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BY
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GENE FREQUENCY IN LABORATORY POPULATIONS OF *DROSOPHILA MELANOGASTER*

INTRODUCTION

Selective differences between alleles in *Drosophila* were described by L'Héritier & Teissier (1934). Later, other experiments revealed that this is a general phenomenon. Reed (Reed & Reed, 1950) observed that phenotypic mating preference was a cause of this selective difference. Merrell (1953) demonstrated at a number of loci that both males and females could express mating preference for genetic alternatives. He argued that a population is better able to maintain itself at an adaptive peak by selective mating than by panmixia. Further, the rate of loss of mutants usually followed a pattern predicted from mating ratios of the mutant to wild type. However, there is not universal agreement on this point (Morpurgo & Nicoletti, 1955; Nicoletti & Solima, 1958). Variation of the mating ratios would alter the rate of removal of the mutant gene. Such a method has been suggested by Strickberger (1962).

Provided that the population is large, the systematic effects of selection may proceed unhindered. Kerr (Kerr & Wright, 1954) deduced that the systematic forces

of selection may be balanced or even outweighed by an accumulation of random deviations in gene frequency—i.e. *genetic drift*. It is important in experiments involving drift and selection that as near to an ideal population structure as possible be achieved. Such a population is described by Falconer (1961). Buri (1956) presented a closely controlled experiment of this sort which involved drift in an autosomal gene.

In this study the nature of selection was observed by altering the mating ratios of the sex-linked mutant white-eyed and wild type flies. The interaction of selection and drift on gene frequencies in a subdivided population in which the population size was very small was observed.

METHOD

Four populations of *D. melanogaster* were started. Each consisted of ten subpopulations or lines in which the sex-linked recessive white (w) competed with its wild type allele. All populations were derived from the F_1 of the cross:

$$\frac{w}{-}\,\male\male \times \frac{+}{+}\,\female\female \qquad \text{Parents,}$$

$$\frac{+}{-}\,\male\male : \frac{w}{+}\,\female\female \qquad F_1.$$

The initial gene frequency of white was 0.5 in all populations. Each generation the male zygotic ratios in each subpopulation were observed. Parents were removed on the 7th day and the new generation scored on the 21st day. In the first three populations each line was started with ten F_1 females, five F_1 males, and five w males. In the fourth population each line was started with two F_1 females, one F_1 male and one w male.

Each generation the following treatment was applied to each line:

Population 1. No treatment. The total number in each line was scored before transferring all the flies into a fresh bottle. The effective population size was calculated as the harmonic mean of the numbers in each generation.

Population 2. Before transferring the population all white-eyed females were removed and discarded.

Population 3. All white-eyed males were removed. The red-eyed males were transferred together with 25 virgin females chosen at random from the population.

Population 4. No treatment. Each line was started with 2 males and 2 virgin females chosen at random from the population. The effective population size was 4.

Generations did not overlap and all lines were reared in $\frac{1}{4}$-pint milk bottles, on cornmeal-agar slopes. The slopes provided a large feeding and breeding area, thus supporting maximum numbers with minimum competition.

Because of recombination a mutant gene competes with its wild type allele independently of other genes. The selective disadvantage of white is large compared with minor differences associated with other loci (Ludwin, 1951). Therefore no further attempt was made to obtain isogenic lines.

The zygotic frequency of the white males was taken as the gene frequency in the population as a whole.

RESULTS

The results fall into two groups—those in which selection is predominant and, secondly, those in which gene frequencies are more likely to be subjected to drift than to selection. Other forces that might disrupt the Hardy-Weinberg equilibrium, such as migration and mutation, are not considered.

Selection experiments

Tables 1 and 2 and Figures 1 and 2 show a decrease in the frequency of white in populations 1, 2, and 3. The fall in frequencies can be attributed in all three populations to a differential mating success among the males. Reed (Reed & Reed, 1950) found that white males and red males mated with red females in the ratio 0.75:1. On this basis an expected rate of fall in the percentage of white was calculated for each population (Table 2). The observed and expected results are compared in Figures 2*a*, *b*, and *c*. There is good agreement in the slope of the curves after the second generation.

The relative numbers in the first population were 4421 (51.4 per cent) females and 4175 (48.6 per cent) males. $X^2_{(1)} = 7.1$, $p < 0.01$. This deviation from a sex ratio of unity is small and considerably less than that observed by Reed. Strictly, this deviation should be included in calculating the expected zygotic values. Omission tends to make the decrease in the frequency of white more conservative.

