GENETICS OF NATURAL POPULATIONS. X. DISPERSION RATES IN DROSOPHILA PSEUDOOBSCURA

TH. DOBZHANSKY AND SEWALL WRIGHT[1]

*Columbia University, New York, and University
of Chicago, Chicago*

INTRODUCTION

THE breeding structure of a population is determined, among other factors, by its effective size (N) and by the migration index (m). The latter constant measures the extent to which the population of a given territory is replaced in each generation by immigrants from the rest of the species or from a territory large enough to have all the genetic variants of a given class at their equilibrium frequencies. The value of the migration index, in turn, is a function of the mobility of the organism. Joint estimates of N and m have been arrived at for certain populations of *Drosophila pseudoobscura*, and some attempt has been made to make separate estimates (DOBZHANSKY and WRIGHT 1941; WRIGHT, DOBZHANSKY, and HOVANITZ 1942). The data reported in the present article were collected in order to test the validity of these estimates.

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METHOD

Experiments on the mobility of insects have been made on mosquitoes, house flies, tsetse flies, grasshoppers, codling moths, and other forms. Individuals of the proper species were caught, marked by paint or colored dust, released at a given point, and subsequently recaptured in the neighborhood. With the exception of JACKSON's (1940) work on tsetse flies, the data give little information on the rules which underlie the dispersal of the species in question. The investigators seem to be most interested in finding out the maximum distance from the point of release at which marked individuals may be encountered. The pioneering work on the dispersal of Drosophila was done by N. W. and E. A. TIMOFEEFF-RESSOVSKY (1940a, b, c). Known numbers of *D. melanogaster* and *D. funebris* marked by easily recognizable mutant characters were liberated at the center of an experimental field. For a week or two after the release of the mutants, baited traps were exposed daily around the point of release, and the

numbers of the mutant and the wild flies which came to each trap were re-
corded, whereupon the flies were released again at the point of capture. The
distribution of the marked flies on the field gave an idea about the rates of their
dispersal; the ratios of the mutant and the wild flies were used to compute the
population densities of the wild flies in the territory examined.

An animal actively moving in a uniform two dimensional environment may
manifest one of at least three types of dispersal. (1) The movements may be
random. The distribution of marked individuals after the lapse of a certain
time, for example a day, will be characterized by a variance, σ^2. The mean dis-
tance from the point of release at which individuals will be found will be r. The
distribution of the marked individuals after two days will have a variance $2\sigma^2$,
and the mean distance will be $\sqrt{2}r$. After n days the variance will be $n\sigma^2$, and
the mean distance $\sqrt{n}r$. (2) The release of a large number of individuals at a
given point raises the population density and may produce a depletion of the
food supply and of the shelter space in the immediate vicinity. The flies may
tend to escape from the areas of high population density to less densely settled
areas. Since the density gradients will become less and less steep as time goes
on, the variance of the distribution of the flies will increase at a faster rate at
the beginning than toward the end of the experiment. (3) If the flies possess
a "homing instinct," each individual will tend to stay within a certain circum-
scribed territory. JACKSON (1940) found such an attachment to a home terri-
tory in tsetse flies. The flies, then, will travel relatively far from the point of
release until they establish home ranges and will become largely stationary
thereafter. The variance and the mean distance will reach a maximum and tend
to become constant.

The experimental fields of the TIMOFEEFF-RESSOVSKYS consisted of traps
placed checkerboard fashion at ten meters from each other. Fields of 63 traps
(7×9 on the sides) and of 121 traps (11×11 on the sides) were used. Since the
marked *D. melanogaster* and *D. funebris* flies barely reach the boundaries of
the fields at the end of the experiments, fields of this size are sufficient for the
purpose. The experimental procedure had to be modified for our experiments
because *D. pseudoobscura* proved to be much more mobile than the species
named above. Checkerboards with traps at 20 meters were tried without suc-
cess; greater distances are impracticable on account of the labor involved. The
traps were then arranged in two lines forming a cross, distances between the
traps were made ten or 20 meters, and the flies were released at the intersection
of the two axes of the cross (fig. 1). Even this arrangement proved satisfactory
only for a few days after the release of the marked flies: with the greatest num-
ber of traps that could be used the flies reached the ends of the arms of the cross
in from two days to a week. As soon as this happened, one of the two axes had
to be sacrificed and the other axis extended by adding traps at the ends, thus
making a single file of traps. Of course, terrains as uniform as possible were
chosen on which to build the experimental fields. Toward the end of the experi-
ments, however, the fields grew to sizes so unwieldy that some non-uniformities
were unavoidable.

TECHNIQUE

The third chromosome recessive orange was used as the marking gene in our experiments. It produces a brilliant red eye color which is distinguishable from the wild type by naked eye to even an untrained observer. Orange heterozygotes have repeatedly been found in natural populations, but no homozygotes have ever been met with. It is obviously important to have the released flies equal in vigor to the wild ones. Throughout the experiments F_1 hybrids of two orange strains were used, one of which was extracted from the population of Keen Camp and the other from Andreas Canyon, both localities on Mount San Jacinto, and thus advantage was taken of the hybrid vigor accruing from the crossing. In 1941 the flies were raised on cornmeal-molasses agar and in 1942 on a cornmeal-molasses-oatmeal agarless medium. Care was taken to avoid overpopulation of the culture bottles or any rough treatment that might injure the flies. Probably the best attestation of the fitness of the released flies is the fact that they reproduced in nature after the release: young orange-eyed flies were repeatedly found on or near the old experimental fields in about a month after the release of the parents. The proportion of the marked flies which were recaptured is much higher in our experiments than in those of the TIMOFEEFF-RESSOVSKYS.

Yet, the use of mutant genes in experiments on natural dispersal may be open to doubt; after all, they are raised in laboratory instead of in natural habitats. Experiments in which wild flies captured in the vicinity of the experimental fields were marked by a spot of the "platinum" nail polish and then released in the same way as the orange flies, however, have given concurrent results. The marking is done as follows: a fly held by its wings in a delicate forceps is brushed gently against a needle dipped in "platinum" nail polish. Care is taken to apply the polish only to the middle of the mesonotum between or slightly in front of the dorsocentral bristles. A small speck in this position makes the fly readily recognizable by naked eye, and the insect is unable to brush it off. One must guard against smearing the base of the wing or the space between the thorax and the head. Any improperly marked fly is rejected. Marking hundreds or thousands of flies is arduous work. Since the flies so marked display the same behavior as orange-eyed flies, the latter were used exclusively in the experiments of 1942.

Marked flies were released at the center of the experimental field late in the afternoon, shortly before the hour when wild flies are most active (see below). On the next and the following days baited traps were exposed from the time when the flies become active till dusk when flies disappear. Paper drinking cups with a layer of fermenting banana on the bottom served as "traps." They were inserted in a ring at the top of a wire stand about 20 inches tall, and the stands were placed upright by forcing their lower ends into the soil. The construction of the experimenta' fields was done with the aid of a string subdivided into ten meter sections. The recording of the flies that have come to the traps was done as follows. The opening of the trap is covered by a glass funnel with a cut off stem. An empty glass vial is applied to the stem, and the flies are made to run into the vial by exploiting their phototropism. The marked and the wild flies

are counted as they walk out of the funnel. When all the flies are in the vial, the latter is closed by a cotton plug and placed at the base of the stand, protected from the sun if necessary. The trap is re-exposed on its stand. Such "revisions" of the traps are repeated at 20 or 30 minute intervals, several observers on different parts of the field working simultaneously. After the last "revision" of the evening, the flies in the vials are released where caught and the traps are taken off. All the traps on the field are revised the same number of times.

