

GENETICS OF NATURAL POPULATIONS. XVIII. EXPERIMENTS  
ON CHROMOSOMES OF *DROSOPHILA PSEUDOOBSCURA*  
FROM DIFFERENT GEOGRAPHIC REGIONS

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THE PROBLEM

Sixteen different gene arrangements have been recorded in the third chromosomes of natural populations of *Drosophila pseudoobscura*, and eight in the third chromosomes of the related species *Drosophila persimilis*. Representatives of the same species which carry different types of third chromosomes have different adaptive values in some environments. If artificial populations with certain proportions of the chromosomal types are set up in population cages, these proportions may undergo rapid changes. Analysis of these changes leads to the inference that the adaptive values of individuals carrying two chromosomes of different types (structural heterozygotes) are higher than those of individuals with two similar chromosomes (structural homozygotes). The superior fitness of the heterozygotes results in populations reaching certain equilibrium states, at which the chromosomal types are present in definite proportions (WRIGHT and DOBZHANSKY 1946). Differential survival which favors structural heterozygotes relative to the homozygotes has been further ascertained through observations on deviations from the HARDY-WEINBERG equilibrium ratios of hetero- and homozygotes among flies which developed in population cages (DOBZHANSKY 1947a).

In the experiments previously reported, the experimental populations were made from flies the ancestors of which had been collected in a single locality—Piñon Flats, on Mount San Jacinto, in Southern California. The gene arrangements found in the third chromosomes of the Piñon Flats population occur, however, in populations of the Pacific Coast from British Columbia to Lower California. The problem naturally arises whether the adaptive properties of flies with the same chromosomes are alike wherever a given chromosomal type occurs, or whether the gene contents of these chromosomes are geographically differentiated. The flies used in the experiments to be reported in the present publication are descendants of wild flies collected in three different localities: Piñon Flats and Keen Camp, both on Mount San Jacinto in southern California, and Mather, in the Sierra Nevada of central California. It will be shown that chromosomes with the same gene arrangement found in geographically distinct populations have different adaptive properties.

MATERIAL

Progenitors of the flies that served as material for the experiments were collected at Piñon Flats and Keen Camp in April 1945 by MR. ALEXANDER SOKOLOFF, and at Mather during the summers of 1945 and 1946 by the writer.

Piñon Flats and Keen Camp are about 13 miles apart, at elevations of 4000 and 4300 feet respectively, but the biotic characteristics of the two localities are quite different (WRIGHT, DOBZHANSKY, and HOVANITZ 1942). Mather is some 300 miles north of the other localities, at elevation of 4600 feet, in the Transition Zone of the Sierra Nevada (DOBZHANSKY 1948).

The population cages used have been described by WRIGHT and DOBZHANSKY (1946); an improved model is shown in DOBZHANSKY 1947c.

#### PLAN OF THE EXPERIMENTS

A mixture of flies with desired proportions of two chromosomal types is introduced into a population cage and allowed to breed. At intervals of one or two months samples of eggs deposited in the cage are taken, and larvae hatched from them are raised under optimal conditions. When larvae mature, the chromosomes in their salivary glands are examined. Each "sample" consists of 300 chromosomes (150 larvae) divided into six "subsamples" of 25 larvae taken on six successive days. The frequencies of the chromosomal types present in the population of a cage at different times are thus determined. If changes in these frequencies are observed, they usually lead to the establishment of an equilibrium condition at which the two competing gene arrangements are present in the population in definite proportions. When the equilibrium is attained no further changes occur.

Since the process of selection results, in most experiments, in establishment of an equilibrium, the adaptive values of the structural heterozygotes must be higher than those of the corresponding homozygotes. For example, the fitness of Standard/Chiricahua heterozygotes is higher than that of Standard homozygotes and of Chiricahua homozygotes. If one of the homozygotes has an adaptive value equal to or higher than the heterozygotes, as is actually observed in one experiment (No. 31, table 7), the outcome of selection is eventually complete replacement of the less fit by the more fit chromosomal type. Mathematical analysis of the rates of change of the frequencies of gene arrangements in population cages permits estimation of the adaptive values of the chromosomal types involved (see equation 11 in WRIGHT and DOBZHANSKY 1946, also DOBZHANSKY 1947a). Taking the adaptive value ( $W$ ) of the structural heterozygotes to be unity, those of the two homozygotes are  $(1-s)$  and  $(1-t)$  respectively, where  $s$  and  $t$  are selection coefficients. The frequency,  $q$ , at which equilibrium between the competing gene arrangements is established can be computed according to the simple formula,  $\bar{q} = t/(s+t)$ .

#### THE INITIAL POPULATIONS OF EXPERIMENTAL CAGES

Since flies carrying different gene arrangements in the third chromosome are phenotypically similar, the task of preparing mixtures of flies with desired proportions of gene arrangements to be placed in population cages is not a simple one. WRIGHT and DOBZHANSKY (1946) and DOBZHANSKY (1947a) set up series of pair matings of flies from strains of certain geographic origin, and examined cytologically several (8) larvae in the progeny of each pair. This permitted to infer the chromosomal constitution of the parents, and hence the

proportions of various chromosome types in the individual progenies. The adult flies that hatched were then placed in the population cages. This method has also been used in the experiments with chromosomes from Keen Camp described below (Cage Nos. 25-27, table 1).

