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John M. Connor
Eastern Illinois University

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Competition and Natural Selection among Laboratory and Naturally Occurring Populations of Drosophila melanogaster

(TITLE)

BY

John M. Connor

B.S., Eastern Illinois University, 1966

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
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IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
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Introduction

It has long been recognized and accepted that organisms are adapted to their physical and biological environments. This is a fundamental concept and principle of biology. However, it has not always been accepted that these various adaptive characteristics are the result of evolutionary processes. Indeed, that evolution is a fact and not a blasphemous word or concept has only been recognized and accepted for a relatively short period. It has only been a century that the scientific method has been found able to supply evidence both from the field and the laboratory that organic evolution has taken place and that the processes are still operative. Before this period, it was believed by lay, religious and even some scientific institutions and circles that species were immutable. It is generally assumed that Linnaeus accepted the doctrine of fixity of species. This is to infer that all species are the result of a single and special creation and that they do not possess the ability within themselves to change.

Charles Darwin initiated an era of scientific exploration and discovery that was to destroy the doctrine of immutability of the species. Darwin provided evidence

and proof that organic evolution was a fact in his The Origin of Species in 1859. In 1900 the simultaneous rediscovery of Mendel's laws of heredity by Correns, de Vries, and Tschermak took place. With these units of heredity or "genes" as they were later termed, an organism contained within itself the ability to adapt to new and different environments. In the following few decades men such as G. G. Simpson, Ernst Mayr, and Theodosius Dobzhansky, to name a few, ushered in the modern synthetic theory of evolution. The theory of evolution was made more coherent by taking into account all of the pertinent facts of modern biology. The next step for evolution as a science appears to be the directed control of evolution by man. However, before science and technology allow man ultimate control of evolution to the extent that a certain type of individual becomes a "mail order" entity, more should be learned about the evolutionary processes. Perhaps some of the fundamental concepts and processes, such as natural selection for the best adapted organism, have not been developed to their fullest extent. One noted scientist believes much still remains to be learned about adaptation. Stebbins (1954) said, "Perhaps the greatest gap in modern evolutionary knowledge is our paucity of precise information on just how and why certain characters are selected under a given set of environmental conditions."

Sewall Wright has said that evolution is basically a statistical transformation of populations. (Stebbins 1966). Thus this thesis is basically an examination of statistical experimental data to elucidate some of the factors involved in the competition and natural selection for certain adaptive characteristics and to ascertain which characteristics are the most adaptive.

Methods and Materials

In order to examine the influence of natural selection on the relative adaptive value of various alleles, population cages were constructed so that large numbers of flies could be reared.

The general construction of the cage was a modified structure of the type suggested by (Strickberger 1962) and (Dobzhansky 1965). The cages were constructed from polyethylene refrigerator pans of a standard size, 12 x 8 x 4 inches. The lids supplied with the pans were totally inadequate; they did not make the cage "fly tight." Plate glass was cut to fit neatly inside the rim. This was then sealed with masking tape. A hole four inches in diameter was cut near one end of the glass and then covered by a plastic bag with punched pin holes for ventilation.

Eight 1 1/2 inch diameter holes were drilled in the bottom of the cage, two holes along one of the sides, and one hole in one of the ends. Several holes three-eighths of an inch in diameter were drilled in the sides. These smaller holes were stoppered with corks and used to remove flies by aspiration. Flies were inserted into the cage by etherizing and placing them in 1 oz. jars that screwed into the side of the cage.

The 1 oz. food cups were inserted into the eight holes in the bottom of the cage. The food used was a synthetic Drosophila medium supplied by the Carolina Biological Supply Company. The food jars were filled to near capacity with both the medium and an equal amount of water to which a pipette of yeast suspension was added. All eight food cups were filled and put into place simultaneously. The appropriate flies would then be added by placing them in the side jars. Flies that did not recover from the ether were replaced.

Each population cage was started with the P_1 generation. The P_1 was so selected that each allele in question was represented with equal frequency. Ten males and ten virgin females of each type were placed in the cage at the same time. Virgins were collected by isolating females that were no more than six or seven hours old.

After the proper generation time the flies were aspirated, etherized, counted and the data recorded. Fifty more flies were then removed from the cage and their characteristics were recorded. These fifty flies which were randomly selected were then used to initiate the next generation. This procedure was repeated for all ensuing generations. After a generation was terminated the cage was cleaned and sterilized

for the next generation. The cages, jars, and lids were washed in hot water and a suitable detergent. The equipment was then washed with 95% alcohol, dried and quickly reassembled for the next generation.

For each generation a thousand flies were counted, when possible, and the characteristics were recorded. In a few instances mold eliminated several hundred flies so that a count of a thousand was impossible. There has been some uncertainty about when to start counting the flies. D. melanogaster has in the laboratory a life cycle that requires an average of ten days to complete at a temperature of 24 degrees centigrade. On the 11th and 12th days after the parents have been placed in a cage, the population of the next generation has seldom, if ever, built itself up to the desired level of a thousand. If the 19th or 20th day is used as the day for counting, it is possible to have adult flies from the next generation present. It has also been hypothesized that if the 13th or 14th day is used for counting, this might be somewhat premature for the emergence of mutant adults if they have a slower developmental period. In effect then, a small degree of artificial selection would be invoked when only the effects of natural selection were desired. Artificial selection might favor the strain which could complete its life cycle the fastest. In naturally occurring populations, this is no

doubt an important factor in selecting for the most adaptive characteristics or genes.

It is quite obvious that the population cage was an artificial situation. However, natural selection or selection by the environment for the fit genotype can still occur. Selection will be relative to the environment. Artificial environment and artificial selection are not the same. With artificial selection one is biased in selecting a particular trait. This artificial environment has not been established with the thought of favoring or biasly selecting a trait. A given environment was made so that the forces of natural selection, adaptation and competition could be elucidated.

The problem of counting too soon and possibly introducing artificial selection was eliminated by counting the flies on the 16th day after the parents had been introduced into the cage. This would standardize procedures and also give the population a better chance to build up to over a thousand. Later the 15th, 16th and 17th days proved to be the days when the greatest majority of the adults emerged for all the strains involved as shown in the results.

The experiments in the population cages were essentially three-fold: one set of experiments was designed to determine the adaptiveness of mutant characters in competition with laboratory wild Drosophila melanogaster,

a similar set of experiments was used to determine the relative adaptiveness of mutants compared to naturally occurring populations of D. melanogaster, and a set to see if these naturally occurring populations had any adaptive superiority between themselves.

Two populations of naturally occurring D. melanogaster were collected in Charleston, Illinois. The term "Town" was used to designate a population occurring near the municipal swimming pool. The "Western" strain was obtained on the west edge of Charleston about 1 1/2 to 2 miles from the Town population. Both populations were collected in September 1966 using trap bottles placed under apple trees. They were verified to be D. melanogaster by Dr. Goodrich of Eastern Illinois University's zoology department.

Mutant characteristics were chosen so that every chromosome had at least one gene locus represented. Sex-linked white eye (w), forked bristle (f), yellow body (y), and miniature wing (m) were utilized. Ebony body (e) III, vestifial wing (vg) II, eyeless (ey) IV, and dark eyes (d) unknown were the autosomal genes used. Two cages of the following crosses were made and maintained until the tenth generation. Three cages had to be started over because of contamination. When contamination was discovered the population was terminated

at that particular generation. The following crosses were made in the population cages:

1. Lab wild x ywm x dark eyes. Repeated three times.
2. Town x wf vg e. Repeated three times.
3. Town x eyeless. Repeated twice.
4. Western x wf vg e. Repeated twice.
5. Western x eyeless. Repeated three times.

Tests for viability, fecundity and mating preferences were performed for all strains used. The flies for these tests were reared in half-pint culture bottles. The medium was the same as that used in the cages. A comparison was made of the viability of the mutant types and their heterozygous wild type sibs by counting the progeny from a backcross of heterozygous females to mutant males.

In the fecundity tests one male and one female of the same type were placed in a culture bottle. Ten culture bottles were used for each type of fly involved in the experiments. The data for the fecundity tests were collected so that a test could be made to determine the time of emergence of the greatest number of individuals. Flies were counted on the 13th, 16th and 20th days after the parents had been introduced into the culture bottle. Counting flies on the 13th day would include all those that had emerged on the 10th, 11th, and 12th days. Counting

Counting flies on the 16th day would include all those that emerged on the 14th and 15th days. Counting on the 20th day would encompass all those that had emerged on the 17th, 18th, 19th and 20th days. These three different sessions of counting flies allowed the determination of a period when largest percentage of adults of each type emerged due to differences in speed of development. The determination of an appropriate period in which to count flies is important. If mutants developed slower and did not emerge until after the population counting was terminated this would result in lower gene frequencies due to artificial selection.

Mating competition tests were also conducted to see if there were any mating preferences between genotypes. The mating success for each genotype was measured by raising the offspring to determine which male was the successful father. Many experiments have shown that, in Drosophila, it is the female that exercises discrimination among suitors, while the male indiscriminately mates with almost any available female. Therefore, wherever possible, experiments were based on "female choice," that is, the female was presented with two classes of males whose mating success was being compared (Strickberger 1962). The general procedure was to have two sets of experiments so that the choice of the mutant and heterozygous females was tested. For example, to

test for the choice of ywm females and wild-type females the following set up was used:

Set 1: Two culture bottles each containing 5 ywm males, 5 wild-type males, and 15 ywm virgin females.

Set 2: Two culture bottles each containing 5 ywm males, 5 wild-type males, and 15 wild-type females heterozygous for ywm.

After the flies were introduced into each culture bottle, they were allowed to remain there for 24 hours. After that time the males were discarded and the females separated, one to a bottle. The phenotype of the new generation determines which male was successful. The above procedure was performed for all genotypes used in these experiments.

