GENETICS OF NATURAL POPULATIONS
IX. TEMPORAL CHANGES IN THE COMPOSITION OF POPULATIONS OF DROSOPHILA PSEUDOOBSCURA

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INTRODUCTION

THE species *Drosophila pseudoobscura* is differentiated into several major and numerous microgeographic races. Inhabitants of large portions of the distribution area can be characterized by the presence or absence or by relative frequencies of certain types of Y chromosome (DOBZHANSKY 1935, 1937a, 1939a), of gene arrangements in the third (DOBZHANSKY and STURTEVANT 1938, DOBZHANSKY 1939a, and unpublished data) and in the X chromosomes (STURTEVANT and DOBZHANSKY 1936 and unpublished data), and of various modifying genes (summary in DOBZHANSKY 1937b). Microgeographic races differ in the incidence of gene arrangements in the third and X chromosomes (DOBZHANSKY and QUEAL 1938, KOLLER 1939, DOBZHANSKY 1939b) and of concealed recessive lethals (DOBZHANSKY and WRIGHT 1941, WRIGHT, DOBZHANSKY, and HOVANITZ 1942). Differences between microgeographic races are smaller than but similar in kind to those between macrogeographic races; it is reasonable to suppose that the latter are compounded from the former. The data to be reported in the present article show that the genetic composition of populations of some localities changes with time. The changes appear to be connected with the annual climatic cycle and are consequently reversible. Nevertheless, since these changes demonstrate a great plasticity of the species genotype, they may be regarded as models of adaptive evolutionary changes on the racial and higher levels.

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MATERIAL AND TECHNIQUE

Population samples were taken at more or less regular intervals at nine collecting "stations" grouped in three "localities" on Mount San Jacinto, California. A map and a brief description of the San Jacinto region is given in WRIGHT, DOBZHANSKY, and HOVANITZ 1942. It should be kept in mind that one of the localities, Andreas Canyon, lies at an elevation of about 800 feet above sea level, the other, Pinon Flats, at about 4000 feet, and the third, Keen

Camp, at about 4300 feet. The stations within a locality are from 200 yards to $2\frac{1}{2}$ miles apart, and the localities 10 to 13 miles apart. Because of the differences in the elevation and other factors, the population density in Andreas is highest in March–April and lowest in summer. The population density at Pinon is greatest in spring and autumn, and at Keen in early summer. No flies can be collected at Pinon and Keen in winter, and at Andreas the flies are very rare in late summer.

Five gene arrangements in the third chromosome are regularly present in populations of Mount San Jacinto. For descriptions of these arrangements, Standard, Arrowhead, Chiricahua, Tree Line, and Santa Cruz, see DOBZHANSKY and STURTEVANT 1938. A sixth arrangement, a new one, has been found in a single chromosome at Keen D; it had arisen by mutation probably shortly before its detection, and in view of its rarity need not concern us here. Two gene arrangements are found in the right limb of the X chromosome: the Standard and the "sex-ratio." Males carrying the latter produce when crossed to any females progenies which consist almost entirely of daughters (STURTEVANT and DOBZHANSKY 1936).

Whenever abundant material was available, the gene arrangements were recorded in approximately 100 third chromosomes from each sample. The wild females, most of which are impregnated before capture, are placed singly in culture bottles and allowed to produce offspring. Examination of the salivary glands in a single F_1 larva suffices to determine the gene arrangements in two third chromosomes (one of maternal and one of paternal origin). Wild males are crossed to laboratory females homozygous for the Standard arrangements in the third and in the X chromosomes. The salivary glands of seven F_1 larvae are examined, which gives the probability of 63 out of 64 chances that both third chromosomes of the father are known. Examination of eight F_1 larvae in the offspring of a wild female gives the information of the gene arrangement in four third chromosomes (two maternal and two paternal). This method may be misleading if a female is fertilized by more than a single male and if the sperms of the different males mix. Since such instances do occur, although rarely, this method has been used only seldom, when an adequate sample of the flies could not be procured. The presence or absence of "sex-ratio" in wild females has been determined by cytological examination of their offspring, and in wild males genetically by observing the distribution of the sexes in their progeny. No significant differences in the incidence of the gene arrangements have been observed between males and females from the same sample; the data for both sexes have, therefore, been combined. It may, however, be noted that owing to the greater efficiency of the examination of the chromosomes in in the offspring of wild females, a major portion of the data has been secured from females, and males have been used chiefly when samples have been small.

In 1939 and 1940 samples were taken regularly at all nine collecting stations. In 1941 only four stations, and in 1942 only three stations, one in each Andreas, Pinon and Keen, were followed. The territory of a "station" has, of course, remained constant throughout, and the traps in which the flies were collected were exposed always on the same trees.

THE DATA

Table 1 summarizes the data on the gene arrangements in the third chromosomes at all stations on Mount San Jacinto. The dates of collecting, the gametic frequencies of the gene arrangements (in percentages), and the total numbers of the chromosomes examined (n) are given. The data are broken up by localities and stations, and within each station by breeding seasons. A "breeding season" is the interval between two consecutive contractions of the population. Thus, at Andreas Canyon the breeding season extends from September to June, although the flies almost certainly continue to breed in midsummer when their population density is very low. At Keen Camp the overwintering population may be rather large, but the ostensible absence of the flies during the winter months makes a convenient break. At Pinon Flats the flies are common in spring and in autumn, but the summer depression is not so striking as it is at Andreas; the "breeding season" at this locality is taken to extend from early spring till late autumn.

The gene arrangement has been determined in a total of 12,807 third chromosomes. As stated above, the data in table 1 are given in terms of the gametic frequencies of the gene arrangements in each population sample. Every fly, however, is a zygote which carries two third chromosomes, a maternal and a paternal one. These two chromosomes may have either similar or different gene arrangements, and our technique of collecting the data has permitted the discrimination of structural homozygotes and heterozygotes. A problem of considerable importance is whether the populations studied are panmictic with respect to the gene arrangements or broken up into castes or clans which interbreed to only a limited extent. Let the gametic frequencies of the gene arrangements in a population be $(a+b+c+\cdots)=1$. In a panmictic population the zygotic frequencies will be in accordance with the terms of the expansion $(a+b+c+\cdots)^2$. Isogamy (preferential mating of individuals with like gene arrangements) will cause structural homozygotes to be more and structural heterozygotes to be less frequent than in a panmictic population; anisogamy will have the opposite effect. DOBZHANSKY and QUEAL (1938) and KOLLER (1939) have examined the zygotic frequencies of the gene arrangements in the third chromosome in populations from the Death Valley region; no significant deviations from the expectancies based on the hypothesis of panmixy have been found. Our data furnish a considerably more extensive material for a test of the validity of that hypothesis than the data of the authors just referred to. The results obtained will be presented in another publication; these results are in complete agreement with the view that the populations are panmictic.

Three gene arrangements, Standard, Arrowhead, and Chiricahua, are common in all localities and stations. The Tree Line arrangement is less common than the three main ones, but it is still present in most samples. Santa Cruz is decidedly rare, but it has been recorded at all but two stations. The differences between localities, stations, and samples are quantitative. Standard is commonest at Andreas (57.6 percent), less common at Pinon (41.1 percent),

TABLE 1

Observed frequencies of the gene arrangements in different samples
ST—Standard; AR—Arrowhead; CH—Chiricahua; TL—Tree Line; SC—Santa Cruz.

