

GENETICS OF NATURAL POPULATIONS.  
III GENE ARRANGEMENTS IN POPULATIONS OF  
*DROSOPHILA PSEUDOOPSCURA*  
FROM CONTIGUOUS  
LOCALITIES

P. C. KOLLER

*California Institute of Technology, Pasadena, California and Carnegie  
Institution of Washington, Cold Spring Harbor, New York*

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INTRODUCTION

SEVENTEEN gene arrangements, related to each other as single or multiple inversions, were described by DOBZHANSKY and STURTEVANT (1938) in the third chromosome of *Drosophila pseudoobscura*. Some of these gene arrangements have a wide, and others a narrow geographical distribution. In some localities the entire population is uniform, but more commonly several arrangements are found together. Differences between populations may be either qualitative or quantitative. Thus, three gene arrangements (Standard, Arrowhead and Chiricahua) were found in each of the eleven populations from isolated mountain ranges in the Death Valley region, California, studied by DOBZHANSKY and QUEAL (1938). The relative frequencies of these arrangements proved, however, to vary rather widely from range to range, there being no pronounced geographical regularity in these variations. Adjacent ranges do not tend to be more similar than remote ones. Differences of this kind are expected to occur in isolated populations whose effective size is not very large (WRIGHT 1931).

The question arises, however, whether a *D. pseudoobscura* population inhabiting a mountain range may be considered to represent a single breeding unit, or whether it is in turn composed of still smaller colonies whose genetic composition can diverge, within limits, due to the same kind of causes, which provoke the differentiation of larger populations described by DOBZHANSKY and QUEAL (1938). To answer this question, samples of the population of *D. pseudoobscura* were taken in different localities on the same mountain range and the relative frequencies of the different gene arrangements found there were determined. As shown below, significant differences between samples are present, thus proving that some genetic diversification can occur even within an ostensibly continuous population.

MATERIAL AND METHODS

The population of *D. pseudoobscura* inhabiting the Panamint Mountains, California, was selected for the analysis. This mountain range, forming the southwestern boundary of Death Valley, has a maximum elevation

of more than 11,000 feet above sea level; its slopes are crevassed with deep canyons running eastward and westward from the crest. The canyons as well as the crest are covered with a forest-like growth consisting chiefly of piñon (*Pinus monophylla*). This growth begins at an elevation of approximately 6,000 feet, and extends to the base of the highest peaks. *D. pseudoobscura* is encountered in the forested zone and not below it. The population inhabiting Panamint Mountains may be considered isolated from those inhabiting other forested mountains in the same region (cf. DOBZHANSKY and QUEAL 1938).

Samples of flies were collected in seven different canyons on the western slope of the Panamints. The altitude of localities varied from 6,300 to about 8,200 feet (fig. 1), and the distance between them from 4 to 6 miles. It may be noted here that the forest cover is practically continuous on the sides of these canyons, on the ridges separating them, as well as on the main ridge, although the northern exposures have, in general, a denser growth than the southern ones. An especially close connection is found between Jail and Hall canyons; Surprise and Pleasant canyons are somewhat further apart. The geographical and ecological conditions are rather similar everywhere, and there is no apparent impediment for migration of flies from one canyon to others.

Collection in Nemo and Wildrose canyons was made on the 26th and 27th of May, and in the other canyons from the 13th to 20th of June 1938. In most of the cases the flies were separated according to sex in order to avoid matings, and were transported in vials to the laboratory. The methods of determining the structure and the frequency of the various gene arrangements were the same as used by DOBZHANSKY and QUEAL (1938). The females were placed separately in cultures and the salivary gland chromosomes of the larvae were analyzed. Usually one larva was taken from each culture, and its chromosomes were examined. When the number of wild flies from a given locality was insufficient, by analyzing the salivary chromosomes of 10 or more larvae, the chromosome structure of the mother as well as that of the father was assumed to be determined. Wild males were mated to orange purple females, both of which genes are located in the third chromosome which had the Standard gene arrangement. Seven larvae from the  $F_1$  generation were dissected and the gene arrangements in the two paternal third chromosomes inferred from the analysis.