TABLE 1  
*A review of the conditions in the different experiments.*

CAGE NO.	ORIGIN	STARTED	TEMP.	LIGHT	NUMBER OF CHROMOSOMES				KINDS OF CHROMOSOMES			
					ST	AR	CH	TL	ST	AR	CH	TL
25	Keen	Nov. 6, 1945	25°	Dark	816	—	1650	—	10	—	13	—
26	Keen	Nov. 7, 1945	25°	Dark	619	1289	—	—	8	11	—	—
27	Keen	Nov. 9, 1945	25°	Dark	—	354	810	—	—	11	13	—
28	Mather	Dec. 22, 1945	25°	Dark	—	357	723	—	—	8	8	—
29	Mather	Dec. 22, 1945	25°	Dark	1119	485	—	—	8	6	—	—
30	Mather	Dec. 22, 1945	25°	Dark	566	—	1136	—	7	—	8	—
31	Mather	Dec. 23, 1945	25°	Dark	547	—	—	667	7	—	—	6
32	Mather	Dec. 24, 1945	25°	Dark	441	1837	—	—	8	10	—	—
33	Mather	Jan. 16, 1946	25°	Dark	—	1067	—	2061	—	6	—	7
34	Piñon	Feb. 25, 1946	Room	Light	2278	394	—	—	14	8	—	—
35	Piñon	Mar. 1, 1946	Room	Light	140	—	1172	—	10	—	11	—
36	Piñon	Mar. 2, 1946	Room	Light	240	1740	—	—	16	12	—	—
37	Piñon	Oct. 9, 1946	25°	Dark	—	370	1432	—	—	12	16	—
38	Piñon	Dec. 16, 1946	25°	Dark	—	2066	400	—	—	12	15	—
39	Mather	Oct. 9, 1946	25°	Dark	—	2345	543	—	—	10	16	—
40	Mather	Oct. 16, 1946	25°	Dark	—	374	2293	—	—	10	16	—
44	Piñon	Feb. 1, 1947	25°	Dark	—	1074	2594	—	—	13	15	—

In 1945 another method was adopted. Strains homozygous for various third chromosomes were prepared by means of a systematic inbreeding of flies from strains descended from wild progenitors. The progress of the inbreeding was controlled by cytological examination in each generation. Several dozen strains homozygous for the Standard, Arrowhead, Chiricahua, and Tree Line gene arrangements of Mather and of Piñon Flats origin were obtained. Population mixtures with any desired frequencies of the chromosomal types can be made by using different numbers of flies from various homozygous strains.

In every experiment six or more strains with the same gene arrangement were used to make up the initial population of a cage. The numbers of the strains used are shown in table 1 in the columns labelled "Kinds of Chromosomes." The numbers given are minimum estimates, since a strain homozygous for a given gene arrangement may contain two or even more different chromosomes with the same gene arrangement but with different complexes of polygenes. The structural homozygotes produced in the population cages are, thus, mostly genic heterozygotes which should have their fitness enhanced by hybrid vigor (for a discussion of this point see WRIGHT and DOBZHANSKY 1946, pp. 130-131). The numbers of flies which constituted initial populations of the experimental cages are given in table 1 in terms of numbers of chromosomes; a fly has, of course, two third chromosomes.

In most of the experiments, the population cages were kept at 25°C in a dark constant temperature room, or in incubators in which the only source of light were the incandescent bulbs used for heating. Some of the cages were, however, kept in laboratory or in apartment rooms with temperatures fluctuating between 21° and 27°C, and alternating light and darkness. The conditions in which the experiments were begun are summarized in table 1; the changes that were subsequently made in some of them are stated in the descriptions of the respective experiments.

The names of the Standard, Arrowhead, Chiricahua, and Tree Line gene arrangements are hereafter abbreviated to ST, AR, CH, and TL respectively.

#### CHROMOSOMES OF THE PIÑON FLATS POPULATION

WRIGHT and DOBZHANSKY (1946) and DOBZHANSKY (1947a) have reported eight experiments in which ST and CH chromosomes of Piñon Flats origin competed in population cages, and a ninth is reported in table 2 of the present article (No. 35). In two experiments (Nos. 9 and 17) the populations were kept in a cold room at 16½°C. No significant changes in the frequencies of ST or CH chromosomes took place in the cages kept at this temperature, just as no changes were observed in three other cages (Nos. 3, 7, and 16) which contained mixtures of ST, AR, and CH chromosomes and were kept at 16½°C. This shows that, in the environments prevailing in population cages kept at 16½°, the adaptive values of homo- and heterozygotes for ST and CH chromosomes are not different enough to give rise to changes in the frequencies of these gene arrangements that would be easily noticeable within time intervals corresponding to several generations.

