GENETICS OF NATURAL POPULATIONS. XLIII. FURTHER STUDIES ON RATES OF DISPERSAL OF *DROSOPHILA PSEUDOOBSCURA* AND ITS RELATIVES[1]

JEFFREY R. POWELL[2], THEODOSIUS DOBZHANSKY[3,5], JAMES E. HOOK AND HARRY E. WISTRAND[4]

[2]*Osborn Memorial Laboratories, Yale University, New Haven, Connecticut 06520 and* [3]*Department of Genetics, University of California, Davis, California 95616*

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ABSTRACT

The amount of gene flow among local populations of a species is determined by the dispersal capacity of that species. Population samples of *Drosophila pseudoobscura, D. persimilis, D. azteca,* and *D. miranda* were collected, marked with ultraviolet fluorescent dusts, and released as soon as possible after capture. One and two days after release, recaptures were made on baits placed at 40-meter intervals in straight lines intersecting the release point. On alternative days, the baits were placed in North-South or in East-West directions. The distribution of the recaptured flies about the release point is very nearly normal. No significant differences between the dispersal rates of the four species are observed; however, males disperse slightly further than females. The variances averaged 50,822 m^2 on the first day and 80,048 m^2 on the second day and the estimated mean distances from the release point averaged 263 m and 361 m respectively. The genetic implications of the results are discussed.

OF the four processes which change gene frequencies in populations, mutation, selection, random genetic drift, and migration, the last named has been studied least. And yet, information about the dispersal capacity of species may well be the key for resolving the controversy between panselectionists and panneutralists (see LEWONTIN 1974 for a review of this controversy). Studies on protein polymorphisms in several species of Drosophila have shown that geographically widely separated populations of a species are usually quite similar in allozyme frequencies (e.g., PRAKASH, LEWONTIN and HUBBY 1969; AYALA, POWELL and DOBZHANSKY 1971). This can be interpreted in two ways. Firstly, the geographic uniformity can be maintained by natural selection, if the selective values of various allozyme genotypes are more or less the same everywhere. Secondly, with adaptively neutral polymorphisms, the uniformity may be a result of migration and gene exchange between geographically separate populations. WRIGHT (1951) pointed out that very little migration will suffice to

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[4] Present address: Department of Biology, Agnes Scott College, Decatur, Georgia 30030.
[5] Deceased December 18, 1975.

prevent genetic divergence of populations owing to random genetic drift (see also MARUYAMA 1970).

In Drosophila, it is the movement of adults that determines the rate of gene exchange between populations. Active dispersal and passive transport must be distinguished (DOBZHANSKY 1973). The latter is due to "accidental" transport by wind, water currents, or human agencies. The study reported here is concerned with active dispersal. It represents a development and, hopefully, improvement of previous experiments bearing on the same problem (DOBZHANSKY and WRIGHT 1943, 1947; CRUMPACKER and WILLIAMS 1973; DOBZHANSKY and POWELL 1974).

MATERIALS AND METHODS

The work reported here was carried out at the Carnegie Institution of Washington Plant Biology Research Station near Mather, California (Toulumne County). The area has been described by CLAUSEN, KECK and HIESEY (1940). It is favorable for Drosophila, especially in the vicinity of the release point. The favorableness of the terrain drops off toward the periphery of the experimental area, but many flies can still be found throughout the area. The release point was at the same *Quercus kellogii* tree used in previous experiments (DOBZHANSKY and WRIGHT 1947; DOBZHANSKY and POWELL 1974). Plastic buckets (20 cm in diameter) with fermenting banana mash were used as baits. The following protocol was used in each experiment.

On one evening, baits were placed in favorable locations in the experimental area to collect as many flies as possible. Collecting ended about an hour prior to the end of the activity period of the flies. The buckets were removed from the area, the flies lightly dusted with ultra-violet fluorescent dusts (Helecon Pigments from U.S. Radium Corporation), and immediately released at the tree designated the release point. Flies usually had about half an hour of activity period in which to find a safe place for the night. CRUMPACKER (1974) has shown these dusts do not harm or alter the behavior of Drosophila in any obvious manner. In all cases, the baits were only exposed about 45 minutes prior to the beginning of evening activity period (about 5:30 P.M., P.D.T.) and removed and sealed immediately after collecting ended.