#### GENE ARRANGEMENTS AND THEIR FREQUENCIES IN THE PANAMINT POPULATIONS

Six previously known gene arrangements have been found in the populations of the canyons, namely: "Standard," "Arrowhead," "Chiricahua," "Santa Cruz," "Tree Line" and "Mammoth" arrangements. Arrowhead

differs from Standard in having one, Chiricahua, Tree Line and Mammoth in having three, and Santa Cruz in having two inversions (DOBZHANSKY

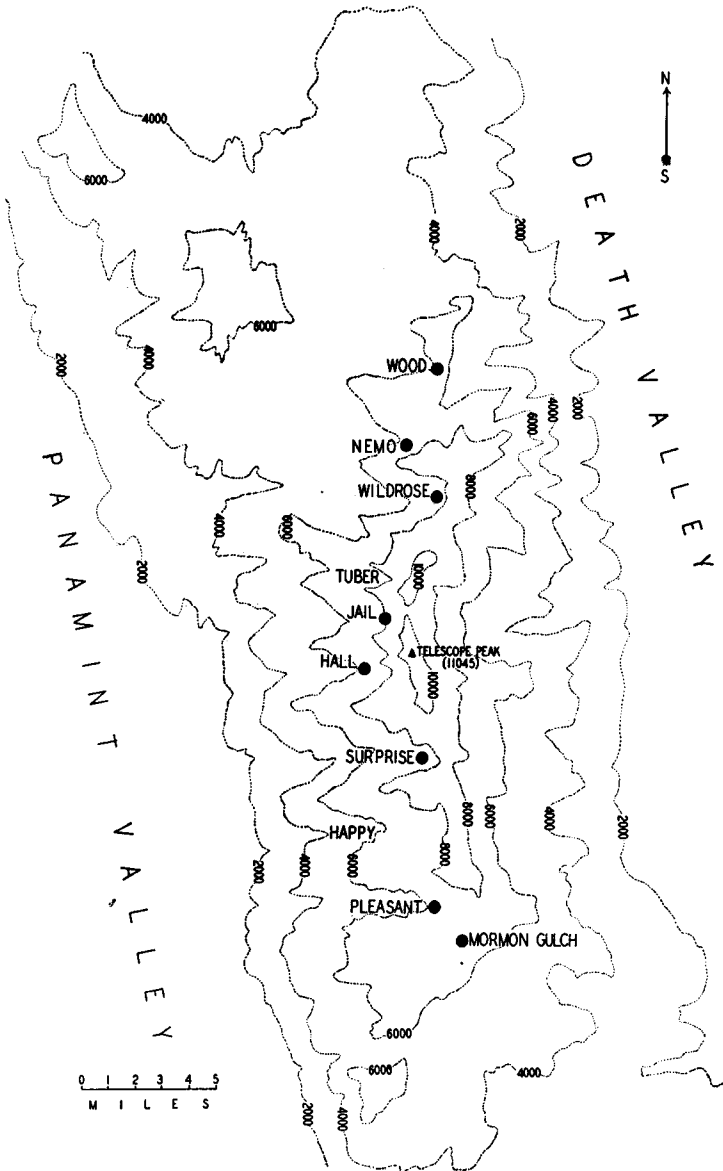


FIGURE 1.—A topographic map of the Panamint Range. Localities in which collection has been made are indicated by circles. (Data from Mormon Gulch are not included in the present paper.)

and STURTEVANT 1938). The distribution and the frequencies of these gene arrangements are given in table 1.

In addition to the six canyons tabulated above, another canyon called Wood Canyon was also explored. It is the northernmost canyon in the Panamint range having tree vegetation. Only one female and two males were trapped. The gene arrangements in the 8 chromosomes (4 from the female, 2 from each male) are as follows: 1 Standard, 6 Arrowhead, and 1 Chiricahua. The small number of chromosomes analyzed prevents us from drawing any conclusions concerning the true genetical constitution of this population.