TABLE 1

Comparison of fecundity

Strain	# Flies	P value	Significance
west	2388	0.999	
town	1751	.001	very high
eyeless	1491	.001	very high
wf vg e	1066	.001	very high
wild	1365	0.999	
dark eye	1597	.001	very high
ywm	1553	.001	very high

TABLE 2

Time of emergence of greatest number of adults

Strain	13th day	16th day	20th day
west	605	948	735
town	668	682	402
dark eyes	503	816	278
ywm	486	771	296
eyeless	471	699	321
wild	511	569	285
wf vg e	181	610	275
Total	3425	5095	2592

TABLE 3

Comparison of viability of
mutant and wild type sibs

Genotype	+ or +/w	w or w/w	+ or +/m	m or m/m
Males	141	54	140	55
Females	144	45	149	40
Total	285	99	289	95
Viability	1.00	.35	1.00	.33
Genotype	**+/d**	**d/d**	**+ or +/y**	**y or y/y**
Males	68	36	141	54
Females	63	26	137	52
Total	131	62	278	106
Viability	1.00	.47	1.00	.38

TABLE 4

Comparison of viability of
mutant and town type sibs

Genotype	+	w/w	+	f/f	+	vg/vg	+	e/e	+	ey/ey
Males	176	71	182	65	204	43	174	73	115	63
Females	156	62	178	40	178	40	153	65	119	66
Total	362	133	360	105	382	83	327	138	234	129
Viability	1.0	.37	1.0	.29	1.0	.22	1.0	.42	1.0	.55

TABLE 5

Comparison of viability of
mutants and western sibs

Genotype	+	w/w	+	f/f	+	vg/vg	+	e/e	+	ey/ey
Males	169	131	176	124	214	96	169	131	137	64
Females	173	136	196	113	191	108	175	134	159	74
Total	372	267	372	237	405	204	344	265	296	138
Viability	1.0	.72	1.0	.64	1.0	.64	1.0	.71	1.0	.48

TABLE 6

Comparison of viability of mutants to normal type flies

Phenotype	% Viability	P value	Significance
y to wild	38	.001	very high
w to wild	35	.001	very high
m to wild	33	.001	very high
d to wild	47	.001	very high
w to town	37	.001	very high
f to town	29	.001	very high
vg to town	22	.001	very high
e to town	42	.001	very high
ey to town	55	.001	very high
w to west	72	.01	high
f to west	54	.001	very high
vg to west	50	.001	very high
e to west	71	.001	very high
ey to west	48	.001	very high

TABLE 7

Female "choice" mating tests

Female Genotype	Successful Males West	Mutant	Double Matings
+/ey	20	9	0
ey/ey	19	2	7
Total	39	11	7
wf vg e hetero	13	0	0
wf vg e homo	17	0	0
Total	30	0	0
Female Genotype	**Successful Males Town**	**Mutant**	**Double Matings**
+/ey	17	3	0
ey/ey	24	1	2
Total	41	4	2
wf vg e hetero	9	0	0
wf vg e homo	8	0	0
Total	17	0	0
Female Genotype	**Successful Males Wild**	**Mutant**	**Double Matings**
ywm hetero	29	3	0
ywm homo	17	10	0
Total	46	13	0
+/d			
d/d	11	15	6
Total			

TABLE 8

Population cage data for
wild x ywm x dark eyes

Generation	Sex Ratio % ♂	Sex Ratio % ♀	Mutant Sex Ratio % ♂	Mutant Sex Ratio % ♀	% Mutants in Population	% of Population with Mutant Character y	w	m	d
P_1	50	50	50	50	66.0	33.0	33.0	33.0	33.0
F_1	48	52	50	50	4.0	2.0	2.0	2.0	2.0
F_2	27	73	75	25	8.2	3.3	3.5	4.0	2.9
P_1	50	50	50	50	66.0	33.3	33.3	33.3	33.3
F_1	58	42	88	12	25.0	20.0	20.0	20.0	6.0
F_2	42	58	72	28	20.0	9.3	9.3	9.0	8.4
F_3	39	61	56	44	22.7	4.8	4.7	5.9	15.0
P_1	50	50	50	50	66.0	33.0	33.0	33.0	33.0
F_1	43	57	72	28	7.0	0.0	0.0	0.0	7.0
F_2	38	62	55	45	6.5	1.9	1.8	1.1	4.3
F_3	45	55	57	43	9.5	1.3	1.2	1.2	7.8
F_4	45	55	46	54	7.8	0.0	0.0	0.0	7.8
F_5	40	60	35	65	9.3	0.1	0.0	0.0	9.3
F_6	57	43	46	54	8.3	0.0	0.0	0.0	8.3
F_7	50	50	46	54	5.8	0.0	0.0	0.0	5.8
F_8	49	51	52	48	7.2	0.0	0.0	0.0	7.2
F_9	55	45	44	56	1.9	0.0	0.0	0.0	1.9
F_{10}	45	55	50	50	3.4	0.0	0.3	0.0	3.1

TABLE 9

Population cage data for
west x wf vg e

Generation	Sex Ratio		Mutant Sex Ratio		% Mutants in Population	% of Population with Mutant Character			
	% ♂	% ♀	% ♂	% ♀		w	f	vg	e
F_1	50	50	50	50	50.0	50.0	50.0	50.0	50.0
F_1	42	58	100	0	2.0	2.0	2.0	.0	.0
F_2	57	43	100	0	4.0	1.8	3.0	.0	.0
F_3	51	49	100	0	.2	.2	.1	.0	.0
F_4	49	51	95	5	3.5	2.5	1.5	.0	.0
F_5	46	54	100	0	2.2	1.4	.9	.0	.0
F_6	43	57	84	16	3.1	2.8	.4	.0	.0
F_7	48	52	100	0	2.0	1.8	.2	.0	.0
F_8	46	54	100	0	.9	1.9	.0	.0	.0
F_9	50	50	100	0	1.3	1.3	.0	.0	.0
F_{10}	56	44	0	0	.0	.0	.0	.0	.0

TABLE 9--Continued

Generation	Sex Ratio		Mutant Sex Ratio		% Mutants in Population	% of Population with Mutant Character			
	% ♂	% ♀	% ♂	% ♀		w	f	vg	e
P_1	50	50	50	50	50.0	50.0	50.0	50.0	50.0
F_1	52	48	0	0	.0	.0	.0	.0	.0
F_2	52	48	0	0	.0	.0	.0	.0	.0
F_3	58	42	0	0	.0	.0	.0	.0	.0
F_4	50	50	0	0	.0	.0	.0	.0	.0
F_5	49	51	0	0	.0	.0	.0	.0	.0
F_6	47	53	0	0	.0	.0	.0	.0	.0
F_7	66	34	0	0	.0	.0	.0	.0	.0
F_8	53	47	100	0	.1	.0	.0	.0	.1
F_9	56	44	0	0	.0	.0	.0	.0	.0
F_{10}	55	45	100	0	.5	.0	.0	.0	.5

TABLE 10

Population cage data for
west x eyeless

Generation	Sex Ratio		Mutant Sex Ratio		% Mutants in Population	% of Population with Mutant Character ey
	%♂	%♀	%♂	%♀		
P_1	50	50	50	50	50.0	50.0
F_1	47	53	0	100	1.1	1.1
F_2	57	43	74	26	2.2	2.2
P_1	50	50	50	50	50.0	50.0
F_1	51	49	50	50	1.8	1.8
F_2	80	20	100	0	1.6	1.6
F_3	50	50	60	40	1.8	1.8
F_4	60	40	100	0	.7	.7
F_5	46	54	36	64	1.8	1.8
F_6	60	40	100	0	.7	.7
F_7	48	52	53	47	1.0	1.0
F_8	45	55	67	33	.6	.6

TABLE 10--Continued

Generation	Sex Ratio		Mutant Sex Ratio		% Mutants in Population	% of Population with Mutant Character ey
	% ♂	% ♀	% ♂	% ♀		
P_1	50	50	50	50	50.0	50.0
F_1	49	51	42	58	5.4	5.4
F_2	54	46	53	47	2.2	2.2
F_3	52	48	60	40	2.4	2.4
F_4	57	43	44	56	3.3	3.3
F_5	71	29	75	25	1.8	1.8
F_6	50	50	21	79	3.3	3.3
F_7	52	48	66	34	.7	.7
F_8	50	50	0	0	.0	.0

TABLE 11

Population cage data for
town x wf vg e

Generation	Sex Ratio		Mutant Sex Ratio		% Mutants in Population	% of Population with Mutant Character			
	♂	♀	♂	♀		ey			
P_1	50	50	50	50	50.0	50.0	50.0	50.0	50.0
F_1	41	59	100	0	9.0	9.0	9.0	.0	.0
F_2	42	58	85	15	9.2	6.1	5.7	.0	1.5
P_1	50	50	50	50	50.0	50.0	50.0	50.0	50.0
F_1	49	51	100	0	2.8	2.8	2.8	2.8	2.8
F_2	67	33	86	14	.7	.4	.6	.0	.0
F_3	63	37	0	0	.0	.0	.0	.0	.0
F_4	43	57	0	0	.0	.0	.0	.0	.0
F_5	54	46	0	0	.0	.0	.0	.0	.0
F_6	57	43	100	0	1.3	1.3	.0	.0	.0
F_7	46	54	100	0	1.1	1.1	.0	.0	.0
F_8	58	42	100	0	.6	.6	.0	.0	.0
F_9	62	38	0	0	.0	.0	.0	.0	.0
F_{10}	51	49	0	0	.0	.0	.0	.0	.0

TABLE 11--Continued

Generation	Sex Ratio		Mutant Sex Ratio		% Mutants in Population	% of Population with Mutant Character			
	% ♂	% ♀	% ♂	% ♀		ey			
P_1	50	50	50	50	50.0	50.0	50.0	50.0	50.0
F_1	58	42	0	0	.0	.0	.0	.0	.0
F_2	51	49	100	0	1.3	.5	1.0	.0	.0
F_3	55	45	100	0	1.6	1.6	.3	.0	.0
F_4	64	36	100	0	1.4	1.4	.0	.0	.0
F_5	48	52	100	0	1.3	1.3	.0	.0	.0
F_6	56	44	0	0	.0	.0	.0	.0	.0
F_7	52	48	0	0	.0	.0	.0	.0	.0
F_8	52	48	100	0	.6	.6	.0	.0	.0
F_9	51	49	0	0	.0	.0	.0	.0	.0
F_{10}	48	52	0	0	.0	.0	.0	.0	.0

TABLE 12

Population cage data for
town x eyeless

Generation	Sex Ratio		Mutant Sex Ratio		% Mutants in Population	% of Population with Mutant Character ey
	% ♂	% ♀	% ♂	% ♀		
P_1	50	50	50	50	50.0	50.0
F_1	47	53	0	0	.0	.0
F_2	49	51	30	70	2.0	2.0
F_3	51	49	50	50	.2	.2
P_1	50	50	50	50	50.0	50.0
F_1	40	60	0	0	.0	.0
F_2	51	49	50	50	.6	.6
F_3	46	54	0	100	.4	.4
F_4	50	50	71	29	.7	.7
F_5	48	52	0	0	.0	.0
F_6	51	49	0	0	.0	.0
F_7	50	50	0	0	.0	.0
F_8	60	40	0	0	.0	.0
F_9	46	54	0	0	.0	.0
F_{10}	59	41	0	0	.0	.0

