GENETICS OF NATURAL POPULATIONS. XV. RATE OF DIFFUSION OF A MUTANT GENE THROUGH A POPULATION OF *DROSOPHILA PSEUDOOBSCURA*

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INTRODUCTION

EXPERIMENTS on dispersion rates in *Drosophila pseudoobscura* have been described by DOBZHANSKY and WRIGHT (1943). These experiments, carried out during the summers of 1941 and 1942 on Mount San Jacinto, California, consisted in releasing suitably marked flies at a certain point on an experimental field, and then for several days recording the numbers of the flies that visited banana traps placed at various distances from the point of the release. The data so obtained permitted estimation of (a) average distances travelled by the flies on days with different temperatures, (b) absolute densities of wild *Drosophila pseudoobscura* on the field at the time of the experiment, and (c) rates of decline of the numbers of marked flies with time.

The drawback of the above experiments is that they describe the speed of dispersion of the released flies and the status of the wild population during only one season of the year. It should be noted that the rate of diffusion of the flies is greatly increased by increasing temperatures, and that in the mountain forests of California the fly populations reach maximal densities in midsummer.

The conditions prevailing during the seasons when the environment is less favorable to the flies remained unknown. To a geneticist the conditions during the latter seasons are most interesting. A new experiment was consequently performed in 1945–1946 at Mather, in the Sierra Nevada of California. This experiment has served in part to recheck the conclusions drawn from the older ones, and in part to furnish data of a new kind. The present article reports the outcome of this new experiment.

LOCATION, MATERIAL, AND METHODS

The experimental work has been done near Mather, at elevation of about 4600 feet, on the western slope of the Sierra Nevada of California. A description of this locality has been published by CLAUSEN, KECK, and HIESEY (1940). In brief, the vegetation belongs to a typical Transition Zone association (yellow pine, incense cedar, Kellogg oak, etc.). Winters are cold with much snowfall; summers mild and very dry. The flies are most abundant in late summer (August).

[1] Observational and experimental data by TH. DOBZHANSKY, mathematical analysis by SEWALL WRIGHT.

As in the older experiments, the third chromosome recessive gene orange has been made use of for marking the flies released at Mather. Orange-eyed flies are easily distinguishable from wild ones in the field. The flies released were F_1 hybrids of two orange strains, one extracted from the population of Keen Camp and the other from that of Andreas Canyon on Mount San Jacinto, California. By using the F_1 hybrids of these strains advantage was taken of the heterosis accruing from crossing two distantly related lines each of which has been somewhat inbred by being kept for several years in small mass cultures in the laboratory. The hybrids were raised in regular laboratory bottles, care being taken to avoid overpopulation. The fitness of the released flies is attested by the fact that they have reproduced in nature in competition with wild flies (see below, cf. also DOBZHANSKY and WRIGHT 1943). Their progeny, though diminished in numbers, has survived the winter of 1945–1946 and was present on the experimental field in summer 1946.

The techniques of trapping and recording the flies have been described by DOBZHANSKY and WRIGHT (1943) and need not be repeated here. To test the flies collected in nature for heterozygosis for the mutant gene orange, a method proposed by PROFESSOR W. P. SPENCER was employed. Tests of wild males were made by crossing individuals to laboratory females homozygous for orange. The crosses were made in "creamers" (small glass vessels) with a small amount of agar-containing culture medium. When small larvae appeared, pieces of "Kleenex" paper tissue soaked in a rich yeast suspension were placed in each "creamer." In testing of wild females from nature these were first placed singly in "creamers" and allowed to produce offspring. A sing'e son (or a single daughter) of each female was then crossed, in a fresh "creamer," to homozygous orange flies. The progeny of the crosses was inspected for presence or absence of orange-eyed flies. If the wild fly tested is homozygous nonorange, its offspring have wild-type eyes. If it is an orange heterozygote, about half of the flies in the test generation have orange eyes.

DROSOPHILA SPECIES IN THE MATHER POPULATION

The three commonest species of Drosophila in the midaltitudinal belt of the Sierra Nevada are *D. pseudoobscura*, *D. persimilis*, and *D. azteca*. These species are indistinguishable to the naked eye, and the first and the second of them are also indistinguishable under a binocular microscope.

Samples of wild flies from all collecting stations in the vicinity of Mather were examined under a microscope, and the male flies classified into *D. azteca* on one hand and a mixture of *D. pseudoobscura* and *D. persimilis* on the other. The females were not classified since they are not as easily distinguishable as the males are. The resulting data are shown in table 1.

D. azteca becomes more and more frequent relative to the other two species as the season progresses, starting with about 20 percent early in June and reaching about 50 percent in late August. It may be noted in this connection that *D. azteca* inhabits chiefly the Transition and the Upper Sonoran life zones of the Sierra Nevada, and that Mather is not far from the upper altitudinal limit of its range.

Two methods of discrimination were used to distinguish *D. pseudoobscura* and *D. persimilis* in our samples. Wild females were allowed to produce offspring, and the salivary glands of the resulting larvae were examined for chromosomes. Chromosomes of the two species differ in the gene arrangement in some sections (TAN 1935). This is the cytological method. Wild males, or sons of wild females, were outcrossed to orange *D. pseudoobscura* females. If the wild male belongs to the species *D. pseudoobscura* the sons are normal, while

TABLE 1

Number of flies of different species and sexes trapped in different seasons.

DATE	♀♀	*pseudoobscura* ♂ +*persimilis* ♂	*azteca* ♂	PERCENT *azteca*
July 8–15, 1945	425	350	197	36
August 10, 1945	—	102	65	39
August 22–September 5, 1945	611	562	572	50
June 4–15, 1946	1230	589	129	18
June 26–30, 1946	201	141	60	30
August 9–10, 1946	292	124	103	45

TABLE 2

Relative frequency of D. pseudoobscura and D. persimilis.

DATE	METHOD	*pseudo-obscura*	*persimilis*	PERCENT *pseudo-obscura*
July 8–15, 1945	Cytological	97	58	63
August 22–September 5, 1945	Genetical	267	170	61
September 5, 1945	Cytological	57	49	54
June 4–15, 1946	Genetical	1275	666	66
June 4–15, 1946	Cytological	89	35	73
August 9–10, 1946	Cytological	79	33	71
Total		1864	1011	64.8

sons of *D. persimilis* males are sterile interspecific hybrids. The sterile hybrids can easily be distinguished from normal males under a high dry power of a compound microscope in unstained squash preparations of freshly dissected testes. This is the genetic method. Table 2 reports the results.

Roughly 65 percent of the total population of *D. pseudoobscura* and *D. persimilis* belong to the former species. The proportions in the different samples are not quite uniform ($\chi^2 = 13.45$, probability of chance occurrence for five degrees of freedom about 0.02), but there is no pronounced seasonal change. The figure 65 percent may, then, be taken as characteristic for the locality.