TABLE I  
*Frequencies (in percent) of the six gene arrangements found in different canyons of the Panamint Mountains.*

| CANYON   |       | STANDARD     | ARROWHEAD    | CHIRICAHUA   | TREE LINE   | SANTA CRUZ  | MAMMOTH     | CHROMO-<br>SOMES<br>TESTED |
|----------|-------|--------------|--------------|--------------|-------------|-------------|-------------|----------------------------|
| Nemo     | ♀     | 48.04 ± 5.38 | 32.35 ± 4.58 | 19.61 ± 3.87 |             |             |             | 102                        |
|          | ♂     | 25.00 ± 8.83 | 45.83 ± 3.16 | 29.17 ± 9.27 |             |             |             | 24                         |
|          | total | 43.65 ± 4.35 | 34.92 ± 4.24 | 21.43 ± 3.60 |             |             |             | 126                        |
| Wildrose | ♀     | 41.43 ± 5.83 | 30.00 ± 8.36 | 24.29 ± 5.09 |             | 2.86 ± 1.73 | 1.43 ± 1.40 | 70                         |
|          | ♂     | 27.91 ± 4.79 | 44.19 ± 5.29 | 25.58 ± 4.69 | 1.16 ± 1.02 | 1.16 ± 1.02 |             | 86                         |
|          | total | 33.97 ± 3.74 | 37.82 ± 3.87 | 25.00 ± 3.46 | 0.64 ± 0.60 | 1.92 ± 1.03 | 0.64 ± 0.60 | 156                        |
| Jail     | ♀     | 43.66 ± 3.16 | 29.92 ± 2.82 | 21.31 ± 2.44 | 0.41 ± 0.37 |             |             | 244                        |
|          | ♂     | 35.71 ± 9.12 | 50.00 ± 9.43 | 14.29 ± 6.55 |             |             |             | 28                         |
|          | total | 47.06 ± 3.00 | 31.99 ± 2.64 | 20.59 ± 2.49 |             |             |             | 272                        |
| Hall     | ♀     | 37.50 ± 4.12 | 45.59 ± 4.24 | 15.50 ± 2.82 | 4.41 ± 1.73 |             |             | 136                        |
|          | ♂     | 25.00 ± 9.64 | 50.00 ± 1.18 | 25.00 ± 9.64 |             |             |             | 20                         |
|          | total | 35.90 ± 3.74 | 46.15 ± 4.00 | 14.10 ± 2.64 | 3.85 ± 1.41 |             |             | 156                        |
| Surprise | ♀     | 34.68 ± 4.24 | 44.35 ± 4.35 | 13.71 ± 3.00 | 7.26 ± 2.23 |             |             | 124                        |
|          | ♂     | 42.00 ± 7.59 | 40.00 ± 6.92 | 14.00 ± 4.89 | 4.00 ± 2.64 |             |             | 50                         |
|          | total | 36.78 ± 3.60 | 43.10 ± 3.71 | 13.79 ± 2.44 | 6.32 ± 1.73 |             |             | 174                        |
| Pleasant | ♀     | 22.45 ± 4.12 | 46.94 ± 5.02 | 30.61 ± 4.58 |             |             |             | 98                         |
|          | ♂     | 26.67 ± 4.59 | 47.78 ± 5.21 | 20.00 ± 4.18 | 5.56 ± 2.31 |             |             | 90                         |
|          | total | 24.47 ± 3.07 | 47.34 ± 3.60 | 25.53 ± 3.16 | 2.66 ± 1.17 |             |             | 188                        |
| Totals   |       | 37.51 ± 1.48 | 39.74 ± 1.49 | 20.15 ± 1.24 | 2.24 ± 0.45 | 0.28 ± 0.11 | 0.09 ± 0.09 | 1072                       |

Table 1 shows that the gene arrangements are present in different proportions in different canyons. While the Standard and Arrowhead arrangements have the highest frequencies, Chiricahua is less frequent and the proportion of the three others (Tree Line, Santa Cruz, Mammoth) is probably so small that they were not encountered at all in the populations of some canyons. The frequencies of gene arrangements in the two sexes are given separately, each observed frequency is accompanied by its standard error. There is an apparent difference between the sexes. This difference is especially marked in the population from Wildrose canyon, where the numbers of chromosomes tested in the two sexes are very close. An analysis of variance was made using the BRANDT and SNEDECOR method of test of significance. The  $\chi^2$  of the difference between sexes in the various canyons is as follows:

|           |       |           |       |
|-----------|-------|-----------|-------|
| Nemo:     | 4.202 | Hall:     | 1.468 |
| Wildrose: | 4.136 | Surprise: | 0.832 |
| Jail:     | 4.684 | Pleasant: | 0.773 |

Neither the values of single  $\chi^2$  (for 2 degrees of freedom) nor the sum of  $\chi^2$  (for 12 d. f.) of the sex-difference in the whole Panamint population are significant.