For recapture one and two days after a release, baits were exposed 40 meters apart along a north-south or east-west transect running through the release point. Forty-one baits were used, one at the release point and 20 in each direction; thus our lines rans 800 meters in two directions from the release point. Because of the ruggedness of the terrain 250 meters or more to the east of the release point, we could place only 6 baits in this direction. On evenings when the east-west transect was used, we placed baits numbered 1–6 in the east direction and 7–20 in the south transect starting at 280 meters. North-south and east-west transects were used alternately on recapture evenings.

After recapture, flies caught at each trap were examined using a portable U-V light source and a dissecting microscope. The number, sex, and when possible the species of the marked and unmarked flies were recorded. Unidentifiable marked flies were placed in vials and kept for species identification later. All other flies were destroyed. Because we did not etherize and classify the flies prior to release, we marked and released all flies captured on a release day. During our experiments 90%–95% of the flies belonged to four species of the obscura group: *D. pseudoobscura*, *D. persimilis*, *D. azteca*, and *D. miranda*. Generally *D. miranda* males and females are visually distinguishable from the other members of the obscura group; *D. azteca* males are easily recognizable. Female *D. pseudoobscura*, *D. persimilis*, and *D. azteca* are morphologically nearly identical, as are *D. pseudoobscura* and *D. persimilis* males. However, all species are clearly identifiable by their enzyme patterns revealed by starch gel electrophoresis (AYALA and POWELL 1972). Marked flies not identified in the field were taken to PROFESSOR F. J. AYALA's laboratory at the University of California, Davis, where he and MISS LORRAINE BARR kindly carried out electrophoresis and species identifications. Because of death, not all flies were identified; there-

fore the numbers reported in Tables 4 and 5 do not coincide exactly. Because of the rarity of Drosophila species other than of the obscura group, we report here data only for the four obscura group species.

We carried out five release experiments between 20 June and 5 July 1974. In four of five experiments we made recaptures one and two days after release. In one (the fourth we made only a second-day recapture. After two days the number of marked flies which can be recaptured is small so third-day recaptures were unprofitable. We used different-colored fluorescent dusts in successive experiments to avoid any confusion which may arise in recapturing flies from previous experiments; occasionally such flies were found, but not often enough to warrant analysis. Temperature and wind velocity data were kept throughout the experiments.

RESULTS

Table 1 gives the days and environmental conditions of each experiment. The time is Pacific Daylight Savings Time. Drosophila show marked diurnal periods of activity; they are active for about 2–3 hours after sunrise and 2 hours before sunset. The exact period is dependent on temperature and sunlight. The environmental factors important for our studies are therefore the conditions prevailing during the activity periods, about 6–9 AM and 6–9 PM. At Mather the evening period is the more important. Many more flies, over a longer period, can be collected in the evening as compared to the morning. Also, it can be seen in Table 1 that Mather is a remarkably windless area during this season. In almost all cases the average daily wind velocity was less than 1/2 of one mile per hour. The evening collecting period is a particularly calm time of day. Thus, we can safely assume that passive transport by wind is playing little or no role in the dispersal of the marked flies.

TABLE 1

Conditions and dates of experiments

Day	Activity	Temperature			Wind velocity	
		7:30 AM	1:00 PM	7:30 PM	Day	6–9 PM
20 June	1st release	—	—	20.5	—	—
21 June	1st day recapture	12	25.5	22.5	.23	0
22 June	2nd day recapture	14	26.5	24	.30	.16
23 June	2nd release	13	27	22	.23	.10
24 June	1st day recapture	11	26	22	.45	.10
25 June	2nd day recapture	12	—	21	.36	0
27 June	3rd release	11	28	25	—	.10
28 June	1st day recapture	13	29	26.5	.38	.06
29 June	2nd day recapture	16	31	27.5	.33	<.05
30 June	4th release	17	30	25	.33	<.05
1 July	No recapture	15.5	28	24	.48	0
2 July	2nd day recapture	12	27	23	.40	.08
3 July	5th release	14	28	24.5	.39	.07
4 July	1st day recapture	15	28	25	.45	.40
5 July	2nd day recapture	13	28	23.5	.52	.05
Average		13.5	27.8	23.7	.37	.09

Temperatures are in degrees centigrade and wind velocity in miles per hour. Average wind velocity for whole day and during collecting period are given in last two columns.