The intensity of selection calculated from changes in the zygotic ratios was not constant between generations in any population. The selection coefficient may be calculated from the change in gene frequencies. For a sex-linked gene the change in gene frequency ($\triangle q$) from one generation to the next is $\triangle q = \frac{-sq\,(1-q)}{1-sq}$, where q is the gene frequency of the first generation and s the selection coefficient against the gene. The mean selection coefficient increased from 0.152 in the first population, under natural selection, to 0.231 in the second population, in which there was complete selection against white females, and to 0.339 in the third population, in which there was complete selection against white males.

TABLE 1

Distribution of white among subpopulations by generation

A. UNDER NATURAL SELECTION WHEN $N_e = 169$

Population 1. Natural Selection

SUBPOPULATION	GENERATION									
	0	1	2	3	4	5	6	7	8	9
1	.5	.344	.279	.225	.178	.117	.072	.055	.125	.136
2	.5	.360	.207	.237	.276	.267	.330	.333	.152	.310
3	.5	.474	.197	.188	.077	.104	.023	.088	.023	.000
4	.5	.240	.330	.177	.204	.206	.100	.136	.133	.161
5	.5	.451	.723	.410	.590	.430	.580	.500	.295	.250
6	.5	.405	.715	.230	.540	.080	.540	.000	.068	.000
7	.5	.517	.444	.182	.161	.105	.125	.356	.114	.034
8	.5	.433	.091	.346	.264	.275	.300	.153	.133	—
9	.5	.124	.160	.077	.000	.000	.000	.000	.000	—
10	.5	.336	.243	.420	.178	.137	.149	.069	.140	—
Total	5.0	3.684	3.389	2.492	2.468	1.721	2.219	1.690	1.050	.891
Number of lines unfixed or newly fixed	10	10	10	10	10	9	9	9	9	7
Mean frequency of white in unfixed or newly fixed lines	.50	.368	.339	.249	.247	.191	.247	.188	.117	.127
Mean population size		174	170	117	225	209	135	273	202	129

$\overline{N}_e = 169.$
$\bar{s} = .152.$

TABLE 1 (Continued)

D. UNDER NATURAL SELECTION WHEN $N_e = 4$

Population IV. Small Population Size

SUBPOPULATION	GENERATION									
	0	1	2	3	4	5	6	7	8	9
1	.5	.437	.540	.687	.700	.000	.380	.485	.456	1.000
2	.5	.304	.430	.000	.000	.000	.000	.000	.000	.000
3	.5	.500	.365	.380	1.000	.429	.745	.000	.203	.177
4	.5	.490	.200	.131	.053	.000	.000	.000	.000	.000
5	.5	.509	1.000	.420	1.000	.490	.320	.000	.000	.000
6	.5	.890	.000	.000	.000	.000	.000	.000	.000	.000
7	.5	.410	.484	.780	.520	.241	.355	.000	.000	.000
8	.5	.526	.590	.795	.406	.563	.850	.730	.750	—
9	.5	—	.000	.195	.000	.000	.000	.000	.000	—
10	.5	.440	.590	.310	.710	.775	.460	.800	.805	—
Total	5.0	4.781	4.199	3.698	4.389	2.498	3.110	2.015	2.214	1.177
Number of lines unfixed or newly fixed	10	10	10	9	8	7	6	6	4	2
Mean frequency of white in unfixed or newly fixed lines	.5	.501	.420	.410	.549	.357	.518	.336	.554	.589

$N_e = 4$.

TABLE 2

Expected percentages of competing genotypes

(Calculated on the assumption that decrease of the white allele is due to selective mating ratio of 1.00 red to 0.75 white males. The differential survival rates of females and males is ignored. The gene frequency of white in the population ($\bar{q}_w$) is calculated from $\bar{q}_w = \frac{2}{3} q_f + \frac{1}{3} q_m$)

A. NATURAL SELECTION

GENERATION	GENOTYPE PER CENT					$\bar{q}_w$
	WW	Ww	ww	WY	wY	
0	—	50.0	—	25.0	25.0	.500
1	14.3	25.0	10.7	25.0	25.0	.476
2	15.3	24.8	9.9	26.8	23.2	.452
3	16.8	24.4	8.8	27.7	22.3	.429
4	18.1	24.0	7.9	29.0	21.0	.405
5	19.5	23.4	7.0	30.9	19.9	.382
6	20.9	22.9	6.2	31.2	18.8	.361
7	22.3	22.2	5.5	32.4	17.7	.329
8	23.8	21.4	4.7	33.4	16.6	.316
9	25.2	20.6	4.2	34.5	15.5	.297