<center>ECOLOGICAL DATA</center>

The available information on the ecology of *Drosophila pseudoobscura* will be published elsewhere, only a summary of the most pertinent facts being given here. The flies display a striking diurnal cycle of activity in their natural habitats, a cycle not at all apparent under laboratory conditions. On a warm and cloudless summer day they begin to visit the traps shortly after dawn. The numbers of flies reach a maximum two to three hours after sunrise, and decline thereafter. No flies arrive in the middle of the day. They reappear two to three hours before sunset, reach a new and frequently a very sharp maximum at about sunset, and disappear completely at dusk. This cycle appears to be determined principally by the changes in the light intensity during the day. The times of the morning and evening maxima change through the year in accordance with the changes in the times of sunrise and sunset. Temperature and humidity fluctuations on successive days affect greatly the total numbers of flies in the traps but not the times when they come, except that below 10°C practically no flies appear at any time. On cloudy and rainy days, and on sunny days in the well shaded parts of the forest, some flies remain active at midday. Crevices of tree bark, especially on oaks, serve as shelter for at least some of the flies during the day, and probably also during the night hours. It is very important that flies raised in the laboratory acquire the activity cycle of the wild flies almost at once after the release. For a day or two a few of the laboratory raised flies begin to come to traps about half an hour earlier than the wild ones, but later even this slight difference is no longer observed.

The productivity of traps exposed in different environments is very unlike. In summer the flies are most abundant in forested localities. The traps exposed close to old oak and pine trees are attended very well, those standing in meadows or brushland are less frequented. The food of the adult consists of yeasts and bacteria. Fungus spores are found in the crops of some specimens and in small amounts. The larval food is unknown, but it is most likely the same as that of the adult. Fermenting sap of bleeding trees is one of the probable sources of the food supply. Seasonal cycles differ according to the climatic conditions: at Andreas Canyon (elevation 800 feet) the population density is highest in spring and lowest in midsummer, while at Keen Camp (4300 feet) and Idyllwild (5300 feet) the highest density is reached respectively in June and early July, no flies at all being obtainable in winter. It is now established that at least in California the flies continue to breed throughout the summer, and young flies appear all the time even during the hot and arid periods.

The productivity of a trap is less if many traps are exposed simultaneously

close to each other than if traps are placed far apart. Experiments conducted in the summer of 1942 at Idyllwild, Mount San Jacinto, demonstrated that traps at 20 meters compete with each other, while traps at 40 and 60 meters show no appreciable interference effect. The effective attractive radius of a banana trap, under the conditions of the experiments, can hardly be more than about 30 meters.

THE MAIN EXPERIMENTS

Four experiments made in the summer of 1942 in the vicinity of Idyllwild, California, will be described in some detail; all other experiments of 1941 and 1942 will be dealt with only briefly, although they involve a variety of conditions not represented in the main series.

First experiment

At 5:30 P.M. on June 2, 3051 orange eyed flies not less than two and not more than seven days old were released at the center (trap No. 12, table 1) of a cross-shaped experimental field east of Saunders Meadow. The traps in this

TABLE 1

Numbers of orange and wild flies in the first experiment.

TRAP NO.	EAST-WEST AXIS								
	1	2	3	4	5	6	7	8	9
1	0–2	0–0	0–1	0–1	0–0	0–0	0–0	0–1	0–0
2	0–1	0–5	0–1	0–2	0–0	0–0	0–3	0–1	0–1
3	0–1	2–7	1–3	1–2	0–0	0–0	0–1	0–2	0–0
4	0–2	1–3	0–0	0–0	0–0	1–0	0–0	1–2	0–1
5	0–1	1–6	1–21	3–11	0–1	1–4	1–3	2–3	0–3
6	0–1	0–5	0–1	0–1	1–0	0–0	0–1	0–3	0–1
7	0–1	7–7	1–0	0–1	0–0	2–4	0–3	1–0	0–1
8	4–1	3–10	1–5	6–7	3–2	14–36	4–24	3–9	1–7
9	1–6	13–9	6–18	3–8	2–2	4–5	4–5	5–7	2–6
10	4–2	28–5	7–4	5–0	2–1	11–3	1–0	1–6	0–2
11	6–4	46–12	32–12	6–1	7–0	7–2	2–3	2–2	2–7
12	68–4	84–5	39–3	22–6	18–0	21–7	2–1	3–2	1–5
13	12–1	48–11	24–1	23–6	3–0	7–5	8–2	4–7	2–1
14	3–6	52–17	18–9	10–7	7–0	6–10	5–0	2–0	1–1
15	1–1	3–2	7–0	6–1	2–1	10–4	3–1	0–0	0–1
16	0–4	10–6	8–7	8–4	4–4	7–6	4–0	0–3	3–5
17	1–7	5–17	3–8	4–5	2–6	4–4	0–1	1–8	0–2
18	0–0	3–14	1–8	0–3	1–1	4–10	0–5	1–9	1–5
19	1–5	3–17	5–15	0–5	0–1	1–11	0–1	1–4	0–4
20	0–4	2–11	2–11	1–2	1–4	1–19	1–9	2–11	0–3
21	0–6	3–43	2–23	4–14	0–0	1–33	0–15	1–19	2–17
22	0–7	4–52	4–80	1–29	0–6	3–43	2–29	2–52	0–23
23	0–2	0–8	1–10	0–5	0–0	0–8	0–11	0–7	0–8
24	—	—	0–7	0–1	0–0	0–3	0–0	0–3	0–6
25	—	—	0–4	0–1	0–1	0–3	0–6	0–2	0–1
26	—	—	0–0	0–0	0–0	0–2	0–7	0–11	0–2
Total	101–69	318–278	163–258	103–123	53–30	105–222	37–131	32–174	15–113

TRAP NO.	NORTH-SOUTH AXIS								
	1	2	3	4	5	6	7	8	9
27	0-1	0-14	1-6	0-2	0-0	0-2	0-0	0-2	0-1
28	0-1	0-5	0-5	0-5	0-0	0-0	0-0	1-4	0-1
29	0-3	0-14	0-8	0-6	0-0	0-2	0-0	0-3	0-5
30	0-6	6-37	4-13	0-10	0-3	2-8	0-10	2-13	0-3
31	0-2	1-24	1-16	2-3	2-1	2-8	0-3	3-10	0-14
32	1-1	1-11	6-5	0-3	0-0	1-3	3-0	1-1	0-4
33	1-0	2-19	1-2	0-0	0-0	1-8	0-0	1-5	0-1
34	2-2	7-14	6-7	1-5	0-1	2-4	2-2	1-3	0-1
35	7-2	15-9	8-5	2-3	0-0	4-7	3-4	2-5	1-15
36	17-5	8-8	4-8	6-1	0-0	3-3	1-2	0-2	0-1
37	9-3	20-4	9-5	0-0	1-1	5-2	1-0	0-2	0-2
38	24-?	20-?	18-?	5-?	4-?	5-?	3-0	3-1	0-1
39	32-?	82-?	59-?	18-?	7-?	21-?	11-20	5-23	3-21
40	5-?	9-?	5-?	0-?	0-?	2-?	0-0	3-2	0-3
41	9-?	18-?	15-?	1-?	2-?	19-?	5-17	3-16	4-26
42	0-?	5-?	4-?	1-?	1-?	3-?	2-20	1-27	1-6
43	0-?	2-?	0-?	0-?	0-?	4-?	0-0	0-4	1-2
44	0-?	3-?	10-?	2-?	2-?	1-?	2-12	1-32	0-9
45	1-?	1-?	7-?	2-?	1-?	4-?	5-19	1-18	0-6
46	0-?	4-?	4-?	5-?	3-?	4-?	2-11	1-11	0-10
47	1-?	2-?	4-?	1-?	0-?	2-?	1-16	2-28	0-6
48	1-?	1-?	1-?	0-?	0-?	2-?	0-4	1-19	0-3
49	—	—	0-?	0-?	0-?	1-?	0-7	1-14	0-7
50	—	—	0-?	0-?	0-?	1-?	1-7	1-15	0-10
51	—	—	0-?	0-?	0-?	0-?	0-1	0-3	1-1
Total	110-?	207-?	167-?	46-?	23-?	89-?	42-155	34-263	11-159