TABLE 2

Numbers of flies released and recaptured in each experiment and density calculations of all obscura group flies

Experiment	No. released	Day	Recaptured		Density (flies/100 m²)
			No.	%	
1	1220	1	71	5.8	2.30
		2	21	1.7	1.50
2	1042	1	101	9.7	1.39
		2	30	2.9	0.66
3	1781	1	95	5.3	4.03
		2	71	4.0	3.23
4	2077	1	—		—
		2	115	5.5	4.36
5	2036	1	282	13.9	4.12
		2	95	4.7	2.40
Total	8156		881	10.8	2.67

Table 2 gives the number of marked flies released and recaptured in each experiment and the estimated densities of obscura group flies. The numbers released are approximations as we did not etherize and count the flies before release. The numbers released were arrived at by averaging the numbers of flies caught on the two days when flies were counted closest to the release day. We assume that we released about as many flies as we recaptured on days nearest to the release day. Recovery of marked flies over two days was 10.8%, which is almost identical to the previous year's recapture rate (DOBZHANSKY and POWELL 1974). The density calculations were made according to the methods described by WRIGHT in DOBZHANSKY and WRIGHT (1943 and 1947). The density measurement includes all four species of the obscura group. Assuming the frequency of species is the same in males and females and is also the same among the flies analyzed by electrophoresis and in nature, we can calculate the relative abundance of each species. The proportion were quite stable throughout the experiments at 54.1% for *D. pseudoobscura*, 17.4% for *D. persimilis*, 26.0% for *D. azteca*, and 2.7% for *D. miranda*.

The numbers of marked and unmarked obscura group flies at each trap on each recapture day are listed in Table 3. The distribution of flies on the experimental plot was far from random. If the flies were distributed randomly the number of flies in each trap should follow a Poisson distribution and the ratio of the variance to mean should equal unity. For different days this ratio varies from 10 to 55. This is in agreement with previous findings (DOBZHANSKY and WRIGHT 1943, 1947; DOBZHANSKY and POWELL 1974). A graphical representation of the data for first day recapture is given in Figure 1. It is evident that the area around the release point is most favorable for Drosophila. This is not surprising as the area was originally chosen for just this reason. However, the whole experimental plot was certainly acceptable for Drosophila. With two exceptions, *every trap produced some* obscura *group flies every day.*

TABLE 3

Numbers of marked flies (before dash) and number of unmarked flies (after dash) caught at each trap on each recapture day

Distance (m)	Direction	21 June N–S	22 June E–W	24 June E–W	25 June N–S	28 June N–S	29 June E–W	2 July N–S	4 July E–W	5 July N–S	Total 1st day marked/unmarked
800	NW	0–3	0–1	0–20	0–1	0–3	0–12	0–20	0–34	0–10	0
760	NW	0–0	0–14	0–14	0–0	0–13	0–74	2–39	0–30	0–23	0
720	NW	1–23	0–8	0–8	0–8	0–12	0–20	2–26	1–16	1–33	.034
680	NW	0–21	1–14	0–12	0–17	1–19	0–57	3–62	1–31	4–47	.024
640	NW	0–23	0–14	0–2	0–14	0–38	0–20	0–43	0–31	2–85	0
600	NW	0–21	0–22	0–7	0–1	0–26	2–40	0–13	0–5	0–12	0
560	NW	0–7	1–4	0–9	0–8	0–18	0–41	0–29	0–9	0–9	0
520	NW	0–3	0–35	0–10	0–5	1–10	0–85	0–12	1–34	0–6	.035
480	NW	0–25	0–34	0–9	1–8	0–14	1–31	1–13	2–53	0–28	.020
440	NW	3–71	0–10	0–12	1–20	2–48	2–45	0–22	4–48	1–30	.050
400	NW	0–6	1–44	3–21	0–4	3–34	4–66	2–24	9–80	2–26	.106
360	NW	1–27	1–10	2–33	0–3	2–56	4–64	2–34	9–105	0–36	.063
320	NW	1–17	0–34	3–14	1–10	4–29	4–81	4–91	15–140	2–70	.115
280	NW	0–18	0–30	5–20	0–3	1–20	4–57	3–36	24–108	2–31	.181
240	NW	0–26	1–15	3–4	2–16	3–68	1–25	6–42	22–40	3–48	.203
200	NW	2–84	0–9	3–12	0–10	1–24	1–7	4–31	13–33	8–94	.123
160	NW	0–6	1–18	5–19	0–2	5–32	2–51	4–20	11–55	2–10	.188
120	NW	13–55	0–51	6–44	0–37	6–107	1–102	11–99	6–45	4–76	.124
80	NW	11–113	4–84	6–52	2–40	15–117	1–66	7–71	15–80	8–67	.130
40	NW	6–92	2–67	3–53	3–26	12–60	4–119	23–175	9–45	7–82	.120
0	Release	9–37	1–105	30–63	7–50	22–232	8–152	8–64	22–75	16–153	.204
40	SE	10–58	0–72	10–27	2–10	3–57	1–24	4–30	15–83	1–13	.169
80	SE	1–25	0–32	5–20	0–14	1–7	5–112	3–28	29–140	3–33	.188

