

GENETICS OF NATURAL POPULATIONS. I. CHROMOSOME
VARIATION IN POPULATIONS OF *DROSOPHILA*
PSEUDOOBSCURA INHABITING ISOLATED
MOUNTAIN RANGES

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INTRODUCTION

IN RECENT years there appears to be a growing interest in the genetics of free-living populations, a subject hitherto almost untouched. Certain species of *Drosophila* prove to be very suitable for investigations in this field. TSCHEWERIKOFF (CHETVERIKOV), DUBININ and their collaborators in Russia, TIMOFEEFF-RESSOVSKY in Germany, GORDON in England, and STURTEVANT in this country have secured much valuable information which opens new vistas and raises a host of new problems (for a short review of the literature see DOBZHANSKY 1937). It has seemed to us that a comparison of the genetic constitutions of several free-living populations from the same general region, and yet isolated from each other, may be of interest. Samples of the populations of *Drosophila pseudoobscura* inhabiting island-like mountain forests in the Death Valley region of California and Nevada were collected. This region is especially favorable for our purposes, since it is as yet practically undisturbed by man's activities.

We wish to acknowledge our obligations to Professor A. H. STURTEVANT for his valuable advice, to Mr. H. D. CURRY whose help enabled us to collect material in certain rather inaccessible localities, and to Messrs. G. T. RUDKIN and EDWARD HELD for their assistance in conducting the experiments.

MATERIAL

The nature and source of the material are so important in the present investigation that we are forced to consider them more carefully than is customary in genetic accounts.

East of the rampart of the Sierra Nevada, in California and the adjacent part of the state of Nevada, there lies an extremely arid desert plateau. This plateau is strewn with mountain ranges and furrowed by deep valleys, extending mostly in the meridional direction (fig. 1). Some of the ranges lift their crests much above six thousand feet, and their upper reaches are covered by open forests consisting of piñon (*Pinus monophylla*), Juniperus, oak, and (on Charleston Peak and the Sierra Nevada), western yellow pine (*Pinus ponderosa*) and other conifers. The valleys intervening

between the ranges are barren except for a very xerophytic vegetation. The mountain forests may, consequently, be described as a series of islands surrounded by a sea of deserts. The contrast between the climatic and ecological conditions encountered on the mountain tops and in the valleys is exceedingly sharp.

The biology of *Drosophila pseudoobscura* in the natural state is very little known. According to the observations of DUDA (1924) and of STURTEVANT (unpublished), its relatives (*D. obscura*, *D. affinis* and other species) feed on the fermenting sap of bleeding trees, and the same is probably true for *D. pseudoobscura*. At any rate, the latter species is restricted to regions having some tree vegetation; occasionally it may be trapped a few thousand feet from the nearest trees, but it has never been found in terrain having only grass vegetation. In arid regions *D. pseudoobscura* is confined to mountains where forests can grow, and in general the denser the forest the more abundant is the fly population. To what extent populations inhabiting different mountain ranges exchange individuals it is very difficult to tell. During the warm season of the year the desert appears to be a formidable obstacle to the distribution of the fly, but an occasional transfer of a stray individual by wind or other agents is not excluded. At the very best, a migration of flies within a continuously forested region is easier than from one range to another across desert valleys. The population inhabiting each mountain range is largely, if not completely, isolated from others.

Samples of the population of *D. pseudoobscura* have been collected in eleven localities shown on the map (fig. 1). Each locality corresponds to a forested mountain range, and in the area studied there exist only two or three ranges where collecting has not been attempted. The entire collecting was accomplished within two months, from the middle of May to the middle of July, 1937; the genetic analysis of the samples has been carried on as nearly simultaneously as possible. The following technique has been adopted. Ten to twenty trap bottles with fermenting banana mush were exposed in each locality, the distance between the traps farthest apart being no less than a quarter and no more than one mile. The traps were left out for a few hours around sunset, and in some cases overnight. The flies that entered the traps were placed in vials with food and transported without delay to the laboratory. In the following presentation each sample of flies is referred to by the name of the locality (island forest) in which it was collected. It must be emphasized, however, that each sample comes from only a small fraction of the area of a given forest; the possibility that the populations inhabiting different parts of the same forest may be different is by no means excluded.