and in the following three experiments were spaced 20 meters apart. The east-west axis of the cross consisted of 23 traps; traps No. 1–18 stood in a ravine with a dense growth of *Pinus ponderosa* and *Libocedrus decurrens;* traps No. 19–23 extended onto a flat with large oaks, *Quercus Kellogii,* and onto a meadow. The north-south axis, traps No. 27–37, 12, 38–48, climbed the drier and more sunlit slopes of the ravine with an open stand of *Pinus Coulteri, Pinus ponderosa, Quercus chrysolepis,* and *Arctostaphylos* sp. The numbers of orange-eyed and of wild flies caught in the traps are shown in table 1. This and the following three tables (tables 1 to 5) are constructed as follows: for each day and for each trap two figures separated by a dash are given; the first of these figures refers to the number of orange-eyed and the second to that of the wild flies recorded. Thus, on the third day of collecting, 32 orange and 12 wild flies were found in trap No. 11 on the east-west axis in the first experiment (32–12, trap No. 11, table 1). No records were made of the numbers of wild flies in traps No. 38–51 on the first six days in the first experiment (the question marks in table 1). On the third day of the first experiment (June 5) the western and the southern arms of the cross were extended by adding three traps to each (No. 24–26 and 49–51, table 1); after nine days so few orange-eyed flies were caught on the field that the experiment was discontinued.

Second experiment

At 6:30 P.M. on June 16, 3297 orange flies two to five days old were liberated at trap No. 16 (table 2) at the center of a cross-shaped field on the slope of a hill west of Saunders Meadow covered with *Pinus Coulteri, Quercus chrysolepis, Q. Kellogii,* and *Arctostaphylos* sp. The east-west axis consisted originally of traps No. 5–27; on June 18 it was extended by adding four traps to each end (No. 1–4 and 28–31), and on June 19 three more traps, No. 32–34, were added to the west arm (table 2). The north-south axis consisted originally of traps No. 42–52, 16, 53–63; on the second and the third days of the experiment both the north and the south arms were extended by adding traps No. 35–41 and 64–70, respectively (table 2). On the sixth day the east and west arms were sacrificed, and the field became linear from north to south. The point of release was now occupied by trap No. 25, the north arm contained traps No. 1–24, and the south arm No. 26–49. The numbers of orange and wild flies in each trap are shown in table 2.

TABLE 2

Numbers of orange and wild flies in the second experiment. EW—east-west axis; NS—
north-south axis. Cross-shaped field for five days, linear on the
sixth and seventh days.

TRAP NO.	1 DAY	2 DAYS	3 DAYS	4 DAYS	5 DAYS	6 DAYS	7 DAYS
	EW	EW	EW	EW	EW	NS	NS
1	—	0–15	0–8	0–19	0–20	0–10	0–32
2	—	0–15	0–11	1–21	2–15	0–31	0–71
3	—	0–6	0–9	0–16	0–20	1–20	0–22
4	—	0–8	1–4	1–29	1–21	0–12	0–31
5	2–10	0–9	1–19	2–22	0–36	1–8	0–24
6	2–32	2–20	1–24	2–24	1–22	0–12	0–11
7	3–10	1–6	4–18	1–22	2–33	0–22	0–32
8	0–0	0–6	0–10	0–13	0–23	0–18	0–42
9	2–10	3–16	2–15	3–54	2–30	0–12	0–13
10	0–14	3–16	2–11	2–18	1–7	2–33	0–22
11	5–8	3–14	1–9	1–12	1–21	0–17	0–22
12	4–7	7–12	4–14	2–17	2–25	2–30	1–43
13	0–3	5–33	2–27	5–19	4–40	0–13	2–37
14	18–39	10–47	9–22	6–33	5–35	0–5	0–12
15	33–34	12–38	21–23	10–40	4–24	0–11	1–28
16	128–27	42–55	9–24	16–30	8–49	1–9	1–16
17	15–12	14–15	13–20	8–31	4–17	0–20	1–43
18	11–28	9–25	8–30	8–59	1–10	0–12	2–35
19	2–7	2–8	7–18	3–14	2–9	0–2	2–8
20	3–11	3–29	1–14	6–31	5–44	4–46	2–20
21	5–10	5–9	7–20	4–41	1–18	4–49	8–64
22	1–19	1–8	1–21	3–32	1–9	1–26	1–44
23	3–25	1–11	3–37	7–62	1–51	8–47	5–55
24	2–10	3–18	1–37	5–24	1–11	6–38	2–68
25	1–8	1–2	1–9	7–14	2–28	1–32	6–110
26	1–22	0–38	1–20	1–21	0–13	6–25	1–27

TABLE 2—*Continued*

Numbers of orange and wild flies in the second experiment. EW—east-west axis; NS—north-south axis. Cross-shaped field for five days, linear on the sixth and seventh days.