DATE	ST	AR	CH	TL	SC	n
Keen A, 1939						
Apr 24	42.9	23.8	23.8	9.5	—	21
May 13	39.1	29.7	29.7	1.6	—	64
Jun 20	31.8	25.8	37.9	4.5	—	132
Jul 25	31.8	31.1	31.8	5.3	—	132
Aug 31	20.0	36.0	38.0	6.0	—	50
Oct 22	26.0	43.5	26.1	4.4	—	46
Total	31.5	30.8	33.0	4.7	—	445
Keen A, 1940						
Apr 13	38.3	20.8	37.5	1.7	1.7	120
May 18	32.0	17.0	48.0	2.0	1.0	100
Jun 8	31.1	28.3	37.7	2.8	—	106
Jul 14	36.0	23.0	40.0	1.0	—	100
Aug 12	34.3	28.7	33.3	3.7	—	108
Sep 14	41.2	17.6	32.4	8.8	—	34
Total	34.9	23.2	38.7	2.6	0.5	568
Keen A, 1941						
May 10	25.8	29.0	42.0	3.2	—	124
Jun 5	40.0	16.7	38.9	4.4	—	90
Jun 25	37.0	22.0	38.0	3.0	—	100
Jul 27	36.0	28.0	32.0	4.0	—	50
Sep 6	38.2	25.0	32.4	4.4	—	68
Total	34.5	24.1	37.7	3.7	—	432
Keen A, 1942						
Apr 2	45.1	17.6	29.4	7.8	—	102
May 2	45.1	14.7	33.3	6.9	—	102
Jun 12	28.2	15.4	46.4	10.0	—	110
Jul 17	26.0	18.0	52.0	4.0	—	100
Total	36.0	16.4	40.3	7.2	—	414
Keen A	34.2	23.7	37.5	4.4	0.2	1859
Keen B, 1939						
Apr 25	21.1	36.8	42.1	—	—	19
May 13	33.3	29.2	33.3	4.2	—	24
May 20	31.1	25.6	40.0	3.3	—	90
Jun 20	24.4	26.9	47.4	1.3	—	78
Jun 29	34.4	23.4	39.1	3.1	—	64
Jul 26	32.3	21.9	37.5	8.3	—	96
Aug 31	37.8	30.5	29.3	2.4	—	82
Total	31.6	26.3	38.4	3.8	—	453
Keen B, 1940						
May 11	21.6	25.5	49.0	2.9	1.0	102
Jun 8	30.7	22.7	45.5	1.1	—	88
Jun 29	34.8	16.3	43.5	5.4	—	92
Jul 29	37.0	26.0	32.0	5.0	—	100
Total	30.9	22.8	42.4	3.9	0.3	382
Keen B	31.3	24.7	40.2	3.8	0.1	835
Keen C, 1939						
May 20	28.8	28.8	39.4	3.0	—	66
Jun 2	19.0	35.0	41.0	5.0	—	100
Jun 29	20.8	28.3	49.1	1.9	—	106
Jul 25	22.7	32.9	43.2	1.1	—	88
Sep 1	25.0	30.0	42.5	2.5	—	40
Total	22.5	31.3	43.5	2.7	—	400
Keen C, 1940						
Apr 14	31.0	19.0	46.0	4.0	—	100
May 11	32.7	25.0	38.5	3.8	—	104
Jun 7	23.5	11.8	61.8	2.9	—	34
Jun 29	34.0	24.5	38.3	3.2	—	94
Jul 29	17.3	28.8	48.1	5.8	—	52
Total	29.7	22.7	43.7	3.9	—	384
Keen C	26.0	27.0	43.6	3.3	—	784
Keen D, 1939						
May 20	32.4	29.4	35.3	2.9	—	34
Jun 3	19.2	37.7	40.8	2.3	—	130
Jul 14	29.0	27.5	37.0	6.5	—	138
Sep 1	26.5	33.8	36.8	2.9	—	68
Total	25.4	32.4	38.1	4.1	—	370
Keen D, 1940						
Apr 14	21.0	30.0	42.0	7.0	—	100
May 18	25.4	27.2	43.9	3.5	—	114
Jun 29	31.7	14.4	49.0	4.8	—	104
Jul 29	40.0	32.0	24.0	3.0	1.0	100
Total	29.4	25.8	40.0	4.5	0.2	418
Keen D, 1941						
May 10	32.2	29.8	33.9	2.4	0.8	124*
Jun 5	38.0	14.0	41.0	6.0	1.0	100
Jul 7	35.2	26.9	34.3	3.7	—	108
Total	34.9	24.1	36.1	3.9	0.6	332*
Keen D	29.7	27.5	38.2	4.2	0.3	1120*
Keen E, 1939						
May 20	30.0	35.0	35.0	—	—	20
Jun 3	26.9	34.3	35.2	3.7	—	108
Jul 14	25.9	33.0	39.3	1.8	—	112
Aug 18	26.9	26.9	46.2	—	—	78
Total	26.7	32.1	39.3	1.9	—	318

* One chromosome with a new gene arrangement

TABLE 1—*Continued*

DATE	ST	AR	CH	TL	SC	n
Keen E, 1940						
Apr 13	30.6	22.2	45.1	2.1	—	144
May 11	22.6	15.1	56.6	5.7	—	106
Jun 7	28.3	23.6	43.4	4.7	—	106
Jun 29	35.6	18.3	40.4	4.8	1.0	104
Jul 14	34.0	16.0	48.0	2.0	—	100
Aug 12	42.9	22.9	28.6	5.7	—	70
Total	31.6	19.7	44.6	4.0	0.2	630
Keen E	30.0	23.8	42.8	3.3	0.1	948
Keen	31.0	25.1	39.8	3.9	0.1	5546
Andreas A, 1939 (Spring)						
Mar 26	91.2	5.9	—	2.9	—	34
Apr 24	73.6	13.2	6.6	1.9	4.7	106
May 13	54.8	30.7	11.3	3.2	—	62
Jun 4	36.8	21.1	36.8	—	5.3	38
Total	65.4	17.9	11.7	2.1	2.9	240
Andreas A, 1939–1940						
Sep 21	52.9	21.6	20.6	2.9	2.0	102
Oct 28	52.0	34.3	10.8	2.9	—	102
Dec 9	46.2	31.7	19.2	2.9	—	104
Jan 13	51.9	31.7	14.4	1.9	—	104
Feb 10	58.8	31.6	6.1	3.5	—	114
Mar 2	62.7	24.6	8.5	4.2	—	142
Mar 28	63.6	17.3	15.5	3.6	—	110
Apr 20	45.0	24.0	26.0	4.0	1.0	100
May 19	43.3	26.7	28.3	1.7	—	60
Total	53.9	27.0	15.6	3.2	0.3	938
Andreas A, 1940–1941						
Oct 19	68.0	19.0	6.0	7.0	—	100
Nov 16	46.1	42.3	7.7	3.9	—	26
Nov 23	54.2	31.3	10.4	4.2	—	48
Dec 31	71.9	21.9	6.2	—	—	32
Feb 1	49.0	33.0	16.0	2.0	—	100
Feb 19	66.3	18.6	11.6	3.5	—	86
Mar 8	71.1	14.9	14.0	—	—	114
Apr 19	70.0	17.0	12.0	1.0	—	100
Total	63.5	22.4	11.6	2.5	—	606
Andreas A, 1941–1942						
Sep 6	59.8	23.8	14.8	1.6	—	122
Oct 4	50.0	26.9	15.4	7.7	—	26
Nov 8	66.0	18.0	11.0	4.0	1.0	100
Dec 6	48.0	34.0	15.0	3.0	—	100
Jan 11	59.6	27.4	9.6	3.4	—	146
Feb 2	64.0	18.0	15.0	3.0	—	100
Mar 14	72.7	20.5	6.8	—	—	44
Apr 2	73.1	13.5	9.6	2.9	1.0	104
May 2	57.8	15.5	20.7	5.2	0.9	116
Jun 12	33.7	26.9	38.5	—	1.0	104
Total	58.3	22.3	16.0	2.9	0.4	962
Andr. A	58.6	23.6	14.5	2.8	0.5	2746
Andreas B, 1939						
Apr 24	62.5	20.0	15.0	2.5	—	40
May 13	53.8	26.9	15.4	1.3	2.6	78
June 4	43.1	26.4	27.8	1.4	1.4	72
Total	51.6	25.3	20.0	1.6	1.6	190
Andreas B, 1939–1940						
Sep 21	56.9	26.7	14.7	1.7	—	116
Oct 28	60.2	26.9	11.1	1.9	—	108
Dec 9	62.8	24.4	11.5	1.3	—	78
Jan 13	60.4	28.1	9.4	2.1	—	96
Feb 10	57.8	24.1	16.4	1.7	—	116
Mar 2	53.2	29.0	15.3	2.4	—	124
Mar 28	62.0	16.7	16.7	4.6	—	108
Apr 20	43.8	22.3	33.0	0.9	—	112
May 19	29.2	33.3	33.3	4.2	—	24
Total	56.0	25.1	16.8	2.2	—	882
Andr. B	55.2	25.1	17.4	2.1	0.3	1072
Andreas	57.6	24.0	15.3	2.6	0.4	3818
Pinon A, 1939						
Apr 24	48.7	33.3	15.4	2.6	—	39
May 13	30.8	35.8	27.5	3.3	2.5	120
Jun 21	32.8	37.1	26.7	2.6	0.9	116
Aug 19	34.7	33.3	23.6	8.3	—	72
Sep 19	49.0	21.0	24.0	4.0	2.0	100
Oct 21	56.0	24.6	13.4	5.2	0.8	134
Total	41.9	30.4	22.2	4.3	1.2	581
Pinon A, 1940						
Mar 3	49.0	16.0	29.0	6.0	—	100
Mar 29	39.5	24.6	30.7	3.5	1.8	114
Apr 21	34.9	18.6	41.9	3.5	1.2	86
May 10	31.4	31.4	35.3	2.0	—	102
Jun 1	29.4	29.4	39.7	1.5	—	68
Sep 14	34.6	25.0	37.5	2.9	—	104
Nov 2	37.5	32.5	26.3	3.8	—	80
Total	37.0	25.1	34.1	3.4	0.5	654
Pinon A, 1941						
Mar 7	56.4	10.9	23.6	8.2	0.9	110
Apr 19	58.2	20.0	17.3	4.5	—	110
May 10	44.0	28.0	24.0	4.0	—	100
Jun 15	37.0	26.1	34.8	2.2	—	92
Jun 28	29.0	38.0	30.0	3.0	—	100
Aug 5	51.9	21.3	25.9	0.9	—	108
Sep 6	61.4	13.6	15.9	9.1	—	44
Oct 4	50.0	25.0	16.7	8.3	—	36
Nov 8	40.9	29.5	20.5	9.1	—	44
Dec 6	48.2	19.6	26.8	5.4	—	56
Total	47.4	23.3	24.5	4.7	0.1	800