THE GENE ARRANGEMENT IN THE THIRD CHROMOSOME

Strains of *D. pseudoobscura* coming from the same or from different localities are frequently unlike in the gene arrangement. The third chromosome proves to be more variable in this respect than the rest; seventeen arrangements related to each other as single or multiple inversions have

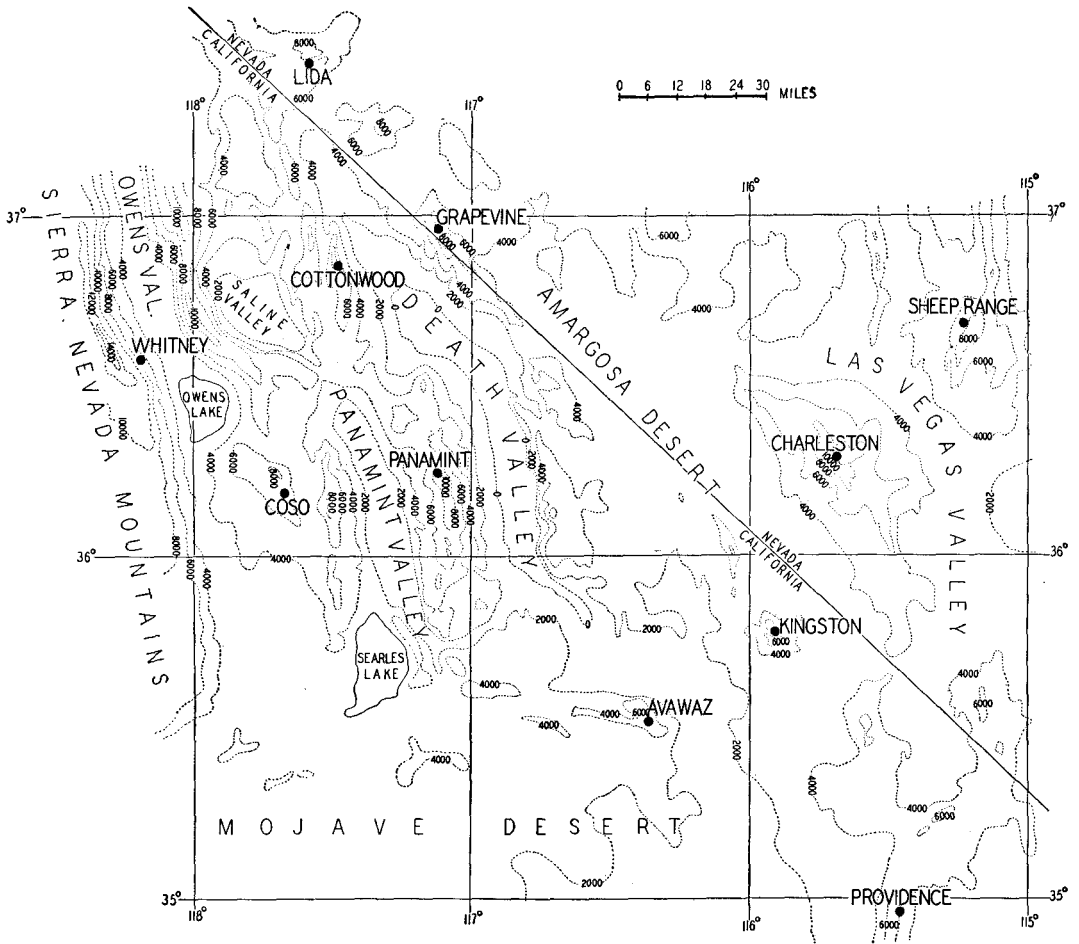


FIGURE 1. Map showing localities from which collections were made. (Note: Avawaz should be spelled Awavaz as in text.)

been recorded (STURTEVANT and DOBZHANSKY 1936a; DOBZHANSKY and STURTEVANT 1938). Populations inhabiting the mountain ranges in the Death Valley region also proved to be variable in the gene arrangement, and the variability observed is of a kind that permits certain inferences as to the relation of these populations to each other.