TABLE 3—Continued

Distance (m)	Direction	21 June N–S	22 June E–W	24 June E–W	25 June N–S	28 June N–S	29 June E–W	2 July N–S	4 July E–W	5 July N–S	Total 1st day marked/unmarked
120	SE	4–44	4–102	3–12	4–26	3–22	7–80	4–23	15–93	0–41	.146
160	SE	2–43	1–49	5–22	0–11	1–15	3–24	6–30	16–172	3–51	.095
200	SE	2–15	0–48	4–20	2–18	1–29	5–75	3–21	12–121	4–35	.103
240	SE	2–23	1–57	1–26	3–11	1–30	2–107	5–27	8–88	3–21	.072
280	S	2–29	1–39	1–15	0–11	2–33	0–6	2–51	2–24	6–22	.069
320	S	0–15	0–19	0–4	0–15	2–21	4–59	1–29	4–28	0–27	.088
360	S	0–16	1–9	0–16	1–16	2–15	1–66	1–36	1–38	1–11	.106
400	S	0–18	0–20	3–11	0–13	1–6	2–36	1–14	3–23	1–12	.121
440	S	0–21	0–25	0–6	1–17	0–8	1–22	0–7	3–10	1–11	.067
480	S	1–21	0–33	0–22	——	0–6	0–49	0–14	2–16	3–41	.046
520	S	0–5	0–36	0–23	——	0–7	1–44	1–17	4–31	1–18	.016
560	S	0–14	0–19	0–18	——	0–19	0–32	0–26	0–24	1–42	0
600	S	0–10	0–40	0–25	——	0–12	0–68	1–30	0–3	1–20	0
640	S	0–12	0–57	0–15	——	0–33	0–84	0–18	1–3	0–42	.016
680	S	0–12	0–21	0–5	——	0–11	0–24	0–47	0–13	1–32	0
720	S	0–22	0–33	0–4	——	0–16	0–12	0–28	0–17	1–55	0
760	S	0–6	0–12	0–4	——	0–7	0–14	0–11	3–30	1–47	.064
800	S	0–0	0–19	0–5	——	0–88	0–38	1–51	0–4	1–90	0
Total		71–1,087	21–1,365	101–738	30–445	95–1,422	71–2,191	115–1,504	282–2,058	95–1,640	

Last column is the ratio of marked to unmarked flies in each trap one day after release; see text for details.