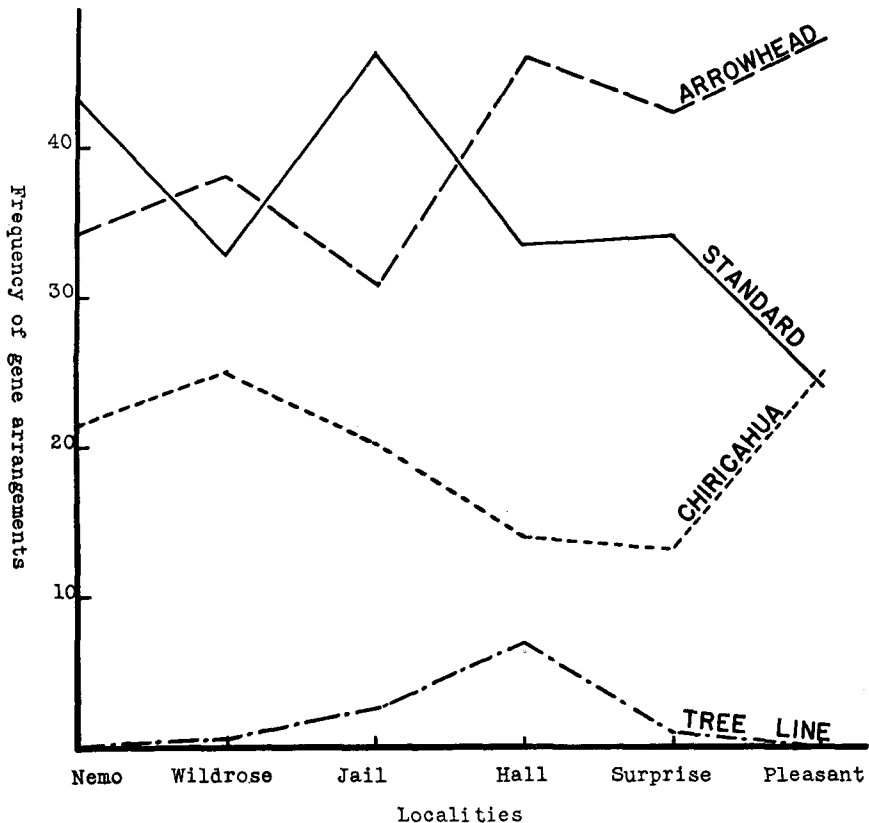


FIGURE 2.—Graph illustrating the frequencies of gene arrangements in the various localities.

Similar statistical analysis was undertaken to determine the significance of the difference with respect to the frequencies of the various gene arrangements observed in the different canyons. The  $\chi^2$  value was calculated to be 33.9782. The probability that the difference between canyons is due to chance alone is less than 0.01 for 10 degrees of freedom. The analysis of variance clearly shows that the variations in the frequencies of the same gene arrangements observed in the different localities are very significant. In view of this fact, a question naturally arises: is there a geographical trend in these variations?

POPULATIONS OF DROSOPHILA PSEUDOOBSCURA

TABLE 2

*The observed and expected frequencies of inversion homozygotes and heterozygotes in populations of different canyons.*