The gene arrangement in a given individual can be determined by

inspection of the chromosomes in the cells of the salivary glands. In structurally homozygous individuals the distribution of the stainable discs in the chromosomes reflects the arrangement involved; if two homologous chromosomes differing in the gene arrangement are present, a characteristic pairing configuration results. For descriptions of each of the seventeen arrangements the paper by DOBZHANSKY and STURTEVANT (1938) may be consulted.

Since females caught outdoors are usually fertilized already, they were placed in individual cultures and allowed to produce offspring. Wild males were crossed to females homozygous for the third chromosome recessives orange (*or*) and purple (*pr*), and having the standard gene arrangement in the third and in all other chromosomes. From the offspring of each wild female a single larva was taken, and a temporary acetocarmine preparation of its salivary glands was made. Such a larva carries one maternal and one paternal third chromosome, and therefore an examination of its nuclei furnishes the information on the gene arrangement in two chromosomes present in the wild population in question. From each male culture seven larvae were taken, and one salivary gland from each larva was fixed and stained in acetocarmine. If the male parent contained two third chromosomes similar in the gene arrangement, all seven larvae show identical chromosome configurations; if two different chromosomes were present, the offspring fall into two equally numerous classes, and the probability is sufficiently great that among seven larvae both classes are represented (only one out of sixty-four heterozygotes is thus not detected). The third chromosomes were carefully examined in every preparation, the rest receiving only a cursory inspection.

Four previously known gene arrangements have been found in populations coming from the localities shown in figure 1. These have been designated as "Standard," "Arrowhead," "Chiricahua," and "Mammoth" respectively (DOBZHANSKY and STURTEVANT 1928). In the offspring of a female collected on Kingston Peak there was found a single larva showing a fifth, and previously unknown, arrangement in the third chromosome. The culture was lost before the new arrangement could be studied in detail. Table 1 shows the frequencies of the four arrangements in the eleven populations; each observed frequency is accompanied by its probable error. The total numbers of the chromosomes examined are given in the rightmost column.

An examination of table 1 shows that the Arrowhead, Chiricahua, and Standard arrangements are present in every population, Arrowhead being much the commonest. The Mammoth arrangement was found in only two localities, a single chromosome in each case. Its frequency is therefore negligible. Nevertheless, some of the populations are significantly different

from others in the relative frequency of the different arrangements. Only three localities, namely Panamint, Awavaz, and Charleston, are inhabited by populations that seem to be identical in this respect. The Coso population is slightly but significantly different from the preceding three. The remaining six populations differ significantly from each other as well as from the four mentioned above, although the sample from Mt. Whitney is too small to be much relied upon.

TABLE I
Frequencies (in percent) of the four gene arrangements encountered in the third chromosome.

MOUNTAIN RANGE	ARROWHEAD	CHIRICAHUA	STANDARD	MAM-MOTH	CHROMOSOMES TESTED
Lida (Mt. Magruder)	76.80±1.80	6.00±1.01	16.80±1.59	0.40	250
Mt. Whitney	69.57±4.57	8.70±2.73	21.73±4.10	—	46
Coso	72.27±1.89	14.45±1.48	13.28±1.43	—	256
Cottonwood	51.20±2.13	9.60±1.25	38.80±2.08	0.40	250
Grapevine (Funeral)	50.86±2.23	18.70±1.73	30.43±2.04	—	230
Panamint (Telescope)	67.41±2.11	18.75±1.75	13.83±1.56	—	224
Awavaz	62.20±3.61	19.51±2.95	18.29±2.88	—	82
Kingston	64.08±2.25	5.34±1.06	30.58±2.17	—	206
Charleston	68.75±1.96	19.14±1.66	12.11±1.38	—	256
Sheep Range	88.11±1.53	1.98±0.64	9.90±1.42	—	202
Providence	82.00±1.50	10.00±1.17	8.00±1.06	—	300