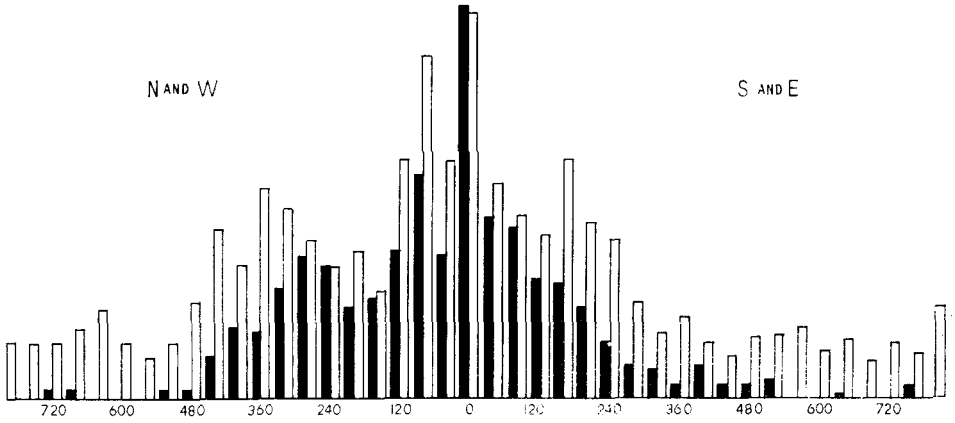

FIGURE 1.—Graphical representation of numbers of marked (solid bars) and unmarked (open bars) flies one day after release. Numbers are meters from release point. The data are combined for all five experiments. Right of "0" is combined data of flies caught in the South and East transects and to the left is combined data of North and West transects. The scale of solid bars is five times that of the open bars.

TABLE 4

Analyses of combined data on the four obscura group species

Experiment no.	N	σ^2 ± S.E.	Kurtosis ± S.E.	Mean	WRIGHT's mean square	WRIGHT's est. mean
		First day				
1	71	33,690 ± 5,654	6.11 ± .34	126.8	52,521	259.8
2	101	29,544 ± 4,157	3.28 ± .49	120.8	33,496	226.6
3	95	40,505 ± 5,877	4.08 ± .50	138.5	52,491	278.4
4	—	——	——	——	——	——
5	282	63,807 ± 5,374	3.04 ± .29	224.2	55,462	276.0
Total	549	50,822 ± 3,067	3.46 ± .21	166.8	49,603	263.0
		Second day				
1	21	72,685 ± 22,431	3.48 ± 1.07	205.7	82,553	352.8
2	31	49,238 ± 12,506	3.05 ± .88	160.0	56,111	303.5
3	71	73,870 ± 12,398	2.24 ± .54	222.0	63,787	329.0
4	114	73,109 ± 9,683	4.56 ± .46	191.9	99,971	376.0
5	95	104,674 ± 15,188	3.29 ± .50	236.2	120,367	433.8
Total	332	80,048 ± 6,213	3.62 ± .27	208.9	90,120	361.2

All measurements are in meters (columns 5 and 7) or meters squared (columns 3 and 6). Kurtosis is the ratio of the 4th moment to the square of the 2nd moment which equals 3 in a normal distribution. WRIGHT's mean square is 1/2 the radial variance which is $\Sigma r^3 f/(\Sigma \bar{r} f + c/2\pi)$ and the estimated mean is $\Sigma r^2 f/(\Sigma \bar{r} f + c/2\pi)$. (See DOBZHANSKY and WRIGHT 1943 and 1947 for details.)

Table 4 presents analyses of the distributions of marked flies one and two days after release. The analyses follow those of DOBZHANSKY and WRIGHT (1943, 1947). Other means of analysis have been suggested (e.g., CRUMPACKER and WILLIAMS 1973; RICHARDSON 1970; WALLACE 1968); however, we have chosen to follow the previous procedures for comparative purposes. The second column of Table 4 gives the number of recaptured marked flies. The third column is the variance about the release point: $\sigma^2 = \Sigma r^2 f$, where r is the distance from the release point and f is the proportion of the marked flies in each trap. The kurtosis test is the ratio of the fourth moment about the release point to the square of σ^2; this equals 3 for a normal distribution. The mean is the average distance from the release point where marked flies were recaptured. Details of WRIGHT's mean square and estimated mean are described in DOBZHANSKY and WRIGHT (1943, 1947). Two things should be especially noted here. Firstly, with the exception of the first experiment, the variance does not double in going from day one to day two. Secondly, the distribution of the flies about the release point is almost normal. The estimates of kurtosis are slightly over 3, though seldom significantly. This indicates a very slight degree of leptokurtosis in the distributions.