TRAP NO.	1 DAY	2 DAYS	3 DAYS	4 DAYS	5 DAYS	6 DAYS	7 DAYS
27	6–30	1–25	5–44	0–42	1–22	8–59	11–135
28	—	2–21	2–29	1–22	0–29	4–51	4–43
29	—	4–28	1–15	1–17	0–42	6–14	3–30
30	—	0–12	1–23	2–25	2–15	2–23	3–33
31	—	0–22	1–22	0–24	1–51	3–33	1–40
32	—	—	0–13	0–24	0–26	3–33	0–67
33	—	—	0–12	0–9	0–6	2–57	1–67
34	—	—	0–14	0–14	0–18	1–41	1–67
	NS	NS	NS	NS	NS		
35	—	—	0–29	0–35	0–61	2–36	2–69
36	—	—	0–21	0–23	0–24	2–49	4–122
37	—	—	0–13	1–26	0–9	1–22	4–56
38	—	0–9	0–24	1–24	0–9	1–33	1–89
39	—	2–41	0–24	3–49	0–13	1–62	3–70
40	—	0–46	0–21	0–18	0–16	3–43	3–89
41	—	2–12	0–15	0–9	0–6	1–60	0–54
42	1–9	1–2	0–10	0–11	0–8	0–46	2–101
43	3–21	0–7	1–8	2–8	1–22	0–30	0–50
44	3–14	1–13	1–8	2–14	0–7	0–36	1–99
45	1–7	2–10	0–7	0–17	0–12	1–14	0–123
46	2–6	2–12	1–11	2–25	1–14	0–20	0–49
47	3–5	1–4	1–8	0–17	1–4	0–5	0–19
48	7–16	11–22	3–22	7–40	3–26	0–2	0–41
49	11–25	14–19	19–57	16–60	6–28	0–5	0–35
50	15–35	8–32	7–29	6–38	5–55	0–16	—
51	34–48	26–63	12–33	16–52	5–35	—	—
52	37–37	20–44	18–45	19–79	10–60	—	—
53	37–13	19–16	6–11	4–31	4–16	—	—
54	29–59	20–31	13–21	9–43	14–46	—	—
55	7–30	7–57	7–42	7–61	2–34	—	—
56	8–11	11–18	9–19	15–57	4–36	—	—
57	4–13	7–24	8–27	8–36	4–39	—	—
58	1–6	3–13	3–17	17–44	8–36	—	—
59	1–3	1–10	1–14	2–8	0–32	—	—
60	3–21	7–27	2–25	2–26	4–15	—	—
61	0–19	2–24	1–29	0–18	3–25	—	—
62	0–20	2–19	0–30	2–51	0–24	—	—
63	2–30	2–54	0–38	2–50	0–46	—	—
64	—	0–33	1–32	1–26	0–33	—	—
65	—	3–60	0–29	1–30	1–32	—	—
66	—	1–47	1–66	3–93	1–46	—	—
67	—	3–33 ·	2–48	2–82	2–82	—	—
68	—	—	2–34	0–41	0–54	—	—
69	—	—	0–50	1–38	1–85	—	—
70	—	—	0–62	1–39	2–66	—	—
Total	456–824	312–1389	229–1625	260–2214	137–1996	78–1350	79–2480

Third experiment

At 6:30 P.M. on June 30, 2868 orange flies two to ten days old were released at trap No. 16 (table 3) on a cross-shaped field in Fern Valley. On the first and second days of collecting the east-west axis of the field consisted of traps No. 1–31; the west arm was extended on the third and fourth days by adding traps No. 68–70. The north-south axis included originally the traps No. 32–46, 16, 47–61; on the third and the fourth days both the north and the south arms

TABLE 3

Numbers of orange and wild flies in the third experiment,
first to fourth days.

TRAP	EAST-WEST				TRAP	NORTH-SOUTH			
	I DAY	2 DAYS	3 DAYS	4 DAYS		I DAY	2 DAYS	3 DAYS	4 DAYS
1	0–26	0–25	0–54	1–28	67	—	—	0–20	0–17
2	0–19	0–24	1–29	0–19	66	—	—	0–17	0–24
3	0–17	1–61	0–50	1–43	65	—	—	0–13	0–13
4	1–21	0–33	0–31	5–30	32	0–19	1–21	0–19	0–14
5	0–12	0–20	0–13	0–20	33	0–10	1–20	1–11	0–9
6	0–16	2–11	1–27	2–28	34	1–17	0–15	0–17	0–11
7	1–28	1–40	5–39	2–24	35	0–16	2–22	1–23	0–22
8	3–111	1–38	9–49	1–45	36	0–23	3–29	2–20	2–22
9	1–53	6–46	5–34	5–36	37	0–21	1–30	2–13	0–17
10	8–42	16–44	4–31	2–18	38	2–11	0–16	0–19	2–10
11	4–9	6–29	2–14	2–6	39	1–12	2–26	2–14	0–7
12	5–4	12–9	5–9	3–6	40	0–21	0–22	1–8	0–9
13	9–7	15–10	7–11	0–5	41	2–15	5–20	1–24	0–15
14	24–8	31–12	10–10	4–11	42	1–4	5–16	5–11	2–7
15	45–21	28–14	10–21	3–14	43	3–14	5–18	0–9	4–10
16	161–30	67–27	12–13	8–19	44	5–7	9–10	2–8	4–6
17	22–6	22–16	13–3	3–19	45	11–5	8–7	1–8	1–5
18	15–8	25–31	11–12	11–19	46	20–8	3–14	5–8	1–17
19	21–26	12–27	7–20	3–27	47	58–16	36–9	14–12	10–7
20	14–16	10–24	11–21	7–18	48	26–14	29–28	20–15	10–10
21	1–12	4–8	4–16	5–55	49	12–10	14–18	8–12	12–17
22	3–8	8–14	4–12	1–11	50	4–10	6–25	8–9	8–23
23	1–9	3–12	3–9	1–16	51	4–6	3–15	4–10	3–11
24	0–3	0–6	1–5	0–5	52	2–16	6–36	7–16	0–12
25	5–60	14–84	16–35	2–25	53	1–10	1–9	6–17	4–5
26	0–30	10–123	11–53	4–41	54	2–10	2–21	2–3	1–11
27	3–48	9–74	11–30	3–26	55	0–12	0–8	1–9	1–7
28	0–39	3–53	2–38	4–42*	56	1–41	2–29	2–22	3–26
29	1–10	1–23	0–32	0–9	57	3–90	4–93	5–74	1–57
30	2–22	1–45	1–25	0–26	58	1–60	5–57	3–56	2–34
31	0–8	2–22	1–4	0–11	59	2–49	1–62	0–36	0–33
68	—	—	0–35	0–18	60	1–58	1–26	0–44	1–26
69	—	—	1–16	0–8	61	0–70	0–50	1–26	0–17
70	—	—	1–16	1–8	62	—	—	2–52	1–22
					63	—	—	1–24	1–37
					64	—	—	0–23	0–25
Rotal	350–729	310–1005	169–817	84–736	Total	163–675	155–772	107–722	74–615

were extended by adding traps No. 65–67 and 62–64 (table 3). On the fifth day, July 5, the south and east arms of the cross were sacrificed, and the two other arms were extended. The field now became ⌐-shaped: the northern arm consisted of traps No. 40–16, and the western arm of No. 16, 47–68 (table 4). The experimental field is mostly level and dry, covered with a sparse stand of large *Quercus Kellogii* and *Pinus ponderosa* and a dense undergrowth of the

TABLE 4

Numbers of orange and wild flies on the fifth to seventh days in the third experiment; traps in a ⌐-shaped file, the point of release at No. 16.

TRAP	5 DAYS	6 DAYS	7 DAYS	TRAP	5 DAYS	6 DAYS	7 DAYS	TRAP	5 DAYS	6 DAYS	7 DAYS
40	0–25	0–11	0–30	24	0–12	0–3	0–4	54	0–9	0–4	0–4
39	0–6	0–7	0–20	23	1–18	1–17	0–14	55	2–2	1–6	0–5
38	0–7	0–3	0–33	22	4–10	0–11	0–11	56	1–24	0–17	1–20
37	0–4	0–10	0–14	21	7–14	1–10	1–14	57	2–39	1–33	0–22
36	0–2	0–0	0–4	20	6–7	2–10	2–17	58	1–51	0–13	1–25
35	0–14	0–7	0–12	19	7–41	4–17	2–34	59	0–42	1–33	1–23
34	0–8	0–11	0–7	18	5–19	3–13	1–28	60	0–15	1–20	2–26
33	1–11	0–16	0–27	17	10–20	2–4	1–12	61	1–26	2–20	1–17
32	0–22	0–26	0–12	16	12–47	1–17	4–21	62	0–27	0–24	1–28
31	0–19	0–8	0–6	47	5–19	3–9	1–3	63	1–55	1–26	1–33
30	0–16	0–10	0–7	48	5–23	0–6	0–5	64	0–13	0–5	0–15
29	0–10	0–9	0–8	49	10–8	3–9	1–3	65	0–26	0–15	1–23
28	5–33	4–20	2–45	50	8–32	2–2	0–10	66	0–18	0–23	0–20
27	3–28	0–7	1–24	51	3–5	0–4	1–6	67	0–10	0–12	0–24
26	11–34	9–28	3–29	52	0–7	0–5	1–3	68	0–54	0–33	0–44
25	11–84	14–55	9–123	53	1–3	2–7	0–6	Total	123–1019	58–656	39–921

fern *Pteris aquilina;* the west arm (traps No. 60–68, table 4) debouches into a more densely wooded territory near a stream.

