heterozygotes. This gives an estimated mean fitness of around 10%.

Some comment must be made on the range of estimated fitnesses of individual chromosomes ( $w$ ) in comparison to the relative uniformity in estimates of  $h$  and  $r$ . The basic reason for this is that the estimate of  $w$ ,  $(r-h)/r(1-h)$ , is very sensitive to small fluctuations in either  $r$  or  $h$ , particularly when either is close to unity. Unfortunately it is precisely those chromosomes with high values of  $r$ , i.e. those with low homozygous viability ( $v$ ), in which heterogeneity between viability estimates is often observed, even from a single sampling. It is striking that in the present experiment the three most discrepant values of  $w$ , two high and one low, are associated with low values of  $v$ . The negative fitness estimate for X43 must of course be spuriously low. This is counterbalanced by the result from X46

where a chromosome having an egg-to-adult viability of 0.06 comes out under the formula with an estimated fitness ten times as high. A comparatively small (although significant) fluctuation in one of the samples is sufficient to account for this high value.

In view of these considerations it might be argued that the safest course in estimating overall fitness is to use only those chromosomes which perform consistently well in the ratio viability test. This would give an upper limit to the fitness if it is assumed that those chromosomes with lower egg-to-adult viabilities do not have higher overall fitnesses on the average. If the present experiment had been carried out using only the nine chromosomes whose viability was significantly greater than 0.5 (i.e. neglecting X3, X8, X38, X43 and X46), the estimate of fitness would have been  $0.19 \pm 0.05$ , coincidentally the same overall mean as obtained for all fourteen chromosomes.

The overall mean fitness estimated in this experiment is considerably lower than the value found recently by Tracey & Ayala (1974) of  $0.32 \pm 0.04$ . The balancer chromosome was eliminated in a number of cages in that study, although this could be accounted for simply by the low fitness of the balancer chromosome used in that study (TM6; SbSer). This could not however account for the overall difference in mean fitness, which could conceivably reflect real differences between the two populations studied.

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#### REFERENCES

- ANDERSON, W. W. (1969). Selection in experimental population. I. Lethal genes. *Genetics* **62**, 653-672.
- MOURÃO, C. A., AYALA, F. J. & ANDERSON, W. W. (1972). Darwinian fitness and adaptedness in experimental populations of *Drosophila willistoni*. *Genetics* **57**, 552-574.
- SVED, J. A. (1971). An estimate of heterosis in *Drosophila melanogaster*. *Genetical Research* **18**, 97-105.
- SVED, J. A. & AYALA, F. J. (1970). A population cage test for heterosis in *Drosophila pseudoobscura*. *Genetics* **66**, 97-113.
- TRACEY, M. L. & AYALA, F. J. (1974). Genetic load in natural populations: Is it compatible with the hypothesis that many polymorphisms are maintained by natural selection? *Genetics* **77**, 569-589.