On the contrary, significant changes in the frequencies of ST and CH chromosomes were observed in each of the seven cages kept at 25° or at room temperature. Thus, cage No. 35 was started on March 1, 1946, with a population having about 11 percent ST and 89 percent CH chromosomes (table 2). Within a month, in early April, the frequency of ST chromosomes doubled, and by early May nearly trebled. In August ST chromosomes were more frequent than CH, and in late December the frequency of ST reached about 70 percent. The frequencies of 70–75 percent ST and 25–30 percent CH chromosomes seem to represent an equilibrium position for these chromosomes of Piñon Flats origin in population cages at 25°C. If a cage is started with an initial frequency of ST above, and of CH below, the equilibrium, CH increase and ST decrease in frequency (cage No. 24, DOBZHANSKY 1947a).

Since the competition of ST and CH chromosomes leads to establishment of equilibrium at which both competitors are present in the population, the adaptive value ( $W$ ) of the ST/CH genotype must be higher than those of the ST/ST and CH/CH genotypes. From the experiments previously published by WRIGHT and DOBZHANSKY (1946) and DOBZHANSKY (1947a) the following estimates have been derived:

<i>Genotype</i>	<i>W</i>		
ST/ST	0.77	$s = 0.23$	
ST/CH	1.00		$\hat{q} = 0.73$
CH/CH	0.39	$t = 0.61$	

From experiment No. 35 taken by itself rather different estimates of the selection coefficients are arrived at, namely:

<i>Genotype</i>	<i>W</i>		
ST/ST-	0.85	$s = 0.15$	
ST/CH	1.00		$\hat{q} = 0.74$
CH/CH	0.58	$t = 0.42$	

It is probable that the data obtained in cage No. 35 underestimate the magnitude of the selection coefficients, because this cage (and No. 36) was kept in a room in which the temperatures during most of April, May, and June averaged below 25°C. The length of a generation at these temperatures was longer than 3.5 weeks, which is the estimate used in the computations of the selection coefficients. Taking all the data into account (including cage No. 35), the estimates  $s = 0.19$ ,  $t = 0.53$ , and  $\hat{q} = 0.74$  are obtained. It may be noted that all the estimates of  $\hat{q}$  agree in showing that the equilibrium frequency of ST chromosomes lies close to 74 percent, which is only slightly higher than actually obtained in experiments (72 percent in cage No. 19, 71 percent in cage No. 35).

TABLE 2

*Percentage frequencies of the different gene arrangements in experiments involving chromosomes of Piñon Flats origin*

TIME <sup>1</sup>	CAGE NO. 35		CAGE NO. 36		CAGE NO. 34	
	ST	CH	ST	AR	ST	AR
Feb. 25-Mar. 2, 1946	10.7	89.3	12.1	87.9	85.3	14.7
E. Apr., 1946	21.7	78.3	26.0	74.0	81.0	19.0
E. May, 1946	28.3	71.7	35.7	64.3	76.7	23.3
E. June, 1946	37.7	62.3	41.3	58.7	77.3	22.7
E. July, 1946	43.7	56.3	46.3	53.7	79.3	20.7
M. Aug., 1946	53.7	46.3	56.7	43.3	75.0	25.0
M. Sept., 1946	54.7	45.3	—	—	—	—
M. Oct., 1946	—	—	64.3	35.7	—	—
M. Nov., 1946	65.7	34.3	—	—	—	—
L. Nov., 1946	—	—	66.7	33.3	—	—
L. Dec., 1946	71.0	29.0	—	—	—	—
E. Jan., 1947	—	—	68.3	31.7	—	—
M. Feb., 1947	—	—	68.0	32.0	—	—

<sup>1</sup> E. = early; M. = middle; L. = late.

Three experiments have been made in which ST and AR chromosomes of Piñon Flats origin were present in population cages. One of these experiments has been reported by WRIGHT and DOBZHANSKY (1946, experiment No. 14), and two are shown in table 2, (cages Nos. 34 and 36). All three were carried at room temperature or at 25°C. In cages Nos. 14 and 36, the initial populations contained appreciably fewer ST than AR chromosomes. The frequency of ST rose rapidly in both cages. In cage No. 36 which was maintained for just under a year, the initial frequency of 12 percent was more than doubled in about 4.5

weeks, and reached about 65 percent in about 7 months; for the subsequent 4 months it advanced to only 68 percent, indicating an approach to equilibrium. Cage No. 34 had initially 85 percent of ST chromosomes; the observed changes were rather erratic but their trend was on the whole downward, reaching 75 percent after about six months. This also indicates an equilibrium frequency in the neighborhood of 70 percent. Estimates of the adaptive values arrived at on basis of all three experiments are as follows:

<i>Genotype</i>	<i>W</i>		
ST/ST	0.81	$s = 0.19$	
ST/AR	1.00		$\hat{q} = 0.72$
AR/AR	0.50	$t = 0.50$	

AR and CH chromosomes of Piñon Flats origin were present in the populations of cages in five experiments (No. 15 in WRIGHT and DOBZHANSKY 1946, No. 23 in DOBZHANSKY 1947a, Nos. 37, 38, and 44 in table 3 of the present paper). Except for No. 15 which was kept at room temperature, the experiments were carried at 25°C.