TABLE 5

Same analyses as in Table 4 for combined data of five experiments for each species and sex

Species, sex and day	N	$\sigma^2 \pm$ S.E.	Kurtosis $\pm$ S.E.	Mean	WRIGHT's mean square	WRIGHT's est. mean
D. pseudoobscura						
1st day ♀♀	172	43,814 ± 4,725	3.96 ± .37	150.7	40,730	214.7
♂♂	127	64,617 ± 8,109	3.30 ± .43	196.9	69,500	328.3
♀♀ and ♂♂	299	52,388 ± 4,285	3.72 ± .28	170.3	62,423	307.6
2nd day ♀♀	97	65,083 ± 9,345	4.20 ± .50	176.1	85,690	357.3
♂♂	78	74,348 ± 11,905	3.78 ± .55	200.0	88,938	367.1
♀♀ and ♂♂	175	68,416 ± 7,314	4.09 ± .37	186.74	85,389	350.2
D. persimilis						
1st day ♀♀	55	46,575 ± 8,882	5.42 ± .66	146.2	69,790	309.8
♂♂	55	42,444 ± 8,094	2.88 ± .66	156.3	43,884	266.6
♀♀ and ♂♂	110	44,509 ± 6,002	4.28 ± .47	151.3	55,256	281.2
2nd day ♀♀	26	72,369 ± 20,072	2.95 ± .96	203.1	77,927	354.7
♂♂	16	144,500 ± 51,088	2.11 ± 1.22	317.5	119,958	454.7
♀♀ and ♂♂	42	100,343 ± 21,897	2.62 ± .76	246.7	98,274	404.7
D. azteca						
1st day ♂♂	77	43,491 ± 7,009	2.52 ± .56	168.1	39,010	249.4
♀♀ and ♂♂	79	42,896 ± 6,825	2.53 ± .55	168.8	40,050	257.7
2nd day ♂♂	40	121,960 ± 27,271	2.41 ± .77	291.0	107,948	418.6
♀♀ and ♂♂	47	126,366 ± 26,067	2.24 ± .71	291.1	116,306	433.2
D. miranda						
1st day	16	74,100 ± 26,198	4.48 ± 1.22	197.5	97,753	374.0
2nd day	10	97,760 ± 43,720	4.65 ± 1.55	220.0	139,818	444.4

Where $N<10$, no analysis was done. Number of flies in this table is less than in Table 4, as this table only includes flies which survived long enough to be identified by electrophoresis.

Table 5 shows the same analyses for each sex of each species. There are no significant differences in dispersal patterns among the four species. Bartlett's test for heterogeneity of variances gives a $\chi^2_3 = 3.27$ ($p>0.5$) for the first day and $\chi^2_3 = 8.62$ ($p\approx0.05$) for the second-day variances. Males seem to disperse on the average further than females. This confirms the findings of DOBZHANSKY and POWELL (1974).

DISCUSSION

Earlier studies on the dispersal of *Drosophila pseudoobscura* (DOBZHANSKY and WRIGHT 1943, 1947) utilized for release and recapture laboratory-reared flies homozygous for the recessive mutant gene orange eye. As many as 3000–5000 individuals were released in each experiment. The orange mutant is sturdy enough to reproduce in nature in competition with wild flies. It is, nevertheless, quite likely that laboratory-reared flies are less mobile than wild ones. Thus, in the newer studies (CRUMPACKER and WILLIAMS 1973; DOBZHANSKY and POWELL 1974; and the present report) wild-collected flies were marked with ultra-violet fluorescent dusts (different colors in successive releases), and released as soon as practicable after the capture. The numbers of flies released were much smaller in the newer experiment (300–2000). Thus the "overcrowding effect" (discussed below) was greater for the orange flies. Nevertheless, wild flies dispersed considerably further than the mutants. It remained to exclude the possibility that the low mobility of orange-eyed flies was due to the early experiments having been conducted at lower temperatures than the more recent ones. The experiments made in 1974 and reported in the present article invalidate this possibility. The temperatures during the 1973 experiments were higher than in 1974. If we correct the variance estimates for the length of the trap lines, the 1973 estimates are slightly lower, not greater, than in 1974. From the accumulated data on dispersion and temperature, it seems that in the range of 20°–29° dispersion is independent of temperature, while below 20° mobility is reduced. Thus we conclude that the older experiments underestimated the dispersal because laboratory-reared mutants were used instead of wild flies.