CONTROL EXPERIMENT

Although homozygous orange-eyed flies have never been found in natural populations, the recessive gene orange is the commonest among striking visible mutant genes carried in concealed condition in both *D. pseudoobscura* and *D. persimilis*. Strains of both species descended from single females collected in nature have repeatedly proved to be heterozygous for orange. Unfortunately, no complete record of these occurrences has been kept. It can be stated, however, that orange heterozygotes occur in different parts of the geographic distribution areas of both species.

Since our main experiment consisted in liberating orange-eyed flies in the Mather locality and in studying the dispersal of the orange homo- and heterozygotes, it was evidently necessary to know how frequent orange heterozygotes were in this locality before the start of the experiment. Samples of wild flies were accordingly collected on the experimental field-to-be between July 8 and 15, 1945. A part of these wild flies, 385 in all, was tested by crossing them to homozygous orange flies. In 384 of these tests the offspring consisted of wild type flies, and in one test both wild type and orange-eyed flies appeared. Since each fly carried two third chromosomes, a total of 770 wild third chromosomes were thus tested, and one of them was found to carry orange.

At the time when these control crosses were being made it was not known that *D. persimilis* as well as *D. pseudoobscura*, two morphologically indistinguishable species, occur together in the Mather population. It is, consequently, known neither how many individuals of each species there were among the 385 specimens tested for orange, nor to which species the single orange heterozygote belonged. It has been found later that approximately 65 percent of the obscura-like flies found in the Mather locality are *D. pseudoobscura* and 35 percent are *D. persimilis* (see table 2). The most probable estimate is, then, that among the 770 tested third chromosomes about 500 belonged to *D. pseudoobscura* and 270 to *D. persimilis*.

In the summer of 1946, more than 750 individuals of *D. persimilis* were tested by outcrossing to orange *D. pseudoobscura* flies. None of them proved to be orange heterozygotes. This shows that the *D. persimilis* population at Mather contains few or no orange mutants. Assuming, then, that the orange heterozygote found in 1945 was a *D. pseudoobscura*, it is probable that 1 out of 493 *D. pseudoobscura* third chromosomes, or about 0.2 percent, contained the orange mutant gene before the start of the experiment. This value, 0.2 percent, will be taken as the "control value" for the frequency of orange in the Mather population of *D. pseudoobscura*.

RELEASE OF ORANGE-EYED FLIES

Between 6.25 and 6.50 P.M. on July 16, 1945, a total of 3840 orange-eyed *D. pseudoobscura* flies were liberated in a grove of old oak trees (*Quercus Kelloggii*) near Mather. On six following evenings (July 17–22), banana traps were exposed and the numbers of orange and nonorange flies visiting them were recorded. The traps were arranged in a single file, north and south from the point of the release, at distances of 20 meters from each other.

The recorded numbers of the orange and nonorange flies found in each trap on each of the six days are shown in table 3. Each entry in this table consists of two figures separated by a dash. The first figure indicates the number of orange and the second that of wild (nonorange) flies. Thus, the entry "33–21" for trap No. 3 on the third day of collecting (July 19th) means that 33 orange and 21 nonorange flies visited this trap on that day. The wild flies here recorded are, of course, a mixture of the three species, *D. pseudoobscura*, *D. persimilis*, and *D. azteca*.

Trap No. 0 was placed at the point of release, at the center of the experimental field. Traps Nos. 1–30 stood north and traps Nos. 31–60 south of the center (see table 3.) Therefore, the distances from trap No. 0 to No. 30, and from No. 0 to No. 60, were 600 meters each, and from No. 30 to No. 60 a total of 1200 meters.

DISTRIBUTION OF WILD FLIES

Inspection of table 3 shows that the wild flies were distributed sufficiently uniformly over the experimental field so that at least a single fly was recorded in each of the 61 trap locations on at least one day. Much greater numbers were, however, caught in some traps than in others. On considering the days separately, wild flies were absent from only 35 of the 351 trap records. Data on the total numbers of flies caught on successive days, and on average numbers found per trap, are given in table 4. These data are compared in table 5 with the analogous data from the four experiments (numbered I to IV) made on Mount San Jacinto and described by DOBZHANSKY and WRIGHT (1943).

It appears from table 4 that the mean number of wild flies caught per trap at Mather rose almost threefold during the six days, a change which might be due either to actual increase in the density of the population, to increased activity, or merely to more favorable temperature at the time of trapping on the later days. The standard deviation of the numbers per trap showed a closely similar increase. If the variations were due merely to accidents of sampling the distribution of numbers per trap should be of the Poisson type with the variance equal to the mean. As shown in the last column, the variance was much greater than can be accounted for as accidents of sampling although, as shown in table 5, the ratio $\overline{\sigma^2/m}$ was less than in any of the experiments on Mount San Jacinto.

That the local heterogeneity, indicated by high $\overline{\sigma^2/m}$ was due to conditions that had some degree of persistence is shown by the correlation between numbers caught on different days in the same trap. These correlations are given in table 6 according to the interval and are compared with averages from the San Jacinto data. The grand average for the 15 correlations in the Mather data is $+0.518$, very similar to the average of $+0.545$ based on 19 correlations from San Jacinto. The average correlation at intervals of one or two days is in both cases somewhat greater than at longer intervals indicating that the heterogeneity was not due entirely to persistent local conditions.

It can be concluded that wild flies occur in all parts of the experimental field on which traps were exposed, but that some neighborhoods are relatively more

TABLE 3

Numbers of orange and wild flies in different traps.