TABLE 3

*Percentage frequencies of AR and CH gene arrangements in experiments involving chromosomes of Piñon Flats origin.*

TIME	CAGE NO. 37		CAGE NO. 38		CAGE NO. 44	
	AR	CH	AR	CH	AR	CH
Oct. 9-16, 1946	20.5	79.5	83.8	16.2	—	—
M. Nov., 1946	41.7	58.3	80.7	19.3	—	—
M. Dec., 1946	54.0	46.0	83.7	16.3	—	—
L. Jan., 1947	—	—	79.7	21.3	—	—
Feb. 1, 1947	—	—	—	—	29.3	70.7
L. Feb., 1947	—	—	75.0	25.0	—	—
E. Mar., 1947	—	—	—	—	40.7	59.3
L. Mar., 1947	—	—	75.3	24.7	—	—
M. May, 1947	—	—	—	—	55.3	44.7
L. June, 1947	—	—	—	—	58.3	41.7
L. July, 1947	—	—	—	—	74.0	26.0
L. Aug., 1947	—	—	—	—	76.7	23.3
M. Nov., 1947	—	—	—	—	75.0	25.0

In four experiments (Nos. 15, 23, 37, and 44) the initial populations had fewer AR than CH chromosomes. The frequencies of AR rose rapidly. In cage No. 44, which is the only one which was maintained sufficiently long for equilibrium frequencies to be approached, the frequency of AR rose to around 75 percent and remained there for about 4 months, after which the experiment was terminated (table 3). Cage No. 38 had initially about 84 percent of AR chromosomes; the frequency of AR declined slightly, and reached values between 75 and 80 percent, which are accordingly indicated as the location of the equilibrium of AR in competition with CH. Computations of the adaptive values from the data of the four experiments gave the following estimates:

<i>Genotype</i>	<i>W</i>		
AR/AR	0.86	$s=0.14$	
AR/CH	1.00		$\hat{q}=0.79$
CH/CH	0.48	$t=0.52$	

## CHROMOSOMES OF THE KEEN CAMP POPULATION

A population cage (No. 25, table 4) was started, at 25°C in early November 1945, with 33 percent ST and 67 percent CH chromosomes of Keen Camp origin. By late February 1946, the frequency of ST rose to 70 percent, and by late March to 75 percent. No significant changes were observed for the next three months, indicating that an equilibrium has been approached or attained. On June 26, 1946 the cage was moved to a refrigerated room with a temperature of 16°C. Population samples taken in September and November failed to disclose significant alterations in the frequencies of the chromosomal types. It

TABLE 4

*Percentage frequencies of the different gene arrangements in experiments involving chromosomes of Keen Camp origin.*

TIME	TEMP.	CAGE NO. 25		CAGE NO. 26		CAGE NO. 27	
		ST	CH	ST	AR	AR	CH
Nov. 6-9, 1945	25°	33.1	66.9	32.4	67.6	30.4	69.6
M. Dec., 1945	25°	52.3	47.7	37.0	63.0	37.0	63.0
L. Jan., 1946	25°	56.3	43.7	52.3	47.7	41.3	58.7
L. Feb., 1946	25°	70.3	29.7	56.3	43.7	43.3	56.7
L. Mar., 1946	25°	75.0	25.0	60.3	39.7	—	—
L. Apr., 1946	25°	76.3	23.7	60.0	40.0	45.3	54.7
L. June, 1946	25°	76.3	23.7	60.3	39.7	—	—
E. Sept., 1946	16°	79.3	20.7	67.0	33.0	—	—
E. Nov., 1946	16°	79.0	21.0	60.0	40.0	—	—
E. Jan., 1947	16°	—	—	58.0	42.0	—	—

may be recalled that ST and CH homozygotes and heterozygotes of Piñon Flats origin possess equal adaptive values at 16°C; the behavior of the population No. 25 is compatible with the supposition that the Keen Camp chromosomes are, in this respect, like those from Piñon Flats. The adaptive values at 25°C, computed from the data in table 4, are as follows:

<i>Genotype</i>	<i>W</i>		
ST/ST	0.91	$s=0.09$	
ST/CH	1.00		$\hat{q}=0.86$
CH/CH	0.42	$t=0.58$	

The equilibrium point for ST chromosomes in competition with CH seems to be slightly higher for the chromosomes of Keen Camp origin than for the chromosomes of Piñon Flats origin (see page 591-592).

A mixture of about 32 percent of ST and 68 percent of AR chromosomes of Keen Camp origin was set in cage No. 26, at 25°C, in November 1945 (table

4). By March 1946 the frequency of ST reached 60 percent, and stayed there till June, indicating an equilibrium. On June 26, 1946 the cage was transferred to 16°C. In September, a sample showed 67 percent ST, but samples taken in November 1946 and January 1947 again contained about 60 percent ST. The adaptive values at 25°C are as follows:

<i>Genotype</i>	<i>W</i>		
ST/ST	0.79	$s=0.21$	$\hat{q}=0.67$
ST/AR	1.00		
AR/AR	0.58	$t=0.42$	

These estimates are probably not significantly different from those obtained for ST and AR chromosomes of Piñon Flats origin.

