FACULTY RESEARCH EDITION

of

The Savannah State College Bulletin

Published by

The Savannah State College

Volume 28, No. 2 Savannah, Georgia December, 1974

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HOMOZYGOUS VIABILITY OF POLYGENES IN A SAVANNAH POPULATION OF DROSOPHILA MELANOGASTER A PRELIMINARY REPORT

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Abstract

Fifteen second chromosomes were extracted from a Savannah, Georgia population of *Drosophila melanogaster* according to the inversion method of Wallace (1956). Viabilities of homozygotes and heterozygotes were examined by counting a total of 39,428 flies. The average homozygous viability was .8258 ± .0490, the average heterozygote viability being 1.0000 ±.0411. The genetic load caused by mild detrimentals (D_m) was .185 in terms of lethal equivalents. The phenotypic correlation coefficient(r) between the viabilities of homozygotes and heterozygotes was .6349 which was significantly different from zero at the 5 percent level. The average dominance of the polygenes was estimated to be .4090 while the average dominance of the newly arisen mutants was 1.3055.

It is well known that a large amount of genetic variability with respect to fitness is maintained in equilibrium random mating population, but the mechanism whereby this is maintained has not been completely clarified. Based on our present knowledge it is reasonable to suppose that the magnitude of genetic variability in population is determined by the action and interaction of numerous factors, such as mutant genes, the mode of interaction among loci, the effect of environment and the nature of selection, breeding system, and population structures. In order to arrive at a hypothesis for the maintenance of variability in the population, polymorphisms existing in a large number of populations must be studied. Moreover, in recent years, various kinds of environmental pollutants have been known as serious factors affecting natural populations. Mukai and Yamaguchi (1974) made a detailed analysis of a population in approximate equilibrium where inversion poly-

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morphisms were encountered. It would be useful to know the present populations so that they might be used as control populations in estimating the effect of polluting agents in future.

The present study was carried out to estimate some of the genetic parameters of a Savannah population of *Drosophila melanogaster* in respect of the second chromosome polygenes controlling viability.

Materials and Methods

Materials: The following two stocks were used in this experiment:

(1) A Savannah population of *Drosophila melanogaster* collected from a location about 1½ miles from the down town area on the Savannah river side.

(2) C160*:+(from W160S);Ins(2) SM1, al^2 Cy sp^2 /In(2)Pm, dp b Pm ds^{33k};+(from W160S); +(from W160S); abbreviated as Cy/Pm(curly/Plum). For more details see Mukai and Burdick (1959).

The experimental materials were maintained in a culture room at about 25°C. Estimation of relative viabilities was conducted at the same temperature. In the maintenance of experimental lines, as well as the estimation of relative viability, 3cm x 10cm vials were employed. The medium throughout the experiment consisted of water 1200ml, dry yeast 50g, agar 14g, molasses 100ml, cornmeal 50g, tegosept solution 5ml, and propionic acid 5 ml.

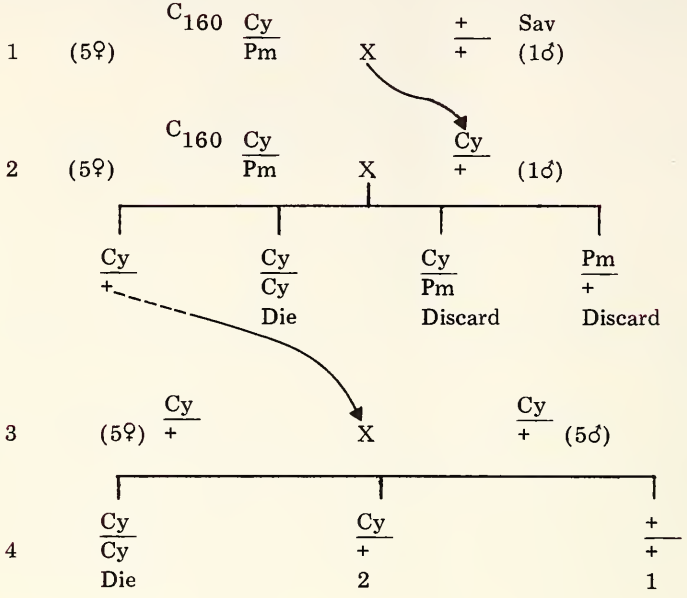
Experimental procedure: The extraction of the second chromosomes from the Savannah population of *Drosophila melanogaster* was according to what is commonly known as the inversion method (Wallace 1956). As shown in Figure 1, males from the Savannah population were individually mated to 5 Cy/Pm females in generation 1, and of the resulting progeny, males of the genotype Cy/+ were again individually mated to the 5 Cy/Pm females in generation 2 and 15 lines were established in this way. These chromosome lines were maintained at 19°C, balanced with SM1 (Cy) chromosomes, which help maintain less viable or lethal chromosome types.