TRAP NO.	1 DAY	2 DAYS	3 DAYS	4 DAYS	5 DAYS	6 DAYS
30	—	—	0–1	0–0	0–0	1–2
29	—	—	1–0	0–0	1–0	2–5
28	—	—	0–1	0–5	0–13	0–10
27	—	—	0–2	1–2	0–1	1–3
26	—	—	2–5	1–8	1–4	0–3
25	0–0	0–1	0–0	0–0	0–0	0–0
24	0–2	1–2	0–1	0–1	3–2	1–3
23	0–8	0–1	0–10	2–8	1–6	1–7
22	0–1	0–0	0–7	0–2	1–3	1–8
21	0–2	0–2	0–1	1–9	0–1	0–12
20	1–0	0–1	0–2	0–2	0–3	1–1
19	0–0	0–0	0–0	0–1	1–0	4–5
18	0–3	0–0	0–4	0–2	0–3	1–4
17	0–4	0–5	1–9	0–5	2–2	0–3
16	1–4	0–5	1–11	2–6	3–6	0–7
15	0–1	0–5	0–5	1–2	0–2	0–7
14	0–0	2–1	1–0	1–0	1–1	1–2
13	0–2	0–2	2–1	1–5	0–1	1–4
12	0–0	0–0	1–2	1–2	2–0	1–2
11	1–0	3–2	5–2	3–0	1–5	5–7
10	1–2	3–2	2–3	2–9	3–6	5–7
9	1–0	0–4	13–4	4–5	6–5	7–5
8	0–0	7–5	6–2	2–4	2–5	6–7
7	0–2	2–2	4–6	9–5	8–8	7–7
6	3–2	16–8	18–13	12–7	34–21	19–38
5	5–3	6–2	13–9	12–10	12–12	6–12
4	5–2	8–3	26–9	21–10	26–16	25–33
3	28–11	26–12	33–21	26–20	16–17	17–38
2	23–12	39–9	46–14	23–12	18–17	12–36
1	26–2	25–3	22–11	18–2	20–10	16–13
0	129–7	78–4	92–4	36–6	47–12	36–20
31	29–4	29–5	27–5	25–5	18–5	11–6
32	33–6	44–7	53–9	37–12	13–6	57–43
33	39–9	25–5	47–9	49–16	21–14	13–16
34	7–1	19–0	22–1	25–9	11–4	11–10
35	3–3	3–2	11–1	6–7	7–2	11–7
36	6–1	6–4	14–5	8–4	3–3	6–8
37	5–0	7–1	3–1	6–3	3–2	15–16
38	2–17	2–1	6–1	6–2	4–2	3–2
39	0–1	2–5	8–8	7–12	2–5	9–7
40	0–1	0–3	2–1	0–4	0–0	6–4
41	1–2	0–8	1–3	2–3	2–5	0–6
42	1–3	2–0	3–10	2–3	2–3	3–23
43	0–1	1–1	2–1	1–0	1–1	2–11
44	0–2	1–11	1–9	0–5	2–10	2–10
45	0–4	1–4	3–3	1–7	2–3	5–28
46	0–7	1–5	1–3	1–9	0–5	2–5
47	0–3	1–16	0–11	1–9	0–5	0–15

TABLE 3—(*continued*)

TRAP NO.	1 DAY	2 DAYS	3 DAYS	4 DAYS	5 DAYS	6 DAYS
48	0–4	0–8	2–7	1–6	3–4	3–11
49	1–0	0–4	2–5	0–2	1–3	2–3
50	0–3	0–2	2–3	1–6	0–9	0–5
51	0–0	0–1	0–6	0–5	1–7	0–8
52	0–4	0–3	0–8	0–6	2–4	2–4
53	0–6	0–4	3–20	0–7	1–24	0–14
54	0–5	0–2	1–11	0–11	0–9	5–10
55	0–24	0–10	1–37	1–9.	1–18	0–15
56	—	0–0	0–5	1–18	1–10	0–10
57	—	0–0	0–4	1–3	1–1.	1–4
58	—	0–1	0–2	0–6	0–7	0–2
59	—	0–4	0–8	0–14	0–9	1–5
60	—	0–3	0–6	0–5	0–4	0–5
Total	351–181	360–201	504–363	361–358	311–366	347–624
t° (F)	—	70°	71°	72°	72°	72°

TABLE 4

Statistics on numbers of the wild flies caught on successive days at Mather. The temperature (F) at time of collection, number of traps set, number of wild flies caught, the mean number (m) per trap, the standard deviation ($\bar{\sigma}$) of the number per trap, and the ratio σ^2/m are shown.

DAY	TEMP.	TRAPS	WILD FLIES	m	σ	σ^2/m
1	—	51	181	3.5	4.5	5.8
2	70°	56	201	3.6	3.4	3.2
3	71°	61	363	6.0	6.2	6.4
4	72°	61	358	5.9	4.5	3.4
5	72°	61	366	6.0	5.6	5.2
6	72°	61	624	10.2	9.9	9.5

TABLE 5

Comparison of data on numbers of wild flies caught at Mather and in four experiments on Mount San Jacinto. $\bar{m}$ is the unweighted average of the daily averages of the numbers of wild flies caught per trap, $\bar{\sigma}$ is the similar average for the standard deviation of the numbers and $\overline{\sigma^2/m}$ is the similar average for the ratio, σ^2/m.

EXPERIMENT	DAYS	$\bar{m}$	$\bar{\sigma}$	$\overline{\sigma^2/m}$
Mather	6	5.9	5.7	5.6
San. Jacinto I	9	5.9	7.4	9.7
San. Jacinto II	7	29.3	17.5	10.6
San. Jacinto III	7	21.2	17.5	15.0
San. Jacinto IV	5	21.7	11.3	5.9

attractive to the flies than others. Estimates of the absolute densities of wild flies at Mather are given below (table 10).

DISTRIBUTION OF RELEASED FLIES

Table 3 shows that the released orange-eyed flies were recaptured mainly in the vicinity of the point where they were liberated. About 88 percent of the orange flies found one day after the release at Mather were found in the seven traps that were 60 meters or less from the point of release, although one orange fly was caught 400 meters to the north and another 380 meters to the south. By the sixth day, the proportion of orange flies in the central seven traps had fallen to 47 percent and one was caught 600 meters to the north (at the end of the line of traps) and one 580 meters to the south. It should be said that the region of release was one that was somewhat above the average in attractiveness for *D. pseudoobscura.* This is indicated by the fact that 24 percent of the wild flies were caught in the central seven traps during the six days, although these constituted only 12 percent of the traps set during the period.

TABLE 6

Correlations between numbers of wild flies caught in the same trap locality on different days. The results for every pair of days were calculated for the Mather data. Only the correlations between the first and subsequent days were calculated for the four experiments on Mount San Jacinto.

LOCALITY		INTERVAL									
		1 DAY		2 DAYS		3 DAYS		4 DAYS		5 DAYS	
		DAYS	r	DAYS	r	DAYS	r	DAYS	r	DAYS	r
Mather		1–2	+0.377	1–3	+0.678	1–4	+0.459	1–5	+0.482	1–6	+0.308
		2–3	+0.562	2–4	+0.490	2–5	+0.457	2–6	+0.449		
		3–4	+0.516	3–5	+0.751	3–6	+0.462				
		4–5	+0.577	4–6	+0.591						
		5–6	+0.604								
	Av.	(5)	+0.527	(4)	+0.628	(3)	+0.459	(2)	+0.466	(1)	+0.308
San Jacinto	Av.	(4)	+0.645	(4)	+0.616	(4)	+0.598	(3)	+0.488	(4)	+0.381
Total	Av.	(9)	+0.579	(8)	+0.622	(7)	+0.538	(5)	+0.479	(5)	+0.366

The orange flies dispersed equally to the north and south. The mean location of capture (m) was never more than about 20 meters from the point of release and was north of the latter on some days, south on others (table 7) the unweighted average of the six means was only 0.8 m. south of the point of release although the total range reached on the sixth day was 1180 m.