A more detailed analysis of the data presented in table I brings to light some additional facts. It must be borne in mind that each of the three arrangements commonly found in the geographical region now under study is encountered also beyond its confines (DOBZHANSKY and STURTEVANT 1928). The Arrowhead arrangement is present throughout the distribution area of the species, except in southern Mexico. The populations inhabiting New Mexico, southern Colorado, northern Arizona, and most of southern Utah show a hundred percent frequency of Arrowhead; westward and north-westward from there the frequency of Arrowhead declines, and reaches a minimum on the Pacific Coast. Standard shows the opposite regularity: its frequency is highest on the Pacific Coast, and decreases as one proceeds eastward, reaching zero just east of the Death Valley region. Finally, Chiricahua is a southern type, very common in Mexico, and the northernmost locality where it has been recorded is in the Toyabe Range, Nevada, lying less than a hundred miles north of Lida. Are, then, the differences observed between the relatively closely adjacent localities in the region studied by us merely an expression of the general geographic trends in the distributions of the gene arrangements? If that were so, one might expect the frequency of Standard to be greatest in the western or

north-western localities, and to decrease as one proceeds eastward. A similar gradient in the direction south-north would be expected for Chiricahua, and an east-west gradient for Arrowhead. Indeed, gradients of this kind have been observed by many students of geographical variation in all sorts of animals and plants (for example, SUMNER 1929).

An examination of table 1 in conjunction with figure 1 reveals however no definite gradients. The greatest frequency of Standard obtains in the centrally located Cottonwood mountains, and decreases westward as well as eastward. Chiricahua is more frequent in the center (Awavaz, Panamint, Charleston) than it is in the south (Providence). Arrowhead is most frequent on the fringes of our region, and least frequent in the center. Not only is there no regularity if our region is treated as a part of the general species area, but there are no definite trends within the region itself. Mountain ranges that lie far apart may be more similar than adjacent ones. Thus, Charleston and Awavaz are alike, while Kingston which is located almost exactly half way between the two is distinctly different from either. The frequency of the Chiricahua arrangement is very low on Kingston Peak and Sheep Range, and high on Charleston which lies between them. Panamint is similar to the rather remote Awavaz and Charleston mountains, and very different from the Cottonwood mountains which represent merely a northern extension of the Panamint. Sheep Range and Providence are more similar to each other and to the remote Lida than to the intervening Charleston and Kingston Peaks. In short, the variation seems to be random. The possible significance of this fact is discussed below.

The data on the gene arrangement in the third chromosome were collected in such a way that in every case two chromosomes present in a given individual were examined. This permits us to study the relative frequencies in natural populations of individuals homozygous and heterozygous for the different gene arrangements. Let the gametic frequencies of the Arrowhead, Chiricahua, and Standard arrangements be a , c , and s respectively ($a+c+s=1$). If mating is random, and the viabilities of the structural homo- and heterozygotes are alike, the expected frequencies of the different types are as follows:

Homozygous Arrowhead— a^2

Homozygous Chiricahua— c^2

Homozygous Standard— s^2

Heterozygous Arrowhead/Chiricahua— $2ac$

Heterozygous Arrowhead/Standard— $2as$

Heterozygous Chiricahua/Standard— $2cs$

A comparison of the observed and expected frequencies is presented in table 2. In general, the two sets of values agree very well, attesting that

TABLE 2

The observed and expected frequencies of the inversion homozygotes and heterozygotes in various populations.

LOCALITY	HOMOZYGOTES			HETEROZYGOTES		
	ARROWHEAD	CHIRICAHUA	STANDARD	ARROWHEAD	ARROWHEAD	CHIRICAHUA
				CHIRICAHUA	STANDARD	STANDARD
Lida	Obs. 74	—	6	14	29	1
	Exp. 73.75	0.45	3.5	11.5	32.2	2.5
Coso	Obs. 70	2	6	28	17	5
	Exp. 66.85	2.7	2.25	26.7	24.6	5.0
Cottonwood	Obs. 34	2	21	13	47	7
	Exp. 32.75	1.5	18.9	12.3	49.6	9.3
Grapevine	Obs. 27	3	12	27	36	10
	Exp. 29.75	4.0	10.65	21.9	35.5	13.1
Panamint	Obs. 49	3	3	32	21	4
	Exp. 50.8	3.9	2.1	28.2	20.9	5.8
Kingston	Obs. 45	1	12	6	36	3
	Exp. 42.3	0.3	9.6	7.1	40.4	3.4
Charleston	Obs. 62	7	5	33	19	2
	Exp. 60.5	4.7	1.9	33.7	21.3	5.9
Sheep Range	Obs. 77	—	—	4	20	—
	Exp. 78.4	0.04	0.99	3.5	17.6	0.04
Providence	Obs. 102	3	2	22	20	1
	Exp. 100.9	1.5	1.0	24.6	19.7	2.4