Fourth experiment

Started at 6 P.M. of July 23 by release of 4810 orange flies two to five days old at trap No. 16 of a cross-shaped field south of Idyllwild. Figure 1 shows the numbers of orange-eyed (large straight numerals in the middle) and of wild flies (smaller slanting numerals on the right) recorded in every trap on the first day of collecting, July 24. Figure 1 may be taken as a scheme of all the cross-shaped experimental fields. Since in one day after the release the orange flies had already reached the ends of the east and west arms (fig. 1), from the second day on the field was transformed into a linear one, from east to west. The east arm included the traps No. 55–44, 1–16, and the west arm No. 16, 17–43 (No. 16, of course, being the point of release). The numbers of the orange and wild flies recovered on the second to the fifth days of the experiment are shown in table 5. The central portion of the field is covered with a rather dense growth of young *Pinus ponderosa*, while the peripheral portions are a more open country with oaks, *Quercus Kellogii*.

Examination of tables 2–5 shows that the numbers of wild flies found in different traps vary within wide limits. Day after day some traps attract more flies than other traps. The orange-eyed flies are found at the beginning of the experiments chiefly at or near the point of release, but in the course of time they tend to occur in the same traps which attract most wild flies. This shows
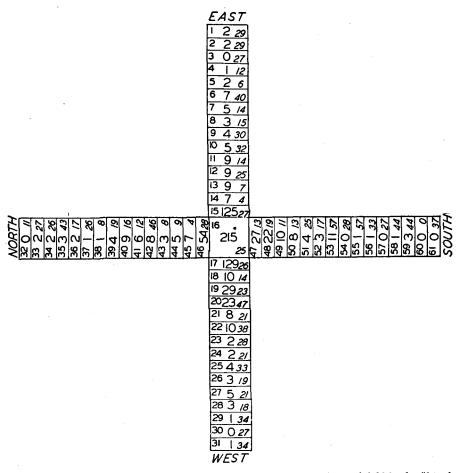
EAST

Trap	Orange	Wild
1	2	29
2	2	29
3	0	27
4	1	12
5	2	6
6	7	40
7	5	14
8	3	15
9	4	30
10	5	32
11	9	14
12	9	25
13	9	7
14	7	4
15	125	27

NORTH → SOUTH

Trap	Orange	Wild
32	0	11
33	2	27
34	2	26
35	3	43
36	2	17
37	1	26
38	1	8
39	4	19
40	9	16
41	6	12
42	8	46
43	3	8
44	5	9
45	7	4
46	54	28
16	215	25
47	27	13
48	22	9
49	10	11
50	8	13
51	4	25
52	3	17
53	11	57
54	0	28
55	1	57
56	1	33
57	0	27
58	1	44
59	3	44
60	0	0
61	0	37

WEST

Trap	Orange	Wild
17	129	26
18	10	14
19	29	23
20	23	47
21	8	21
22	10	38
23	2	28
24	2	21
25	4	33
26	3	19
27	5	21
28	3	18
29	1	34
30	0	27
31	1	34

FIGURE 1.—The results of the first day of collecting on the experimental field in the "fourth experiment." The figure at the left in each cell indicates the number of the trap; the figure in the middle, a number of orange-eyed flies; the figure on the right, the number of wild flies.

that the terrains on which our experimental fields were built were not quite uniform. We have pointed out above that traps standing near old trees or in dense vegetation in moister places attract more flies than do traps in more open or drier situations. The flies are attracted to places where they find food and shelter. Fortunately, these non-uniformities were never large enough to produce striking displacements of the flies in one direction from the point of the release of the marked flies.

Another, and more important, non-uniformity in our experiments is intro-

duced by the variation of temperature on different days (table 6). Temperature and humidity records were kept for all the evenings when flies were being collected. The readings were made at about half-hour intervals. As pointed out above, the flies in their natural habitats display two sharp maxima of activity,

TABLE 5

Numbers of orange and wild flies on the second to fifth days in the fourth experiment; traps in a single file, the point of release at No. 16.

TRAP	2 DAYS	3 DAYS	4 DAYS	5 DAYS	TRAP	2 DAYS	3 DAYS	4 DAYS	5 DAYS
55	0-62	0-78	0-109	0-69	17	40-17	11-20	3-18	3-13
54	0-99	0-105	0-183	0-63	18	6-4	2-4	0-9	0-7
53	0-27	0-40	0-203	0-31	19	28-23	8-24	6-27	2-19
52	0-47	0-102	0-174	0-76	20	11-29	5-15	6-24	2-22
51	0-23	0-17	1-31	0-47	21	6-27	3-21	3-14	0-17
50	0-69	0-54	0-69	0-19	22	8-40	2-40	2-39	6-46
49	0-17	0-14	0-24	0-23	23	2-27	0-29	5-33	2-42
48	0-12	0-7	0-9	0-8	24	3-22	2-17	0-10	3-26
47	0-19	0-7	0-12	0-10	25	2-33	2-28	3-33	1-26
46	0-11	0-5	0-13	0-7	26	1-17	2-18	1-15	0-23
45	0-5	0-3	0-13	0-9	27	3-16	3-26	1-27	0-30
44	1-5	0-4	0-25	1-6	28	3-12	1-24	1-31	0-21
1	5-23	1-28	1-29	2-55	29	2-27	2-27	2-23	0-15
2	0-22	1-21	0-33	1-18	30	0-18	2-25	0-33	2-32
3	1-19	·2-24	1-20	1-18	31	2-19	1-8	1-15	0-21
4	1-6	1-2	0-10	1-6	32	0-26	0-14	1-23	0-18
5	0-6	0-9	0-6	0-6	33	0-24	0-20	0-19	0-19
6	2-71	3-27	2-27	5-25	34	0-19	0-16	0-13	0-17
7	4-11	1-9	4-13	0-8	35	0-30	0-19	0-22	0-15
8	1-15	3-8	1-10	2-9	36	1-14	0-23	1-16	0-26
9	4-27	0-26	0-23	2-21	37	0-19	0-19	0-14	0-19
10	8-29	4-29	1-11	1-13	38	0-45	0-34	0-30	0-55
11	11-21	3-26	2-8	2-28	39	0-38	0-39	2-19	0-11
12	19-32	7-23	4-15	0-18	40	0-22	0-13	0-8	0-15
13	14-16	2-17	0-5	4-13	41	0-60	1-44	1-25	1-38
14	2-9	2-8	0-9	1-5	42	0-22	0-10	0-17	0-16
15	45-34	10-33	6-22	4-30	43	0-47	0-50	0-40	0-24
16	70-43	15-15	11-24	2-22	Total	306-1477	102-1368	73-1727	51-1296

one a short time before sunset and the other in a few hours after sunrise. We believe that the temperature at the time of these maxima of activity is most important as far as the fly movements are·concerned. The temperatures at the times of the evening maxima (F°) are shown in table 6. We have only a few records of the temperatures during the morning maxima of activity on the same days. However, the summer climate at Idyllwild is remarkably equable, and the morning and the evening temperatures on the same day are in general closely correlated.