TABLE 1—*Continued*

DATE	ST	AR	CH	TL	SC	n
		Pinon A, 1942				
Apr 2	51.0	21.6	19.6	7.8	—	102
May 2	48.0	17.0	25.0	9.0	1.0	100
Jun 12	29.8	22.8	40.4	7.0	—	114
Jul 17	41.9	21.8	30.6	5.6	—	124
Total	42.7	20.9	29.3	6.8	0.2	440
Pinon A	42.5	25.0	27.3	4.6	0.5	2475
		Pinon B, 1939				
Apr 24	54.6	22.7	9.1	13.6	—	22
May 13	25.0	35.8	32.5	5.0	1.7	120
Jun 21	21.1	28.9	42.1	5.3	2.6	38
Aug 19	36.9	33.3	27.4	2.4	—	84
Sep 19	53.3	24.4	22.2	—	—	90
Oct 21	53.3	26.0	19.3	0.7	0.7	150
Total	41.5	29.4	25.6	2.8	0.8	504
		Pinon B, 1940				
Mar 3	40.3	17.7	33.9	8.1	—	62
Mar 29	48.2	20.9	28.2	2.7	—	110
Apr 21	34.4	37.8	25.6	1.1	1.1	90
May 10	25.0	23.0	44.0	8.0	—	100
Jun 1	20.6	30.4	43.1	5.9	—	102
Total	33.4	26.3	35.1	4.7	0.4	464
Pinon B	37.6	27.9	30.2	3.7	0.6	968
Pinon	41.1	25.8	28.1	4.4	0.5	3443
Grand Total	41.7	25.0	29.4	3.7	0.3	12807

and least common at Keen (31.0 percent); the corresponding figures for Arrowhead are 24.0, 25.0 and 25.1 percent, and for Chiricahua 15.3, 29.4, and 39.8 percent. The differences for Standard and for Chiricahua are obviously significant. The totals for stations within a locality and for breeding seasons within a station agree with each other more closely. But an inspection of the data for different samples within a station and a breeding season discloses that appreciable changes occur from month to month, especially at Andreas and Pinon and to a lesser extent at Keen.

For purposes of presentation it is desirable to anticipate at this point the results of the more rigorous tests to be described below. The relative frequencies of Standard and Chiricahua at Andreas and at Pinon change from month to month; the changes follow the seasonal climatic cycle. In figures 1–3 the percentage frequencies of the gene arrangements (ordinates) are plotted against the months of the year (abscissae). Every sample taken during the four years of observation is shown by a dot. The curves represent the monthly averages of the frequencies of the respective gene arrangements. At Andreas and Pinon the frequency of Standard decreases from March to June and increases thereafter. Chiricahua is most frequent in early summer and reaches a low level during the winter months. Arrowhead is more stable than the two other arrangements, but it seems to be more frequent in spring than in summer and in winter. The changes at Keen are not so striking as those at Andreas and Pinon, but Chiricahua is apparently more frequent in May and June than in August and September. The amplitude of the changes in the composition of the populations within a breeding season is greater than the amplitude of the differences between breeding seasons within a station, between stations within a locality, and almost equal to the differences between the localities. The principal variable in the data is a cyclic change within a breeding season.

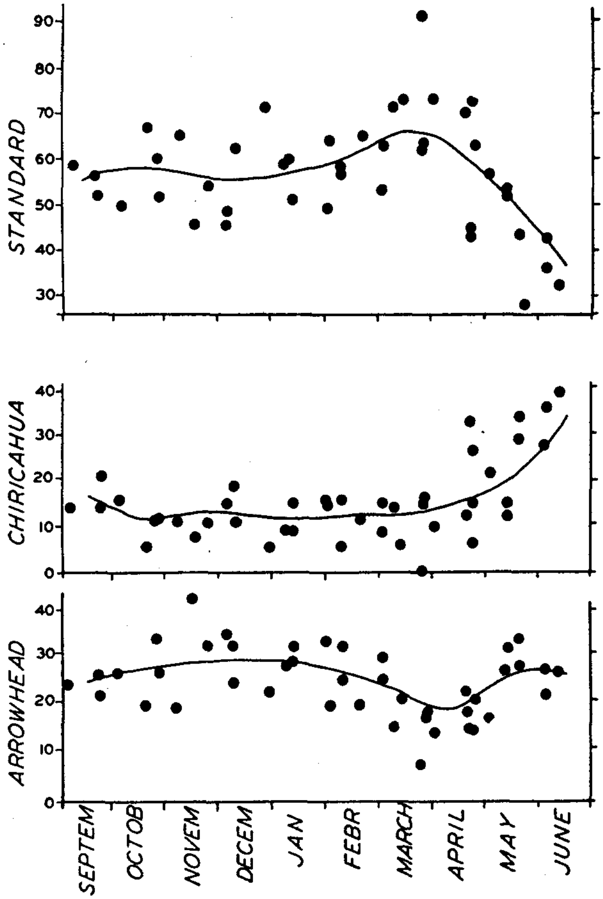

FIGURE 1.—Frequencies (in percent) of the three most common gene arrangements in the third chromosome which occur in the population of Andreas Canyon. Dots—individual observations; curve—monthly totals. This and the following two figures (Figs. 2 and 3) are based on observations which extended during four breeding seasons; the data for these four seasons are combined according to the month of collecting.

CHANGES WITHIN A BREEDING SEASON

The population of every station has been followed from two to four breeding seasons. In all, 25 sets of samples for different stations and seasons are shown in table 1. The degree of heterogeneity within a station and a breeding season can be estimated by means of a χ^2 analysis. On the assumption that the observed heterogeneity is due to sampling errors alone, the expected numbers of chromosomes with each gene arrangement in every sample may be deduced from the seasonal totals entered in table 1. The numbers of Tree Line and Santa Cruz chromosomes, however, are too small in most samples for such an analysis; they are added to the Arrowhead chromosomes. The chromosomes are therefore divided into three groups: those with Standard, with Chiricahua, and with "Others" gene arrangements. The results of the computations are presented in table 2.

TABLE 2

Variability observed within a station and a breeding season.

STATION AND SEASON	χ^2	df	P
Andreas A, Spring 1939	44.52	6	<0.01
Andreas A, 1939–1940	44.37	16	<0.01
Andreas A, 1940–1941	30.59	14	<0.01
Andreas A, 1941–1942	77.82	18	<0.01
Andreas B, Spring 1939	6.22	4	0.20–0.10
Andreas B, 1939–1940	41.34	16	<0.01
Pinon A, 1939	28.71	10	<0.01
Pinon A, 1940	16.62	12	0.20–0.10
Pinon A, 1941	40.77	18	<0.01
Pinon A, 1942	16.53	6	0.02–0.01
Pinon B, 1939	39.77	10	<0.01
Pinon B, 1940	28.92	8	<0.01
Keen A, 1939	11.29	10	0.50–0.30
Keen A, 1940	9.38	10	0.50–0.30
Keen A, 1941	8.54	8	0.50–0.30
Keen A, 1942	18.59	6	<0.01
Keen B, 1939	7.87	10	0.70–0.50
Keen B, 1940	10.48	6	0.20–0.10
Keen C, 1939	4.74	8	0.80–0.70
Keen C, 1940	11.97	8	0.20–0.10
Keen D, 1939	4.54	6	0.70–0.50
Keen D, 1940	22.73	6	<0.01
Keen D, 1941	9.67	4	0.05–0.02
Keen E, 1939	3.29	6	0.80–0.70
Keen E, 1940	18.18	10	0.10–0.05