The dispersion of the released flies on the experimental field can be described in terms of the variance (σ^2) of the distance at which these flies are found from the point of release on successive days of the experiment (DOBZHANSKY and WRIGHT 1943). If the flies scatter over the field at random, and equally fast on all days, variance should increase in proportion to the time elapsed since the release of the orange flies. The variance (in meters^2) observed on successive days is as follows:

1 day —4051	4 days—15444
2 days—7252	5 days—23378
3 days—14202	6 days—28377

A comparison of the standard deviations (σ) in the Mather experiments with those found in the four experiments performed on Mount San Jacinto is shown in table 7. The Mather figures are about equal to those in experiments II, III, and IV on San Jacinto performed at similar temperatures. The standard deviations are much lower in experiment I on San Jacinto during which the temperatures were much lower than in all other experiments.

TABLE 7

Comparison of the Mather experiments with those on San Jacinto with respect to standard deviation in meters (σ) and kurtosis (Ku) of released flies along the lines of traps. The number (n) of orange flies recaptured on each day and the center of location in meters north (+), or south (−) of the point of release (m) are also given for the Mather data.

	MATHER				SAN JACINTO							
					I		II		III		IV	
DAY	n	m	σ	Ku	σ	Ku	σ	Ku	σ	Ku	σ	Ku
1	351	− 5.6	64	13.0	39	9.8	59	7.6	58	10.4	68	8.3
2	360	+ 1.2	85	7.7	57	5.7	92	5.0	94	4.4	95	5.9
3	504	− 4.7	119	7.9	74	4.2	102	4.4	131	2.8	136	4.2
4	361	− 3.8	124	7.8	72	4.3	117	3.6	129	3.0	177	4.0
5	311	+20.5	153	6.1	64	4.5	122	4.0	133	2.7	171	3.0
6	347	− 8.1	169	5.4	84	3.5	159	3.6	171	1.8	—	—
7	—	—	—	—	93	3.1	161	2.7	190	1.9	—	—
8	—	—	—	—	114	2.4	—	—	—	—	—	—
9	—	—	—	—	97	3.9	—	—	—	—	—	—

The reliability of these figures is, however, questionable, because the variance of dispersion along a line of traps passing through the point of release does not adequately indicate the amount of dispersion unless the distribution of captures is normal. Departures from normality are indicated sufficiently accurately for our purpose by the ratio of the fourth moment about the point of release to the square of the second moment, which is three in the case of the normal distribution. It was shown that this ratio was far greater than three on the first day after release in all of the San Jacinto experiments and only approached (or fell below) three several days later. The data at Mather show the same trend but much higher values on all days (table 7). High kurtosis indicates that the dispersive movements were heterogeneous: short range wandering movements on the part of most flies but relatively long flights by some. The fourth moment is, of course, greatly affected by a few extreme distances and thus appears much less than it actually is, if the line of traps does not cover the entire range. The high kurtosis even on the sixth day at Mather may reflect the relative adequacy of the range sampled (1200 meters at Mather, 500 meters in experiment I (relatively adequate because of slow dispersion), 960 meters in experiment II, 920 meters in experiment III and 1080 meters in experiment IV. The subnormal values of the kurtosis on the sixth and seventh days in experiment III especially suggest curtailment of the range (table 7).

Whatever heterogeneity there may be with respect to dispersion, there should be the same contribution on each day to the mean square radial distance from the point of release, if direction of movement is random and if the distribution of radial distances which flies cover is the same on each day. The

TABLE 8

Estimates of variance in kilometers² (σ^2) and standard deviation in kilometers (σ) for the whole population in one direction $\sigma^2=\frac{1}{2}\Sigma r^3\bar{f}/(\Sigma r\bar{f}+c/2\pi)$ in Mather and in San Jacinto experiments on each day. Temperature in F°.

DAY	MATHER			SAN JACINTO I			II			III			IV		
	t°	σ^2	σ	t°	σ^2	σ	t°	σ^2	σ	t°	σ^2	σ	t°	σ^2	σ
1	?	0.0095	0.098	56	0.0032	0.056	70	0.0073	0.086	70	0.0085	0.092	71	0.0106	0.103
2	70	0.0126	0.112	67	0.0050	0.071	71	0.0128	0.113	72	0.0128	0.113	72	0.0152	0.123
3	71	0.0264	0.162	66	0.0074	0.086	70	0.0136	0.117	77	0.0176	0.133	74	0.0239	0.155
4	72	0.0275	0.166	59	0.0072	0.085	71	0.0160	0.127	71	0.0177	0.133	78	0.0394	0.199
5	72	0.0392	0.198	55	0.0061	0.078	68	0.0190	0.138	74	0.0173	0.132	69	0.0286	0.169
6	72	0.0433	0.208	65	0.0080	0.090	73	0.0299	0.173	75	0.0215	0.147			
7				62	0.0087	0.093	63	0.0254	0.160	74	0.0285	0.169			
8				63	0.0119	0.109									
9				60	0.0105	0.102									

mean square radial distance for a radially symmetrical frequency distribution is given theoretically by the expression $\int_0^{2\pi}\int_0^\infty r^3 z\,dr\,d\vartheta/\int_0^{2\pi}\int_0^\infty rz\,dr\,d\vartheta$ where r is the radial distance, z the corresponding ordinate of the frequency function (inadvertently omitted in the formula as given in the preceding paper) and ($r\,dr\,d\vartheta$) the element of area. As brought out in the preceding paper, an approximation can be obtained by calculating $\sum r^3\bar{f}/(\sum r\bar{f}+c/2\pi)$ where $\bar{f}$ is the mean frequency at distance r and c is frequency at the point of release.

The dispersion variance that is of most interest, however, is that of the whole population in a single direction. The north-south variance involves not only the observed dispersion along the line of traps through the point of release but the dispersion along all lines parallel to this. With kurtosis greater than three, the variance along these parallel lines is greater than that along the line through the center. This total variance in one direction should be just half the radial variance discussed in the preceding paragraph. Table 8 shows this variance (in kilometers²) and the standard deviation (in kilometers) in relation to temperatures on each day at Mather and in the four experiments on San Jacinto. The variance in one direction increased about 0.007 km.^{2} per day at Mather and in experiment IV, at about half this rate (after the first day) in experiments II and III, and only by about 0.001 km.^{2} per day in experiment I. It appears that it would require some five months for the standard deviation in one direction to reach one kilometer under the most favorable conditions found in these experiments. On comparing the standard deviations estimated for the whole population in table 8 with those observed along the line of traps through the point of release (table 7) it may be seen that the latter (on reduction to kilometers) are usually smaller, especially on the early days when kurtosis was high. The average ratio in the eight cases in which Ku is greater than 7.5 is 0.70, in six cases to which Ku is from 4.5 to 6.1 is 0.80, in the 11 cases in which Ku is from 3.5 to 4.4. is 0.89, in the six cases in which Ku is from 2.7 to 3.1 (close to the normal value 3.0) it is 1.00, and in the three cases in which Ku is markedly subnormal (1.8 to 2.4) it is 1.11. This illustrates the point that the observed standard deviation along a line of traps through the point of release should agree with the standard deviation of the whole population in the same direction only if the distribution is a bivariate normal one.