Cage No. 27 (table 4) was started in November 1945 with a population of 30 percent AR and 70 percent CH chromosomes from Keen Camp (at 25°C). AR chromosomes increased in frequency rather slowly, and reached 45 percent in April of 1946. The following estimates of the adaptive values are obtained:

<i>Genotype</i>	<i>W</i>		
AR/AR	0.54	$s=0.46$	$\hat{q}=0.47$
AR/CH	1.00		
CH/CH	0.60	$t=0.40$	

These values are very different from the estimates obtained for AR and CH chromosomes of Piñon Flats origin.

#### CHROMOSOMES OF THE MATHER POPULATION

The initial population in cage No. 30 contained about 33 percent of ST and 67 percent CH chromosomes derived from ancestors collected at Mather (table 5). During the eight and a half months which this cage was held at 25°C, the frequency of ST rose to about 77 percent and appeared to have approached an equilibrium. On September 12th, this cage was transferred to a cold room at 16°C. No significant change in the frequencies of the gene arrangements appeared until January of the following year. The adaptive values of the chromosomal types at 25°C are estimated as follows:

<i>Genotype</i>	<i>W</i>		
ST/ST	0.78	$s=0.22$	$\hat{q}=0.77$
ST/CH	1.00		
CH/CH	0.28	$t=0.72$	

These estimates are not very different from those obtained for ST and CH chromosomes of Piñon Flats origin if the experiment No. 35 is disregarded (cf. page 591-592).

Two experiments, Nos. 29 and 32 (table 5), involved ST and AR chromosomes of Mather origin. In No. 29, the initial population contained about 70 percent ST and 30 percent AR chromosomes. This cage was kept for about seven months at 25°C, and the frequency of ST chromosomes in its population declined to about 55 percent and seemed to reach an equilibrium at that value.



Cage No. 32 contained initially about 19 percent ST and 81 percent AR chromosomes (table 5). During the  $8\frac{1}{2}$  months when this cage was kept at 25°C the frequency of ST rose to between 50 and 55 percent, which appears to be close to the equilibrium frequency. The adaptive values of the chromosomal types in these cages at 25°C are as follows:

<i>Genotype</i>	<i>W</i>		
ST/ST	0.64	$s = 0.36$	
ST/AR	1.00		$\hat{q} = 0.54$
AR/AR	0.575	$t = 0.425$	

It is evident that, with ST and AR chromosomes of Mather origin, the equilibrium frequency of ST is appreciably lower than it is with similar chromosomes of Piñon Flats and Keen Camp origin.

On September 17, 1946, after the population in cage No. 32 reached an equilibrium at a level of 50–55 percent of ST chromosomes, this cage was removed from the temperature 25° and transferred to a cold room at 16°C. Two

TABLE 5  
*Percentage frequencies of the different gene arrangements in experiments involving chromosomes of Mather origin.*

TIME	TEMP.	CAGE NO. 29		CAGE NO. 32		CAGE NO. 30		CAGE NO. 28	
		ST	AR	ST	AR	ST	CH	AR	CH
Dec. 22, 1945	25°	69.8	30.2	19.4	80.6	33.3	66.7	33.1	66.9
L. Jan., 1946	25°	62.7	37.3	23.1	76.9	49.7	50.3	41.5	58.5
L. Feb., 1946	25°	56.3	43.7	30.0	70.0	62.7	37.3	44.7	55.3
L. Mar., 1946	25°	57.3	42.7	37.7	62.3	64.0	36.0	45.0	55.0
M. May, 1946	25°	58.7	41.3	44.7	55.3	71.3	28.7	39.7	60.3
L. June, 1946	25°	54.7	45.3	54.3	45.7	77.3	22.7	43.3	56.7
L. July, 1946	25°	54.0	46.0	49.7	50.3	72.7	27.3	—	—
E. Sept., 1946	25°	—	—	52.0	48.0	77.7	23.3	—	—
E. Nov., 1946	16°	—	—	44.7	55.3	74.7	25.3	—	—
M. Jan., 1947	16°	—	—	52.7	47.3	78.3	21.7	—	—
E. Mar., 1947	4°	—	—	56.0	44.0	—	—	—	—
M. June, 1947	4°	—	—	57.3	42.7	—	—	—	—

months later, in November 1946, the population sample taken proved to contain 45 percent ST, which represented an ostensible decrease. But in January 1947 the frequency of ST again rose to about 53 percent. These fluctuations seemed to indicate that the transfer from the high to the low temperature was followed by a drop in the frequency of ST, with a subsequent recovery. To test the possibility that exposure of the population to alternating high and low temperatures might modify the equilibrium frequencies of ST and AR chromosomes, between January 20 and mid-March 1947 the cage No. 32 was placed on alternate weeks in a dark cold room at 4°C and at room temperature in a room accessible to daylight. The sample taken in March 1947 disclosed no significant change (table 5). From mid-March to mid-June of 1947 the cage was placed overnight at 4°C and during the daylight hours at room tempera-