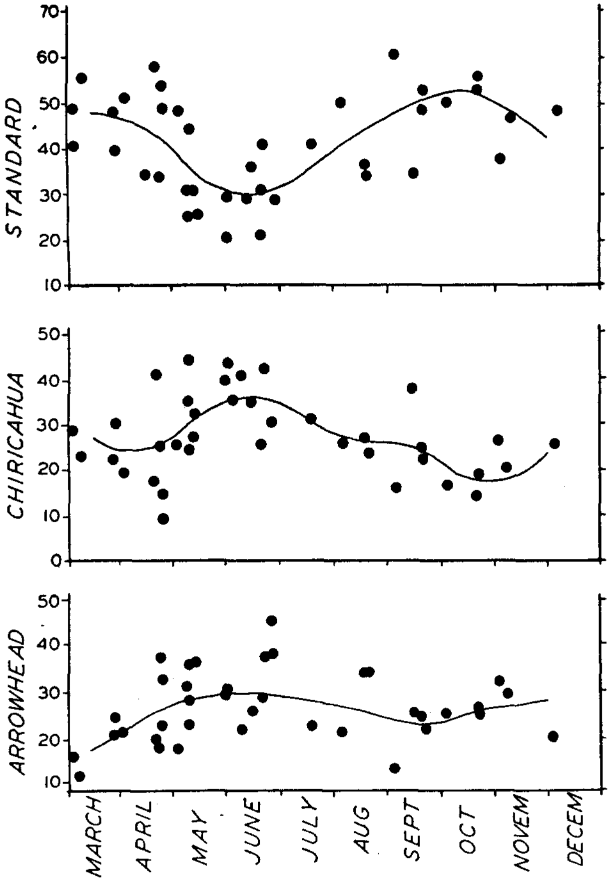

FIGURE 2.—The population of Pinon Flats. For further explanation see Fig. 1.

The data for Andreas Canyon fail to show a significant intra-seasonal change only for the station Andreas B in the spring of 1939. This is not surprising, since only three samples were taken at this station from April 24 to June 4, 1939. Furthermore, the figures in table 1 show that Standard appeared to be more frequent in April than in June, which is the same direction of change as observed at the adjacent station, Andreas A, where the change is statistically significant. At Pinon Flats intra-seasonal changes are established for every station and season except for Pinon A in 1940 (table 2). But even in this case the frequency of Standard dropped from 49 percent in early March to 29 percent on June 1, and rose to 37 percent on November 2; Chiricahua rose from 29 percent on March 2 to 42 percent on April 21, and dropped to 26 percenton November 2. This is the same type of change which is established at Pinon A and Pinon B in other years (table 1). At Keen Camp significant intra-seasonal changes are ostensibly rare (table 2). The population of Keen A has changed during 1942 but apparently not during 1939, 1940, or 1941. At Keen B and C no significant changes have been recorded. The population of Keen D underwent changes during 1940 and 1941 but not during 1939. At Keen E there was no change during 1939 but during 1940 there may have been some instability.

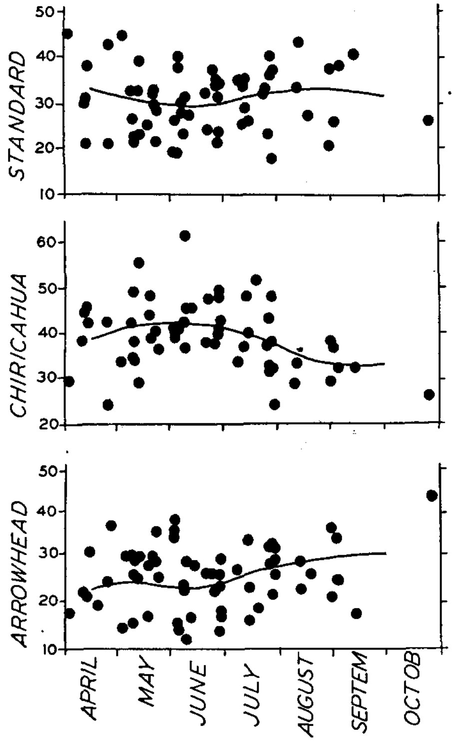

FIGURE 3.—The population of Keen Camp. For further explanation see Fig. 2.

The χ^2 analysis estimates the probability that the heterogeneity of the samples taken within a breeding season is or is not due to sampling errors.

This analysis does not discriminate between haphazard and directed changes. Examination of table 1 shows that changes, at least at Andreas and at Pinon, are not haphazard. There is a clear tendency for the successive samples to be more nearly similar than the samples taken several months apart, except where the annual cycle is closed. The changes run parallel at different stations within a locality and in different years. The lowest frequencies of Standard at Andreas and Pinon have been observed eight times in June, thrice in May, and only once in November. The highest annual frequencies of Standard fell four times in March, four times in April, and once in September and October. The highest frequencies of Chiricahua are reached mostly in May and in June, but the lowest frequencies may fall in any month from September to April. The frequencies of Arrowhead fluctuate apparently irregularly. The directed nature of the intra-seasonal changes is attested by figures 1 and 2. If the changes in successive breeding seasons were unrelated, they would tend to cancel each other and the joint monthly averages would show no trends; actually, the curves connecting the monthly averages in figures 1 and 2 do show definite trends.

The situation at Keen Camp may or may not be different from that obtaining at Andreas and Pinon. Since significant intra-seasonal changes have been observed in only three out of 13 sets of samples (table 2), clear trends are hardly to be expected. It should be noted, however, that since the collecting season at Keen is shorter than at Andreas and Pinon, the detection of the changes at Keen is correspondingly more difficult.

DIFFERENT BREEDING SEASONS AT THE SAME STATION

The problem next to be considered is whether or not the population of a station may change from one breeding season to another. Since significant alterations in the composition of the populations within a breeding season occur at least at Andreas and at Pinon, we must be on guard not to mistake spurious inter-seasonal changes for real ones. The samples have not been taken at quite regular intervals, and some samples are greater than others. If, then, during one breeding season more or larger samples were taken—for example, in spring than in autumn—a spurious difference between seasonal totals may result. For this reason we disregard the samples taken at Andreas A and B in the spring of 1939 and the samples taken at Pinon B in 1940 and at Pinon A in 1942. Hence, no inter-seasonal comparisons at all can be made for Andreas B and Pinon B, but data for three complete breeding seasons are available for Andreas A and for Pinon A. The χ^2's are calculated as for the intra-seasonal changes, except that four classes of chromosomes are distinguished: those with Standard, Chiricahua, Arrowhead, and "Others" gene arrangements ("Others" are Tree Line and Santa Cruz combined). The results are shown in table 3.

The populations which inhabited Andreas A in 1939–1940, 1940–1941, and 1941–1942 appear to be significantly different (table 3). The meaning of this difference is nevertheless open to question, since no samples were taken at this station in May and in June of 1941. In other years the frequency of Standard reached a minimum and that of Chiricahua reached a maximum during these months (see above). The seasonal total for 1940–1941 shows a lower frequency of Chiricahua and a higher frequency of Standard than do the seasonal totals for other breeding seasons at the same station. The seasonal totals for 1939–1940 and 1941–1942 do not differ significantly (table 3). The aberrant results for the season 1940–1941 are most probably accounted for by the incompleteness of the data for the critical months of May and June. No certain inter-seasonal changes have been observed at Andreas A.

TABLE 3

Different breeding seasons at the same station.

STATION AND SEASONS	χ^2	df	P
Andreas A, 1939–1940, 1940–1941, 1941–1942	18.37	6	<0.01
Andreas A, 1939–1940, 1941–1942	5.91	3	0.20–0.10
Pinon A, 1939, 1940, 1941	36.61	6	<0.01
Keen A, 1939, 1940, 1941, 1942	33.64	9	<0.01
Keen B, 1939, 1940	1.76	3	0.50–0.30
Keen C, 1939, 1940	10.12	3	0.02–0.01
Keen D, 1939, 1940, 1941	11.18	6	0.10–0.05
Keen E, 1939, 1940	19.42	3	<0.01

The inter-seasonal differences observed at Pinon A are very significant, and they cannot be discounted on any such grounds as the changes at Andreas A. To be sure, more samples were taken during the autumn of 1941 than during the corresponding months in 1939 and 1940, and this may be a partial explanation of the high apparent frequency of Standard and the low frequency of Chiricahua in the total for 1941 (table 1). But the frequency of Chiricahua was appreciably and consistently higher during the summer months of 1940 than during the summers of 1939 and 1941. Similarly, Standard chromosomes were rather more frequent in 1941 than in 1939 and 1940. The frequency of Chiricahua at Pinon B in 1940 was higher than in the corresponding months in 1939. The population of Pinon seems to change its composition from year to year as well as from month to month. Whether or not the intra-seasonal and the inter-seasonal changes are independent is quite another matter. The possibility must be considered that the climatic variations from year to year are reflected in the composition of the populations in the same manner as the succession of the seasonal climates. The winter of 1940–1941 was richer in precipitation than the preceding and the following winters; the fly populations contracted much less in the summer of 1941 than they did in 1940 or 1942; the conditions in the summer of 1939 were about intermediate. In the midsummer of 1941 the flies were, in fact, rather abundant at Pinon Flats, while in other years they were abundant only in spring and in autumn. The contention that the composition of the population in 1941 differed from that in other years because of this vagary of the climate cannot be proved by the available data, but it seems not improbable.