POPULATION DENSITY

The total number of flies that would be caught in a grid in which traps are spaced at 20 m intervals in parallel lines can be estimated from the formula $K[2\pi\sum r\bar{f}+c]$, where K is a constant that is less than one if captures are reduced by the presence of parallel lines of traps (DOBZHANSKY and WRIGHT, 1943). These estimates are shown in the second column of table 9.

TABLE 9

The number of orange flies which it is estimated would be caught in a grid of traps at 20 m intervals in parallel lines 20 m apart by the formula $(2\pi\Sigma r\bar{f}+c)K$, and the ratio of this estimate to the total number actually released. This ratio is also given for the four experiments at San Jacinto.

MATHER			SAN JACINTO			
			I	II	III	IV
DAY	ESTIMATE	RATIO	RATIO	RATIO	RATIO	RATIO
Released	(3840)	100	100	100	100	100
1	2230K	58K	19K	50K	61K	66K
2	3300K	86K	63K	53K	94K	63K
3	6270K	163K	50K	42K	81K	33K
4	4850K	126K	22K	58K	45K	31K
5	5010K	131K	11K	31K	71K	23K
6	6370K	166K	36K	44K	47K	—
7	—	—	15K	48K	34K	—
8	—	—	16K	—	—	—
9	—	—	5K	—	—	—

If conditions were the same on all days, these figures should fall off at the same rate as the whole population of released flies. Instead of this, the estimates for all later days are greater than that on the first day and the maximum is reached on the last day. However, the captures of wild flies per traps show an even greater increase. This general parallelism makes it probable that conditions were more favorable for trapping or that the activity of the flies was greater on the later days. In the preceding paper the estimated numbers of orange flies capable of being captured in a system of traps such as described was divided by the ratio of wild flies per trap to that on the first day to correct for activity. The data from San Jacinto, whether corrected or not, indicated a statistically significant falling off in the orange population at a rate of about nine percent per day. The Mather data show a rise to the third day followed by a greater decline when corrected, in contrast with the three fold increase when uncorrected. They give no aid, however, in estimating the true rate of decline.

More disconcerting perhaps is the fact that on all days from the third to the sixth the estimated number of orange flies capturable in a 20 m grid came out much greater than the actual number of orange flies released, except for the competition factor K. Only one such case occurred in the experiments on San Jacinto. This may mean that K is less than 0.5 (flies being attracted from greater distances than indicated before) or else that there was more dispersion along the line of traps than at right angles to it, contrary to the assumption of a radially symmetrical dispersion. On San Jacinto dispersion was demonstrated to be more or less radially symmetrical by the use of a cross shaped arrangement of traps. This was not done at Mather but there was nothing in the terrain to suggest channelling of dispersion in one direction. It is possible however that we have overestimated somewhat the total amount of dispersion at Mather.

The density of the wild population at Mather may be estimated for comparison with those made from the San Jacinto experiments. It will be assumed as before that the released population decreased 9.2 per cent per day as estimated from the San Jacinto data. This means an estimate of 3840×0.908^n on the nth day after release. Independent estimates can be obtained for each day by the formula (DOBZHANSKY and WRIGHT 1943)

$$\text{wild}/400\text{m}^2 = K(\text{wild}/\text{trap}) \times 3840 \times 0.908^n / K(2\pi r\bar{f} + c).$$

The term $K(2\pi r\bar{f}+c)$ is the estimated number of orange flies capturable in a 20 m grid, such as discussed above. It is assumed that the wild flies actually caught per trap should also be multiplied by K to give the corresponding estimate for wild flies capturable per trap (each at the center of an area of 400 m^2) in such a grid. The K's cancel. These estimates (divided by 4 to give density in terms of flies per 100 m^2) are given in table 10 including all days on San Jacinto instead of merely the first two previously published. In averaging these for each experiment, the figures for each day have been weighted by the term $n_1n_2/(n_1+n_2)$, where n_1 and n_2 are the total numbers of wild and orange flies captured. The estimates for Mather, July 16–July 22, 1945, average 0.9 flies/100 m^2, and are consistently lower than on San Jacinto (3.8 flies/100 m^2 in early June 1942, 9.8 flies/100 m^2 in mid-June 1942, 6.7 flies/100 m^2 in early July 1942 and 8.9 flies per 100 m^2 in late July 1942).

The conclusion that the population density of *D. pseudoobscura* at Mather is lower than it is on San Jacinto is much strengthened if one recalls that the figures for "wild flies" given in table 10 for Mather refer to a mixture of *D. pseudoobscura*, *D. persimilis*, and *D. azteca*. Only *D. pseudoobscura* occurs on Mount San Jacinto. About 36 percent of the flies caught in July of 1945 at Mather were *D. azteca* (table 1), and about 35 percent of the remainder were *D. persimilis* (table 2). Hence, only about 42 percent of the "wild flies"

TABLE 10

Estimates of the density of the wild population based on the captures on each day of wild flies as compared with captures of orange flies released in known numbers and assumed to decrease at a rate of 9.2 percent per day. The averages for all days are based on weights depending jointly on the total numbers of wild (n_1) and of orange (n_2) flies caught on each day. [$wt=n_1n_2/(n_1+n_2)$].

DAY	MATHER		SAN JACINTO							
			I		II		III		IV	
	WT.	FLIES PER 100 m^2	WT.	FLIES PER 100 m^2	WT.	FLIES PER 100 m^2	WT.	FLIES PER 100 m^2	WT.	FLIES PER 100 m^2
1	119	1.39	66	3.42	294	8.34	376	8.52	531	8.22
2	126	0.91	238	4.22	237	8.53	369	6.39	214	7.51
3	199	0.74	164	3.62	186	9.85	228	5.03	88	11.65
4	163	0.78	77	3.58	221	9.47	139	7.25	65	10.97
5	157	0.73	24	1.51	123	13.26	105	5.04	47	14.15
6	216	0.95	111	3.01	70	9.93	51	4.08		
7			50	3.38	74	14.00	37	6.86		
8			50	4.32						
9			22	8.83						
Av.	980	0.89	802	3.80	1205	9.76	1305	6.67	945	8.86

caught in July 1945 belonged to the species *D. pseudoobscura*. If the population density of "wild flies" per 100 square meters was 0.89 (table 2), the figure for *D. pseudoobscura* becomes about 0.37 of a fly per 100 square meters. This is less than one-tenth of the population density in midsummer on San Jacinto (table 10). The relative rarity of the flies at Mather compared to San Jacinto was realized from the start of the experiments in the former locality because the absolute numbers of flies visiting the traps there were strikingly smaller.