| CANYON   |      | STANDARD | ARROWHEAD | CHIRICAHUA | STANDARD  | STANDARD   | ARROWHEAD  |
|----------|------|----------|-----------|------------|-----------|------------|------------|
|          |      | STANDARD | ARROWHEAD | CHIRICAHUA | ARROWHEAD | CHIRICAHUA | CHIRICAHUA |
| Nemo     | obs. | 12       | 7         | 4          | 21        | 10         | 9          |
|          | exp. | 12.00    | 7.46      | 2.89       | 19.20     | 11.79      | 9.43       |
| Wildrose | obs. | 6        | 11        | 2          | 19        | 19         | 16         |
|          | exp. | 9.00     | 11.15     | 4.87       | 20.04     | 13.24      | 14.75      |
| Jail     | obs. | 28       | 13        | 6          | 44        | 28         | 16         |
|          | exp. | 30.12    | 13.92     | 5.77       | 40.94     | 27.36      | 17.91      |
| Hall     | obs. | 10       | 15        | 3          | 28        | 5          | 11         |
|          | exp. | 10.05    | 16.61     | 1.95       | 25.85     | 7.90       | 10.15      |
| Surprise | obs. | 7        | 10        | 1          | 37        | 7          | 14         |
|          | exp. | 11.77    | 16.16     | 1.65       | 27.58     | 8.12       | 10.34      |
| Pleasant | obs. | 5        | 15        | 4          | 26        | 9          | 30         |
|          | exp. | 5.63     | 21.07     | 6.13       | 21.78     | 11.70      | 22.72      |
| Total    | obs. | 68       | 71        | 20         | 175       | 78         | 96         |
|          | exp. | 75.41    | 84.65     | 21.76      | 159.78    | 81.02      | 85.84      |

| CANYON   |      | STANDARD   | ARROWHEAD  | STANDARD  | ARROWHEAD | CHIRICAHUA | ARROWHEAD |
|----------|------|------------|------------|-----------|-----------|------------|-----------|
|          |      | SANTA CRUZ | SANTA CRUZ | TREE LINE | TREE LINE | TREE LINE  | MAMMOTH   |
| Nemo     | obs. |            |            |           |           |            |           |
|          | exp. |            |            |           |           |            |           |
| Wildrose | obs. | 2          | 1          | 1         |           |            | 1         |
|          | exp. | 1.12       | 1.13       | 0.34      |           |            | 0.37      |
| Jail     | obs. |            |            |           | 1         |            |           |
|          | exp. |            |            |           | 0.32      |            |           |
| Hall     | obs. |            |            | 3         | 3         |            |           |
|          | exp. |            |            | 2.25      | 2.77      |            |           |
| Surprise | obs. |            |            | 6         | 4         | 1          |           |
|          | exp. |            |            | 4.05      | 4.74      | 1.52       |           |
| Pleasant | obs. |            |            | 1         | 3         | 1          |           |
|          | exp. |            |            | 1.32      | 2.27      | 1.28       |           |
| Total    | obs. | 2          | 1          | 11        | 11        | 2          | 1         |
|          | exp. | 1.16       | 1.19       | 9.03      | 9.54      | 4.84       | 0.37      |

It is obvious from the data that the Tree Line arrangement is most frequent in the middle region of the Panamint range. While the frequencies of Arrowhead arrangement gradually increase towards the south, the reverse is true for the Standard arrangement (fig. 2). Furthermore, adjacent canyons tend to be more nearly similar than do remote canyons. This is best expressed in populations inhabiting Hall and Surprise canyons.

#### RANDOMNESS OF MATINGS

The distribution of inversion homo- and heterozygotes in the different canyons is given in table 2.

The observed and expected frequencies agree very well. There is a slight, statistically insignificant excess of heterozygotes. The reverse condition was found by DOBZHANSKY and QUEAL (1938); they observed a small increase in the number of inversion homozygotes.

It was found that females sometimes mate with two or more males in succession. Evidence that double matings may occur in nature was found during the present study. The frequency and structure of the gene arrangements in 10  $F_1$  larvae of one wild female was found to be as follows: 4 Standard/Arrowhead; 2 Standard/Chiricahua; 2 Arrowhead/Arrowhead and 2 Standard/Standard. According to the first three classes, the genetical constitution of the parents is Standard/Arrowhead  $\times$  Chiricahua/Arrowhead. Consequently, no larvae of Standard/Standard constitution could be expected in the  $F_1$  generation. The presence of this class is probably due to the fact that the female mated twice, the second male having a chromosome with the Standard gene arrangement.

The other evidence showing that multiple matings occur in nature was obtained when the "sex-ratio" conditions were analyzed in the  $F_1$  generations of wild females. It was reported by STURTEVANT and DOBZHANSKY (1937) that either very few or no sons appeared in the  $F_1$  generation of a female if she was mated to a male carrying "*sr*" ("sex-ratio" gene or genes). Some  $F_1$  cultures of wild females were encountered during the present study in which the proportion of males was found to be between 20-40 per cent. A complete sex-ratio condition in the Panamint strain allows 0-5 per cent of males in the  $F_1$  generation. The greater number of males may have been brought about by a second mating with a normal male.