Figure 1

Competition between wild x ywm x dark eyes

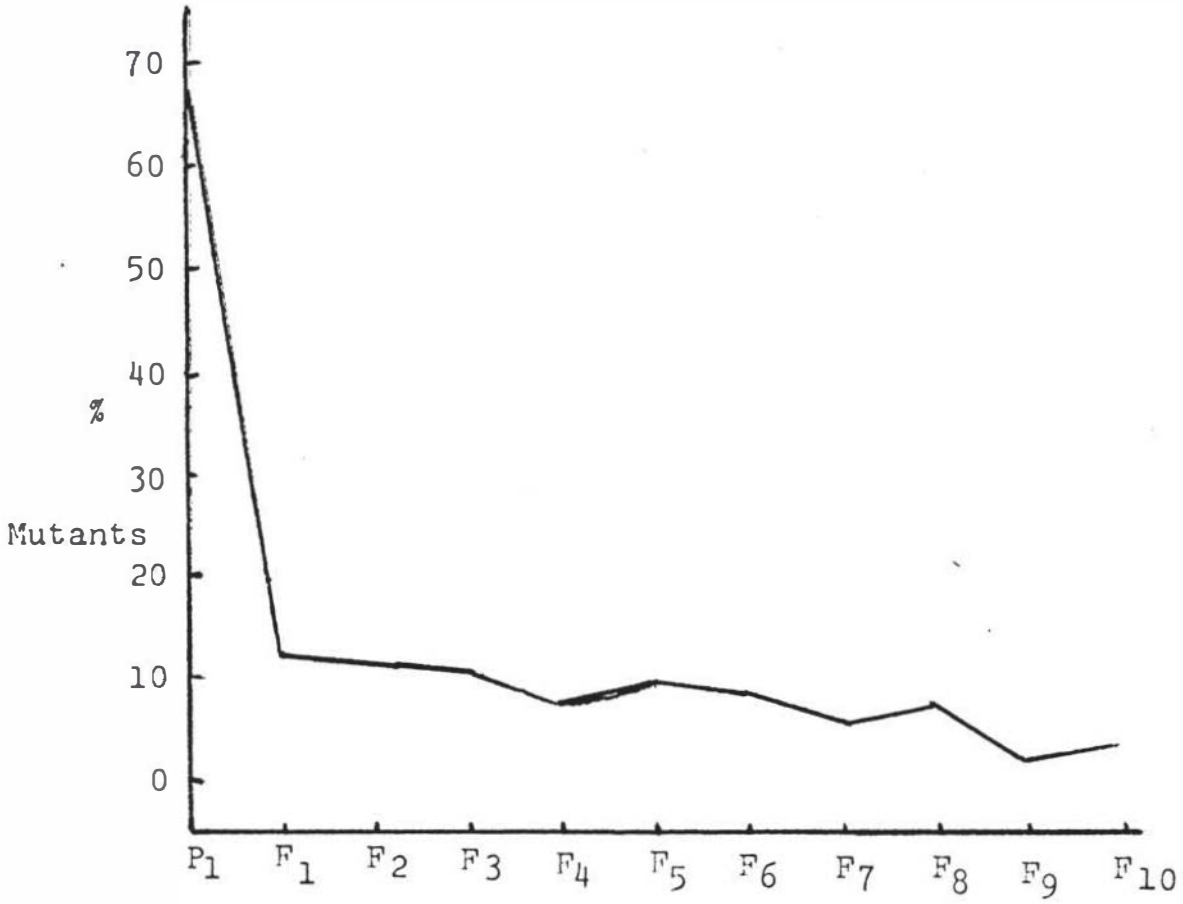


Figure 2

Competition between yellow body
and wild type alleles

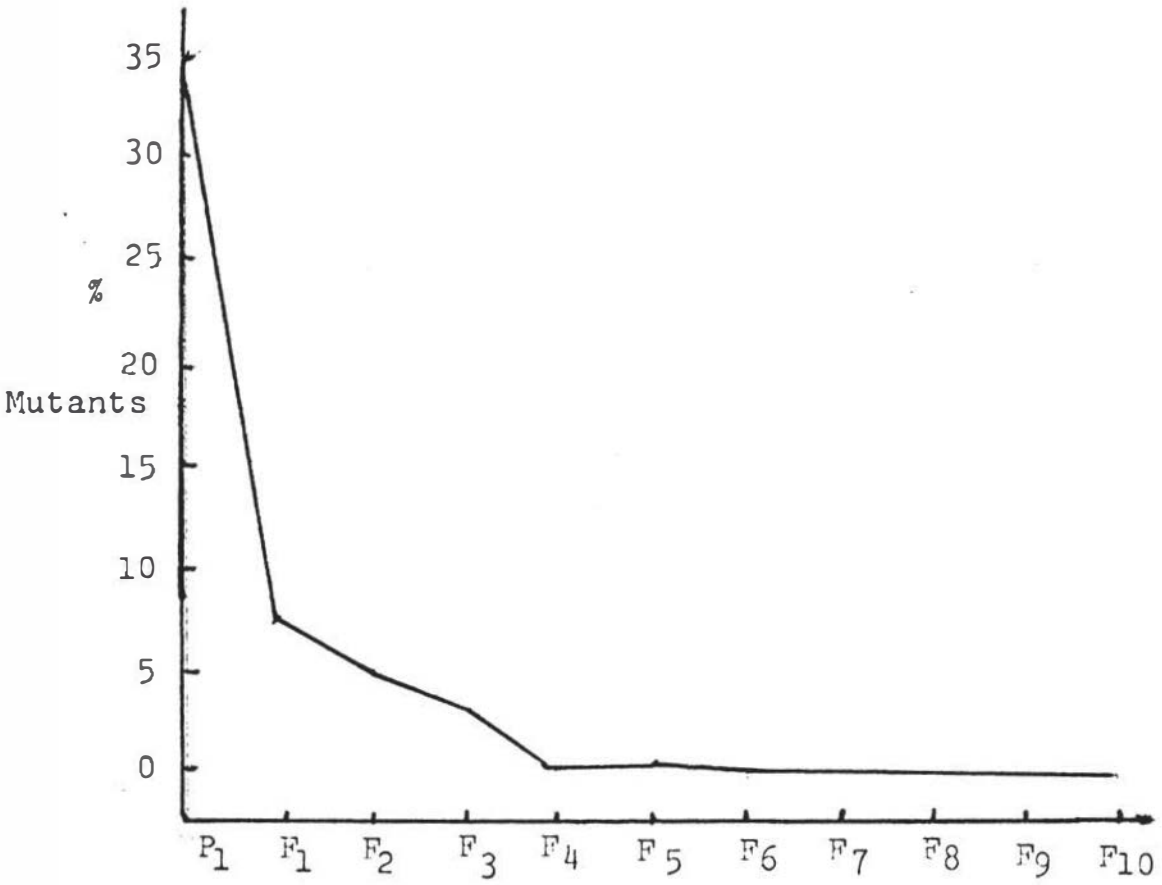


Figure 3

Competition between white eye
and wild type alleles

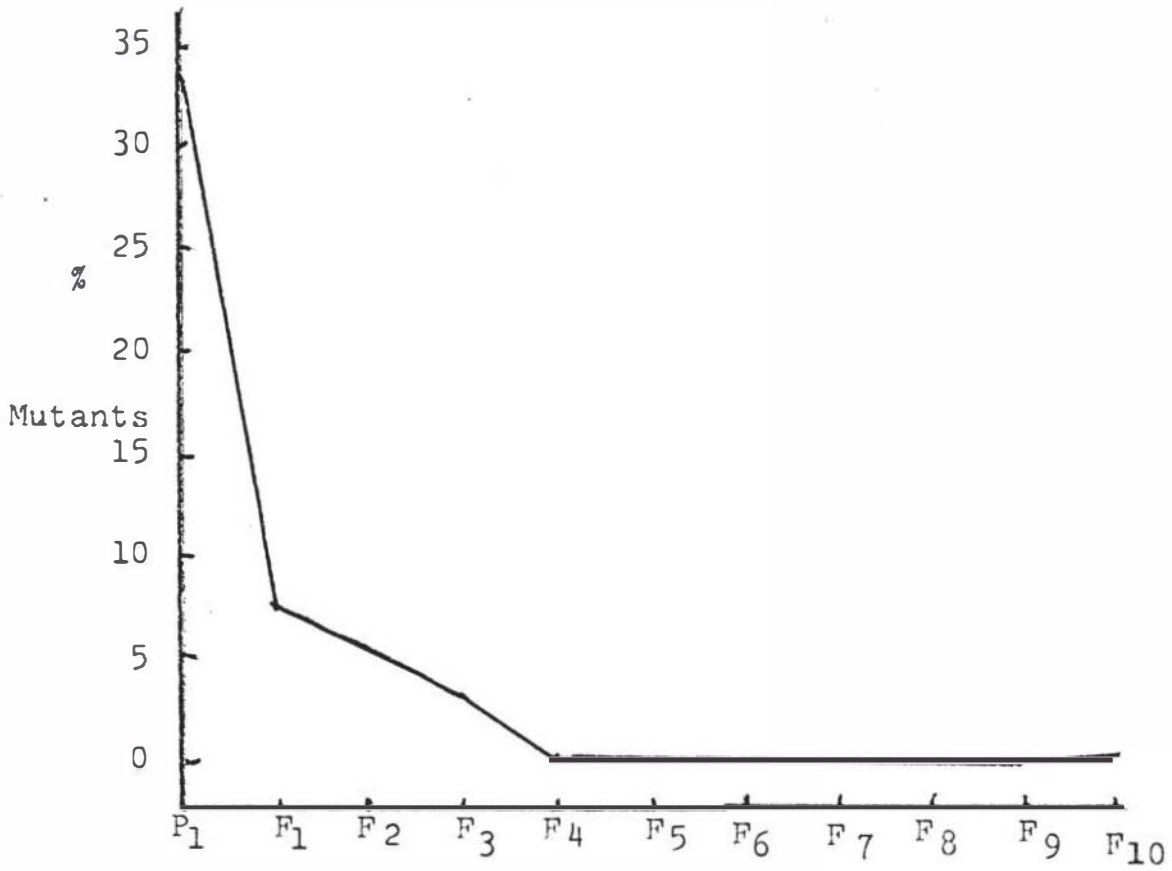


Figure 4

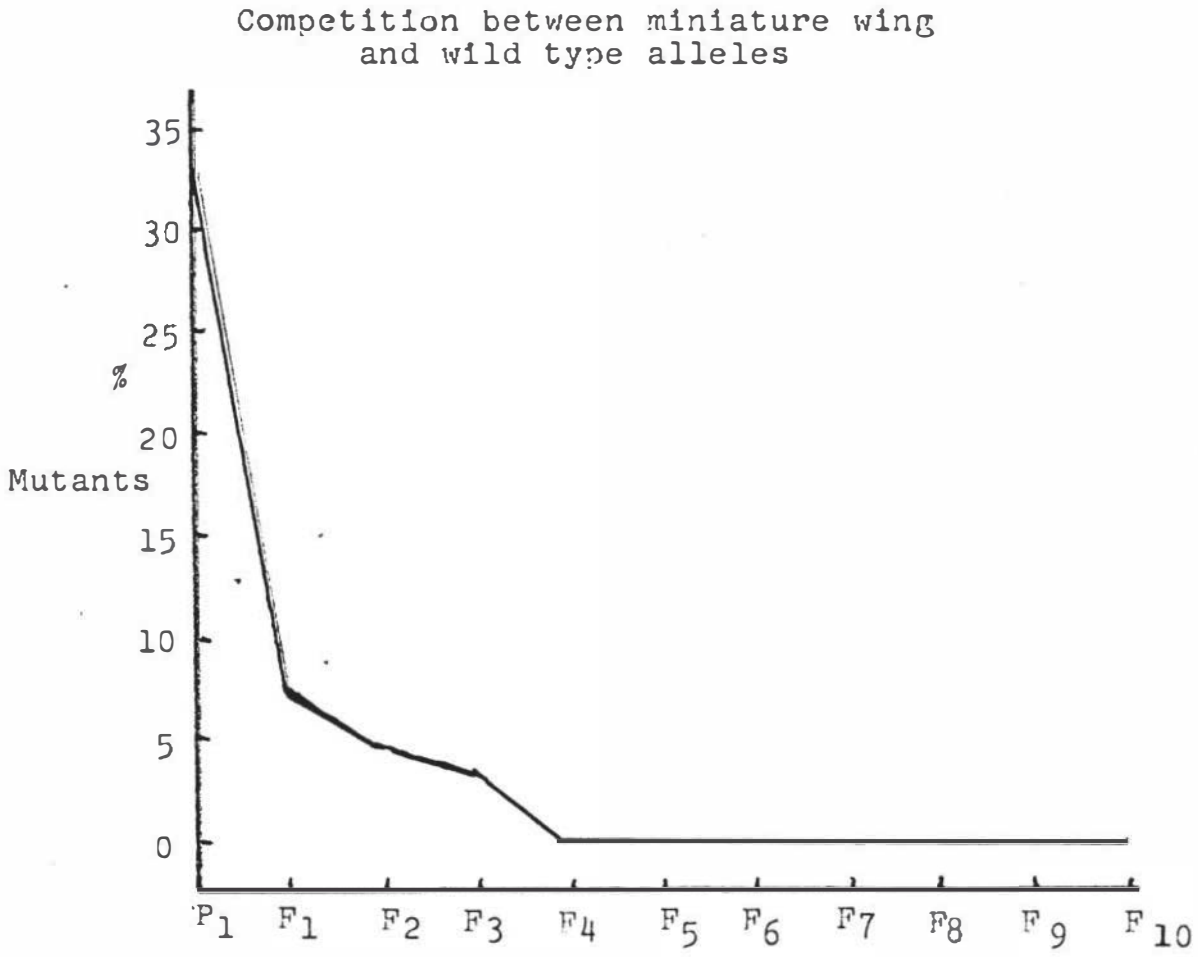

Competition between miniature wing and wild type alleles
35
30
25
%
20
Mutants
15