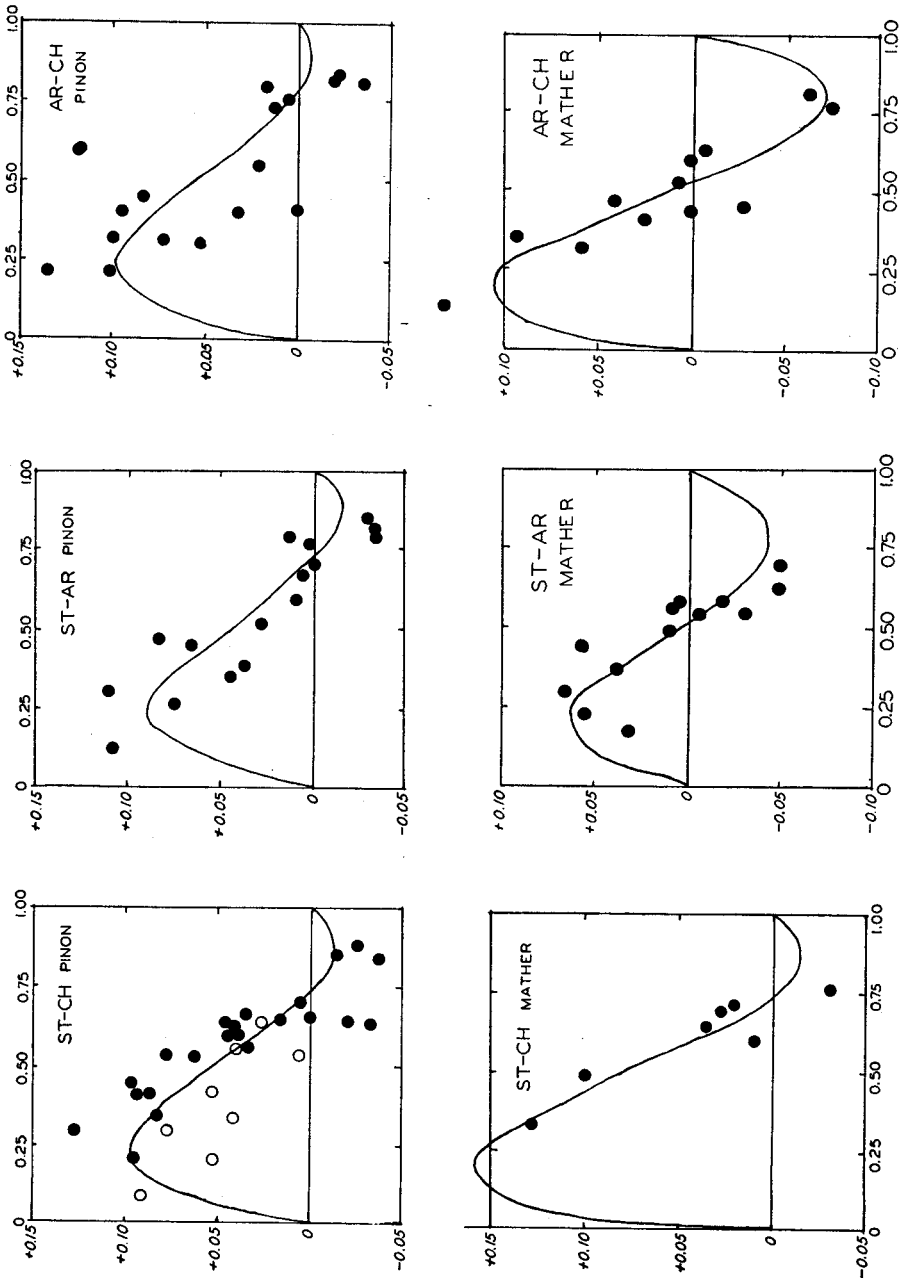


FIGURE 1. Increments of frequencies of ST (or AR) gene arrangements per generation in different experiments for different initial frequencies of the same gene arrangement (regression of  $\Delta q$  over  $q$ ). Vertical axis—increments of frequencies ( $\Delta q$ ); horizontal axis—initial frequencies ( $q$ ). Dots—observed values; curves—theoretically computed values. The open circles in the diagram for ST-CH from Pinon Flats represent the data from the aberrant experiment in cage No. 35.

ture. No changes in the frequencies of ST and AR were observable in the sample taken in mid-June (table 5). The experimental population in this cage was about 18 months old when it was finally discarded.