#### VARIATIONS IN THE FREQUENCIES OF GENE ARRANGEMENTS FROM YEAR TO YEAR

The frequencies of the various gene arrangements in the population of the Wildrose canyon were determined in 1937 (DOBZHANSKY and QUEAL 1938) and in 1938 (my data). The localities where the collecting was done are almost exactly the same: DOBZHANSKY's trap bottles being spaced

somewhat more widely than mine. The time of collecting was the middle of May in 1937, and the end of the same month in 1938. A comparison of both sets of data is presented in table 3.

TABLE 3

*The frequencies of various gene arrangements in Wildrose Canyon on two successive years.*

| YEAR | STANDARD   | ARROWHEAD  | CHIRICAHUA | SANTA CRUZ | TREE LINE | MAMMOTH  | CHROMO-<br>SOMES<br>TESTED |
|------|------------|------------|------------|------------|-----------|----------|----------------------------|
| 1937 | 13.83±1.56 | 67.41±2.11 | 18.75±1.75 |            |           |          | 224                        |
| 1938 | 33.97±3.74 | 37.82±3.87 | 25.00±3.46 | 1.92±1.03  | 0.64±0.6  | 0.64±0.6 | 156                        |

$$\chi^2 = 33.7512 \quad D.f. = 2 \quad P = < .01$$

Three gene arrangements, namely Santa Cruz, Tree Line and Mammoth, were detected in 1938, but not in 1937. Santa Cruz and Tree Line are recorded in the Death Valley region for the first time, while Mammoth has been known to occur on other mountain ranges (Lida, Cottonwood) but not on Panamint. The failure to detect these gene arrangements in 1937 may be due either to sampling errors, or to increases of their frequencies in the population. It is highly improbable that they arose there de novo, since spontaneous changes in the gene arrangement are extremely rare; the variations in the gene arrangement in *D. pseudoobscura* described in an earlier paper (KOLLER 1936) were probably present in the experimental strains long before the cytological study was made.

The most important conclusion following from the data presented in table 3 is that the frequencies of the gene arrangements in the same population are not constant from year to year. In 1938 the frequencies of Standard and Chiricahua chromosomes were higher, and of Arrowhead, lower than in 1937. The  $\chi^2$  gives the value 33.7572 which is highly significant. Comparable data for the frequencies of the gene arrangements were also obtained for another locality, namely, for the Mount Whitney canyon (Sierra Nevada). Populations of race A and race B of *D. pseudoobscura* were collected in this canyon in mid-July of 1937 (DOBZHANSKY and QUEAL 1938), and again in mid-July of 1938. Table 4 shows the results.

In 1938 two new gene arrangements, namely, Tree Line and Olympic, were found in the Mount Whitney canyon. The frequencies of other gene arrangements underwent no striking changes. To test the statistical significance of the differences observed, the  $\chi^2$  values were calculated and proved to be 4.107 for race A and 3.984 for race B respectively. For two degrees of freedom, the P values are between 0.20 and 0.10, hence not significant.

A third set of similar data concerns the population of San Gabriel canyon in 1936 and 1937 (DOBZHANSKY and STURTEVANT 1938). The fol-



lowing frequencies of the various gene arrangements were found in this locality:

| Year | Standard | Arrowhead | Chiricahua | Tree Line | Chromosomes tested |
|------|----------|-----------|------------|-----------|--------------------|
| 1936 | 14.8     | 27.8      | 40.7       | 16.4      | 57                 |
| 1937 | 57.5     | 27.7      | 10.6       | 4.3       | 47                 |

Despite the small numbers of the chromosomes tested, the differences are clearly significant: the  $\chi^2$  value is 30.3942. The conclusion is justified that pronounced changes in the frequencies of the gene arrangements have taken place in populations inhabiting the Wildrose and San Gabriel canyons, but not in Mount Whitney canyon.