10
5
0
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Figure 5

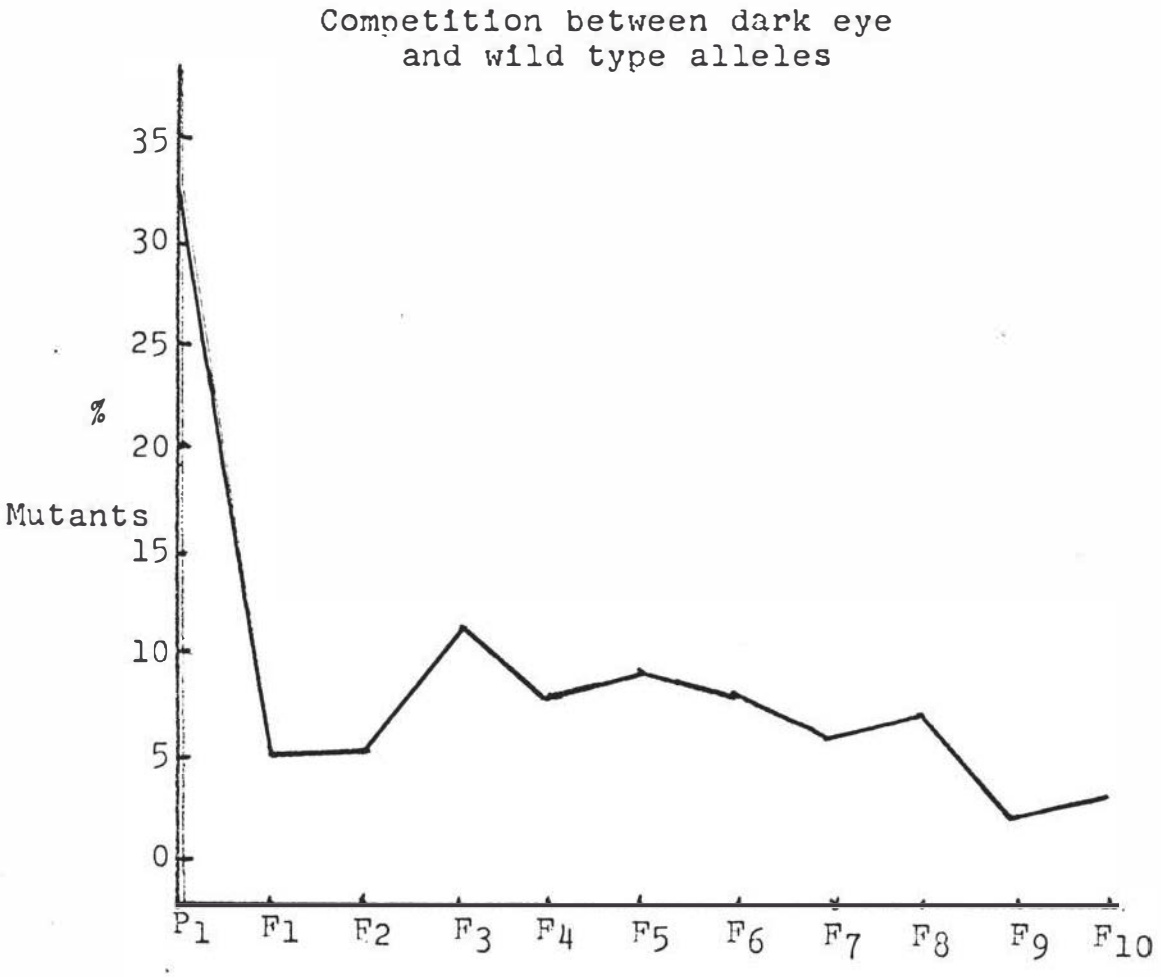

Competition between dark eye and wild type alleles
35
30
25
%
20
Mutants
15
10
5
0
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Figure 6

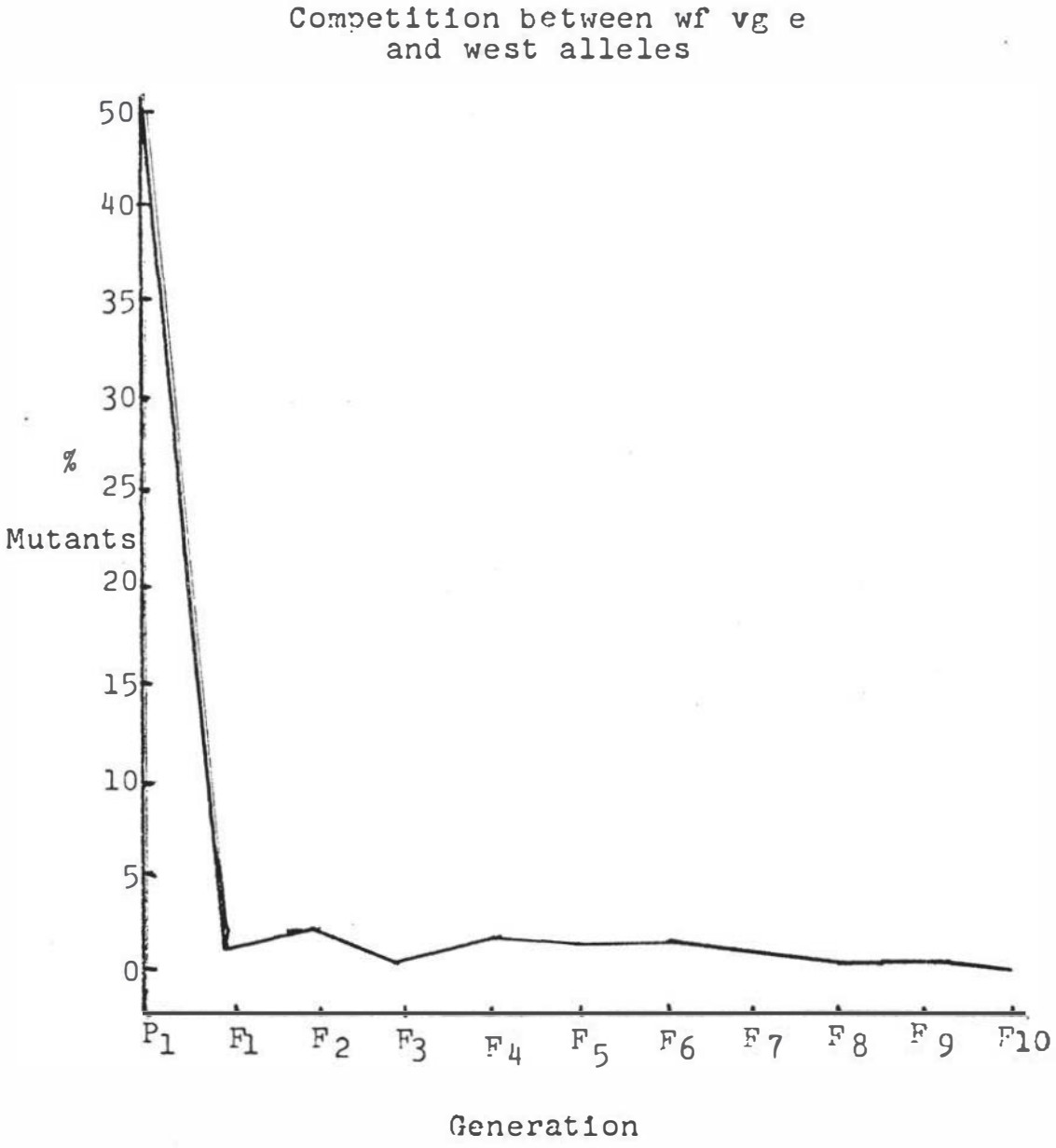

Competition between wf vg e
and west alleles
50
40
35
30
%
25
Mutants
20
15
10
5
0
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Figure 7