THE DISTRIBUTION OF THE WILD FLIES

In making a detailed analysis of the data it will be well to consider first the

implications relating to the wild flies. These were distributed sufficiently uniformly throughout the regions studied that some were caught in nearly all the traps on each day. In the first experiment in which the average number caught per trap was small (one to 13 on different days) at least one wild fly was caught in 309 of the 369 traps (84 percent). In the other experiments, in which the average caught per trap was higher on all days (14 to 52), there were only three among 1072 traps which failed to yield at least one wild fly.

On the other hand, the distributions were obviously not random. In a random distribution, the numbers on a given day should exhibit a Poisson distribution with variance approximately equal to the mean. But, as brought out in table 6, the variance of numbers per trap was always much greater than the mean ($\sigma^2/m = 9.7$ in experiment I, 8.6 in experiment II (first five days)) 14.1 in experiment III (first four days) and 5.4 in experiment IV (single line, five days).

TABLE 6

Statistics of wild flies caught on successive days in experiments I to IV. The first column gives the day, and the second column the temperature (F), the third column the number (n) of flies caught in those traps in which counts were made on the first day, the fourth column gives the mean number per trap (m), the fifth column the standard deviation of the numbers (σ), and the sixth column the ratio, σ^2/m as an index of randomness of dispersion ($\sigma^2/m = 1$ if Poisson distribution). The figures in experiment I are based on 34 traps, spaced 20 m apart in three arms of a cross. In experiments II, III, and IV they are based on 45, 61, and 61 traps respectively, similarly spaced, in four arms of a cross. Similar data (n', m', σ' and σ'^2/m') are given in additional columns relating to two arms of the cross in which trapping was continued for a greater number of days in experiments II, III, and IV (23, 31, and 31 traps respectively).

| | | I N.E.W. | | | | | | | |
DAY	TEMP.	n	m	σ	σ^2/m				
1	56°	95	2.8	2.1	1.6				
2	67°	437	12.9	11.9	11.0				
3	66°	327	9.6	14.1	20.5				
4	59°	159	4.7	5.5	6.4				
5	55°	35	1.0	1.7	2.7				
6	65°	261	7.7	10.3	13.7				
7	62°	139	4.1	6.8	11.2				
8	63°	208	6.1	9.1	13.6				
9	60°	151	4.4	5.4	6.5				
Total		1812	5.9	7.4	9.7				
		II N.E.S.W.				II' N.S.			
DAY	TEMP	n	m	σ	σ^2/m	n'	m'	σ'	σ'^2/m'
1	70°	824	18.3	12.9	9.0	475	20.7	14.3	9.9
2	71°	981	21.8	15.6	11.1	576	25.0	17.9	12.8
3	70°	997	22.2	11.6	6.0	535	23.3	13.5	7.8
4	71°	1461	32.5	17.4	9.4	816	35.5	19.4	10.6
5	68°	1197	26.6	14.1	7.5	669	29.1	15.7	8.5
6	73°	—	—	—	—	718	31.2	17.1	9.4
7	63°	—	—	—	—	1203	52.3	33.8	21.8
Total		5460	24.3	14.3	8.6	4992	31.0	18.8	11.5

		III N.E.S.W.					III' N.W.		
DAY	TEMP.	n	m	σ	σ^2/m	n'	m'	σ'	σ'^2/m'
1	70°	1404	23.0	21.6	20.3	538	17.4	13.1	9.8
2	72°	1777	29.1	22.4	17.2	879	28.2	24.8	21.9
3	77°	1323	21.7	15.3	10.8	540	17.4	11.2	7.2
4	71°	1179	19.3	12.4	8.0	550	17.7	11.6	7.6
5	74°	—	—	—	—	717	23.1	17.5	13.2
6	75°	—	—	—	—	427	13.8	11.2	9.2
7	74°	—	—	—	—	575	18.5	22.1	26.4
Total		5683	23.3	17.9	14.1	4222	19.5	15.9	13.6

		IV N.E.S.W.					IV' E.W.		
DAY	TEMP.	n	m	σ	σ^2/m	n'	m'	σ'	σ'^2/m'
1	71°	1465	24.0	12.8	6.8	740	23.9	10.1	4.3
2	72°	—	—	—	—	715	23.1	13.1	7.4
3	74°	—	—	—	—	631	20.4	9.1	4.0
4	78°	—	—	—	—	616	19.9	9.6	4.7
5	69°	—	—	—	—	655	21.1	11.7	6.5
Total		1465	24.0	12.8	6.8	3357	21.7	10.7	5.4

That the departures from randomness were due to persistent local conditions is shown by the correlation between the numbers caught in the traps on the first day and on subsequent days (table 7). The average correlation between first and second day was .645 based on 171 traps. There was only a slight falling off in the correlation between first and third day (.616), and first and fourth day (.598) based on the same 171 trap stations on each day. That between first and fifth day (.488) is based on the same 110 trap stations in experiments I, II, and IV but does not include experiment III. The average correlation between first day and sixth to ninth days (a total of 136 trap stations in experiment I only) was appreciably lower (.381). On taking into account the rate of

TABLE 7

The correlation between the numbers of wild flies caught in traps on the first day and the numbers caught in the same traps on subsequent days. The number of traps is indicated in parentheses under the designation of the experiment (I to IV). The standard errors would be somewhat larger than indicated by the formula $SE_r = (1-r^2)\sqrt{n}$ because of correlation between adjacent traps. The unweighted averages are given in the last column.

DAYS	I (34)	II (45)	III (61)	IV (31)	AV.
1–2	.552	.699	.633	.693	.645
1–3	.547	.540	.740	.560	.616
1–4	.532	.542	.647	.657	.598
1–5	.565	.417	—	.507	.488
1–6	.379	—	—		
1–7	.311	—	—		.381
1–8	.455	—	—		
1–9	.380	—	—		

dispersion of the flies, discussed later, it becomes apparent that these correlations must depend on more or less persistent local conditions. The tendency to aggregate about old oak and pine trees appears to be the major factor here.

ACTIVITY AND TEMPERATURE

In experiment I (table 6), the average number of wild flies caught per trap varied rather closely with the temperature which was lower throughout this experiment (55° to 67°) than on any day of any other experiment with one exception (63° on the seventh day of experiment II). The average number caught per trap in experiment I was much lower than in the other experiments, but this might be attributed to earliness of season as well as to an effect of low temperature. However, there can be little doubt that the exceptionally low catches on the first and fifth days at temperatures of 56° and 55° respectively reflect low activity of the flies at these temperatures. As will be brought out later, the catches of orange flies and the amounts of dispersion corroborate this conclusion.