The data for Keen Camp (table 3) are rather irregular. No inter-seasonal changes have been detected at Keen B and D, but at Keen A, C, and E some changes are indicated. In addition, the changes at Keen A appear to be directed: Arrowhead has decreased in frequency from 31 percent in 1939 to 23–24 percent in 1940 and 1941 and to 16 percent in 1942. The figures for Keen stations other than A show the same trends toward reduction of the frequencies of Arrowhead, although the statistical significance of these trends is doubtful. It looks as though the population of the whole Keen Camp locality has been losing Arrowhead chromosomes during the whole period of observation. The relative rarity of intra-seasonal changes at Keen (see above) makes this conclusion somewhat stronger than it would have been otherwise.

DIFFERENCES BETWEEN STATIONS WITHIN A LOCALITY

Two sources of error must be guarded against in making comparisons of stations within a locality: the intra-seasonal and the inter-seasonal changes within a station. The stations Andreas A and Andreas B are only about 200 yards from each other. Comparison of all the data for these stations gives $\chi^2 = 9.10$, which, for 3 degrees of freedom, has the probability of chance occurrence between 0.05 and 0.02, which is usually considered to indicate a significant difference. The observations at Andreas B, however, lasted only from April 1939 to May 1940, while those at Andreas A extended from March 1939 to June 1942 (table 1). Comparison of the stations only during the period when both were under observation gives $\chi^2 = 6.27$, df = 3, P = 0.10; the difference is not significant. Comparison of the total data for Pinon A and Pinon B (distance about 800 yards) gives $\chi^2 = 9.17$, df = 3, P between 0.05 and 0.02. Again, the duration of the observation period at Pinon B was less than at Pinon A. If identical time intervals are compared, $\chi^2 = 2.02$, df = 3, P between 0.70 and 0.50. The difference is not significant.

The distances between stations at the Keen Camp locality are relatively large: Keen C and Keen E are about two and a half miles apart; the environments at the Keen stations are rather diversified. In 1939 samples were collected at all stations. Comparison of the yearly totals gives $\chi^2 = 24.72$, df = 12, P between 0.02 and 0.01. Chiricahua was more frequent and Standard less frequent at Keen C than at Keen A or B. Unfortunately, the collecting at Keen A and B was started in April and at the other Keen stations late in May, which makes the validity of the observed heterogeneity between the stations doubtful. In summer of 1940 the five collecting stations at Keen were again followed. Comparison of the year's totals gives $\chi^2 = 12.43$, df = 12, P between 0.50 and 0.30; the heterogeneity is not significant. In 1941 collections were made only at Keen A and D, with no significant differences detected: $\chi^2 = 0.59$, df = 3, P between 0.90 and 0.80.

The available evidence indicates that populations of stations within a locality do not differ in the relative frequencies of the third chromosome gene arrangements. WRIGHT, DOBZHANSKY, and HOVANITZ (1942), however, have shown that third chromosome lethals found within a station are alleles more frequently than lethals found at different stations within a locality. These results are not necessarily contradictory: the differentiation of the local populations need not go parallel with respect to different classes of genetic variants. The recessive lethals are not subject to strong selection pressures while in heterozygous conditions; the gene arrangements appear to respond to the environmental changes induced by the annual climatic cycle.

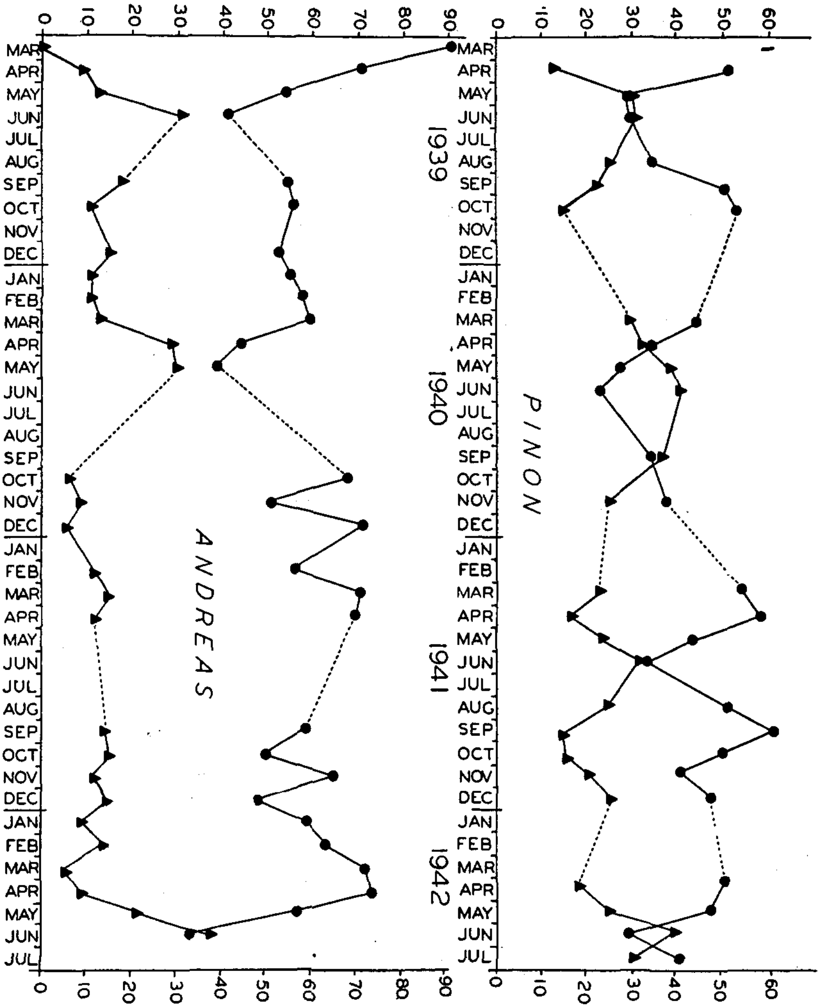

FIGURE 4.—The frequencies of Standard (circles) and of Chiricahua (triangles) gene arrangements in the third chromosome in the populations of Pinon Flats and of Andreas Canyon. Abscissae—time, ordinates—percents.

SEASONAL CHANGES

Various hypotheses have been tried out in attempts to discover which agent or agents are responsible for the production of the fairly striking intra-seasonal changes described above. It is conceivable that the flies spend their lives in so small a territory that several elementary breeding units occur within the area of a collecting station. If so, different samples might represent now one and now another part of the area, and the differences between the samples might reflect this lack of uniformity. This hypothesis is excluded by the unpublished experiments which prove that the average radius of the daily activities of the flies is of the same order of magnitude as the diameter of a typical collecting station. Furthermore, this hypothesis fails to account for the observed parallelism of the variations at different stations within a locality and for the correlation between the compositions of successive samples.

In contrast to the first hypothesis, it can be imagined that the flies range over territories of some tens of square miles in area and that they live in discrete droves or clans which maintain an internal cohesion in their wanderings. Fantastic as it is, this hypothesis is difficult to exclude entirely. It fails to explain the observed cyclic nature of the changes, and it is contradicted by the results of unpublished experiments alluded to above which show that in an approximately uniform two-dimensional environment individual flies move more or less at random.

A third hypothesis, which for a time appeared plausible enough (DOBZHANSKY 1940, 1941), is as follows: If the sources of food on which the species subsists in nature are abundant at only a few scattered points in the inhabited territory, it is possible that only a minute fraction of the individuals which compose the population of a station will locate the food and produce offspring. The fecundity of *Drosophila pseudoobscura*, under favorable conditions, is measured in thousands of eggs. The population of a territory as large as a station might, therefore, be descended from a small number of "lucky" individuals. If so, the incidence of the gene arrangements in the population might fluctuate from generation to generation owing to the accidents of sampling involved in the choice of the parents. This hypothesis had to be rejected for the following reasons. (A) Examination of the contents of the crops of flies caught in nature has shown that most individuals are able to find food every day even during the arid midsummer season in the mountains of southern California (unpublished data). (B) The mobility of the flies varies, depending upon temperature, from ten to about one hundred and fifty meters per day. The absolute population density is mostly high enough so that a food source in an area of about one hundred meters in diameter will attract many flies. However, when the population density diminishes during unfavorable seasons the accidents of sampling may become important (unpublished data). (C) The observed changes in the incidence of gene arrangements run parallel at different stations within a locality. Except when the population reaches a minimum, the number of flies within a locality is much greater than could be descended from only a few parents. (D) The observed changes follow a seasonal cycle.