TABLE 6  
*Percentage frequencies of AR and CH gene arrangements in experiments involving chromosomes of Mather origin.*

TIME	CAGE NO. 39		CAGE NO. 40	
	AR	CH	AR	CH
Oct. 9-16, 1946	81.2	18.8	14.0	86.0
M. Nov., 1946	72.3	27.7	35.0	65.0
M. Dec., 1946	63.0	37.0	47.0	53.0
L. Jan., 1947	61.3	38.7	54.0	46.0
E. Apr., 1947	62.3	37.7	56.3	43.7

AR and CH chromosomes from Mather were involved in three experiments, all conducted at 25°C (No. 28, table 5, Nos. 39 and 40, table 6). In Nos. 28 and 40 the initial populations contained respectively 33 and 14 percent AR, and the frequencies of AR increased for several generations. In No. 39 a high frequency, 81 percent, of AR was initially present and it declined in the course of the experiment. Unfortunately none of the three experiments were carried long enough to be certain that equilibrium values were reached. The following estimates of adaptive values are obtained from the three experiments:

<i>Genotype</i>	<i>W</i>		
AR/AR	0.81	$s = 0.523$	
AR/CH	1.00		$\hat{q} = 0.534$
CH/CH	0.60	$t = 0.599$	

Experiments Nos. 31 and 33 (table 7) involved chromosomes with the TL gene arrangement, in combinations with respectively ST and AR chromosomes, all of Mather origin. The unique feature of the experiment No. 31 is that no equilibrium was arrived at in the population concerned, and instead one of the gene arrangements has supplanted its competitor. The cage No. 31 had 45 percent of ST and 55 percent of TL chromosomes in the initial population in late December of 1945. By late March 1946, the frequency of ST rose to about 77 percent, by June to 89 percent, by September to 98 percent, and by November to 98.7 percent. It appears certain that TL chromosomes were headed for extinction. The experiment was discontinued because with very low frequencies of TL chromosomes the accidents of sampling in a limited population might vitiate the results. The adaptive values of the three genotypes involved in the experiment No. 31 are:

<i>Genotype</i>	<i>W</i>	
ST/ST	1.12	$s = -0.12$
ST/TL	1.00	
TL/TL	0.33	$t = 0.67$

TABLE 7

Percentage frequencies of TL, ST, and AR gene arrangements in experiments involving chromosomes of Mather origin (at 25°).

TIME	CAGE NO. 31		CAGE NO. 33	
	ST	TL	AR	TL
Dec. 23, 1945	45.1	54.9	—	—
Jan. 16, 1946	—	—	34.1	65.9
L. Jan., 1946	62.3	37.7	—	—
M. Feb., 1946	—	—	57.7	42.3
L. Feb., 1946	71.7	28.3	—	—
M. Mar., 1946	—	—	64.7	35.3
L. Mar., 1946	77.3	22.7	—	—
M. Apr., 1946	—	—	68.7	31.3
M. May, 1946	82.0	18.0	69.3	30.7
L. June, 1946	89.0	11.0	66.0	34.0
L. July, 1946	93.0	7.0	75.3	24.7
E. Sept., 1946	98.0	2.0	74.3	25.7
E. Nov., 1946	98.7	1.3	80.0	20.0
M. Dec., 1946	—	—	76.0	24.0

Individuals homozygous for ST chromosomes have an adaptive value higher than the heterozygotes, while the TL homozygotes are semilethal.

Since individuals both homozygous and heterozygous for TL are inferior to ST homozygotes, the question naturally arises why are the TL chromosomes retained at all in natural populations instead of being eliminated by natural selection? Experiment No. 33 (table 7) supplies an answer, for it shows that TL chromosomes form highly adaptive heterozygotes with another normal constituent of the Mather population, namely AR. Cage No. 33 was started with a population of 34 percent AR and 66 percent TL chromosomes, and was kept at 25°C. The frequency of AR rose rapidly, and about six months later an equilibrium was seemingly attained at a level of about 75 percent AR. The estimates of the adaptive values are as follows:

<i>Genotype</i>	<i>W</i>		
AR/AR	0.69	$s=0.306$	
AR/TL	1.00		$\hat{q}=0.74$
TL/TL	0.12	$t=0.88$	

Compared to AR/TL heterozygotes, individuals homozygous for AR have an appreciably reduced fitness, while TL homozygotes are well in the semilethal range.

#### DISCUSSION

Because of the variation of the gene arrangement in the third chromosome of *Drosophila pseudoobscura*, natural populations of this species in some geographic regions are mixtures of structural heterozygotes and structural homozygotes. Structural heterozygotes carry two third chromosomes with different

gene arrangements, while homozygotes have chromosomes with similar gene orders. Experiments of WRIGHT and DOBZHANSKY (1946), DOBZHANSKY (1947a), and those reported in the present article, have shown that, at Piñon Flats and Keen Camp localities in southern California and at Mather in the Sierra Nevada, the structural heterozygotes are superior in fitness to the homozygotes. The adaptive superiority of the heterozygotes (heterosis) makes the populations very plastic, that is, able to respond by rapid adaptive changes to variations in environmental conditions. At the same time, natural selection prevents any of the gene arrangements from being eliminated from the populations altogether, which would reduce the adaptive plasticity of these populations.

The Tree Line (TL) gene arrangement from the Mather population is an exception to the rule of superior fitness of heterozygotes, because the heterozygotes for TL and Standard (ST) gene arrangements (TL/ST) are inferior to the ST/ST homozygotes, although superior to TL/TL homozygotes. Accordingly, in an experimental population consisting of TL and ST chromosomes the former have been wholly eliminated by natural selection. But this exception proves the rule, inasmuch as TL chromosomes form superior heterozygotes with Arrowhead (AR) chromosomes from the Mather locality, AR/AR and TL/TL homozygotes being inferior in adaptive value to AR/TL heterozygotes. TL chromosomes induce heterosis in combination with some but not with other chromosomes which exist in the same population. This explains both the retention of TL chromosomes in the Mather population, and the fact that they are relatively rare compared to ST, AR, and CH chromosomes.