Homozygote and heterozygote viabilities were estimated as in Wallace (1956) and Mukai et al. (1974). Crosses were made between 5 Cy/$+_i$ females and 5 Cy/$+_i$ males from generation 3 with 4 simultaneous replications in each chromosome line number. In the offspring (generation 4), Cy/$+_i$ and $+_i/+_i$ flies segregate at an expected ratio of 2:1. The viabilities of random heterozygotes were estimated in a way similar to the above, combining two successively numbered lines i.e., Cy/$+_i$ x

*Received from Dr. Mukai's laboratory

FIGURE 1

Mating scheme for the extraction of chromosomes and testing their viabilities.



$Cy/+_{i+1}$ in order to secure random combinations of different chromosome lines. As in the case of homozygotes, five pair matings were conducted with 4 simultaneous replications. In both cases, 7 days after crosses were made all 10 flies were discarded. All emerged flies were counted at 4 different times until the 18th day after crosses were made. Cy flies and wild-type flies from the vial were considered a single observation. The viability was expressed as the ratio of the number of wild-type flies to the number of Cy flies plus one (Haldane 1956). Crosses were made at two different times (replications). There were 5 chromosome lines in the first replication and 10 lines in the second replication. Homozygote and heterozygote viabilities were estimated at the same time within replications. Before analyses were made all viabilities were standardized to the average viability of the heterozygote within replications.

The genetic load(s) due to mildly deleterious genes on the second chromosomes(D_m), was calculated by the formula (Temin et al. 1969):

$$(1)\quad S = e^{-s}$$

where S is the viability estimate of homozygotes relative to heterozygotes. The average dominance of the polygenes ($\bar{h}$) was estimated by the formula (Mukai and Yamaguchi 1974):

$$(2)\ \beta_{Y.X.} = \bar{h}$$

where $\beta_{Y.X.}$ is the regression coefficient between the heterozygote viability(Y) and the sum of the corresponding homozygous viabilities(X). The average dominance of the newly arisen mutants(h_N) was calculated according to the formula (Mukai and Yamaguchi 1974):

$$(3)\ h_N = \frac{\text{Variance (Y)}}{\text{Covariance (X, Y)}}$$

The analysis of the variance of the data was according to standard statistical procedures (Snedecor and Cochran 1967).

Results and Discussion

In two different experiments, a total of 15 second chromosomes were extracted and their homozygote and heterozygote (random combination of the chromosomes) viabilities were estimated. The basic statistics and genetic parameters with respect to the second chromosome viability was presented in Table 1. Of a total of 39,428 flies counted, 19,905 were

TABLE 1

Basic statistics and genetic parameters obtained in the study of homozygous viability of polygenes in *Drosophila melanogaster*.

	Homozygotes	Heterozygotes
Number of chromosome lines	15	15
Total number of flies counted	19,905	19,523
Average number of flies counted for each chromosome line	1,327.00	1,301.55
Average number of replications in each line	3.9	3.9
Average number of flies counted in each observation (each vial)	340.26	333.73
Average viability index*	.4177	.4722
Average viability index (standardized)**	.8258	1.0000
Error variance on line basis	.0156	0.0260
Error variance on individual observation basis	.0958	0.0668
Genetic variance ($\sigma^2 G$)	.0299	0.0262

*Viability index = ++/Cy+ + 1 (Haldane 1956)
**On heterozygote basis

homozygotes and 19,523 were heterozygotes. No lethal line was detected because there was no line which showed a viability less than 10 percent (< 0.1) in a homozygous condition relative to the heterozygous condition (Greenberg and Crow 1960). All the chromosome lines studied showed viabilities more than 50 percent (> 0.5) and therefore they are considered mild detrimentals(D_m). The average viabilities of the homozygotes and heterozygotes respectively were 0.4177 and 0.4722. The standardized viability of the homozygotes was .8258 ± .0490 (assuming the heterozygote viability to be 1.0000) and it was 1.0000 ± .0411 for the heterozygotes. The genetic variance of the homozygotes was .0299 while it was .0262 for the homozygotes. The analysis of variance for the viabilities of homozygotes is presented in Table 2. It is evident that there is a

TABLE 2

Analysis of variance for the viabilities of homozygotes with respect to polygenes on the second chromosome in *Drosophila melanogaster.*

Source	Sum of squares	Degrees of freedom	Mean square	F	Expected mean square
Between lines	2.5534	14	.1824	2.78**	$\sigma^2 E + 3.9\ \sigma^2 G$
Within lines (error)	2.8868	44	.0656		$\sigma^2 E$
Total	5.4402	58			

**Significant at the 1 percent level
$\sigma^2 G = .0299$

significant diversity among these lines with respect to viability of polygenes. The analysis of variance for the viabilities of the heterozygotes is shown in Table 3. As seen from the table, significant differences are shown among the viabilities of heterozygotes, the estimated genetic variance, as expected being slightly smaller than that of homozygotes. The distribution of heterozygote viabilities is presented in Figure 2 together with that of homozygotes.