WRIGHT (in DOBZHANSKY and WRIGHT 1943) chose as the simplest model of dispersion of marked flies released at a single point a random model analogous to Brownian movement. It was evident at the outset that this model can be only a first approximation. Since no two-dimensional environment is spatially and temporally uniform, the flies will tend to remain in some neighborhoods and escape from others. The experiments have indeed shown minor but consistent discrepancies from the model. In all four studies (San Jacinto and three at Mather) the distributions tend to be more or less leptokurtic rather than strictly normal. In the DOBZHANSKY and WRIGHT (1943 and 1947) studies leptokurtosis was quite significant on the first few days after release, but declined with time to normality. The 1973 and 1974 studies show a nearly normal distribution, but still with occasional slight leptokurtosis. There are two possible explanations for leptokurtosis. Firstly, some of the released flies may have been less vigorous than others. The less vigorous portion of the released population remained at or near

the release point while the rest of the flies dispersed normally. If the less vigorous and less mobile individuals have a higher mortality rate than the rest of the population, the leptokurtosis will decrease with time. This was the case in the early studies with mutants.

Another cause of leptokurtosis might be the non-uniformity of the environment. As indicated in Figure 1, the area around the release point is more attractive for Drosophila than is the periphery of our plot. If the released flies are preferentially choosing favorable areas, then leptokurtosis would occur. This leptokurtosis should not decrease with time.

Figure 1 shows that released flies tend to accumulate in attractive areas, i.e. areas where the natural populations are the densest. The ratio of marked to unmarked flies at a trap is given in the last column of Table 3. The relative constancy of this ratio indicates that the dispersion is not entirely random but that flies seek out favorable territories. However, we would like to emphasize that in the 1973 and 1974 experiments at Mather, the leptokurtosis was slight and in most cases the test for kurtosis was not significantly different from the expectation of a normal distribution.

The random movements model leads to the expectation of a direct proportionality of the variance to time. Table 6 summarizes data from several experiments. Except for the variance in the San Jacinto experiments, the increase is less than expected. This is especially true of the 1973 Mather experiments, but this may in part be an artifact. If some flies are going beyond the ends of the trap lines, then the variances are underestimated. In comparing the 1973 and 1974 data, it is clear that our trap lines in 1973 were not long enough, while in 1974 they were long enough, so that very few or no flies were beyond the last traps after two days. Indeed, only two marked flies were caught at 800 meters, one *D. azteca* female and one *D. miranda* female. Thus we can be reasonably confident that essentially all *D. pseudoobscura* and *D. persimilis* were within our experimental area in 1974. The variances after two days were still less than twice as great as after one day. Less dispersion on day two than on day one may be due to a

TABLE 6

Increments of variance (upper figure) and Wright's mean square (lower figure) from 1st to 2nd day after release for Drosophila pseudoobscura

	San Jacinto	Mather 1945	Mather 1973	Mather 1974
1st day	3,245	4,051	16,646	52,388
	7,400	9,500	27,259	62,423
2nd	7,394	7,252	26,976	68,416
	11,375	12,600	27,256	85,389
Percent increment	128	79	66	24
	54	33	0	57

All figures are in m^2. San Jacinto data from DOBZHANSKY and WRIGHT (1943), Mather 1945 data from DOBZHANSKY and WRIGHT (1947), and Mather 1973 data from DOBZHANSKY and POWELL (1974).

relatively more favorable area around the release point as compared to the periphery. This might cause a centripetal force to hold the flies nearer the release point than random movement would predict. However, Professor J. S. WILLIAMS (personal communications) has calculated that with our experimental design, random movement predicts an increase of the variance by a factor of 1.7 from day one to day two. This is almost exactly the observed increase.

WALLACE (1970) has speculated that release experiments such as ours may not accurately reflect the normal behavior of flies because of overcrowding at the release point. The flies may be "agitated" and disperse abnormally. This possibility may be tested with our data. If the "agitated" flies disperse more than normal, there should be a positive correlation between the numbers released and the distance they fly. Our release numbers in 1973 and 1974 varied between 300 and 2,000 flies. Since there were fewer traps in 1973 than in 1974, we have recalculated the 1974 variances leaving out flies captured in traps more than 440 meters from the release point. The correlation coefficient between the numbers released and variances after one day is $+0.79$ ($p<.01$). This appears to support the notion that crowding affects the dispersal patterns. However, the correlation may not be due to crowding alone. On days when we caught few flies for marking and release, the environmental conditions were less favorable for Drosophila activity than on days of abundant captures. If environmental conditions on successive days are correlated, we would expect a correlation between the numbers released and the distance dispersed. The cause of the correlation would not be overcrowding or agitation, but rather fluctuations in activity due to temporal fluctuations in the favorableness of the environment.