MASS RELEASE OF ORANGE FLIES

On July 23, 1945, the trapping of the flies was discontinued because some of the orange flies liberated on July 16 (see table 3 and page 310) had reached, and probably gone beyond, the ends of the trap lines. Trap lines longer than 1200 meters could not be constructed with the available number of collectors.

From July 23 till August 11 inclusive, approximately 1000 orange-eyed flies per day were liberated at the same point at which the orange flies were released on July 16. A grand total of about 25,134 orange flies were thus set free. Liberation of such numbers of flies on a single evening would, of course, raise unduly the population density of the flies near the point of release. Releasing them gradually was designed to permit the environment to absorb the newcomers. The hour of the release, between six and seven PM, was adjusted to let the orange flies out when the wild flies were active in the same neighborhood.

Between August 10 and 16 inclusive, groups of ten to 15 traps were exposed in the vicinities of the points lying 250, 500, 750, and 1000 meters north and south from the point of release, 1250 and 1500 meters south, and near the point of release itself. Since several traps placed very closely together attract much fewer flies than the same number of traps spaced at distances of more than ten meters apart (DOBZHANSKY and EPPLING 1944), the traps were placed near trees or bushes in irregular files approximately perpendicular to the north-south axis of the experimental field. No collections could be made at 1250 and 1500 meters north of the point of release because of the rugged terrain there (Tuolumne Canyon). Owing to the small number of collectors, the trapping could not be made simultaneously at the different points. The 500, 750, and 1000 meter points were sampled first, then the 0 and 250 points, and finally the 1250 and 1500 meter points. Only a single collection was made at 250 and 1500 meters, while near the point of release the trapping continued for four days. This partly explains the very unequal number of flies collected at different stations (table 11). The flies that visited the traps were, as usual, liberated where collected (see DOBZHANSKY and WRIGHT 1943).

Table 11 shows that in mid-August 1945 the adult population near the point of release consisted of decidedly more orange than nonorange flies. Since only about 42 percent of the "wild flies" actually belong to the species *D. pseudoobscura* (see above), there is no doubt that orange-eyed individuals constituted more than half of all individuals of this species which visited the traps within a circle with a radius of 500 meters centered on the point of release. The proportions of orange in the total population decreased, however, as the distance from the point of release increased. The decrease of the frequency of orange was more rapid southward than northward from the center. This may seem to indicate that the flies traveled northward more frequently than they did southward, but such an inference is not necessarily correct. Indeed, the density of the population of wild flies was greater in the territory south of the point of release than it was north of the same point. Hence, if orange flies disperse uniformly in all directions from the point of release, a greater relative frequency of orange is expected to be found in the territory in which wild flies are less abundant. Although orange flies tend to show the same preferences for different microenvironments as wild flies do, their distribution seems to be somewhat more uniform (table 11).

The problem now to be considered is how the distribution of the orange flies observed between August 10 and 16 compares with that found between July

17 and 22 (see above). The best way of computing the variance from the data presented in table 11 is to use the ratios of the numbers of orange and wild flies trapped at the various collecting stations. The use of the ratios obviates in part the complications due to varying densities of the fly population and variable numbers of traps in different parts of the experimental field. These ratios are included in table 11. It is also assumed that collecting at 1250 and 1500 meters north of the point of release would have given the same numbers of orange flies as found at 1250 and 1500 meters south of this point.

On August 10–16, 1945, the variance of distribution of the orange-eyed flies along the line of traps turns out to be 0.086 kilometers^2, and the correspond-

TABLE 11

Numbers of orange and wild type flies collected between August 10 and 16, 1945, at different distances (in meters) from the point of release.

DISTANCE	DAYS OF COLLECTING	TOTAL ORANGE	TOTAL WILD	RATIO ORANGE/WILD	ORANGE PER DAY
Point of release	4	674	208	3.24	168.5
250 North	1	43	18	2.39	43.0
250 South	1	40	21	1.90	40.0
250 Total	2	83	39	2.13	41.5
500 North	7	48	42	1.14	6.86
500 South	7	46	134	0.34	6.57
500 Total	14	94	176	0.53	6.71
750 North	4	6	23	0.26	1.50
750 South	4	12	96	0.13	3.00
750 Total	8	18	119	0.15	2.25
1000 North	7	12	139	0.09	1.71
1000 South	5	6	100	0.06	1.20
1000 Total	12	18	239	0.075	1.50
1250 South	3	6	110	0.055	2.00
1500 South	1	1	103	0.010	1.00

ing standard deviation 0.293 kilometers. These figures should be compared with the variance and standard deviation observed on the sixth day of the initial experiment (July 22, cf. table 7) which are 0.028 kilometers^2 and 0.169 kilometers respectively. The variance has, consequently, trebled between July 22 and August 10–16. The kurtosis of the distribution on August 10–16, measured as before, is 7.5 or somewhat higher than that on July 22. Because of this high kurtosis, an estimate of the variance of the whole population in one direction, made with the aid of the formula $\sigma^2 = \frac{1}{2}\sum r^3\bar{f}/(\sum r\bar{f}+c/2\pi)$, comes out nearly twice as great as that along the line of traps, viz., 0.156 kilometers^2. The standard deviation of this dispersion is 0.395 kilometers.

Another way to compute the variance is to take in consideration only the collecting stations at 500 meters, 1000 meters, and at the point of release. This gives the variance 0.055 kilometers^2 (table 15), which is an underestimate because it is computed from a truncated distribution; however, it has the advantage of being comparable to the figure for the August 22–September 5 collecting (see below).

The orange-eyed individuals which came to the traps exposed on the experimental field between August 10 and 16 were doubtless recaptures of the flies liberated at the center of this field between July 16 and August 11. Very few, if any, orange-eyed progeny of the released parents could have hatched from pupae and be old enough to enter traps by mid-August. Furthermore, since the longevity of the flies in natural habitats is much lower than in the laboratory (DOBZHANSKY and WRIGHT 1943), most of the flies recaptured between August 10 and 16 must have been liberated only a few days before the recapture. The observations made in mid-July showed the variance of the distribution of orange flies to increase at a rate of approximately .0047 km^2 per day along the line of traps (see above). The higher of the two estimates of variance for mid-August seems, consequently, to be about what we might expect if the variance continued to grow at a uniform or accelerated rate. An acceleration is indeed expected because late July and the first half of August were warmer at Mather than mid-July. Since the rate of dispersal of flies increases with temperature, the flies released in August must have traveled for relatively greater distances.

SAMPLING IN LATE SUMMER OF 1945

Between August 22 and September 5, 1945, samples of the population were taken again in the neighborhood of the point of release, and at 500 and 1000

TABLE 12

Numbers of orange and wild type flies collected between August 22 and September 5, 1945, at different distances (in meters) from the point of release.