Correlation coefficient between homozygote and heterozygote viabilities:

The phenotypic correlation between homozygote and heterozygote viabilities was calculated on line basis. The result is .6349. This estimate is significant from zero at the 5 percent level. Since the expectation of correlation between the errors of homozygote and heterozygote viability is zero, the genetic correlation between the homozygote and heterozygote viabilities ($r_{GG'}$) can be calculated by the following formula (Mukai et. al. 1964):

$$\hat{r}_{GG'} = \frac{\hat{Cov}\ (\text{Homo and Heterq})}{\sigma\hat{G}\ \ \sigma\hat{G}'}$$

where Cov(Homo and Hetero) indicates the covariance between the homozygote and the heterozygote viabilities. The result obtained on the basis of Cov(Homo and Hetero) = .0178 $\sigma\ \hat{G}$ = .1729 $\sigma\ \hat{G}'$ = .1618 is .6357.

TABLE 3

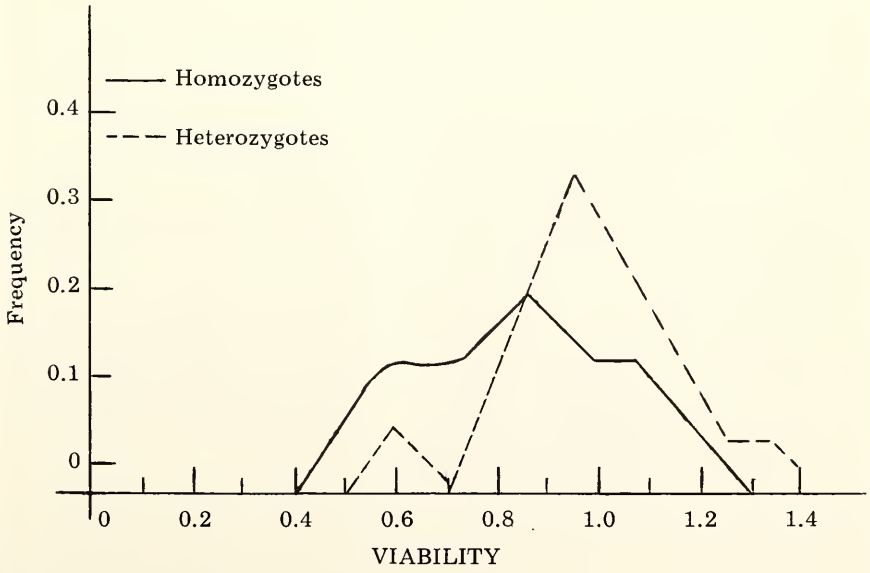
Analysis of variance for the viabilities of heterozygotes with respect to polygenes on the second chromosome in *Drosophila melanogaster.*

Source	Sum of squares	Degrees of freedom	Mean square	F	Expected mean square
Between lines	2.3073	14	.1648	2.62**	$\sigma^2 E + 3.9\sigma^2 G$
Within lines (error)	2.7625	44	.0628		$\sigma^2 E$
Total	5.0698	58			

**Significant at the 1 percent level
$\sigma^2 G = .0262$

FIGURE 2

Frequency distribution of homozygote and heterozygote Viabilities of the second chromosomes. The average viability of heterozygotes is assumed to be 1.0000.



Average dominance of viability polygenes: All the heterozygotes whose constituent chromosomes have both viability indices larger than 0.6 were chosen for estimating the average degree of dominance of the viability polygenes. In total there were 14 heterozygotes which satisfied the above condition (homozgous viability > 0.6). The average degree of dominance was estimated by formula (2). The covariance between heterozygote viabilities and the sum of the corresponding homozygous viabilities is .1352 and the variance of the sum of the corresponding homozygote viabilities is .3303 giving a regression coefficient of .4093. This estimate of average dominance for the second chromosome viability polygenes is within the range of values reported by many authors for natural populations (Mukai et. al. 1972, Temin et. al. 1969 and Mukai & Yamaguchi 1974). Similarly, average dominance of newly arisen mutants (h_N) was calculated by formula (3). Variance Y was .1765 and covariance XY was .1352 and therefore the average degree of dominance of the newly arisen mutants was 1.3055. The value obtained in this study is also within the range of values obtained by Mukai and Yamaguchi (1974) for the Raleigh population. The experimental results of Temin et. al. (1969), Mukai and Yamaguchi (1974) and the present study indicate that the average dominance of viability polygenes is much higher than that of "recessive" lethal genes which Crow and Temin (1964) calculated to be .015 at approximate equilibrium frequencies in a natural population. Chisholm and Nambiar (1974) in a recent study concluded on the basis of D_m/L ratio in a cage population that the dominance of the mildly detrimental genes is several times larger than the lethal genes.

Using formula (1) as described in the initial part of this paper the viability index was translated into D_m load. The value obtained was .180 which is slightly higher than the values reported for mildly detrimental genes for natural populations (Temin et. al. 1969 and Temin 1966). Probably this might be due to fewer genomes being studied in this investigation.

From the above experimental results it could be concluded that the few genetic parameters studied on a Savannah population are basically the same or within the ranges as other populations. However, further tests are necessary to understand fully the state of the present population.

We are grateful to Dr. Terumi Mukai, Professor, Department of Genetics, North Carolina State University, Raleigh for providing us with the stock of C160 flies from his laboratory and to Dr. Margaret C. Robinson, Head of the Department of Biology, Savannah State College, Savannah for affording us the facilities to complete this study.

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