It has been suggested that the lines of traps artificially increase the dispersal because of a channelling effect of flies attracted to the baits in search of food. This is unlikely. Firstly, the baits were exposed for only a short time each day, albeit at the height of activity. Secondly, trap lines were never the same on day one and day two of the same experiment. Finally, the anomalous placement of traps in the E-W transect allows a test of this hypothesis. Traps which should have been numbers 7–20 in the east were placed in positions 7–20 south. If there is a channelling effect, on day one when a E-W transect is used here should be fewer marked flies in traps 7–11 south than in 7–11 west because of the 280-meter gap between the release point and the first trap in the south direction. Examination of Table 3 shows that not to be the case. Indeed, already in 1944, DOBZHANSKY and EPLING reported the results of a simple experiment of exposing baits for several consecutive days away from the transect on which lines of baits were placed. If a "channelling effect" existed the baits not on the transect should have attracted fewer flies than the baits within the transect. This was not observed.

Although the experimental procedures and analysis of CRUMPACKER and WILLIAMS (1973) were considerably different from ours, their conclusions agree quite well. Their estimates of mean distance traveled by *D. pseudoobscura* in one day is 176 m while ours is 170 m (ordinary mean) or 307 m (Wright's estimated mean). Since their furthest trap from the release point was just over 300 meters and the total number of flies recaptured was 20 in one experiment and 65 in

another, it is remarkable that their results coincide so well with ours. Thus there is as yet no evidence to indicate geographical differences in the dispersal behavior of *D. pseudoobscura* populations.

An important implication of our dispersal studies is that the mobility of species of the obscura group is great enough to prevent genetic differentiation on a microgeographic scale like that observed by HAMRICK and ALLARD (1972) in *Avena barbata*. The gene flow in Drosophila is great enough to homogenize gene frequencies over short distances, say less than 1 km, even in the face of fairly strong diversifying selection. A difference in gene frequencies correlated with habitats over short distances might, however, arise in Drosophila if the carriers of different genotypes were actively seeking some habitats in preference to others. On the other hand, the dispersal of Drosophila is not great enough to prevent local differentiation on a somewhat greater scale. This was proved by the experiments of DOBZHANSKY and WRIGHT (1947). Orange mutant flies were released in the summer of 1945 at a certain point at Mather; in the summer of 1946, flies heterozygous for orange were still present in the locality, and were most frequent in the vicinity of the release point. It must, of course, be stressed that the mobility of flies may be much greater in unfavorable territories than in favorable terrains like in Mather.

The active dispersal of *D. pseudoobscura* and its related species is now known to be considerably greater than suggested by the old experiments with flies marked by a mutant gene. Yet it is probably insufficient to account for gene flow between populations living hundreds of kilometers apart. The preferred habitats of *D. pseudoobscura* are pine-oak forest throughout western North America, from British Columbia southward to Mexico and Guatemala. These preferred habitats are often separated by many kilometers of less favorable, or unihabitable, terrains. Passive transport, rather than active dispersal, would have to be invoked for long distance gene flow. Unfortunately, rates of passive transport are most difficult to study experimentally.

DOBZHANSKY and WRIGHT (1943) and CRUMPACKER and WILLIAMS (1973) estimated the panmictic unit of *D. pseudoobscura* to be one to seven thousand individuals. Our recent results suggest even larger estimates. Table 7 presents

TABLE 7

Estimates of effective population size of Mather population of D. pseudoobscura

τ	Ne
5	15,860
10	31,720
15	47,580
20	63,440
25	79,300

Calculations are based on WRIGHT's (1946) formula, $Ne = (4\pi\sigma^2\tau/3)$ (density), where σ is the dispersal parameter and τ is the number of days an adult on average is expected to be capable of producing offspring.

some estimates of effective population sizes based on data presented above. Random genetic drift can be important in such populations only if selection coefficients are very small or zero. However, it should be kept in mind that our release-recapture experiments were done during the yearly population peaks. Considerable fluctuations must occur during the winter or times of unfavorable weather. The effective population size is the harmonic mean of the population sizes over time. Low population levels affect this mean more than high. Severe winter bottlenecks make the effective population size over a year much smaller than our summer estimates indicate. It would be most interesting to obtain density measurements for early spring and late fall in these areas.

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Corresponding editor: R. C. LEWONTIN