the above assumptions of the randomness of mating and equal viability are correct. A more detailed examination of table 2 shows however that the observed figures for homozygotes are somewhat more frequently higher than lower than the expected ones, and the reverse is true for the heterozygotes. The differences are in no case statistically significant. This small discrepancy, if real, may have two explanations. First of all, a small fraction of the heterozygotes might have been misclassified as homozygotes (see above). Secondly, the fly samples from each locality were collected in a number of trap bottles placed at some distance from each other. If the flies spend their life in the immediate vicinity of the place where they were born, the mating may not be absolutely random, and a certain amount of inbreeding may be involved. This latter possibility is theoretically very interesting, but no conclusions can be drawn from the data now available. What is demonstrated is merely that the natural populations are not segregated into non-interbreeding sections each of which has a given gene arrangement.

THE "SEX-RATIO"

Certain males of *D. pseudoobscura* produce, when crossed to females of any genetic constitution, mostly or only daughters and few or no sons.

This peculiar "sex-ratio" condition is known to be inherited through the X chromosome, and to be associated with an inversion in the right limb of the latter, the association apparently being invariable. The "sex-ratio" is often encountered in wild populations of *D. pseudoobscura*, but the frequency is higher in the southern than in the northern part of the specific area (STURTEVANT and DOBZHANSKY 1936b). It proved to be rather common in most of the populations from the Death Valley region.

To detect the presence or absence of the "sex-ratio," wild males or single sons of wild females were crossed in individual cultures to two or three *or pr* females. In the F₁ generation some of the cultures produced few or no sons, indicating that the father carried the "sex-ratio" in its X chromosome. Complete counts are unnecessary to distinguish the "sex-ratio" from the normal cultures, because in the former only very few or no males are found. Since the salivary gland chromosomes of the F₁ larvae were studied in order to determine the gene arrangement in the third and the other chromosomes, some "sex-ratio" cultures were in fact detected before any adult flies appeared in them. Nevertheless, no special attention was paid to the presence or absence of the "sex-ratio" inversion in the right limb of the X chromosome in these cultures, so that the statistical data of the frequency of the "sex-ratio" presented in table 3 are based on the genetical and not on cytological determinations.

TABLE 3
Frequency (in percent) of the "sex-ratio" condition in the X chromosome.

LOCALITY	ELEVATION (FEET)	DATE OF COLLECTING	SEX-RATIO	CHROMOSOMES TESTED
Awavaz	5000	May 22	23.08	26
Providence	5000?	May 7, 8	16.06	137
Sheep Range	6000	June 5	11.57	121
Kingston	4800	May 21	11.38	123
Cottonwood	7800	June 23, 24	10.66	122
Lida	8000	June 15, 17	9.09	66
Grapevine	7500	June 22	8.33	72
Panamint	8300	May 20	8.09	136
Charleston	8200	June 4	6.72	119
Coso	6500	July 14, 15	4.70	149

From 4.7 percent (in Coso) to 23.1 percent (in Awavaz mountains) of the X chromosomes were found to carry the "sex-ratio." Table 3 shows also the approximate elevation above sea level of the localities in which the collecting was done, and the date of collecting. There seems to be a weak negative correlation between the elevation and the frequency of the "sex-ratio"; the existence of such a correlation has been suspected on the basis of another set of data (STURTEVANT and DOBZHANSKY 1936b).

Taken at their face value, the figures in table 3 suggest that the frequency of the "sex-ratio" in localities of equal elevation diminishes as the season advances, but the reality of this relationship is certainly far from established.