#### "SEX-RATIO" AND MUTANT GENES

The "sex-ratio" gene is localized in the right limb of the X chromosome, and is associated with a triple inversion. Any male which carries it produces only a few or no sons, owing to the fact that during the spermatogenesis no Y-carrying sperms are formed. The "sex-ratio" gene (*sr*) was found to be widely distributed in free-living populations of *D. pseudoobscura* and other related species (STURTEVANT and DOBZHANSKY 1936). Its frequency in the populations of different canyons of the Panamint range is given below:

| CANYONS  | NO. OF X<br>CHROMOSOMES<br>WITH "SR" | NO. OF X<br>CHROMOSOMES<br>TESTED | PERCENT OF X<br>CHROMOSOMES<br>WITH "SEX-RATIO" |
|----------|--------------------------------------|-----------------------------------|---|
| Nemo     | 2                                    | 11                                | 18.18   |
| Wildrose | 10                                   | 44                                | 22.73   |
| Jail     | 7                                    | 44                                | 15.9  |
| Hall     | 0                                    | 9                                 | 0   |
| Surprise | 3                                    | 23                                | 13.04   |
| Pleasant | 6                                    | 44                                | 13.64   |
| Total    | 28                                   | 175                               | 16.00   |

In 1936, DOBZHANSKY and QUEAL (1938) found that 8.09 percent of the 136 X chromosomes in the Wildrose population tested carried the "sex-ratio" gene.

The populations of the different canyons were tested for the presence of two third-chromosome genes: orange and purple. For this purpose, the wild males were crossed to orange purple females and the F<sub>1</sub> generation was inspected; 596 third chromosomes were thus analyzed, and one chromosome was found to be carrying the gene orange. One half of the F<sub>1</sub>

offspring in this culture had the orange eye color. No purple mutant genes were found during the present study.

TABLE 4

*The frequencies of various gene arrangements in Mount Whitney Canyon in two successive years.*

| RACE YEAR | STANDARD        | ARROWHEAD  | CHIRICAHUA | TREE LINE | OLYMPIC   | WAVONA     | KLAMATH   | CHROMO-<br>SOMES<br>TESTED |
|-----------|-----------------|------------|------------|-----------|-----------|------------|-----------|----------------------------|
| A {       | 1937 21.73±6.07 | 69.57±6.78 | 8.70±4.16  |           |           |            |           | 46                         |
| {         | 1938 20.42±4.16 | 56.50±5.11 | 18.08±3.92 | 3.19±1.76 | 1.06±1.01 |            |           | 94                         |
| B {       | 1937 20.30±4.61 |            |            |           |           | 78.40±4.75 | 1.30±1.21 | 74                         |
| {         | 1938 25.71±5.21 |            |            |           |           | 67.14±5.61 | 7.14±3.07 | 70                         |

For Race A:  $\chi^2=4.107$  D.f.=2 P=0.20-0.10  
 For Race B:  $\chi^2=3.984$  D.f.=2 P=0.20-0.10

## DISCUSSION

The analysis of the chromosome structure has shown that the population of *D. pseudoobscura* inhabiting the Panamint Mountains is not uniform. Population samples from the different canyons proved to be not alike. The population of the Panamints is differentiated into smaller breeding units having more or less different genetic constitutions. Whether or not the entire population of a canyon may be considered an elementary breeding unit can be decided only by further investigations. Anyway, the subdivision of an inhabited territory (mountain range) into geographical units (canyons) is, in this case, reflected in a corresponding subdivision of the fly population.

No local differentiation can occur in a panmictic population inhabiting a territory of any size. Local colonies which do not interbreed absolutely at random may or may not drift apart in their genetic constitution. Indeed, if the colonies exchange a sufficient number of migrants every generation, a genetic uniformity will continue to prevail. If, however, the migration rate is small, a differentiation is liable to occur. As shown by WRIGHT (1931 and other works), a reduction of the effective size of the breeding population is followed by random fluctuations in the frequencies of the genes (or chromosome structures) present in it. The amplitude of the fluctuations is negatively correlated with population size: the smaller the size the larger the fluctuations.

Since the frequencies of the chromosomal types in the different canyons of the Panamint range are not alike, the fly population is certainly not panmictic. Whether or not migration of flies from canyon to canyon occurs, in any case the migration rate is not sufficient to prevent the origin of differences between the local colonies. In fact, our data suggest the existence of geographical gradients for some of the gene arrangements (fig. 2).