TABLE 2 (Continued)

B. COMPLETE SELECTION AGAINST WHITE FEMALES

GENERATION	GENOTYPE PER CENT					$\bar{q}_w$
	WW	Ww	ww	WY	wY	
0		50		25.0	25	.500
1	14.3	25	10.7	25.0	25	.476
2	19.5	23.7	6.8	34.1	15.9	.355
3	27.0	19.4	3.6	36.3	13.7	.269
4	31.0	16.7	2.3	39.7	10.3	.211
5	34.4	14.1	1.5	41.3	8.7	.172
6	37.6	11.5	0.9	42.8	7.2	.137
7	39.2	10.2	0.6	44.1	5.9	.115
8	40.7	8.8	0.5	44.9	5.1	.096
9	42.0	7.7	0.3	45.6	4.4	.085

C. COMPLETE SELECTION AGAINST WHITE MALES

GENERATION	GENOTYPE PER CENT					$\bar{q}_w$
	WW	Ww	ww	WY	wY	
0		50.0		25.0	25.0	.500
1	14.3	25.0	10.7	25.0	25.0	.476
2	26.8	23.2	0	26.8	23.2	.309
3	38.4	11.6	0	38.4	11.6	.155
4	44.2	5.8	0	44.2	5.8	.077
5	47.1	2.9	0	47.1	2.9	.039
6	48.6	1.4	0	48.6	1.4	.019
7	49.8	0.2	—	49.8	0.2	.003
8	49.9	0.1	—	49.9	0.1	.001
9	49.9	0.1	—	49.9	0.1	.001

Drift experiment

The chance fluctuations in gene frequencies between isolated subpopulations in the same generation or within subpopulations from generation to generation are known as *genetic drift*. Genetic drift does not occur in a population where, in a generation, the change in gene frequency due to selection is greater than ten times the variance of gene frequencies due to chance (Kerr & Wright, 1954). In population 1, the change in gene frequency (measured by the change in the frequency of white males) due to selection was $\triangle q = 0.027$ (see Table 1A). The variance due to chance fluctuations in the frequencies of white males in population 4 was $\sigma^2_{\delta q} = 0.026$. Drift was therefore operating within the small subpopulations, with the result that the change in gene frequency brought about by selection against the white allele would be considerably reduced or lost entirely. The data presented in Figure 1 indicate that there was no systematic decrease in the frequency of white among all the unfixed or newly fixed subpopulations. Grouping all shifts in frequency gave a value of $X^2_{(1)} = 0.8$, $p = 0.36$.

Virgin females were used to start each subpopulation. Thus in each generation the effective population size was 4. The distribution of percentages of white males in each generation among the ten subpopulations each founded by two pairs of

individuals is shown in Table 3. Newly fixed subpopulations are distinguished from those fixed in previous generations. The gene frequency distributions by generation are graphically presented in Figure 3. These data show that the gene frequencies (measured by the male ratios) spread from an initial value of 0.5 throughout the whole range from 0 to 1 in two generations. At this stage not all frequencies are equally probable, but by generation 3 a stable form appears to be reached. Over generations 3–9 the fixation rate did not significantly differ from uniformity (see Table 3). The theoretical distribution of gene frequencies among subpopulations derived from a base population whose frequency was 0.5 was calculated by Kimura (1955). All frequencies between 0 and 1 become equally probable at generation $t = 2N_e$. In the case of a sex-linked gene this becomes generation $3N_e/2$. When $N_e = 4$, $t = 6$.

The gene frequencies of the white allele in the subpopulations could not be accurately measured by the male ratios; however, in several subpopulations at certain generations, all the males were white. This could only occur if the female parents were homozygous for white—i.e. if 4 of the 6 parental genes were white. The gene frequency of white was at least 0.67. That this should occur in spite of the 15 per cent disadvantage of white found in population 1 indicates that the systematic pressure of selection was overcome by the greater dispersive influence of drift.