CHROMOSOMAL VARIATION IN RACE B

All of the above data concern race A of *D. pseudoobscura*. Race B of the same species has been found only in two out of the eleven localities shown in figure 1, namely on Mt. Whitney and in Coso mountains. On Mt. Whitney more than three times as many race B as race A flies came into the traps, while in Coso 3 race B individuals were encountered together with 149 of race A. The geographical distribution of race B lies west and north-west from the Death Valley region, Coso mountains being in fact the extreme south-eastern locality where this race has been thus far encountered.

The gene arrangement was studied in 74 race B third chromosomes from Mt. Whitney and in 6 chromosomes from Coso. On Mt. Whitney 15 chromosomes, or 20.3 percent, showed the Standard, and 1, or 1.35 percent, the Klamath arrangement. The remaining 58, or 78.4 percent, of the chromosomes had a gene arrangement which has not been encountered previously. This new arrangement, designated as "Whitney," differs in a single inversion from Klamath and in two inversions from the Standard (Klamath and Standard differ in a single inversion). The distal end of the Whitney inversion lies proximally from the distal end of the Klamath one, and the proximal end of Whitney lies nearer to the base of the chromosome (section 69A) than in Klamath. The gene arrangement in Whitney is therefore on the whole more similar to that in the Standard than to that in Klamath. Out of the six chromosomes from Coso, three had the Whitney and three the Standard arrangement.

The discovery of a new arrangement in the third chromosome of *D. pseudoobscura* (the eighteenth in the species) is in itself not surprising. What is more unexpected is that the new arrangement has been found to be so frequent on Mt. Whitney, on the eastern slope of the Sierra Nevada, while it has not been encountered at all among race B individuals from the Sequoia National Park (Giant Forest and Lodgepole Camp), from which samples of flies had been previously studied (DOBZHANSKY and STURTEVANT 1938). The Giant Forest and Lodgepole Camp localities lie less than a hundred miles from Mt. Whitney, on the eastern slope of the Sierra Nevada. On the contrary, two other gene arrangements known from Sequoia Park have not been found on Mt. Whitney. This suggests that populations of *D. pseudoobscura* are very local, and that few migrants pass from one locality to the other. One must note however that the Giant Forest and Mt. Whitney localities are separated by the alpine desert of

the highest part of the Sierra Nevada, which may constitute a natural barrier for the distribution of *D. pseudoobscura*.

DISCUSSION

It has been shown above that three distinct gene arrangements in the third chromosome, namely Standard, Arrowhead, and Chiricahua, are encountered in every one of the eleven populations studied. The relative frequencies of these arrangements, however, vary within rather wide limits; there is no geographical trend or regularity in these variations, so that populations from adjacent localities may be more different from each other than populations from remote ones. In order to evaluate properly the significance of these observations one must recall certain other facts discussed in detail by DOBZHANSKY and STURTEVANT (1938). The gene arrangements known in the third chromosome of *D. pseudoobscura* are members of a single phylogenetic series. Some arrangements differ from others in a single inversion, while others are related only through a chain of discrete intermediate forms, each link in the chain representing a single inversion step. Thus, Arrowhead and Standard differ in a single inversion, while it takes three inversions to pass from Standard to Chiricahua, four to derive Chiricahua from Arrowhead, three to derive Mammoth from Standard, and two to get Mammoth from Chiricahua, or vice versa. It is significant that in the mountains of the Death Valley region we find only the gene arrangements just named, and do not find the intermediates between them (which, however, are encountered in other, more or less remote, geographical localities). This means that the variety of the gene arrangements now observed in the Death Valley region has arisen elsewhere, or at any rate that its origin has taken place at a certain more or less remote time. Only Standard and Arrowhead may be conceived to transform into each other by "mutation," although we not only lack evidence that they do so regularly, but even have reasons to doubt that this is the case.