The frequency of Arrowhead seems to be highest in the southern part of the Panamints, and to decrease northward. Standard shows the opposite regularity. Tree Line is most frequent in the central portion of the range. In general, adjacent canyons are more similar than remote ones. This may be the result of occasional migration between the canyons. It is noteworthy that no geographical gradients are observed between *D. pseudo-obscura* populations inhabiting separate mountain ranges; the migration of flies from range to range is certainly less probable than migration from canyon to canyon (DOBZHANSKY and QUEAL 1938).

The other important observation concerns the significant differences between the frequencies of the various gene arrangements on two successive years in the same canyon. This has been observed in the Wildrose canyon of the Panamint and in the San Gabriel canyon further south. On the other hand, populations of race A and race B remained stationary during the same period in Mount Whitney Canyon in the Sierra Nevada. It follows that yearly fluctuations in the genetical structure of a population may or may not occur. Such fluctuations can be accounted for on the same basis as the differentiation of the local populations in general. They may be due to a small effective size of the population in a breeding unit. It is very probable that the fly populations in the Death Valley region undergo sharp seasonal reductions and increases; the number of flies is reduced in winter due to cold, and perhaps also at the height of the summer due to extreme aridity. The reduction of population is normally proportional, that is, it affects all the genetical constituents to the same degree. But occasionally it may lead to a disproportionate change in the genetical structure. During the expansion of a population the relative frequencies of the genes or chromosome structures attained at the time of the greatest reduction are, more or less, faithfully perpetuated. On such a basis the genetic structure of a population in a locality may remain stationary over a period of years, or it may fluctuate; the fluctuation is, in general, greater when the minimum effective breeding size is smaller.

Whether or not the various gene arrangements in the third chromosome differ in adaptive value (due to position effects) is unknown. It is most probable that they are neutral in this respect. The whole complex of facts at hand can consistently be accounted for on the assumption of random variations in the frequencies of the gene arrangements and without the intervention of selection. The agreement of the observed and expected frequencies of the inversion homo- and heterozygotes shows that (1) random mating prevails, and (2) that the viabilities of the homo- and heterozygotes are alike. The occurrence of inversions or other structural changes in a chromosome does not *per se* lead to isolation or formation of endogamous groups within a population.

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## SUMMARY

1. The frequencies of the gene arrangements in the third chromosome of *Drosophila pseudoobscura* were determined in populations inhabiting the different canyons of the Panamint Mountains.

2. Six different gene arrangements are present in the populations, and their relative frequencies vary from canyon to canyon.

3. Populations of adjacent canyons are somewhat more similar than those of the more remote ones. The geographical gradient may be due to migration, which, however, is not effective enough to level the differences between the canyons.

4. The observed and expected frequencies of the inversion homozygotes and heterozygotes in the canyon populations are in agreement, indicating random mating and equal viability.

5. Significant yearly variations were found in the populations of two localities, but were not observed in a third.

6. The genetic differences between the canyon colonies, as well as the yearly variations in the frequencies of the gene arrangements, are probably due to the smallness of the effective breeding size of these colonies.

7. Local genetic diversification can arise in a population occupying a continuously habitable territory. How small the elementary breeding units are in such a territory remains to be determined.

## LITERATURE CITED

- DOBZHANSKY, TH. and QUEAL, M. L., 1938 Genetics of natural populations. I. Chromosome variation in populations of *Drosophila pseudoobscura* inhabiting isolated mountain ranges. *Genetics* **23**: 239-251.
- DOBZHANSKY, TH. and STURTEVANT, A. H., 1938 Variations in the gene arrangement in the chromosomes of *Drosophila pseudoobscura*. *Genetics* **23**: 28-64.
- KOLLER, P. C. 1936 Structural hybridity in *Drosophila pseudoobscura*. *J. Genet.* **32**: 79-102.
- STURTEVANT, A. H. and DOBZHANSKY, TH., 1936 Geographical distribution and cytology of "Sex-ratio" in *Drosophila pseudoobscura* and related species. *Genetics* **21**: 473-490.
- WRIGHT, S., 1931 Evolution in Mendelian populations. *Genetics* **16**: 97-159.