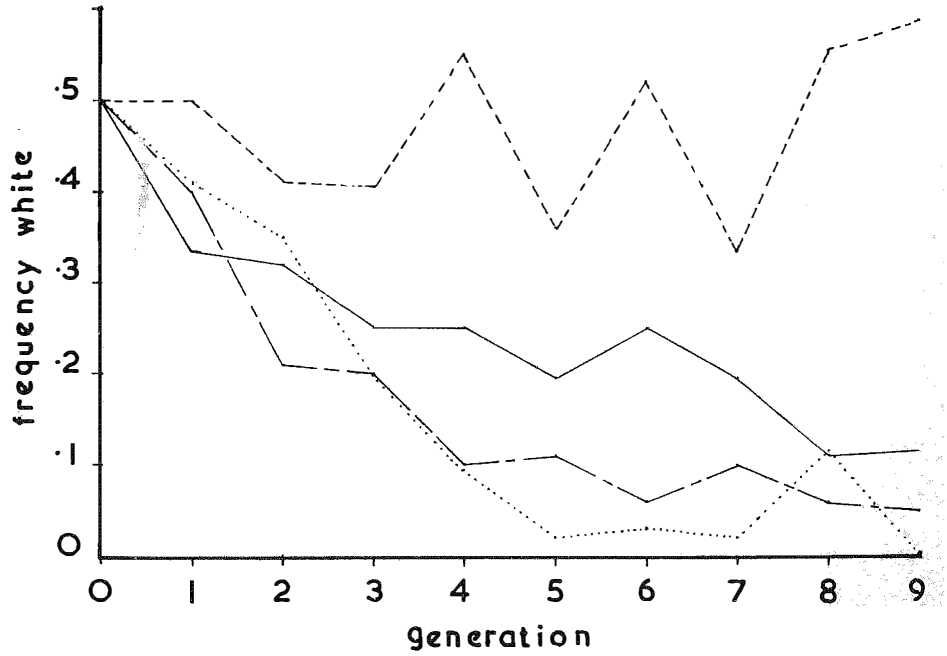

FIG. 1.—Gene frequency distribution by generation in four populations. The solid line represents the mean frequency of white males under natural selection, $N_e = 169$. The broken line represents complete selection against white females. The dotted line represents complete selection against white males. The dashed line represents the effect of natural selection in a small population, $N_e = 4$, previously fixed subpopulations excluded. Graphical representation of Tables 1A, 1B, 1C, and 1D.