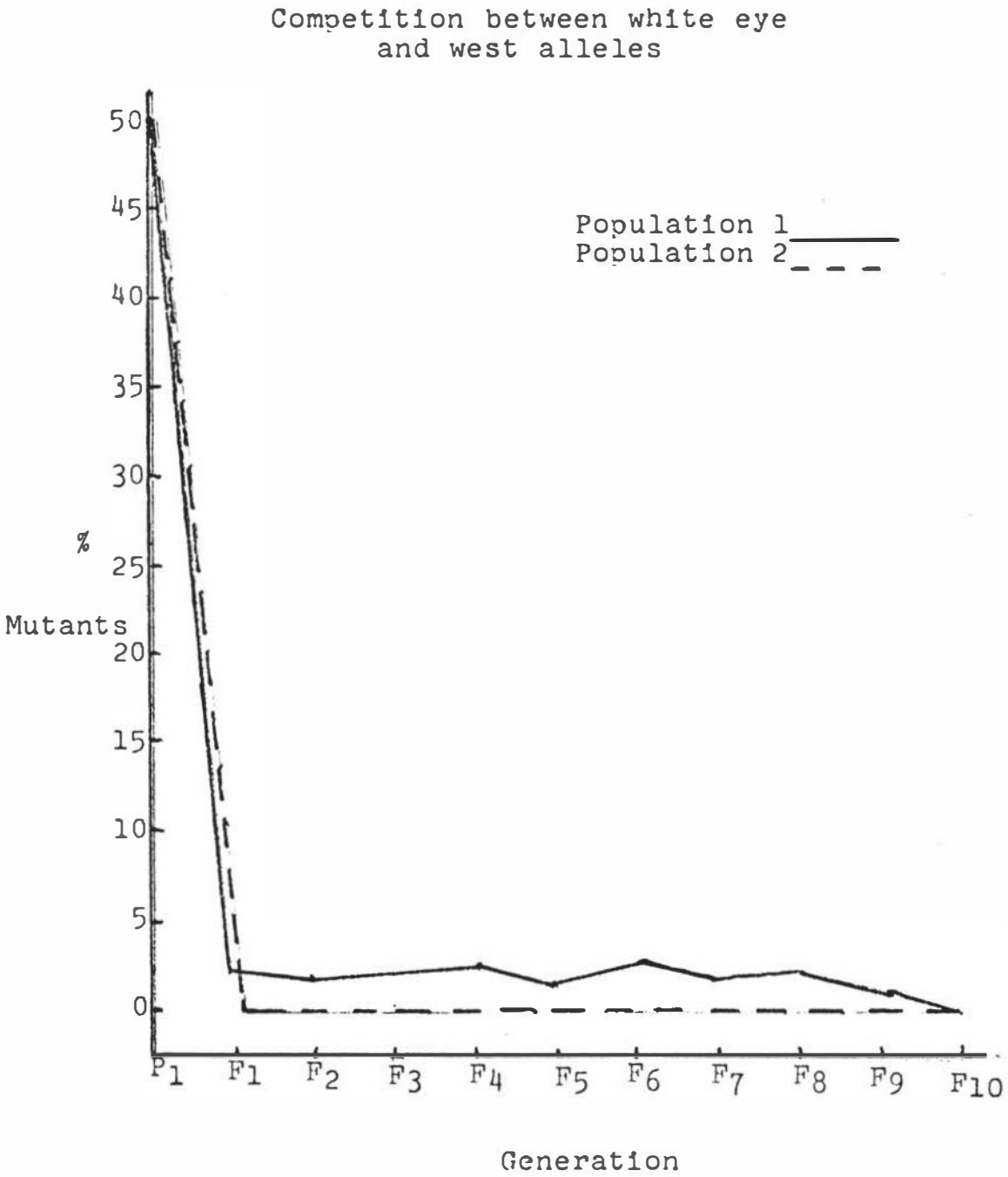

Competition between white eye and west alleles
Population 1
Population 2
50
45
40
35
30
25
20
15
10
5
0
%
Mutants
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Figure 8

Competition between forked bristles and west alleles

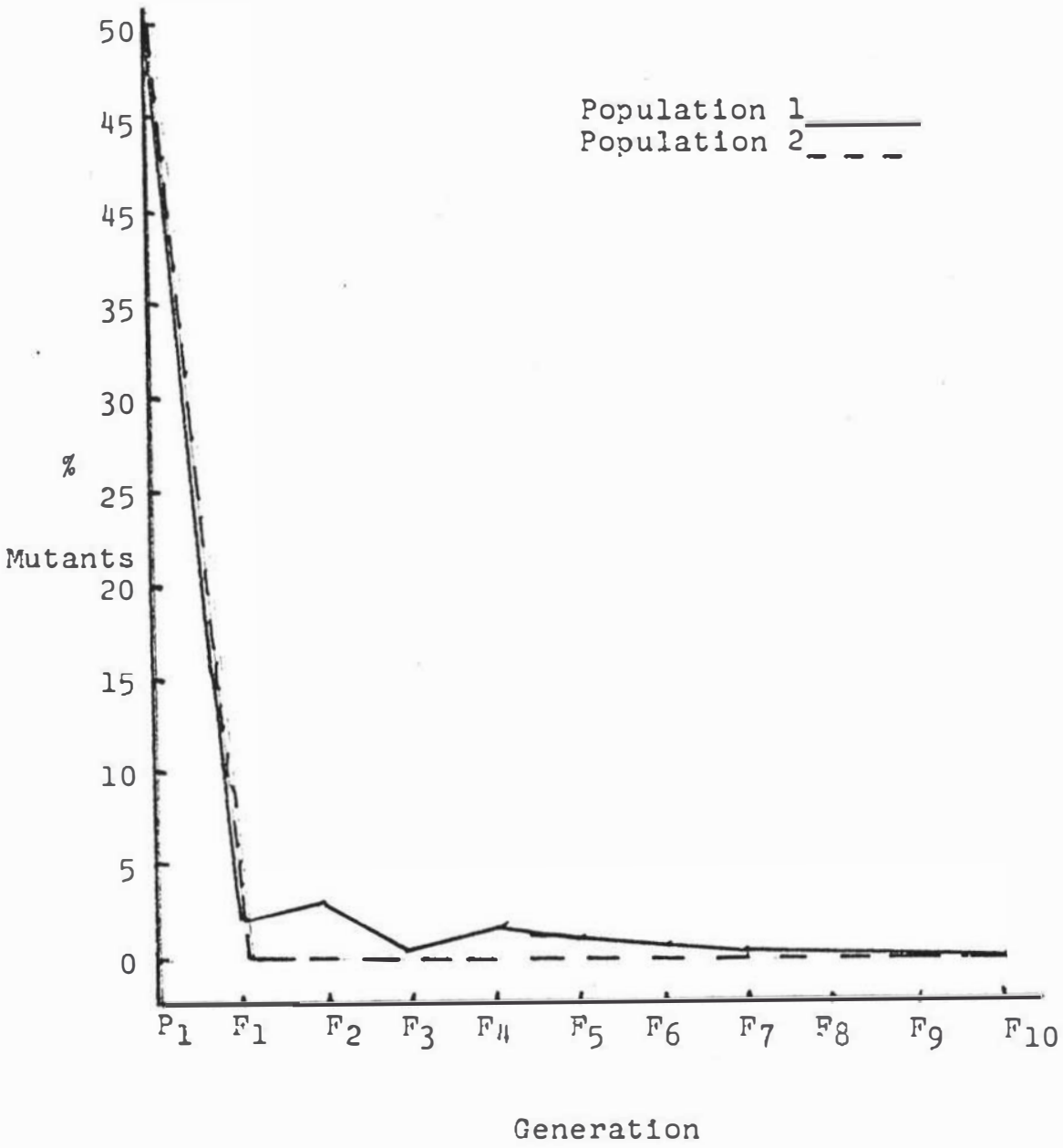


Figure 9

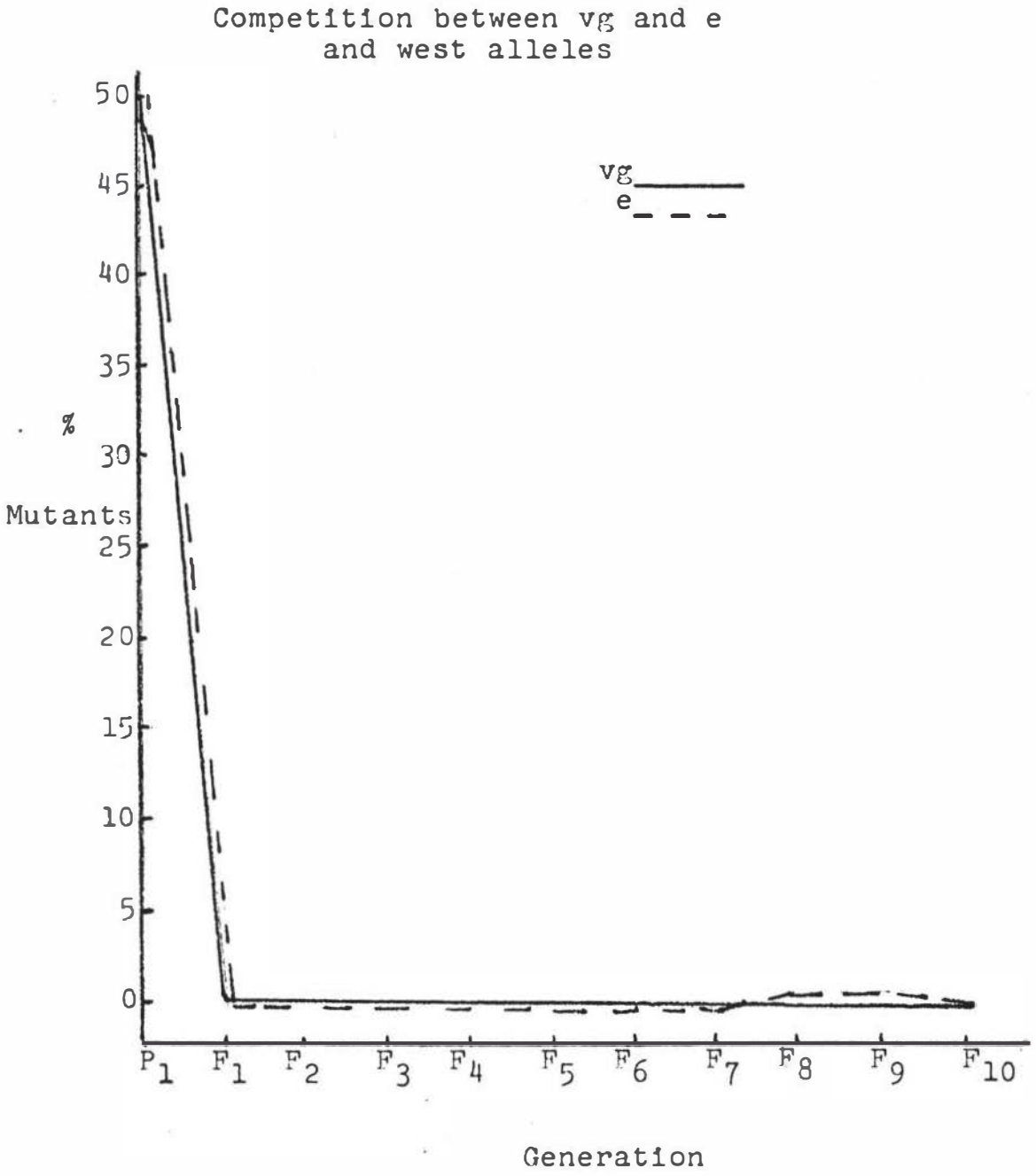

Competition between vg and e and west alleles
vg
e
50
45
40
35
%
30
Mutants
25
20
15
10
5
0
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Figure 10