The available data seem to fit best a fourth hypothesis, which assumes that the carriers of different gene arrangements in the third chromosome have different ecological optima. At Andreas Canyon and at Pinon Flats the Standard gene arrangement is favored in spring and the Chiricahua arrangement in early summer. Natural selection alters the composition of the populations

TABLE 4

Observed frequencies (in percentage) of the gene arrangements in different months.
ST—Standard, AR—Arrowhead, CH—Chiricahua, TL—Tree Line, SC—Santa Cruz.

	ANDREAS						PINON						KEEN					
	ST	AR	CH	TL	SC	n	ST	AR	CH	TL	SC	n	ST	AR	CH	TL	SC	n
January	57.5	28.9	11.0	2.6	—	346	—	—	—	—	—	—	—	—	—	—	—	—
February	58.9	25.4	13.0	2.7	—	516	—	—	—	—	—	—	—	—	—	—	—	—
March	64.5	20.1	12.6	2.8	—	676	47.2	18.1	28.6	5.4	0.6	496	—	—	—	—	—	—
April	61.0	18.2	17.4	2.1	1.2	562	46.8	24.9	23.6	4.2	0.4	449	33.2	22.4	39.8	4.3	0.3	606
May	51.8	24.1	20.0	3.2	0.9	340	33.6	29.0	31.3	5.1	0.9	642	30.3	24.6	41.2	3.6	0.3	1174
June	37.4	25.7	34.6	0.5	1.9	214	29.2	30.6	35.9	3.8	0.5	630	29.9	23.8	42.1	4.1	0.1	1846
July	—	—	—	—	—	—	42.3	26.3	27.3	4.1	—	388	31.3	26.6	38.0	4.0	0.1	1276
August	—	—	—	—	—	—							33.2	28.6	34.8	3.4	—	388
September	56.8	24.1	16.5	2.1	0.6	340	47.3	22.2	26.6	3.3	0.6	338	31.3	30.5	34.0	4.3	—	256
October	58.9	27.1	10.1	3.9	—	336	54.1	25.3	16.6	3.4	0.6	150						
November	59.8	25.3	10.3	4.0	0.6	174	41.7	27.8	25.0	5.6	—	180	—	—	—	—	—	—
December	53.5	29.6	14.6	2.2	0.2	314							—	—	—	—	—	—
Total	57.65	23.99	15.30	2.62	0.45	3818	41.13	25.82	28.14	4.39	0.52	3443	30.98	25.11	39.83	3.93	0.14	5546

accordingly. Since the gene arrangement which is favored at one season is discriminated against at other seasons, the net result over the whole year is typically no change at all—comparison of the totals for successive years shows usually no significant differences. The climatic variations from year to year, however, may disturb the regularity of the seasonal cycles and may produce the occasionally observed relatively slight differences in the composition of the population on successive breeding seasons. The fact of cardinal importance on which this hypothesis is primarily based is the cyclic nature of the observed changes in the composition of the populations.

It has already been pointed out (p. 171, fig. 1–4) that, at least at Andreas and Pinon, the frequency of Chiricahua has reached a maximum in May, June and July on every one of the four years during which the observations have been made. Standard reaches its minimum while Chiricahua is at its maximum, and *vice versa*. It is important to examine this contention very carefully. Table 4 presents the data for the entire period of observations broken up by months of collecting and by locality. The seasonal changes at Andreas are very significant; if the chromosomes are divided into those with Standard, Arrowhead, Chiricahua, and "Others" gene arrangements, the χ^2 turns out to be 128.23, df = 27, P much less than 0.01. The changes at Pinon resemble those at Andreas; they are highly significant: $\chi^2 = 253.36$, df = 21, P negligible.

It is important to ascertain whether cyclic changes occur also at Keen Camp. A statistical test is negative: $\chi^2 = 21.74$, df = 15, P between 0.20 and 0.10. The greatest contribution toward this χ^2 is made by Arrowhead chromosomes which contribute relatively little in the tests for Andreas and Pinon. Taken at their face value, the data suggest that Chiricahua is more frequent in May and June than it is in late summer and in autumn, and that Arrowhead is more frequent in August and September than it is during the earlier months (fig. 3, table 4). Significant changes within a breeding season have been observed at Keen A in 1942 and at Keen D in 1940 and 1941 (see above). At Keen A, the frequency of Standard decreased and that of Chiricahua increased from April till July of 1942; the seasonal change at Keen D in 1941, however, was in the opposite direction (see table 1). In some years samples at Keen stations have been taken over periods of five to six months (Keen A in 1939 and 1941, Keen B in 1939, Keen E in 1940), and yet no significant changes have been observed. The conclusion seems inescapable that seasonal changes at Keen, if any, are less pronounced and less regular than those at Andreas and Pinon during comparable time periods. Nothing is known, of course, about the changes that might occur at Keen during the period from November to March when no population samples have been collected.

The possible mechanisms through which a gene arrangement may influence the adaptive value of its carrier will be discussed below.

DIFFERENCES BETWEEN THE POPULATIONS OF LOCALITIES

Comparison of the totals for localities (tables 1 and 4) suggests that the Standard gene arrangement is more frequent at Andreas (57.65 ± 0.80 percent) than at Pinon (41.13 ± 0.84), and more frequent at Pinon than at Keen (30.98

±0.62). Chiricahua is more frequent at Keen (39.83±0.66) than at Pinon (28.14±0.77) and at Andreas (15.30±0.58). The frequencies of Arrowhead are uniform (24–26 percent). Tree Line is slightly commoner at Pinon (4.39±0.11) than at Andreas (2.62±0.08), Keen being intermediate. Santa Cruz is rare throughout. The data for separate breeding seasons agree very well with those for the entire period of observation. Localities ten to thirteen miles apart may therefore be inhabited by populations which differ in the incidence of the gene arrangements. This conclusion, although it is supported by other data (DOBZHANSKY and QUEAL 1938, KOLLER 1939, DOBZHANSKY 1939b, also unpublished information) as well as by those reported in the present article, is important enough to deserve a most careful scrutiny.

The collecting seasons at Keen, Pinon, and Andreas fall at different periods of the year. The frequencies of at least Standard and Chiricahua arrangements are known to undergo seasonal changes at Andreas and at Pinon. May it be that the populations of the three localities are really identical but they are out of step in their seasonal cycles? The data in tables 1 and 4 must be re-examined from this point of view. Let us compare the status of the populations of the three localities in the months of April, May, and June only; we find that the differences in the incidence of the gene arrangements are almost as striking as they are in the yearly totals ($\chi^2 = 256.28$, df = 6, P negligible). The same is true if the months of September and October alone are considered ($\chi^2 = 94.73$, df = 6, P negligible). The situation, however, is different if the data for May and June at Andreas, June and July at Pinon, and July and August at Keen are compared. A very significant difference is still apparent ($\chi^2 = 47.71$, df = 6, P less than 0.01), but this difference is due principally to Andreas being different from Pinon and Keen, the latter two being very nearly similar. If the data for June alone are taken for Andreas, and compared with June and July at Pinon and July and August at Keen, no significant differences are any longer manifest ($\chi^2 = 5.99$, df = 6, P between 0.50 and 0.30). Such a comparison, however, is not a fair one, because only 214 chromosomes have been obtained in June at the Andreas locality. To sum up: the populations of the three localities are different, but the amplitude of the seasonal variations at Andreas and at Pinon is so great that the inter-locality differences are at times almost or entirely submerged.

POSSIBLE SELECTIVE AGENTS

The assumption that the gene arrangement in the third chromosome affects the adaptive value of its carrier is a novel one and is contrary to the surmise which the writer had entertained in the past. Yet, Chiricahua chromosomes are favored at Andreas and at Pinon in late spring and in early summer, while Standard chromosomes are favored at other seasons and especially in early spring. The prevailing temperatures may be the selective agents, although both at Andreas and at Pinon the frequencies of Chiricahua drop and those of Standard rise again by the time the populations emerge from their summer eclipse stage. July and August are the hottest and driest months in both localities, yet in September the frequencies of Standard are higher and those of Chiricahua are lower than they were in June. A more plausible view is that Standard is favored while the populations are at their highest density levels in the year, and that Chiricahua is favored while the populations are dwindling toward their summer eclipse stage, presumably because of a relative food scarcity. Experiments which may possibly shed some light on this problem are being planned.