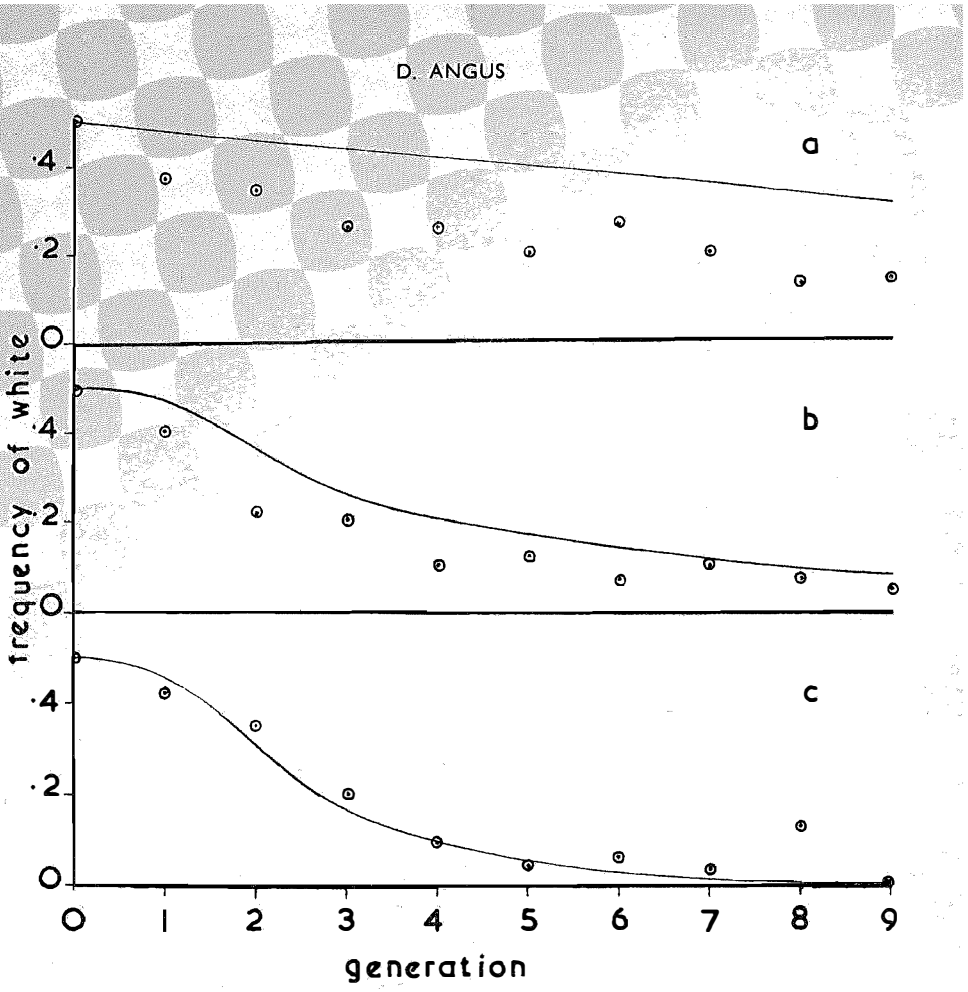

FIG. 2.—Frequency distribution by generation of white males under different intensities of selection. The continuous curve represents the theoretical gene frequency of white calculated in Tables 2A, 2B, and 2C. The open circles represent the genotypic frequency of white males.
a—No selection other than that occurring naturally.
b—Complete selection against white females.
c—Complete selection against white males.

Since genetic drift has no direction, the amount by which the gene frequencies of subpopulations can differ may be measured as the variance of the ratios of their initial frequencies. If p_0 and q_0 are the initial allelic frequencies, where $p + q = 1$, then $\sigma^2_{\delta q} = p_0q_0/2N$, where 2N is the total number of genes and N the effective population size. This becomes $\sigma^2_{\delta q} = 2p_0q_0/3N$ for a sex-linked gene, and measures the amount by which any one subpopulation could vary from the base population in one generation, or the amount of variance expected among subpopulations in one generation. In the next generation each subpopulation has its own gene frequency and variance. This will result in the dispersal of gene frequencies among subpopulations (see Fig. 3).

At the same time the total variance for the whole population, including fixed subpopulations, increases. The value for any generation t can be calculated from the formula $\sigma^2_{\delta q} = p_0 q_0 (1-(1-2/3N)^t)$ (Wright, 1942). In Table 4 and Figure 4 the observed and expected variances are presented by generation, including and excluding previously fixed subpopulations. The maximum theoretical value of the variance is found when all subpopulations are fixed. While unfixed subpopulations occur, the maximum value of the variance among subpopulations, excluding those previously fixed, will be that at which all frequencies become equally probable, i.e. $t = 3N/2$. This produced an asymptote at $\sigma^2 = 0.17$. There is general agreement of the data with expectation, the variances on the whole being rather smaller than expected from so small a population size.

Table 1D shows the male ratios in the small subpopulations. By generation 2 all ratios from 0 to 1 occurred, and one subpopulation was fixed. In subsequent generations more subpopulations became fixed (see Fig. 5). It is of interest to compare the observed and expected amount of fixation. When the stable frequency distribution occurred, the number of lines fixed was 2/3N per generation. The expected amount of fixation to occur in any one generation t may be calculated from the expression $1-6p_0q_0(1-2/3N)$ (Wright, 1952). The observed and expected results are compared in Table 5 and presented graphically in Figure 5. When the stable form is reached, about 50 per cent of all subpopulations are fixed (Kimura, 1955). The observed results gave a value of about 0.5 at generation 6, i.e. $t = 3N/2$ when $N = 4$. In all subpopulations the allele fixed was wild type. The rate of fixation approached $2/3N = 0.17$ per generation at the stable form. The observed fixation rate after the stable form was reached varied from 0.1 to 0.3 subpopulations per generation.

TABLE 3

Distribution of percentages of white males by generation among ten subpopulations each founded by two pairs of individuals. Newly fixed subpopulations are distinguished from those fixed in previous generations

Group Percentages (White)	Generation										Generations 3–9
	0	1	2	3	4	5	6	7	8	9	
Old 0				1	2	3	4	4	6	5	
0			2	1	2	2	—	3	—	—	8
17			1	2	—	1	—	—	1	1	5
33		2	1	2	1	—	3	—	—	—	6
50	10	6	3	1	1	3	1	1	1	—	8
67		—	2	1	2	—	1	1	1	—	6
84		1	—	2	—	1	1	1	1	1	6
100			1	—	2	—	—	—	—	1	3
Total	10	9	10	10	10	10	10	10	10	7	42

Mean fixation rate 0.1 per generation.
$X^2_{(6)} = 3.01$; $p = .8$.