DISTANCE	DAYS OF COLLECTING	TOTAL ORANGE	TOTAL WILD	RATIO ORANGE/WILD	ORANGE PER DAY
Point of release	8	274	515	0.532	34.25
500 North	7	39	231	0.169	5.57
500 South	7	27	302	0.089	3.86
500 Total	14	66	533	0.124	4.71
1000 North	2	3	105	0.029	1.50
1000 South	9	4	113	0.035	0.44
1000 Total	11	7	218	0.032	0.64

meters north and south from it. The numbers of orange and normal-eyed flies recorded at this time are given in table 12. Comparison of tables 11 and 12 discloses that during approximately two weeks which elapsed between the two samplings the proportions of orange flies in the adult population on the experimental field have dwindled very appreciably. This is doubtless explained by death of many of the released flies. On the other hand, some of the orange flies found in late August and early September were the progeny of the releaesd parents which developed outdoors. This was established by inspecting some of the flies under a microscope; at least two undoubtedly young flies with orange eyes were found among about one hundred inspected ones.

The variance computed from the data in table 12 is 0.092 kilometers^2, and the standard deviation 0.293 kilometers (table 15). This value for variance is only slightly higher than that obtained for the August 10–16 data, namely 0.086 kilometers^2 (see above). However, this value represents undoubtedly an underestimate because of the curtailment of the range over which collections were made (only at the point of release, at 500, and at 1000 meters in August 22–September 5, also at 250, 750, 1250, and 1500 meters on August 10–16, cf. tables 11 and 12). A fairer comparison can be obtained by calculating the variance for the earlier date from the same collecting stations. This comes out 0.055 kilometers^2, or considerably below that for August 22–September 5. A very appreciable increase of the variance during the second half of August is expected, because the warmest period of the summer was reached at about the middle of August and toward the beginning of September the weather became much cooler. Still another estimate can be obtained as follows. The estimate of the variance for the whole population on August 10–16 is 0 156 kilometers^2, or 2.8 times greater than the variance along the line of traps, 0.055 kilometers^2. Multiplying the figure for variance on August 22–September 5 (0.092) by 2.8, we obtain 0.258 kilometers^2 as the variance, and 0.51 kilometer as the standard deviation, on August 22–September 5 (table 15). This is probably an overestimate since it involves the assumption that kurtosis late in August remained as high as it was at the earlier date.

The released orange flies have interbred with the native wild ones. Copulating pairs consisting of two orange, one orange and one wild and two wild individuals were observed repeatedly in the traps in the course of the experiment. Since the presence of some young orange-eyed flies was recorded on the experimental field between August 22 and September 5, some orange heterozygotes must have been present there at that time. Accordingly, some of the phenotypically wild type flies collected on the field were shipped to the laboratory in New York and tested for heterozygosis for orange. The wild males were crossed singly to virgin laboratory-bred orange-eyed females. The wild females were allowed to produce offspring, and a single son or a single daughter of each female was outcrossed to orange. Presence or absence of orange flies in the next generation shows whether or not the wild type parent was heterozygous for orange. Each cross tests two third chromosomes present in a fly. Since both *D. pseudoobscura* and *D. persimilis* occur at Mather, a male from the progeny of each outcross to orange was dissected and its testes were examined under the microscope. The progeny of *D. persimilis* flies outcrossed to the orange mutant of *D. pseudoobscura* are sterile hybrids, and their testes are easily distinguishable from those of males of either pure species. The results obtained are summarized in table 13. Since approximately 0.2 percent of third chromosomes in flies found on the experimental field before the release of the orange flies carried the mutant gene orange (see control), the observed percentages of the orange-containing third chromosomes must be corrected by subtracting 0.2 percent.

Since very few chromosomes were tested and few heterozygotes were found, calculation of variance from the data in table 13 does not seem to be justified. All that these data show is that orange heterozygotes were present on the experimental field in late August and early September of 1945, and that they

TABLE 13

Numbers of third chromosomes of Drosophila pseudoobscura tested and of those carrying orange. Flies collected between August 22 and September 5, 1945.

DISTANCE	CHROMOSOMES TESTED	ORANGE	RATIO ORANGE/WILD	PERCENT ORANGE
Point of release	130	11	0.092	8.46
500 North	14	3	0.049	4.69
500 South	74	3	0.042	4.05
1000 South	36	1	0.029	2.78

were more common in the vicinity of the point of release than away from this point.

DISTRIBUTION OF ORANGE IN JUNE OF 1946

Flies were collected again in the vicinity of the point of release and of the points 500 meters north and south of there between June 4 and 15, 1946. On June 26 and 30 collections were made at approximately 1000 meters north and south from the point of release. No orange-eyed flies were found among several thousand individuals examined. The absence of orange homozygotes does not, however, preclude the possibility that individuals heterozygous for this gene were present.

Accordingly, wild males were crossed in individual cultures to orange females, and the progeny was examined for presence or absence of orange-eyed flies. One son of each male was dissected and its testes were inspected under a microscope to distinguish between the cultures which had *D. pseudoobscura* and those which had *D. persimilis* fathers. Wild females were allowed to produce offspring, and a son or a daughter of each female was outcrossed to orange. The progeny was also examined for orange, and a single grandson of each wild female was dissected to determine the species to which its wild ancestor belonged. The data thus obtained are summed up in table 14.

The data in table 14 disclose the very significant fact, namely that the orange-carrying chromosomes were still clustered about the point of release in June of 1946, or about ten months after the liberation of the orange flies. The observed deviations from a uniform ratio of orange to wild flies would occur by accidents of sampling with a probability of less than 0.01 ($\chi^2 = 10.3$, two degrees of freedom).

The variance along the line of traps comes out 0.182 kilometers^2, or almost exactly double the figure obtained for the August 22–September 5, 1945, sampling. Even if the variance for June 1946 be rated up by the factor 2.8 to give an estimate for the whole population, again assuming persistence of the kurtosis 7.5 (see above), the resulting figure for the variance is only 0.510, indicating a standard deviation of only about 0.7 kilometer about ten months after the release of the flies (table 15).

The variance observed in late August and early September of 1945 was reached as a result of dispersal of orange flies liberated from two to six weeks

TABLE 14

Numbers of third chromosomes of Drosophila pseudoobscura tested and of those carrying orange. Flies collected between June 4 and 30, 1946.

DISTANCE	CHROMOSOMES TESTED	ORANGE	RATIO ORANGE/WILD
Point of release	646	18	0.0287
500 North	746	13	0.0177
500 South	698	12	0.0175
500 Total	1444	25	0.0176
1000 North	334	2	0.0060
1000 South	312	1	0.0032
1000 Total	646	3	0.0047

TABLE 15

Variance (in kilometers²) and standard deviation (in kilometers) along the line of traps considering only the samples taken at 0, 500, and 1000 meters from the origin. In the last two columns the variance and standard deviation are estimated for the whole population by multiplying the variance in the second column by 2.8 (see text).

