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Eighteen different third chromosome lethals were used in equal frequencies to start 4 populations at different temperatures and sizes (relatively large populations in cages at 18° and 25°C, designated L-18 and L-25; and small

populations in vials at 18° and 25°C, designated S-18 and S-25). All third chromosomes carried one of the 18 lethals. The populations were maintained for about a year. After this, lethal frequencies were determined for each population. The two lethals in highest frequencies were selected from each population, without determining if the two different lethals in each population were among those selected for any other population, to initiate new populations with a level of 25% for each lethal and 50% quasi-normal third chromosomes from the natural population (American Samoa). Samples were taken at intervals (generation time varies with population size and temperature, about 24 days for L-25 and S-18, 11 days for S-25 and 42 days for L-18) for over 2 years. Frequencies were estimated for each lethal by crossing single males carrying a third chromosome in balanced condition with a marker to appropriate balanced lethal females from stock cultures. If no wild type appeared in the offspring of this cross the sampled chromosome contained the lethal in question.

Frequencies of two lethals in four experimental populations of *D. melanogaster*

S#*	Population L-25				Population L-18				Population S-25				Population S-18			
	#	L-25-17	#	L-25-30	#	L-18-2	#	L-18-21	#	S-25-1	#	S-25-16	#	S-18-2	#	S-18-27
0		0.25		0.25		0.25		0.25		0.25		0.25		0.25		0.25
1	45	0.18	43	0.16	20	0.05	18	0.17	25	0.08	24	0.13	34	0.06	25	0.32
2	21	0.10	32	0.09	81	0.07	70	0.29	20	0.10	28	0.20	26	0.19	13	0.31
3	100	0.11	100	0.18	82	0.07	88	0.14	41	0.15	42	0.19	35	0.09	38	0.13
4	45	0.20	55	0.07	40	0.0	40	0.20	37	0.14	49	0.14	82	0.23	98	0.07
5	94	0.05	90	0.08	97	0.02	80	0.11	71	0.27	54	0.22	40	0.20	62	0.03
6					53	0.04	62	0.07	87	0.07	84	0.21				
7									79	0.02	89	0.23				

*S# = Sample Number

The table shows the frequencies of each lethal through a number of generations (estimated 20 for L-25, 11 for L-18, 42 for S-25, and 23 for S-18). They were all maintained above the expected level for lethal heterozygotes selected one half of the time, $\hat{q}_n = -sq_{n-1}(1-q_{n-1}) / 1-2sq_{n-1}$ where $s = 0.5$. With the exception of one lethal, L-18-2, the total frequency values are higher than would be expected for a neutral effect in the heterozygote, $\hat{q}_n = -q_{n-1}^2 / 1+q_{n-1}$, at the 0.001 level of significance. The 95% confidence limits shows overlap for a neutral effect of all lethals with no overlap with expected values when $s = 0.5$. These observations indicate a heterotic effect for the 8 lethals with the possible exception of L-18-2.

When the lethals were crossed with 9 remaining balanced stocks that survived from the 18 original stocks, 3 lethals were found in 5 different populations (one in three populations L-18-21, L-25-17, and S-25-1; one in two populations L-18-21 and L-25-30; and one in one population S-18-2). L-18-21 carried two of the original lethals that must have arisen through crossing over and recombination. One of these two lethals is allelic with L-25-30, the other with L-25-17 and S-25-1. The persistence of some lethals under different environmental conditions indicates a heterotic effect independent of the environment in which they are found. To bear this out, one lethal persisted in 3 different populations, as to size and temperature, and was found in linkage with a second lethal (indicating epistatic interaction between lethals) that was found in two different populations.

It may be concluded that chromosomes with genes or gene complexes that are lethal for homozygotes can be selected for their heterotic effects, as indicated by their persistence in different experimental populations. The level at which lethal genes are heterotic in natural populations may have been underestimated with data on fitness values of particular lethals and tests for allelism. And, while these results are not absolute, there are indications (6 of 18 lethals recovered in frequencies at or above the level expected for a neutral effect in heterozygotes) that a very high percent of lethals found in natural populations benefit the heterozygote. This work was supported by Grant GM 12222 from the National Institutes of Health.