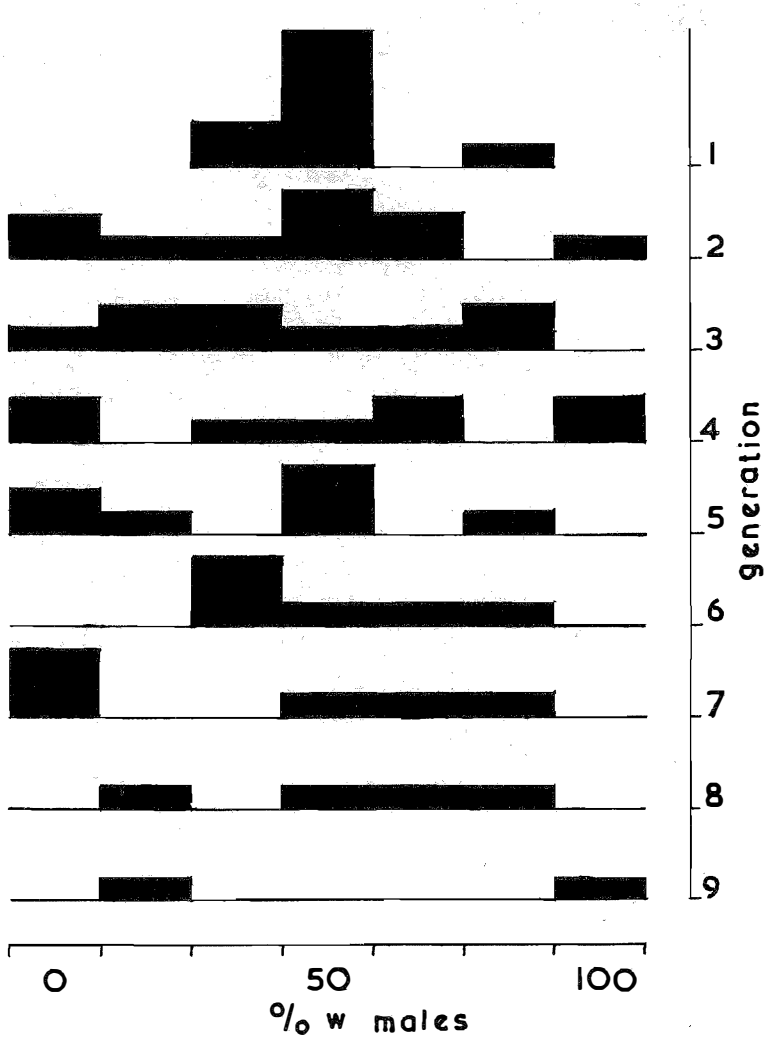

FIG. 3.—Distribution of percentages of white males by generation. Previously fixed subpopulations excluded. Graphical representation of Table 3.

DISCUSSION

Selection

The resemblance between the zygotic ratios observed and the expected gene frequencies of the first three populations indicates that no major factor other than selective mating was operating. This is in full agreement with Reed's results. The discrepancies are mainly the result of the sampling variance of gene frequencies between generations, and they also to a lesser degree derive from selection which

produces inequality in the male and female gene frequencies. This causes a small oscillation in the gene frequency of each sex about the population mean. The discrepancies between the expected and observed results in the first two generations of populations 2 and 3 (see Figs. 2*b*, *c*) reflect that between generations 0 and 1 the populations were not subjected to the same pressures as later generations. The effect of this discrimination would not show in generation 1 since all the parental females were heterozygous and the male zygotic ratio would be in proportion to the gene frequencies in the female parents. In the next generation fewer white males than red would be produced, and these in turn would be less successful than red males. A steady reduction in the frequency of white results.

Selection against white females (population 2, Fig. 2) caused a reduction in the frequency of white males which could only be produced by heterozygous mothers. The reduction in relative numbers combined with their inferior mating ability caused a sharper decrease in white than occurred in population 1.

In the third population (Fig. 2*c*) selection against white males resulted in no white females occurring after the second generation. All white males were produced by heterozygous mothers. In addition the relative mating success of red to white males was 1 : 0. This represents the theoretical maximum rate of selection against white.