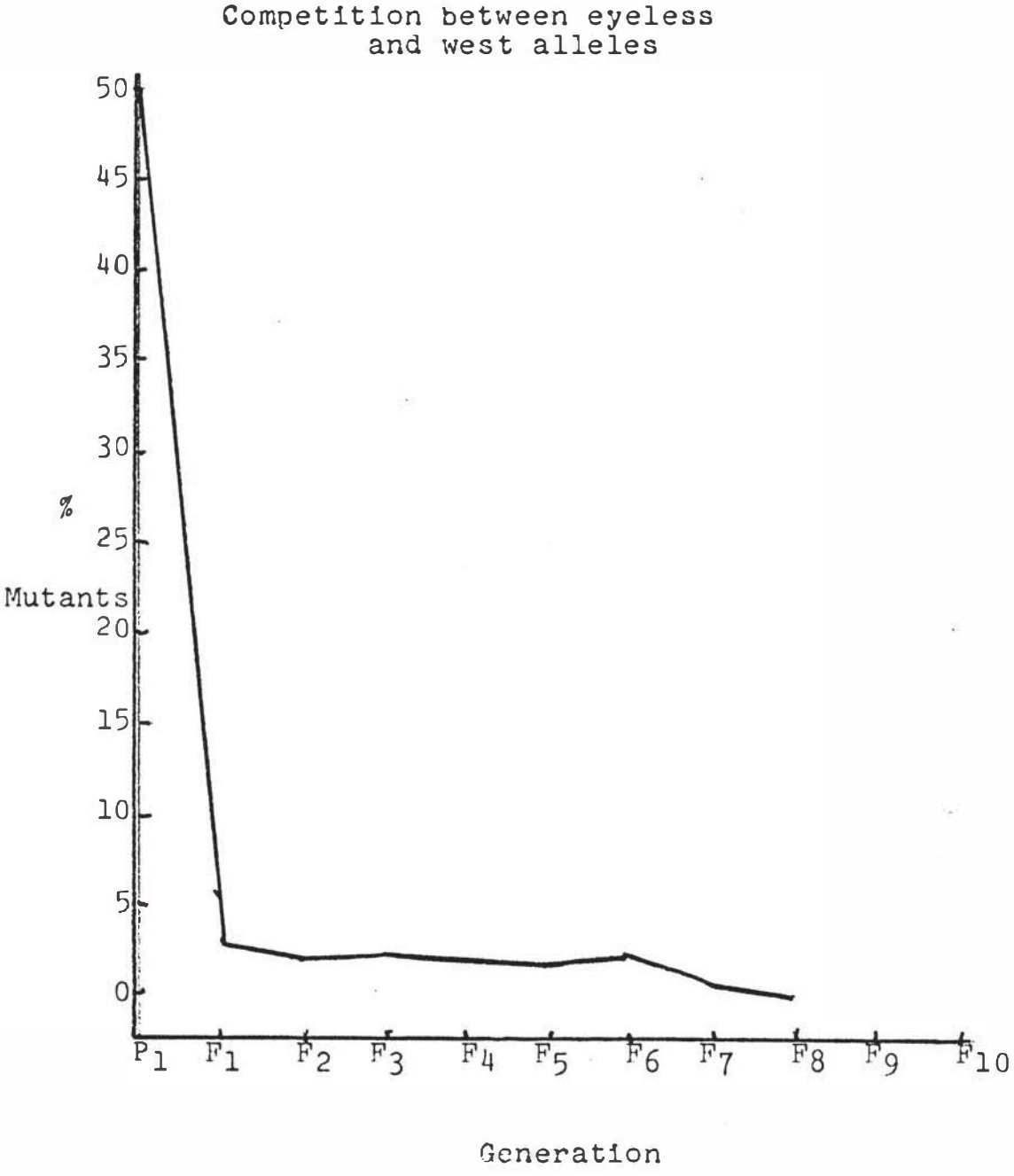

Competition between eyeless and west alleles
50
45
40
35
30
%
25
Mutants
20
15
10
5
0
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Figure 11

Competition between wf vg e
and town alleles

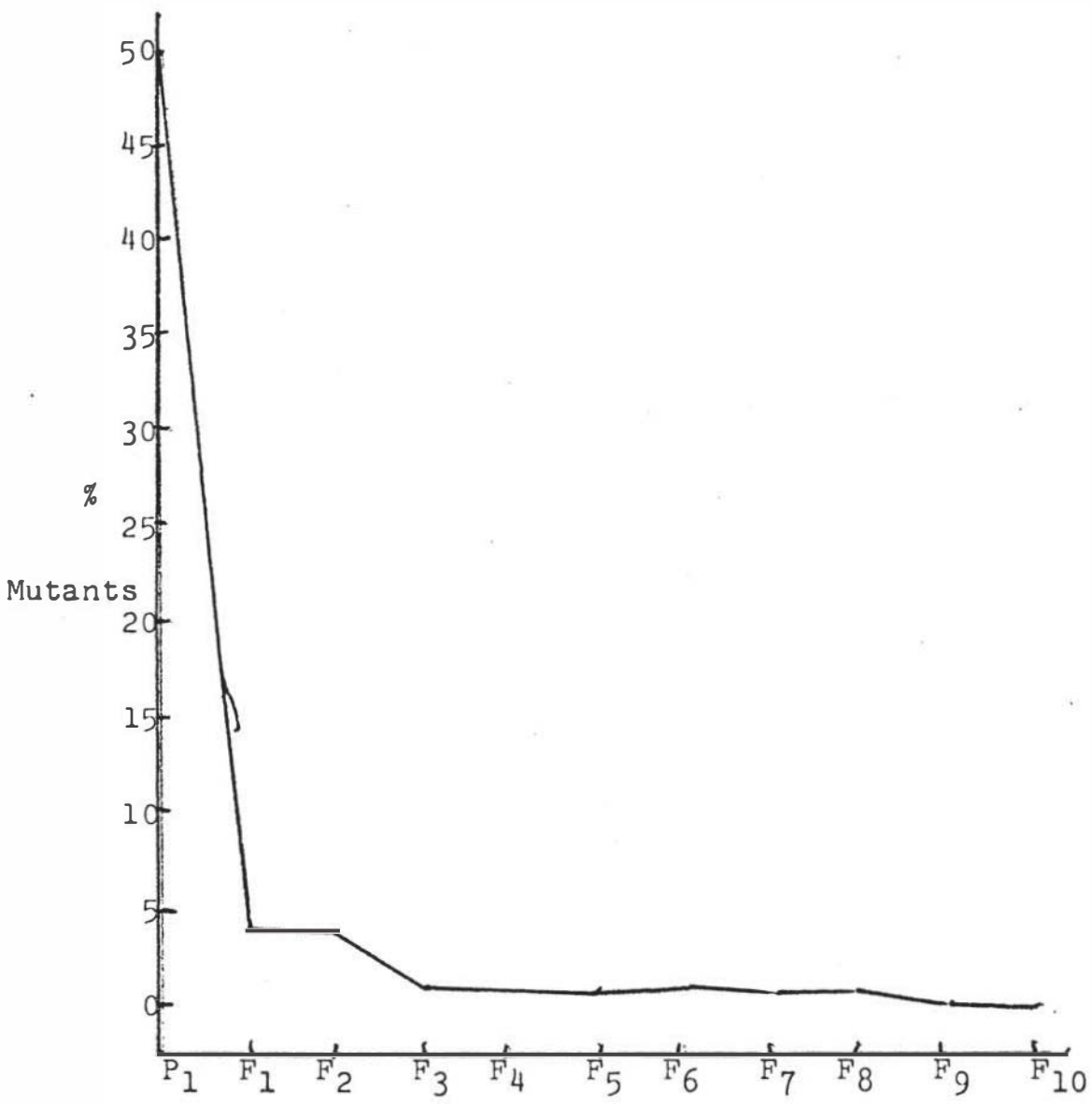


Figure 12

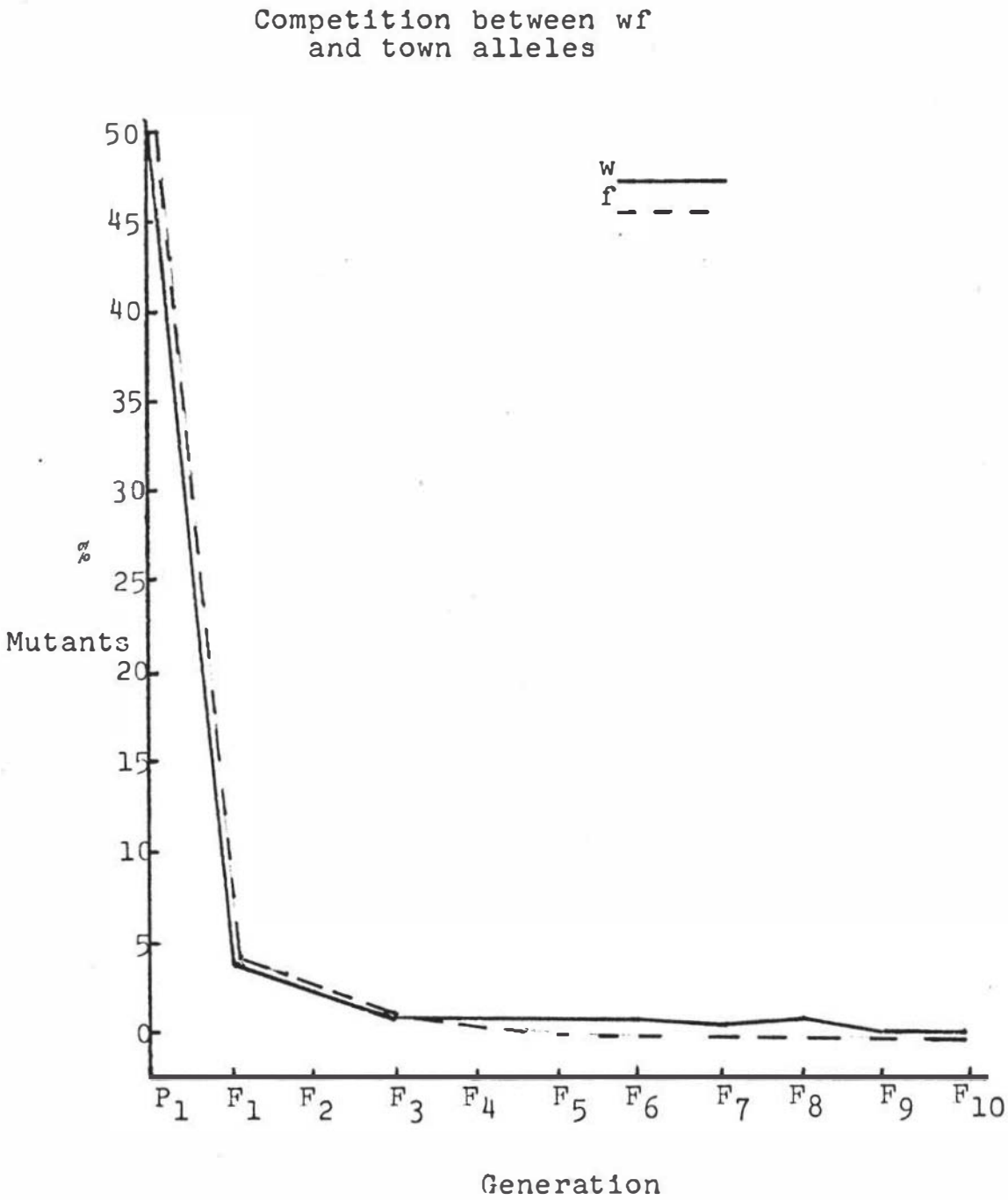

Competition between wf and town alleles
w
f
50
45
40
35
30
25
20
15
10
5
0
%
Mutants
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Figure 13