It is very improbable that the gene arrangements in the third chromosome of *Drosophila pseudoobscura* exert their effects on the physiology of their carriers because of the differences in the alignment of the genes (position effect). Such a view is contradicted by the absence, or at least the relative weakness, of the seasonal changes in the frequencies of gene arrangements at Keen Camp in contrast to their great amplitude at Andreas and Pinon. Furthermore, the summer environment at Keen resembles the spring environments at Andreas and at Pinon to a greater extent than it does the summer environments in the latter two localities. The position effect hypothesis would lead one to expect that the frequency of Standard should be higher and the frequency of Chiricahua lower at Keen than at Pinon and Andreas. Exactly the opposite is observed (tables 1 and 4). The position effect hypothesis fares even worse if one takes into account the total geographic distribution of the gene arrangements. Standard is frequent on the Pacific Coast, rapidly declines in frequency as one proceeds eastward, is rare in the Great Basin and the Rocky Mountains, and absent in Mexico and Guatemala. Arrowhead is the predominant gene arrangement in the Great Basin and declines in frequency westward, eastward, and southward from there. Chiricahua reaches the highest known frequencies in the state of Chihuahua, Mexico, and in southern California (DOBZHANSKY and STURTEVANT 1938 and unpublished data). An analysis of the gross geographic distribution of the gene arrangements has led EPLING (unpublished) to the conclusion that it reflects the history of the species rather than the contemporary environments prevailing in different parts of the species area.

The facts are in a much better agreement with the view that the variations in the adaptive values observed among chromosomes with different gene arrangements result from chance association of mutant genes with now one and now another gene arrangement. The establishment of such an association can easily be visualized, provided that the species is broken up into colonies isolated by distance or by distribution barriers. A mutant gene which is advantageous at a certain season arises in a chromosome with, for example, the Standard arrangement. The descendants of this chromosome may attain a considerable frequency within the colony, and if the gene in question lies in the part of the chromosome in which crossing over is rare in inversion heterozygotes, the association may persist for a long time. In another colony the same mutant gene, however, may arise in a chromosome with a different gene arrangement. Thus, in some colonies a gene favorable at a given season may be associated with chromosomes with the Standard arrangement, in other colonies with Arrowhead, and in still others no such association may exist. The fact that most chromosomes in natural populations of *Drosophila pseudo-*

TABLE 5

Observed frequencies of "sex-ratio" in different samples. SR—frequency in percentage, n—number of chromosomes examined.

DATE	SR	n
Andreas A, Spring 1939		
Mar 26	31.2	16
Apr 24	23.7	93
May 13	17.8	45
Jun 4	11.1	27
Total	21.0	181
Andreas A, 1939–1940		
Sep 21	14.2	113
Oct 28	17.1	123
Dec 9	16.7	84
Jan 13	14.8	128
Feb 10	13.3	113
Mar 2	12.5	231
Mar 28	10.6	106
Apr 20	10.9	92
May 19	23.1	39
Total	14.0	1029
Andreas A, 1940–1941		
Oct 19	15.0	60
Nov 24	15.2	33
Dec 31	0.0	12
Feb 1	7.8	77
Feb 19	7.1	56
Mar 8	13.7	153
Apr 19	20.3	69
Total	12.8	460
Andreas A, 1941–1942		
Sep 6	11.4	79
Oct 4	11.1	18
Nov 8	35.7	98
Dec 6	9.6	83
Jan 11	8.3	96
Feb 2	3.0	33
Mar 14	9.8	41
Apr 2	19.2	73
May 2	19.3	83
Jun 12	23.1	78
Total	16.9	682
Andreas A	15.1	2352
Andreas B, 1939		
Apr 24	18.5	27
May 13	28.3	53
Jun 4	23.4	47
Total	24.4	127
Andreas B, 1939–1940		
Sep 21	14.8	128
Oct 28	9.9	111
Dec 9	15.8	57
Jan 13	16.4	67
Feb 10	19.8	96
Mar 2	10.2	187
Mar 28	12.9	85
Apr 20	15.3	85
May 19	7.1	14
Total	13.6	830
Andreas B	15.1	957
Andreas	15.1	3309
Pinon A, 1939		
Apr 24	8.7	23
May 13	8.6	116
Jun 21	11.6	86
Aug 19	7.1	28
Sep 19	7.6	106
Oct 21	11.5	183
Total	9.8	542
Pinon A, 1940		
Mar 3	11.2	107
Mar 29	9.6	104
Apr 21	6.6	61
May 10	15.2	92
Jun 1	11.4	44
Sep 14	13.2	76
Nov 2	7.7	39
Total	11.1	523
Pinon A, 1941		
Mar 7	13.7	117
Apr 19	13.2	151
May 10	14.3	84
Jun 15	8.9	56
Jun 28	23.2	82
Aug 5	16.3	98
Oct 4	24.0	25
Nov 8	9.4	32
Dec 6	3.4	29
Total	14.5	674
Pinon A, 1942		
Apr 2	18.0	78
May 2	7.1	84
Jun 12	12.4	81
Jul 17	23.9	88
Total	15.4	331
Pinon A	12.6	2070
Pinon B, 1939		
Apr 24	0.0	16
May 13	15.3	124
Jun 21	26.9	26
Aug 19	8.5	71
Sep 19	8.3	72
Oct 21	9.1	187
Total	11.1	496
Pinon B, 1940		
Mar 3	17.1	41
Mar 29	10.2	98
Apr 21	14.3	63
May 10	18.8	85
Jun 1	15.7	83
Total	14.9	370
Pinon B	12.7	866
Pinon	12.6	2936
Keen A, 1939		
Apr 24	7.1	14
May 13	17.0	47
Jun 20	17.0	135
Jul 25	17.7	113
Aug 31	17.7	51
Oct 22	23.3	30
Total	17.4	390
Keen A, 1940		
Apr 13	8.7	92
May 18	10.2	88
Jun 8	11.9	42
Jul 14	22.1	77
Aug 12	20.0	80
Sep 14	5.6	18
Total	14.1	397

TABLE 5—*Continued*

DATE	SR	n
Keen A, 1941		
May 10	14.5	117
Jun 5	14.3	49
Jun 25	17.1	76
Jul 27	15.8	38
Sep 6	21.9	41
Total	16.2	321
Keen A, 1942		
Apr 2	14.9	74
May 2	6.8	74
Jun 12	15.9	88
Jul 17	15.6	77
Total	13.4	313
Keen A	15.3	1421
Keen B, 1939		
Apr 25	14.3	14
May 13	11.8	17
May 20	12.5	64
Jun 20	16.0	50
Jun 29	21.1	52
Jul 26	25.6	78
Aug 31	17.7	51
Total	18.4	326
Keen B, 1940		
May 11	23.4	94
Jun 8	20.0	55
Jun 29	19.1	63
Jul 29	18.6	70
Total	20.6	282
Keen B	19.4	608
Keen C, 1939		
May 20	21.3	47
Jun 2	21.7	69
Jun 29	14.9	74
Jul 25	16.7	66
Sep 1	20.0	15
Total	18.4	271
Keen C, 1940		
Apr 14	7.9	63
May 11	12.4	97
Jun 7	16.7	18
Jun 29	16.1	31
Jul 29	23.8	21
Total	13.0	230
Keen C	16.0	501
Keen D, 1939		
May 20	20.0	25
Jun 3	16.5	127
Jul 14	11.6	112
Sep 1	14.3	42
Total	14.7	306
Keen D, 1940		
Apr 14	13.6	88
May 18	20.8	96
Jun 29	18.2	66
Jul 29	14.3	77
Total	16.8	327
Keen D, 1941		
May 10	14.8	101
Jun 5	15.7	89
Jul 7	17.7	85
Aug 12	7.9	101
Total	13.8	376
Keen D	15.1	1009
Keen E, 1939		
May 20	14.3	14
Jun 3	22.6	115
Jul 14	16.1	62
Aug 18	18.6	86
Total	19.5	277
Keen E, 1940		
Apr 13	13.4	112
May 11	14.7	95
Jun 7	18.1	83
Jun 29	21.6	37
Jul 14	15.3	59
Aug 12	12.5	48
Total	15.4	434
Keen E	17.0	711
Keen	16.2	4250

obscura contain deleterious recessives (DOBZHANSKY, HOLZ, and SPASSKY 1942) will, of course, counteract too high an increase in frequency of the descendants of an individual chromosome, even if that chromosome contains a mutant which is *per se* favorable. The optimum condition is probably the presence in a population of a variety of chromosomes with different gene arrangements and different gene contents. A similar conclusion has been arrived at through a different argumentation by STURTEVANT and MATHER (1938).

THE "SEX-RATIO"

In the populations of Mount San Jacinto the gene arrangement is constant in chromosomes other than the third and the X. Two types of X chromosomes occur: the Standard and the "sex-ratio." Males which carry "sex-ratio" produce almost unisexual progenies. The situation with the "sex-ratio" gene arrangement is peculiar in that, as first shown by Gershenson (1928), it should increase in frequency automatically until the species becomes homozygous for it. Actually, its frequency in populations of *Drosophila pseudoobscura* varies from zero to about 30 percent. The level to which the "sex-ratio" is allowed to accumulate is evidently controlled by natural selection, although precisely how selection acts to restrict the spread of the "sex-ratio" is unknown (STURTEVANT and DOBZHANSKY 1936). Variations in the frequency of such a character in different localities and at different seasons, however, are not unexpected.