The difference in sex ratio from unity is correlated with the degree of crowding in the bottles. Keeping the flies on food slopes increases the population capacity of the bottles by reducing the degree of competition, and this results in a sex ratio approaching unity

Morpurgo & Nicoletti (1955) were unable to demonstrate selective mating when the sex ratio was 1 : 1. Nicoletti & Solima (1958) stated that selective mating was subordinate to larval competition and other factors in contributing to gene evolution.

In this experiment larval competition was kept low, the sex ratio was very close to 1 : 1, and under three different intensities of selection it was demonstrated that the progressive reduction in gene frequency of *white* could be principally related to selective mating.

TABLE 4

Comparison of expected and observed variances by generation, including and excluding previously fixed subpopulations

Generation	Observed		Expected	
	Total	Fixed Lines Excluded	Total	Fixed Lines Excluded
0	0	0	0	0
1	.026	.026	.042	.042
2	.091	.091	.076	.076
3	.091	.083	.105	.105
4	.167	.146	.129	.129
5	.086	.087	.150	.150
6	.099	.050	.166	.166*
7	.111	.146	.180	.166
8	.108	.098	.192	.166
9	.139	—	.201	.166

*Asymptote.

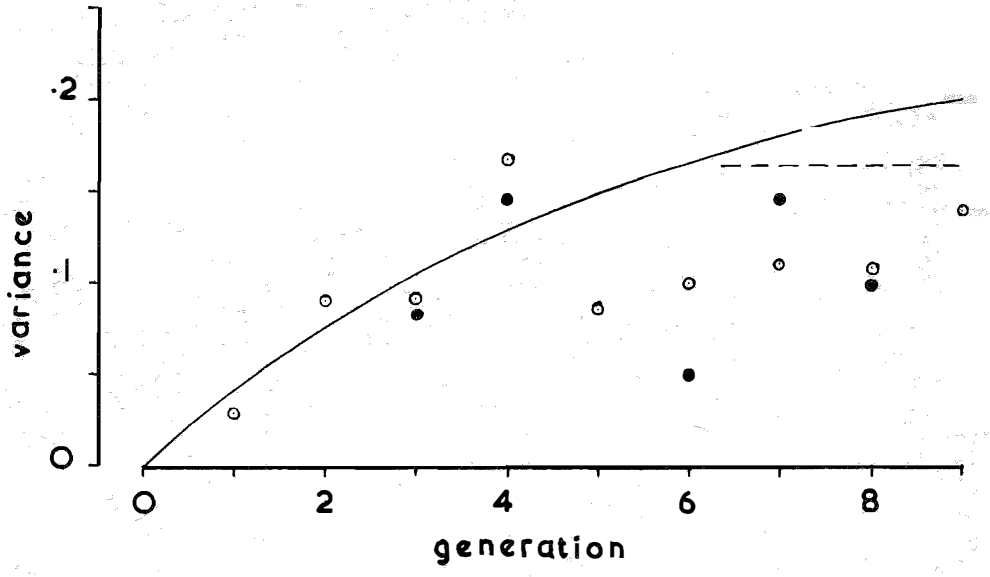

FIG. 4.—Theoretical variances of the total frequency distribution by generation, including fixed subpopulations and based on $N_e = 4$, are represented by the smooth curve. Open circles show the observed variances of the distribution, including previously fixed subpopulations. Closed circles indicate the observed total variances, excluding previously fixed subpopulations. The asymptote (=0.166) indicates approximately the theoretical maximum value of this variance.

Drift

The increase in variance in small populations due to drift is accompanied by a decrease in heterozygosity. No direct data were obtained on the amount of heterozygosity in the population, since only male ratios were recorded. Indirectly, a decrease in heterozygosity was observed in that 70 per cent of all subpopulations became homozygous by the ninth generation (see Fig. 5).

The degree to which the estimate of variance observed among subpopulations may agree with the theoretical parameter will be proportional to the number of subpopulations contributing to the estimate. In the data the maximum number of subpopulations observed was ten. Only a general measure of agreement can be expected between the observed and expected variances. Further, the observed variances were based on male ratios, while the expected variances are based on gene frequencies. The experiment was not designed to show equivalence between theory and practice but that a strong relationship exists.

The ratio of white alleles to red alleles fixed was 0 : 6. This number is too small to test for significance; however it may indicate an interaction between selection and drift.