MATERIAL	DATE		TRAPS		POPULATION	
			σ^2	σ	σ^2	σ
Flies	August 10–16,	1945	0.055	0.24	0.156	0.40
Flies	Aug. 22–Sept. 5,	1945	0.092	0.29	0.258	0.51
Chromosomes	June 4–30,	1946	0.182	0.43	0.510	0.72

previously. This variance was only a little more than doubled during the nine and a half months that elapsed between early September of 1945 and mid-June of 1946. The evident lack of strict proportionality between dispersal and time is not at all strange because the rate of dispersal is greatly modified by temperature. Below 50°F the flies move very little if at all (DOBZHANSKY and EPLING 1944). Since freezing temperatures occur at Mather during winter (CLAUSSEN, KECK, and HIESEY 1940), there can be little migration of flies for about five or six months each year. The migration rates during spring and autumn must be low, and only during July and August the high temperatures induce rapid dispersal.

DISCUSSION

Despite the high sampling errors involved, some conclusions are clearly justified by the data presented above. The experiments performed on Mount San Jacinto (DOBZHANSKY and WRIGHT 1943) and in Mather (described in the present article) agree in showing that in a fairly uniform two-dimensional environment *D. pseudoobscura* flies disperse more or less at random. To be sure, some microenvironments, such as proximity of old oak or pine trees, are clearly attractive to wild as well as to laboratory-bred flies. Nevertheless, we have never found discrete foci of concentration of the flies in nature, nor have we observed directional movements resembling those described by TIMOFÉEFF-RESSOVSKY and TIMOFÉEFF-RESSOVSKY (1940) in *D. funebris* and *D. melanogaster*, and interpreted by these authors as due to the influence of wind. It is fair to note in this connection that all our experimental fields were in localities remarkably free of strong winds during the seasons when the field work was in progress.

The rate of dispersal varies greatly with temperature. As judged by the failure of the flies to come to traps at temperatures below 50°F, the movements of the flies are negligible in cold weather. On days with temperatures of about 70°F at the time of the evening activity of the flies, the average distances between the locations of a fly on successive days are close to 120 meters. Values close to 200 meters per day are probably reached with evening temperatures of about 78°F.

It is, therefore, understandable that in the Mather experiment the amount of dispersal during August was greater than during July, while from September till June the flies traveled only as much as they did during a part of July and August. DUBININ and TINIAKOV (1946) believe that *D. funebris* near Moscow has a period of rapid migrations during June (which is a relatively cool month), followed by a period of a more sedentary existence later in the summer when temperatures are as a rule higher. There is nothing in our data to indicate such alternation of migratory and sedentary phases in *D. pseudoobscura*. The published data of DUBININ and TINIAKOV do not, in our opinion, prove such an alternation in *D. funebris* either. The very interesting experiments of these authors consisted in releasing flies homozygous for a certain inversion and in observing its distribution on a territory two kilometers long and 200 meters wide. In about 60 days after the release, populations about one kilometer distant from the origin showed mixtures of inversion homozygotes and heterozygotes in proportions approaching the binomial square ratios. If released and wild flies interbreed at random, such proportions can be formed in a single generation, not in two generations as DUBININ and TINIAKOV (1946, p. 542) supposed. The results of DUBININ and TINIAKOV are compatible with the assumption that the dispersal of *D. funebris* occurs at rates resembling those found in *D. pseudoobscura*.

If the flies disperse at random, the variance of their distribution increases, with temperature held constant, in proportion to the time elapsed since the release. The standard deviation, and the average distance at which a released fly or its progeny are found from the point of origin, increase as the square root of the time interval. Thus, if flies disperse at a rate of m meters per day on the average, they will be found after n days at an average distance of $m\sqrt{n}$ meters from the origin. As a consequence, the rate of diffusion of a mutant gene through a population is fairly slow even in such relatively mobile but randomly moving forms as *D. pseudoobscura*. Orange-eyed flies were released at Mather between July 16 and August 11, 1945. About ten months later, between June 4 and 30 of 1946, more than half of the progeny of the released flies was still concentrated within a circle with a radius of one kilometer from the origin. Although some further dispersion doubtless took place in July of 1946, there can be no doubt that within a year the flies and their progeny have not moved very far from the point of release.

To help a nonmathematical reader visualize the observed rate of diffusion of the gene orange, the following very crude figures can be mentioned. We take the figure 0.72 kilometers to represent the standard deviation (in one direction) of the distribution of the progeny of orange flies about ten months after their release (table 15). This is probably an overestimate for ten months, but may be fairly close as an estimate of the standard deviation one year after the release. Now, if the progeny of the flies one year after the release is normally distributed, then half of this progeny will be found within a circle with a radius of about 0.85 of a kilometer from the origin. About 95 percent of the progeny will be found within a circle with a radius of 1.76 kilometers, and about 99 percent of the progeny within a circle with a radius of 2.2 kilometers.

SUMMARY

3840 orange-eyed flies were liberated at a certain point near Mather, California, on June 16, 1945. On the six following days traps were exposed along a line 1200 meters long running through the point of release, and the numbers of orange and wild flies visiting these traps were recorded. Analysis of the data confirms the conclusions reached from similar experiments made earlier on Mount San Jacinto (DOBZHANSKY and WRIGHT 1943). At temperatures close to 71°F, the variance of the distribution of flies increased at a rate of about .007 square kilometers per day in one direction, reaching a standard deviation of .21 kilometers in the six days.

More orange-eyed flies were released at the same point near Mather between July 23 and August 11, 1945. A total of 25,134 flies were thus set free. Between August 10 and 16, the standard deviation of the distribution of orange flies on the experimental field was estimated to lie between 0.24 and 0.40 kilometers. Two weeks later the standard deviation rose to between 0.29 and 0.51 kilometers.

Between June 4 and 30, 1946, flies were collected at the point of release and at 500 and 1000 meters north and south of this point. No orange homozygotes were found but some flies proved to be orange heterozygotes. The concentration of orange heterozygotes was higher near the point of release than further away from this point. The standard deviation of the distribution of heterozygotes is estimated between 0.43 and 0.72 kilometers. Taking the higher estimate this means that ten months after the release of the orange-eyed flies about 95 percent of their progeny are found within a circle with a radius of 1.76 kilometers or less centered on the point of release.

The population density of wild *D. pseudoobscura* in midsummer at Mather is found to be around 0.4 of a fly per 100 square meters of the territory. This is

only about one-tenth to one-twentieth of the density found in the corresponding season at Idyllwild, on Mount San Jacinto.

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