A summary of the data on the occurrence of "sex-ratio" in populations of Mount San Jacinto is presented in table 5. In all, 10,495 X chromosomes have been examined from the three localities. The "sex-ratio" has been found at all the stations and in all but two very small samples. Its frequency, however, appears to vary a great deal. The variations are analyzed in table 6. Stations within a locality are alike in the incidence of the "sex-ratio." No significant changes either within or between breeding seasons have been observed at the Keen stations, but at Andreas and at Pinon changes do occur. Thus, the behavior of the "sex-ratio" parallels that of the gene arrangements in the third chromosome. In both instances the variations within a breeding season are apparently the primary phenomenon, while the variations between the seasons are in part, but only in part, accountable for by the incomplete regularity of the sampling in different months and in different years.

TABLE 6

Variations in the frequency of the "sex-ratio" within a breeding season, at different breeding seasons, and at different stations within a locality.

	ANDREAS			PINON			KEEN		
	χ^2	df	P	χ^2	df	P	χ^2	df	P
Within season	74.78	36	<0.01	45.64	31	0.05–0.02	55.47	51	0.60
Between seasons	19.39	4	<0.01	12.41	4	0.02–0.01	9.17	8	0.50–0.30
Stations	0.005	1	0.95–0.90	0.011	1	0.95–0.90	6.70	4	0.20–0.10

The situation is clarified further by breaking up the data according to the month but regardless of the year of collecting (table 7). The behavior of the "sex-ratio" is analogous to that of the Chiricahua gene arrangement in the third chromosome: at Andreas and at Pinon its frequency increases in late spring, reaches a maximum in May, June, or July, and drops thereafter to its winter level. The changes are statistically significant: for Andreas $\chi^2 = 47.86$, $df = 9$, P negligible; for Pinon $\chi^2 = 17.94$, $df = 8$, P between 0.05 and 0.02. The data are consistent throughout, except for a very high value for the month of November at Andreas (table 7); this value depends, however, upon a single aberrant sample. No significant changes occur at Keen: $\chi^2 = 10.77$, $df = 5$, P between 0.10 and 0.05, or else slight changes of the same type as at Andreas and Pinon. The total frequency of "sex-ratio" at Keen (16.2 percent) is greater than at Pinon (12.6 percent), while Andreas is intermediate (15.1 percent). The differences are statistically significant ($\chi^2 = 15.45$, $df = 2$, $P < 0.01$), but they cannot be considered established because of the errors introduced by the intra- and inter-seasonal changes it the separate stations and localities.

OTHER DATA

Aside from the body of data presented above, there exist other data which show that the relative frequencies of gene arrangements may vary with time. DOBZHANSKY and STURTEVANT (1938) observed a significant change between autumn and the following spring in a population of San Gabriel Canyon, California. This population, however, has not been studied further. A population sample taken in 1938 at Wildrose Canyon, Panamint Mountains, California, by KOLLER (1939) differed in composition from that taken in 1937 by DOBZHANSKY in the same neighborhood. Further samples were taken at four collecting stations in Wildrose Canyon in 1939 and 1940. No new changes have been observed, but it is to be noted that the collecting was done always in late May or early in June. PROFESSOR J. T. PATTERSON has very generously sent to the writer for examination the population samples taken at frequent intervals in 1939, 1940, and 1941 at Aldrich, near Austin, Texas. In Texan populations the commonest gene arrangement in the third chromosome is Pikes Peak, Arrowhead is less common, and Tree Line, Olympic, and Estes Park occur as admixtures (for descriptions of these gene arrangements see DOBZHANSKY and STURTEVANT 1938). A total of 1279 third chromosomes have been examined. Slight but significant changes occur at Aldrich: the relative frequency of Arrowhead is highest in March and declines as the season advances, while Pikes Peak displays a seasonal trend which is the reciprocal of that of Arrowhead. Furthermore, in 1939 Arrowhead was less and Pikes Peak was more common at Aldrich than in 1940. In 1941 the species, according to Patterson, was abnormally rare; the small sample obtained showed a very low frequency

TABLE 7

Frequency of the "Sex ratio" (in percentage) in different months.

	ANDREAS		PINON		KEEN	
	SR	n	SR	n	SR	n
January	13.1	291	—	—	—	—
February	12.0	375	—	—	—	—
March	12.2	819	11.8	467	—	—
April	17.8	439	12.5	392	11.8	457
May	20.9	234	13.2	585	15.3	976
June	21.1	152	15.1	458	17.7	1319
July	—	—	23.9	88	17.3	935
August	—	—	12.2	197	15.3	417
September	13.8	320	9.5	254	17.8	146
October	13.8	312	11.1	395		
November	30.5	131	7.0	100	—	—
December	13.1	236			—	—

of Arrowhead. The differences between the seasonal totals for 1939 and 1940 are statistically significant.

DISCUSSION

Until recently biologists generally conceded that evolutionary changes, apart from those engendered by artificial selection and by polyploidy, are too slow to be observed directly. Instances of rapid transformation, however, have accumulated to such an extent that this concession is no longer necessary (for a review see DOBZHANSKY 1941). These instances are roughly of three sorts: changes in microorganisms, emergence of new varieties of wild species adapted to conditions altered by man (the best example of this being the cyanide resistant forms of scale insects), and cyclic changes connected with the alternation of the seasons. To the last class belong the remarkable observations of TIMOFEEFF-RESSOVSKY (1940) on *Adalia bipunctata*, which reveal a situation singularly like that in *Drosophila pseudoobscura*. *Adalia bipunctata* is a beetle which occurs in several color phases determined by a series of alleles of a certain gene. The populations of any one locality are usually mixtures of several color phases; populations of different geographical regions differ as a rule in the relative frequencies of the same color types which can be found in any one of them, although certain types are geographically restricted. In the environs of Berlin, the darkly pigmented types increase in relative frequency from spring to autumn, but, owing to a greater mortality of the dark phases during the hibernation, the lighter types become again more frequent in spring.

It is evident that in at least some species the genetic composition of populations is more plastic than it was believed hitherto. The pressure of the environment varies in intensity as well as in kind in different localities and in different seasons; some populations are able to respond to these variations by startlingly rapid reconstructions of their genotype. As shown above, the frequency of the Chiricahua gene arrangement in the population of the Andreas Canyon is about doubled between March and June of each year (table 4). This time interval can hardly correspond to more than two generations. Even if every chromosome with the Chiricahua gene arrangement contains genetic factors favorable in the summer environment (which may well be doubted), a change so swift as the above indicates a selection coefficient of an unexpectedly high magnitude (s approximately 0.4). The drop in the frequency of the Chiricahua arrangement during the last summer at Andreas is almost as precipitous as its rise in spring. Selection coefficients of the order $s=0.1$ must be assumed to operate to bring about the observed changes in the frequencies of the gene arrangements in the third chromosome and of the "sex-ratio" at Andreas and Pinon Flats. Yet, it is customary to think that the adaptive changes in race and species formation are built with the aid of much smaller selective advantages.

The changes observed in Adalia and Drosophila seem to follow the seasonal climatic cycle. If they are constantly recurring and completely reversible, they represent, from the point of view of long range evolutionary progress, largely a wasted motion. It may even be that species undergoing changes as rapid as these never actually reach the highest theoretically possible adaptive levels: the species may at any one time be adapted best to the conditions which have just lapsed. Such a situation is likely to obtain in many organisms which inhabit the Temperate Zone, and in general any country with pronounced seasonal climatic changes. Organisms which produce several generations per year will be most subject to this unending race with the environment, but an essentially similar situation may obtain also in organisms with long developmental periods.

SUMMARY

In 1939 and 1940 population samples were taken at approximately monthly intervals at nine collecting "stations" in three "localities" on Mount San Jacinto, in California. In 1941 four of these stations, and in 1942 three stations, were followed. The relative frequencies of the various gene arrangements in the third and X chromosomes in these samples have been determined. In all, 12,807 third and 10,495 X chromosomes have been examined.

In the populations of at least two of the three localities the relative frequencies of the gene arrangements change from month to month. The changes are regular and cyclic. They seem to follow the annual climatic cycle.

The composition of the population of a locality may change also from year to year, but such changes, as far as known, are not as striking as the seasonal ones.

The populations of stations within a locality are alike at any one time. The populations of localities ten to fifteen miles apart may be permanently different.

It is surmised that the changes observed are caused by natural selection favoring the carriers of different gene arrangements at different seasons of the year. Chance associations of the gene arrangements with genetic factors producing physiological modifications, rather than position effects, are probably responsible for the phenomena observed.

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