TABLE 5

Comparison of observed and theoretical frequencies o fixation and loss of the white allele among ten subpopulation over nine generations

GENERATION	OBSERVED	EXPECTED
0	0	0
1	0	0
2	.10	0
3	.20	.13
4	.30	.28
5	.40	.40
6	.40	.50
7	.60	.58
8	.60	.65
9	.71	.71

$N_e = 4$.

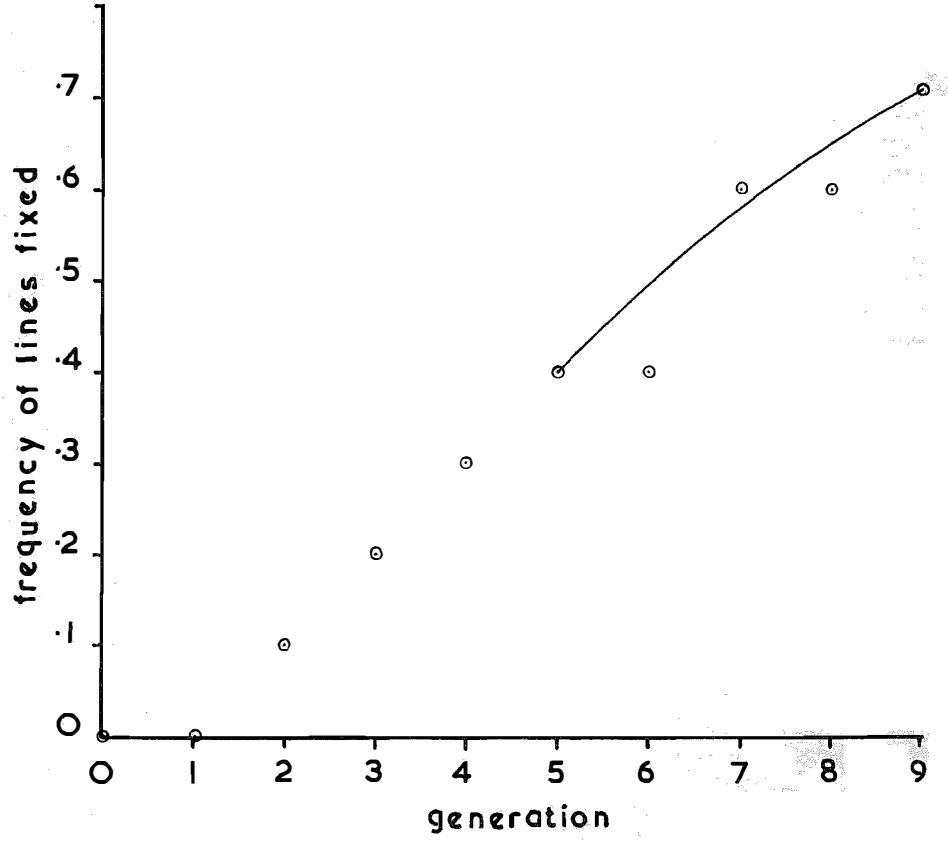

FIG. 5.—Fixation occurring among subpopulations during nine generations. $N_e = 4$. The circles show percentage of subpopulations in which the red allele was fixed. The smooth curve represents the expected total amount of fixation of both alleles, calculated from the expression $1-6p_0q_0P$ where $P=(1-2/3N)$.

SUMMARY

1. Competition between white and wild type alleles in three populations of ten isolated subpopulations of effective size about 169 resulted in the decrease of the white allele.

2. In all cases selection against white could be related to the relative mating success of the two male phenotypes. Red males were 25 per cent more successful than white males.

3. Study was made of the change in frequency in white between generations in cultures over nine generations with a random sample of two pairs of individuals. Considerable drift occurred. Ten cultures were set up with initial frequency of 0.5 in $\frac{1}{4}$-pint milk bottles. No consistent changes in frequency occurred in the unfixed or newly fixed lines.

4. The fixation rate after generation 3 did not significantly differ from uniformity.

5. It was not possible to assess the effect of selection, but grouping changes in frequency in unfixed and newly fixed subpopulations indicated these were caused by accidents of sampling.

6. The effective population size was 4.

7. The observed fixation rate agreed with the expected fixation rate.

8. Curves representing the expected increase in the total variance of gene frequencies were calculated using an effective size of 4. A general agreement between the data and curves was obtained and inconsistencies noted.

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