What are, then, the driving causes of the historical process which has resulted in the differentiation of the populations inhabiting separate mountain ranges? Since the differences observed are merely quantitative, and since, taken as a whole, the Death Valley populations are intermediate between populations living in the surrounding territories, the possibility of migration as one of the causes must be considered. Arrowhead is more frequent to the east and less frequent to the west of the Death Valley region than anywhere in that region itself. For Standard the relations are the reverse of those for Arrowhead, while Chiricahua is most frequent to the south of Death Valley. If the rate of exchange of individuals between populations inhabiting parts of the distribution area of the species is great

enough, a chain of populations intermediate between the extremes will result. By "great enough" we mean a migration rate sufficient to outweigh other causes leading toward diversification of local populations. The populations inhabiting the Death Valley region form, however, no geographical chains linking together the populations of the surrounding country. We have seen that the characteristics of a population inhabiting a given mountain range are independent of those of the populations in the neighboring mountains. Each population seems to be sufficiently isolated from the others, and migration, if it occurs at all, is not a factor of paramount importance in determining the characteristics of a colony.

The possibility that the gene arrangement may not be indifferent for the viability of its carrier, and that selection has caused one or the other arrangement to be frequent on a given mountain range, must be considered. The localities where collecting was done differ in altitude, climate, flora, and other conditions. The frequency of "sex-ratio" shows indeed a suggestive correlation with the altitude of the locality. The "sex-ratio" cannot, however, be likened to the variations in the gene arrangement in the third chromosome; while the former produces an easily discernible effect, namely unisexual progenies, the latter do not seem to be correlated with any physiological or morphological characteristics of their carriers. There is also no trace of a correlation between the frequency of any gene arrangement in a given locality and any peculiarities of the latter. Since, furthermore, every one of the three gene arrangements is present in every locality, and presumably has been indigenous there for countless generations, the supposition that these chromosome structures are subject to selection is extremely improbable, although, by the very nature of things, it cannot be completely excluded.

By far the most probable explanation of the observed differences between populations of the separate mountain ranges is that the frequency of a gene or a chromosome structure is subject to random fluctuations. WRIGHT (1931, and other works) has shown that, theoretically, such fluctuations must occur in populations whose size is not infinitely large, and that the smaller the population the greater is the amplitude of the fluctuations in a given time interval. In a species segregated in numerous colonies this process will sooner or later lead to a differentiation, provided only that its intercolonial migration rate is not great enough to cancel the effects of the fluctuations. The mountain ranges of the Death Valley region, isolated from each other by the intervening deserts, furnish a set of conditions that might favor such a differentiation. Suppose, for example, that this region was inhabited originally by a homogeneous population in which the frequencies of the three commonest gene arrangements were like those now found in Panamint, Awavaz, and Charleston mountains

(fig. 1 and table 1). A segregation of this population into colonies restricted each to an isolated mountain forest might have resulted in the course of time in a diversification. In some populations, like those inhabiting the three mountain ranges just named, the original frequencies have been retained. Other populations have deviated to a smaller or greater extent from the original condition. But there is not, nor is there expected to be, any geographical trend or regularity in those fluctuations. Adjacent mountains are as likely to retain as they are to lose the similarity in the composition of their populations.

The factor that is decisive for an evaluation of the above hypothesis is how large is the effective size of the breeding population in the colonies of the flies inhabiting each mountain range? The greater the size, the shorter the time interval during which this differentiation may be supposed to have taken place, the less probable is the hypothesis, and vice versa. We hope to be able to present some information bearing on this problem at a later date.

SUMMARY

1. *Drosophila pseudoobscura* inhabits mountain forests in the Death Valley region, but not the intervening deserts. Samples of the fly populations were collected in eleven localities (fig. 1).

2. Three different gene arrangements in the third chromosome are present in every population studied. The difference between these arrangements is due to inversion of chromosome sections.

3. Inversion heterozygotes and homozygotes are present in every population in theoretically predictable proportions (table 2).

4. The relative frequency of each arrangement varies from locality to locality (table 1). Only three out of the eleven localities are inhabited by populations that seem to be identical with respect to the relative frequencies of the gene arrangements.

5. Populations inhabiting adjacent localities are no more likely to be similar than populations from remote ones.

6. It is concluded that the rate of migration of flies between localities is small. The genetic compositions of the populations inhabiting different localities may drift apart in the course of time.

7. A certain proportion of the X chromosomes carry the "sex-ratio" condition (table 3). There is a slight correlation between the frequency of the "sex-ratio" and the elevation of the locality above sea level.

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