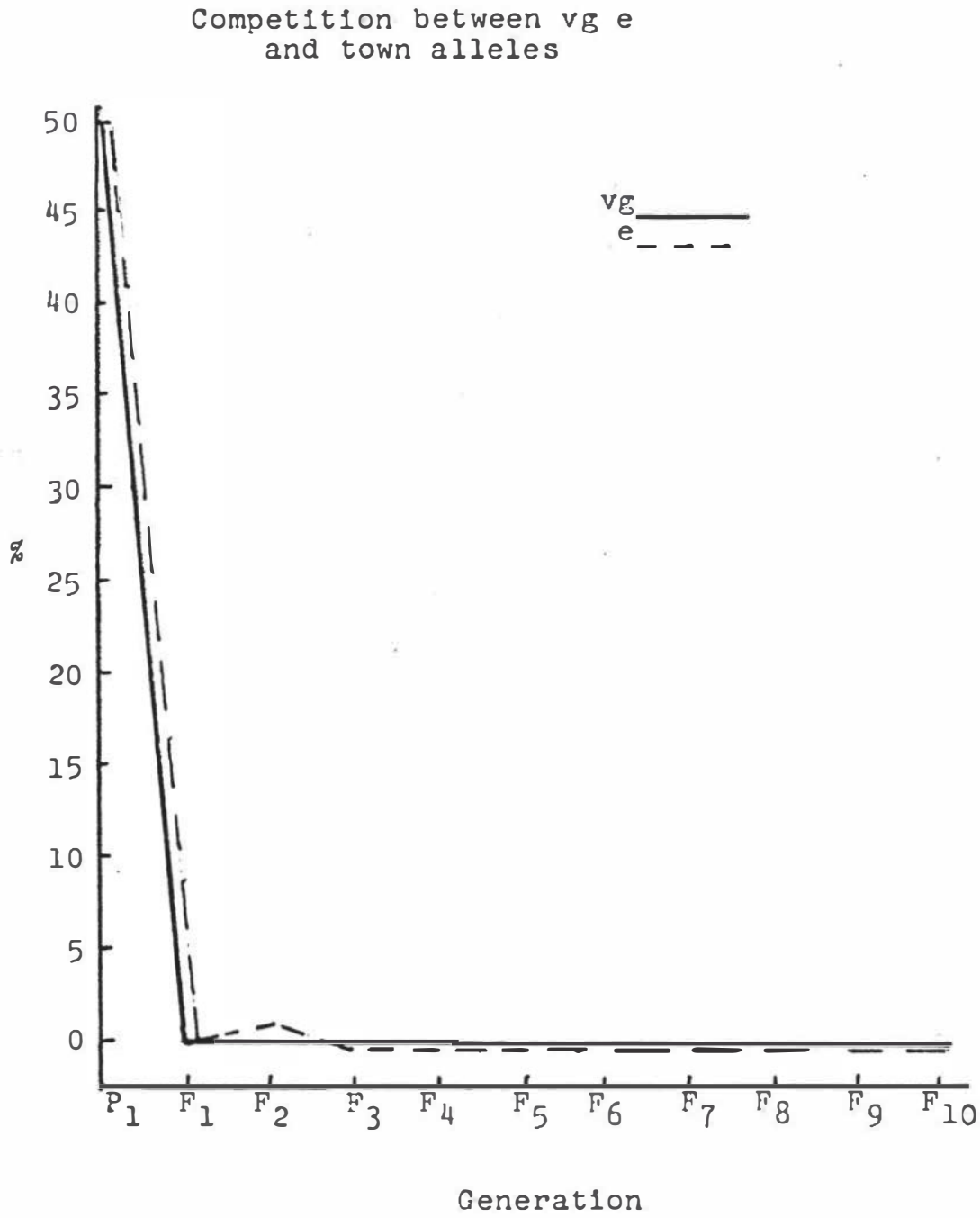
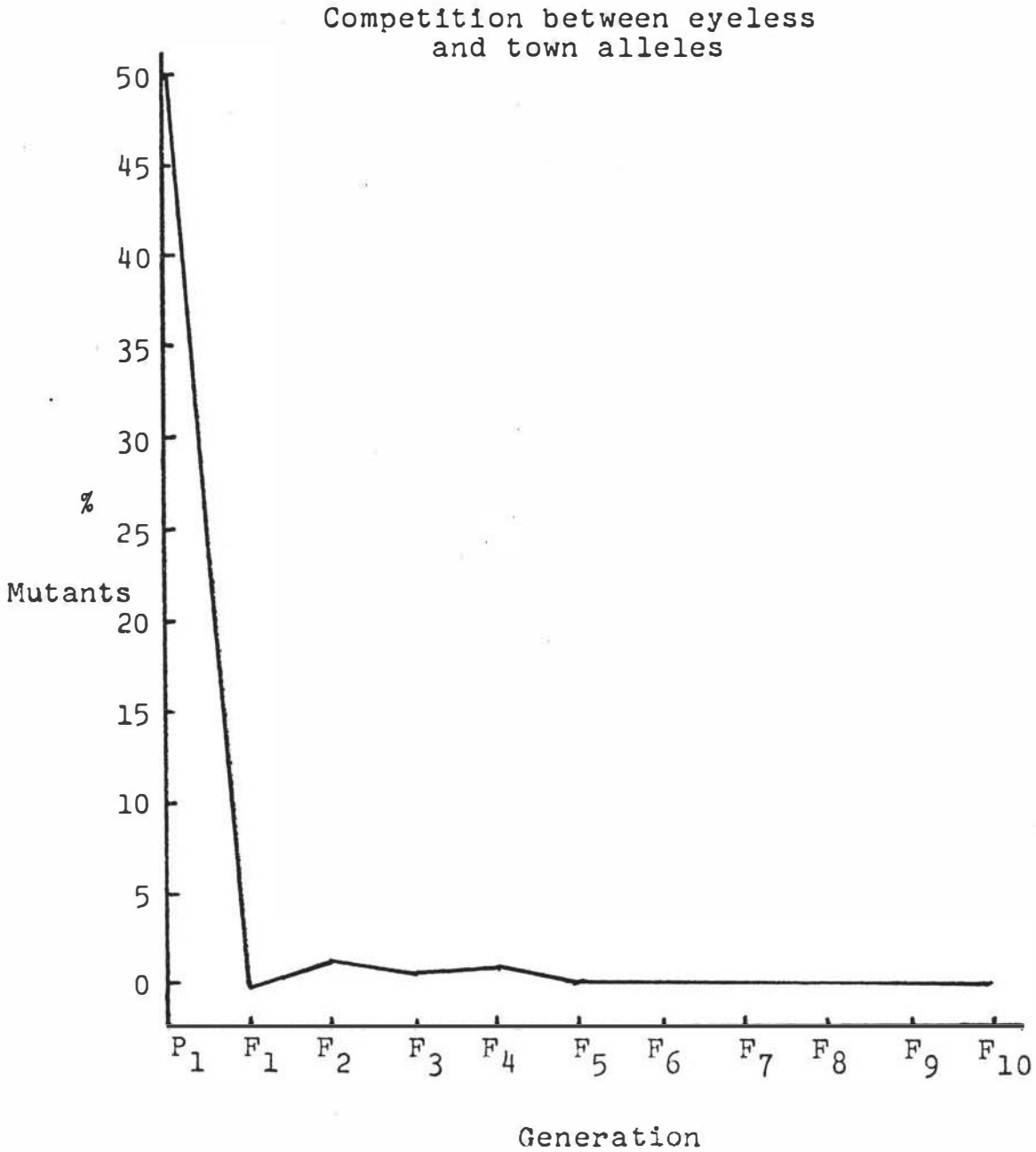

Competition between vg e and town alleles
50
45
40
35
30
25
20
15
10
5
0
%
vg
e
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Figure 14


Competition between eyeless and town alleles
50
45
40
35
30
%
25
Mutants
20
15
10
5
0
P1
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
Generation

Discussion

The environment of the population cages utilized in the experiments to determine the relative adaptive value for various alleles appears to be ideal. Many of the deleterious and selective components found in a natural environment are missing. There is no predation, extreme or radical temperature changes, starvation, or disease factors. Superficially it seems that any type of fly will have valuable adaptive characteristics because no selection pressures for a more favorable genotype will be invoked.

The experiments that have been performed relate much about the ways in which organisms compete with each other, and how a particular genotype can gain an evolutionary advantage over another. Beliefs and attitudes of the layman concerning the processes of evolution reveal a "survival of the fittest" conception where nature is "red in tooth and claw." However, this physical combat, which results in the death of the less successful individuals, is one of the least common ways in which the "struggle for existance" takes place; the nature of competition is often more subtle. (Stebbins 1966) For example, an organism that has the ability to grow and develop faster can eventually crowd out the least successful competitors. The ability of a genotype to leave a larger number of viable offspring

than a less successful genotype is another way in which competition can be manifested. Thus factors such as fecundity and viability are important components of natural selection.

It can be inferred from Figure 1 that selective competition for a superior genotype is taking place. This is the interpretation of the initial precipitous drop in gene frequencies from the P_1 through F_1 and F_2 generations. Thus in the first two or three generations equilibrium between different alleles has not been reached. According to the Hardy-Weinberg principle, which is a mathematical expression of the frequencies of the member of a pair of allelic genes, alleles in a population tend to establish an equilibrium with reference to each other. However the Hardy-Weinberg formula is only valid if neither allele has a selective advantage over the other, if neither mutates more frequently than the other and if mating is at random. If all these criteria are followed then gene frequencies are expected to remain in equal proportions generation after generation. Thus it is evident from the graphs that selection is taking place. Tables 1, 6 and 7 show that fecundity, viability and mating preference respectively are all significant factors working to minimize the gene frequencies of less successful mutant genotypes.

Table 8 shows that wild type genes have a decided superiority over their mutant alleles. Figure 1 indicates that the trend is for continued selection against all mutant alleles for each ensuing generation. A leveling off and hence genetic equilibrium appears eminent with the F_4 through F_8 generations. However, this leveling off and the attainment of a low gene grequency by the mutant alleles does not necessarily mean that equilibrium has been attained. Merrell and Underhill (1955) warn that the rate of elimination is so slow at low frequencies that the decision as to whether or not equilibrium has been reached is a very difficult one unless the experiment is continued for a long period. They collected data for over 350 days which gave a possible thirty generations in which to reach an equilibrium. The ten generations used in these experiments was probably too short a period in which to establish equilibrium for any set of mutant alleles.