On the other hand, there is no relation, that can be relied upon, between temperature and catch per trap in experiments II, III, and IV. It happens that the largest average per trap (52.3 on the seventh day of experiment II) came at the *lowest* temperature (63°) in these experiments. This might suggest an optimum at about 63°. The average catch for these three experiments was so nearly the same that they may be thrown together without serious error. The correlation between mean number per trap and temperature is $-.64$, based on 19 entries (m table 6 where available, otherwise m'). The regression, of catch on temperature is $-1.57 \pm .45$ flies per degree Fahrenheit or 3.5 times the standard error. These values, however, are greatly affected by the record on the one exceptional day referred to above. Omitting this, the remaining 18 days yield a correlation of only $-.28$ and a regression of $-.49 \pm .42$.

THE FORM OF DISTRIBUTION OF THE RELEASED FLIES

The first question in connection with the orange flies concerns the relation between observed distribution along a single line of traps, or along two lines forming a cross, and the total actual distribution in the area. It is obvious from inspection of tables 1 to 5 that most of the flies were still close to the point of release after a day and that they were moving out rapidly in all directions on subsequent days. This scattering, however, is not wholly at random. The numbers in the various directions (table 8) differ much more than expected purely from chance, ($x^2 = 630$ n = 66) but the evidence that the wild flies tend to cluster at certain points makes a purely random scattering unlikely *a priori*. There was in fact an excess of orange flies in the same directions in which wild flies were caught in excess. Table 8 shows the numbers of wild flies and of orange flies captured on each day at the point of release (c) and in each direction from this. In the case of the wild flies, only those points are considered in which traps were put out on the first day. All traps are considered in the case of the orange flies. The two populations are not strictly comparable in any case because of the changing distributions of the orange flies, in comparison with the relative stability of the wild population. The 2×2 correlation tables

TABLE 8

The numbers of wild flies and of the released orange flies caught at the central trap (C) and in north (N), east (E), south (S), and west (W) lines of traps on successive days. In the case of the wild flies, the same 11 trap stations in each direction are considered on each day of experiments I and II, the same 15 traps in each direction in experiments III and IV. In the case of the orange flies all traps are included. In experiment I, wild flies were not recorded in the south arm of the cross.

| | DAY | WILD | | | | | | ORANGE | | | | | |
		C	N	E	S	W	TOTAL	C	N	E	S	W	TOTAL
I	1	4	26	22	—	43	95	68	37	15	73	18	211
	2	5	159	69	—	204	437	84	60	101	147	133	525
	3	3	80	66	—	178	327	39	40	49	127	75	330
	4	6	38	34	—	81	159	22	11	24	35	57	149
	5	0	6	6	—	23	35	18	3	15	20	20	76
	6	7	47	54	—	153	261	21	20	40	69	44	194
	7	1	21	43	—	74	139	2	10	12	32	23	79
	8	2	50	36	—	120	208	3	11	15	23	14	66
	9	5	47	29	—	70	151	1	1	5	10	9	26
II	1	27	223	167	225	182	824	128	117	69	92	50	456
	2	55	228	217	293	188	981	42	90	46	88	46	312
	3	24	238	192	273	270	997	9	63	48	56	53	229
	4	30	361	274	425	371	1461	16	75	36	77	56	260
	5	49	271	296	349	232	1197	8	32	25	50	22	137
	6	32	265	—	421	—	718	1	30	—	47	—	78
	7	110	393	—	700	—	1203	6	28	—	45	—	79
III	1	30	203	394	472	305	1404	161	46	101	117	88	513
	2	27	286	416	486	562	1777	67	45	119	110	124	465
	3	13	212	422	361	315	1323	12	23	59	84	98	276
	4	19	181	333	296	350	1179	8	16	31	58	45	158
	5	47	365	—	—	305	717	12	71	—	—	40	123
	6	17	222	—	—	188	427	1	40	—	—	17	58
	7	21	376	—	—	178	575	4	22	—	—	13	39
IV	1	25	300	311	425	404	1465	215	107	190	91	230	833
	2	43	—	341	—	331	715	70	—	118	—	118	306
	3	15	—	290	—	326	631	15	—	40	—	47	102
	4	24	—	241	—	351	616	11	—	23	—	39	73
	5	22	—	273	—	360	655	2	—	27	—	22	51

of excess and deficiency in the number of wild and orange flies in the various directions on each day are shown below. A few cases in which the number in a direction was the exact average are omitted. On certain days only two directions are available for comparison, on others three or four directions. They are given separately.

| | orange | | | | orange | | | | orange | |
	+	−			+	−			+	−
wild	+ 7	1		wild	+ 7	2		wild	+ 18	7
	− 7	7			− 4	8			− 5	18
	2 directions				*3 directions*				*4 directions*	

Since there is only one degree of freedom for each pair of entries in the cases in which counts were made in only two directions, two degrees of freedom for each set of three entries for days with counts in three directions and three degrees of freedom from the sets of four entries for days with counts in four directions, the frequencies above were multiplied by $\frac{1}{2}$, $\frac{2}{3}$, and $\frac{3}{4}$, respectively. The value of χ^2 for the combined table, weighted in this way is 13.7, which, with one degree of freedom, is highly significant.

There was very little wind during the experiments, making it unlikely that there was any systematic drift of the released flies from this cause. It is probable (as pointed out) that differences in terrain were in part responsible for the differences in the numbers caught in different directions. In the main, however, it appears from the tables that local differences in conditions are responsible. We will accordingly treat the distributions as centered at the point of release rather than at the intersections of the east-west and north-south means.

The simplest hypothesis with respect to the dispersion is that the distribution on any day is a radially symmetrical bivariate normal one except as modified by local conditions. In this case, the distribution along a line through the center should have the same form and variance as that along any line whether through the center or not and hence should be representative of the total in a given direction. Unfortunately it is obvious from inspection that the observed distributions are far from normal, at least on the first day or two. There are excessive frequencies at the point of release, associated with excessive scattering of other flies—that is, distributions that are leptokurtic instead of normal. In a normal frequency distribution the fourth moment about the mean is three times the square of the second moment about the mean (and less than three

TABLE 9

The kurtosis of the distribution of orange flies along a line of traps, as measured by $n\Sigma r^4 f/(\Sigma r^2 f)^2$. The figures under I, II, III, and IV are based on four arms of the cross, while the figures under II', III', and IV' are based on the two arms that were continued to the ends of the experiments. The last column gives the weighted average of I, II, III, and IV. II', III', and IV' were used where II, III, and IV were not available.

DAY	I	II	II'	III	III'	IV	IV'	AV.
1	9.82	7.64	7.07	10.41	10.25	8.34	8.44	8.88
2	5.69	5.02	4.93	4.41	3.57	—	5.86	5.21
3	4.24	4.39	5.28	2.76	2.32	—	4.15	3.84
4	4.30	3.61	4.01	3.04	3.03	—	3.97	3.68
5	4.45	4.03	4.62	—	2.66	—	3.01	3.59
6	3.47	—	3.55	—	1.77	—	—	3.21
7	3.05	—	2.65	—	1.93	—	—	
8	2.43	—	—	—	—	—	—	2.73
9	3.89	—	—	—	—	—	—	

times if the moments are taken about any other origin). Table 9 shows the value of $n\Sigma r^4 f/(\Sigma r^2 f)^2$ on all days of the four experiments, r being the distance from the point of release (in 20 meter units) and f the corresponding frequency.