Two hypotheses may be advanced regarding the genetic nature of the differences in fitness observed between the hetero- and homozygotes for various gene arrangements. First, each type of chromosome may carry a complex of polygenes different from those carried in other gene arrangements. The gene arrangements differ in inversions of chromosome sections; the inversions suppress most of the gene recombination in inversion heterozygotes (DOBZHANSKY and EPLING 1948), and thus bind together adaptively valuable polygene complexes which are inherited *en bloc*. Secondly, the rearrangement of genes in chromosomes may influence physiological traits of their carriers through position effects.

Several previously published facts favored, although they did not prove, the first of the above hypotheses. Chromosomes with the same gene arrangement found in geographically different populations behave differently (DOBZHANSKY 1943, 1947b, 1948). On Mount San Jacinto, in southern California, ST chromosomes are more frequent in the lower localities (Andreas Canyon and Piñon Flats) than in the higher one (Keen Camp), Chiricahua (CH) chromosomes show the opposite relationship with altitude and AR chromosomes do not change in frequency. In the Sierra Nevada of California the frequencies of ST decrease with altitude, AR increase, and CH change relatively little. At Andreas Canyon and Piñon Flats, the frequencies of ST chromosomes wane and those of CH wax from March to June, between June and September the reverse change occurs, while during fall and winter the relative frequencies of

all chromosomes remain stable. At Keen Camp, less than 15 miles away from Piñon and Andreas, no seasonal cyclic changes are observed, but the frequencies of ST continuously increased and those of AR and CH decreased for at least eight consecutive years. In the Sierra Nevada, ST chromosomes become more and AR less frequent as the summer progresses, with CH remaining relatively constant; the converse change which closes the cycle must occur in winter or early in spring.

In a large territory comprising parts of Arizona, New Mexico, Utah, and Colorado populations of *Drosophila pseudoobscura* consist preponderantly of homozygotes for AR chromosomes (DOBZHANSKY 1944). Yet, AR homozygotes (of California origin) had a far lower adaptive value than AR/ST, AR/CH, and AR/TL heterozygotes in our experiments. Despite the similarity in gene arrangements, AR chromosomes from California have different complexes of polygenes than AR chromosomes from Arizona and neighboring states.

The experiments described in the present article show in a conclusive manner that chromosomes with the same gene arrangement coming from localities even as close as Piñon Flats and Keen Camp (about 13 miles) may have different adaptive properties. Chromosomes from Mather, about 300 miles from Piñon and Keen, are again different. In another publication data will be presented that will show that in heterozygotes which carry chromosomes with different gene arrangements (such as ST and CH) from different localities (such as Piñon and Mather), heterosis disappears and the fitness of heterozygotes becomes equal to or lower than in the corresponding homozygotes. The adaptive properties of a chromosome are, consequently, determined not by the gene arrangement but by the quality of the genes it contains. This does not exclude the possibility that some position effects are, nevertheless, produced by the inversions, but the adaptive values of the chromosomes are not determined by position effects alone. The implications of this finding for the understanding of the evolution of the adaptive mechanisms in *Drosophila pseudoobscura* will be discussed elsewhere.

#### SUMMARY

Populations containing mixtures of Standard (ST), Arrowhead (AR), Chiricahua (CH) and Tree Line (TL) chromosomes have been maintained in population cages. In some experiments, the chromosomes were derived from progenitors collected at Piñon Flats, in others from Keen Camp, and in still others from Mather, California. The distance between Piñon Flats and Keen Camp is about 13 miles; between either of these two localities and Mather about 300 miles.

Regardless of the geographic origin, the structural (inversion) heterozygotes are superior in fitness to the corresponding structural homozygotes. Accordingly, the process of natural selection does not result in elimination of one and establishment of the other competing chromosome types; instead, an equilibrium is reached at which both competitors are retained with certain definite frequencies. This rule has two exceptions. First, when ST chromosomes from Mather compete with TL chromosomes from the same locality, the former

crowd out the latter entirely. Secondly, the differences in fitness between the chromosomal types are observed at 25°C, while at 16°C the adaptive values of these types are more nearly similar or even identical.

The adaptive values of the chromosomal types depend upon the geographic origin of the flies. Thus, AR/AR homozygotes are much superior in fitness to the CH/CH homozygotes of Piñon Flats origin, while AR/AR of Mather origin are only slightly superior to CH/CH from Mather. Similarly, ST/ST homozygotes are relatively much superior to AR/AR homozygotes if the chromosomes involved are of Piñon Flats origin than if they are of Mather origin. This shows that the chromosomes with the same gene arrangement found in different localities have different gene contents. In the population of any one locality, the gene contents of chromosomes with different gene arrangements are mutually adjusted by natural selection, so that highly adapted (heterotic) heterozygotes are produced.

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