Yellow body has an adaptive value inferior to that of the normal wild type and disappeared from the population by the sixth generation. Ludwin (1951) produced data that showed "wild type flies increase in proportion while yellow flies decrease in proportion. No yellow females were observed after the third count. The data indicate clearly that the frequency of the yellow gene is rapidly decreasing due to selective forces acting against yellow flies."

The selection is for the genotype with the greater viability as illustrated by Table 6. Utilizing the chi-square method for probability the difference in viability is very highly significant. However, the y allele, according to the results in Table 1, has a fecundity significantly greater than wild. Table 7 reveals that mating preferences favor the wild genotype. The wild type male is more successful than the yellow male when both are in "competition" for either the y/y or the y/+ female. This has been verified by Diederich (1941) and Merrell (1948). Merrell discovered that the wild type male is successful in mating in 95% of the cases when in competition with the yellow male for the heterozygous female.

White eye and miniature wing are also adaptively inferior to the wild alleles. Figures 2, 3 and 4 for per cent mutants in the population produce almost identical curves. All three are extinct by the F_4 generation. Table 6 indicates that all three of these sex-linked genes have approximately the same viability. The viability of ywm alleles compared to wild type is very highly significant. The 35% viability of white allele does not correspond with high viability found by other researchers. Reed and Reed (1949) "It was found that the flies with white eyes and those with red eyes were equally viable." Their conclusion for the decrease

of the white gene was due to selective mating. Diederich (1941) also verifies the selective mating pressure against yw. "When yw females were exposed to as many yw as wild males, 79% of those fertilized were fertilized by wild males; and 91% of wild females in parallel trials. When equal numbers of yw and wild females were exposed simultaneously to as many yw as wild males, 66% of the yw females and 94% of the wild females were fertilized by wild males." Thus non-random mating is capable of producing evolutionary changes.

How dark eye is inherited is not definitely known. It was first isolated at the University of Illinois. Dark eye does not appear to be a polygenic or a sex-linked trait. It is not of vital importance to know how the trait is inherited to perform the fecundity and mating choice tests. In the viability tests the dark eye has been treated as if it were a single pair of genes. Two inferences can be elucidated from Figure 5: the dark eye allele is of less adaptive value than wild and it is superior to ywm. Table 1 indicates that dark eye has a greater fecundity than the wild type. The difference is very highly significant. The dark eye allele also has a fecundity greater than ywm. However, the P value is .30 which makes the difference in fecundity an expected and acceptable event.

The viability of dark eye is 47% that of wild type. This is a very highly significant departure. See Table 6. The viability of dark eyes differs from y by an acceptable degree; from wm by a significant amount. Thus it appears from the viability data that dark eyes have a lesser adaptive value than wild, but a greater adaptive value than ywm. However, the greater gene frequency and thus a superior adaptive value of dark compared to ywm is not entirely due to its greater viability as shown in Table 7. From these data it appears that mating between wild and dark eyes is at random. The use of the chi-square method to determine the P value and the significant difference reveals that the slight amount of departure from equality is a highly probable event. The adaptive value of the alleles involved in the populations of wild x dark eye x ywm can be formulated as wild alleles > dark eye > y = w = m.

Population cage data for west x wf vg e indicates that the mutant alleles are less adaptive in this particular environment than are the "normal" alleles. Figure 6 reveals that the per cent of mutants in the population experiences the tremendous initial decline in the F_1 and F_2 generations as do all the mutant strains. From the F_4 generation to the F_{10} the general trend is for a decrease in the number of mutants in the population and

thus a continued lowering of gene frequencies for mutant alleles. Evidently the population has not established equilibrium with respect to all the alleles. However, equilibrium with respect to vg and e occurs in the F_1 generation because they become extinct. As is shown in Table 9 the mutants recorded in the population are white eyed and forked bristled. From this data alone it can be inferred that wf genes are of greater survival value than vg or e.

The reasons for the lesser adaptive value of wf vg e alleles compared to the normal genes are due to very highly significant differences in fecundity and viability. See Tables 1 and 6. The w allele has a viability that is 72% that of the west or normal allele. This does not closely agree with the results of Reed and Reed (1950). They found in their experiments that white-eyed flies were not less viable than normal individuals. Also the 50% viability of vg/vg is significantly lower than that reported by other workers. A viability of about 91% was recorded by Merrell and Underhill (1955). Low fecundity and viability are not themselves totally responsible for the selective pressure experienced by the population from the P_1 to the F_1 generation. Mating preferences again are greatly responsible for the low adaptive value of wf vg e alleles as shown in Table 7. The preference for red eyes over white eyes has

already been discussed on page 43. Work done by Merrell and Underhill (1955) whow that normal wings are highly preferred to vestigial wings. No reference has been found that discloses the success of ebony body males in competition with normal males for females. It cannot be inferred from Table 7 the mating success of ebony body males because competition was between a combination consisting of wf vg e. However, the frequency of e would be lowered in the F_1 generation because of preference for normal over w and vg. It is known from the data (see Table 6) that the viability of e/e is less than west. Timofreff and Ressovsky reported (Moody 1962) that the viability of ebony was lower than normal. The lower adaptive value of ebony compared to normal was also reported by (L'Heritier and Teissier 1937.) Merrell (1948) reports that in regard to the forked bristles, mating is at random. However, since f is in combination with w and vg it is discriminated against in the P_1 and will be selected against in all ensuing generations when in combination with w or vg. From the data it can be reasoned that the superiority of west alleles $>$ w $>$ f $>$ e $>$ vg.

Table 9 consists of data from two separate populations. In the first population (see Figures 7 and 8) the genes wf establish themselves at a level that approaches equilibrium. However, in population two these

genes become extinct with the F_1 generation and no mutants appear for ten generations. This is unusual even though the wf genes are of lower adaptive value due to reduced fecundity, viability, and non-random mating. One of the three following things may have happened: either no wf vg e females were fertilized by wf vg e males, no wf vg e females were fertilized by west males, or it is the result of genetic drift.

No wf vg e females having been fertilized by wf vg e males is probable since w and vg are greatly selected against. The failure of wf vg e females to be fertilized by west males is unlikely to have happened since wf vg e females prefer west males and males will mate indiscriminately and with frequent repetition. The mating of wf vg e females by west males would produce homizygous males and heterozygous females in the F_1 generation. Mutants would then be found in the next generation. Therefore the failure of mutant flies to be recorded could possibly be due to chance. By chance alone the 50 flies randomly selected for the $F_1 \times F_1$ could have been homozygous for the normal alleles. A chance event such as this is termed genetic drift or the Sewell Wright effect. The terms are synonymous and refer to chance occurrences in small populations. The effect could have been in the other direction. That is, the gene frequency for wf vg e could have been unusually high if the 50 flies selected

for the F_1 would have been mostly wf males and heterozygous females. Thus in the ensuing generations there could be a high fixation of the characteristics wf if it were not for their reduced fecundity and viability.

Population size and the chance of genetic drift occurring has been discussed by Wright (1943), "The simplest model is that in which the total population is assumed to be divided into sub-groups, each breeding at random within itself . . .Whatever the size of the subpopulation considered the variability (in gene frequency) depends upon the size of the inbreeding unit. There is an important amount of differentiation among large regions if the unit group is as small as 10, appreciable differentiation if the unit group is as large as 100, but little if it is as large as 1000." Thus the variability in gene frequency due to chance is little expected with the population as high as a thousand. However, genetic drift is the most suitable explanation for the extinction in one generation of wf vg e.

The population cage data for town x wf vg e have similarities much like that of west x wf vg e. See Table 11. The alleles vg and e become extinct in the F_1 generation. The viability of vg and e is reduced to a very highly significant difference. See Table 6. The fecundity of wf vg e is lower by a very highly significant amount. An enigma is evident that involves the e gene. Ebony body should have a greater adaptive

value than wf because in this situation ebony body has a greater viability than w or f; w is selected against in mating, f is neutral. Therefore, another factor or factors are selecting against e. Although it cannot be justly explained from these data why e is of lower adaptive value than w or f, it is hypothesized that mating preferences select against e also. The formulated expression for relative adaptive value is town alleles > >w >f >e >vg.

The data indicates that eyeless is of less adaptive value than its allele in west and town. See Figures 10 and 14. Tables 1 and 6 show that significantly reduced fecundity and viability are partially responsible for the evolutionary disadvantage. Mating choice results (Table 7) indicate that there is strong mating preference against the ey/ey male. This can explain the initial precipitous drop from the P_1 to F_1 generation. As a result of heterozygous matings in the F_1 x F_1 the gene frequency or per cent mutants in the population can increase in the next generation.

On the basis of Table 1 it can be inferred that west town wild. Each is lower in fecundity by a P value that is very highly significant. A possible explanation for the difference between weat and town is that this might be the result of separate geographical races. Small sample size might also be a factor.

The greatly reduced fecundity of the lab wild type is believed due to lowered viability as a result of approximately forty years of inbreeding. Its fecundity is even lower than that of some mutants. See Table 1. It has been discovered by Lints and Lints (1966) that viability of wild type was decreased after 63 generations of inbreeding.

In almost every case when west and town are in competition with the same mutant alleles, the mutants show a greater viability when in competition with west than in competition with town. The factor or factors operative here in producing such a magnitude of variance between west and town cannot be explicately known from these data. Several explanations can be hypothesized. If west does have greater viability, as well as fecundity, than does town, then heterosis will favor larger populations of western homozygous individuals. West shows greater viability than town for all mutants except eyeless. Unknown factors due to separate local populations might possibly have some influence on these results. Another factor might be small sample size. From these data it can be concluded that west has a slightly greater adaptive or survival value than does town.

Summary and Conclusions

Uniform population cages were constructed so that large numbers of flies could be reared. The data from the cages were utilized to determine which genes in a population had the greater adaptive value. Several cages of wild type flies versus yellow body, white eyed, and miniature winged flies plus dark eyed flies were established. Two separate populations of naturally occurring Drosophila melanogaster were collected. These were termed "town" and "west". Each was put into competition with white eyed, forked bristle, vestigial winged and ebony bodied flies. The adaptive value of eyeless was compared to town and west also. Graphs and tables of the population cage data revealed which alleles had an evolutionary advantage. Fecundity, viability and mating choice tests were performed to determine why certain genes were adaptively superior to others.

1. Wild type genes have an adaptive superiority over yellow bodied, white eyed, miniature winged, and dark eyed alleles. The greater evolutionary advantages of wild over ywm are a result of greater viability and non-random mating. The significantly reduced fecundity of wild type flies is believed due to long continued inbreeding.

2. Dark eye is superior to ywm because random mating occurs between wild and dark eyed flies. Selection against dark eye is believed due to lowered viability.

3. Town and west are adaptively superior to mutants wf vg e and eyeless because of the significantly reduced fecundity, viability and non-random mating pressures against mutants.

4. Extinction of wf vg e in one generation cannot unequivocally and completely be contributed to reduced fecundity, viability and non-random mating. Extinction is believed due to genetic drift or chance factors that occur when populations are small.

5. West appears to have an adaptive superiority slightly greater than town as a result of greater fecundity and viability. The difference is believed to be an expression of separate local populations with slightly different gene pools, each adaptive in its own microgeographical area.

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