The figures under I, II, III, and IV are based on the cross shaped plots with the frequency in the central trap doubled, as an element in both the east-west and the north-south distribution. The figures under II′, III′, and IV′ are based on the two lines of traps that were continued to the ends of those experiments. The

TABLE 10

Estimates of the number of orange flies, that would have been caught on successive days of each experiment if traps had been placed throughout the region of dispersal in a grid with 20 meter spacing, assuming no competitive effect. Without this assumption, all estimates must be multiplied by an unknown constant, K. Column (1) gives the experiment and day, column (2) the ratio, R, of wild flies caught on the day in question in the traps involved in table 6 to that on the first day (second day in experiment I) to be used as an index of activity, column (3) gives an estimate of orange flies by the formula $2\pi\Sigma rf$ which gives no weight to flies caught at the point of release and is undoubtedly an underestimate. In column (4) this is divided by the index, R, of column (2), column (5) gives an estimate by the formula $2\pi\Sigma rf+c$ which is probably a slight overestimate; in column (6) this is divided by the index, R, of column (2). The last column gives the ratio of the estimates with (5) and without (3) inclusion of the central station. These are based on all four arms of the cross (except that only three arms were available for calculation of the ratio, R, in experiment I).

	(1) DAY	(2) R	(3)	(4) (3)/(2)	(5) (3)+c	(6) (5)/(2)	(7) (5)/(3)
I	1	.217	498	(2295)	566	(2601)	1.136
	2	1.000	1830	1830	1914	1914	1.046
	3	.748	1481	1980	1520	2032	1.026
	4	.364	655	1799	677	1860	1.034
	5	.080	303	(3787)	321	(4012)	1.059
	6	.597	1067	1787	1088	1822	1.020
	7	.318	468	1472	470	1478	1.004
	8	.476	496	1042	499	1048	1.006
	9	.346	160	462	161	465	1.006
II	1	1.000	1516	1516	1644	1644	1.084
	2	1.191	1695	1423	1737	1458	1.025
	3	1.210	1379	1140	1388	1147	1.006
	4	1.773	1904	1074	1920	1083	1.008
	5	1.453	1013	697	1021	703	1.009
III	1	1.000	1598	1598	1759	1759	1.101
	2	1.266	2630	2077	2697	2130	1.026
	3	.942	2303	2446	2315	2458	1.005
	4	.842	1291	1537	1299	1546	1.006
IV	1	1.000	2975	2975	3190	3190	1.072

standard error in the case of a normal distribution is approximately $\sqrt{24/n}$ where n is the total number of independent entries. The entries cannot be considered to be wholly independent here because of the tendency of the flies to cluster in particular localities. Nevertheless, there can be no doubt that the departures from three are highly significant for several days. Leptokurtic distributions of this sort would result from the superposition of two normal distributions, one of small standard deviation relating to flies that move only short

distances if at all and one of large standard deviation relating to flies that make at least one long flight. In the course of time it is likely that all surviving flies will fall in the latter category, giving a progressive approach toward normality such as is observed.

THE DECLINE IN NUMBERS IN THE RELEASED POPULATION

In order to make approximate estimates of the properties of the total distribution, it will be assumed that the latter may be represented sufficiently well for this purpose by a radially symmetrical figure in which the ordinate (z) at a given distance (r) in any direction from the center (point of release) is proportional to the average ($\bar{f}$) of the frequencies at this distance in the four (or two) observed directions. The total frequency in the bivariate distribution can be represented by $\int_0^{2\pi}\int_0^{\infty}\text{rzdrd}\theta$, θ being the angle between the direction of the fly from the center and a given axis, and rdrdθ the element of area. The total number that would have been caught if traps had been placed at all intersections in a grid of lines spaced at 20 m intervals both ways instead of at 20 m intervals along single lines may thus be estimated roughly as $2\pi\Sigma r\bar{f}$, assuming no competition between traps.

It is probable, however, that there is some competition between traps as close as 20 meters. DOBZHANSKY and EPLING (in press) concluded from carefully controlled tests that traps in a 20 m×20 m grid catch only about 50 percent to 70 per cent as many flies as traps in a 40 m×40 m or more widely spaced grid. The estimate of the potential catch in a grid with 20 m×20 m spacing may then be represented by $2\pi K\Sigma r\bar{f}$ where K is an unknown constant, probably between .50 and one, designed to measure the competitive effect in a grid as compared with a single line.

This formula makes no allowance for the catch at the point of release, especially important on the first day. It does not appear to be possible to make accurate allowance for this, since the catch per trap cannot be considered as strictly proportional either to the ordinate at the appropriate distance or to the frequency in the 20 m×20 m square centered at this point in the model bivariate distribution. It is probable, however, that the frequency in the central trap (c) should be given something approaching full weight, giving as an upper limit for the total catch in a 20 m×20 m grid, $2\pi\Sigma r\bar{f}+c$ if K = 1.

Table 10 gives both estimates (omitting factor K), $(2\pi\Sigma r\bar{f})$ in column 3 and $(2\pi\Sigma r\bar{f}+c)$ in column 5. The ratio (5)/(3) is given in column 7. Table 11 gives similar estimates for the single lines that were continued to the ends of the experiments. In no case do the two estimates differ to an important extent except on the first day in which that in which c is added is on the average 10 percent the larger. We shall use this larger estimate in later discussions.

In the case of the orange flies there are four reasons for changes in the actual numbers caught from day to day: (1) a systematic tendency to decrease because of the dispersion from the center with consequent increase in the average distance from the lines of traps, (2) real changes in the size of population (necessarily decreases since no orange flies were added), (3) changes in the proportion caught due to differences in activity, (4) accidents of sampling. The for-

mulae discussed above are intended to obviate the first of these. It may be seen by inspection that their application gives population estimates which do not fall off at the rapid rate found (with a few exceptions) in the actual captures. Indeed in experiments I, II, and III the estimates for the first day are less than those for certain later days by amounts too great to be attributed to

TABLE 11

Similar estimates to those of table 10 but based on the two arms of the cross in which trapping was continued to the ends of the experiments.

	(1)	(2) R	(3)	(4) (3)(2)	(5) (3)+c	(6) (5)/(2)	(7) (5)(3)
II	1	1.000	1772	1772	1900	1900	1.072
	2	1.213	2240	1847	2282	1881	1.018
	3	1.126	1423	1264	1432	1272	1.006
	4	1.718	2331	1357	2347	1366	1.007
	5	1.408	1219	866	1227	871	1.006
	6	1.512	1451	960	1452	960	1.000
	7	2.533	1561	616	1567	619	1.005
III	1	1.000	1398	1398	1559	1559	1.115
	2	1.626	2790	1716	2857	1757	1.024
	3	1.004	2422	2412	2434	2424	1.005
	4	1.022	1106	1082	1114	1090	1.007
	5	1.333	2020	1515	2032	1524	1.006
	6	.794	1357	1709	1358	1710	1.001
	7	1.069	983	920	987	923	1.003
IV	1	1.000	3704	3704	3919	3919	1.058
	2	.953	2975	3122	3045	3195	1.023
	3	.841	1558	1853	1573	1870	1.009
	4	.821	1470	1790	1481	1804	1.008
	5	.873	1106	1267	1108	1269	1.002

accidents of sampling. There were clearly considerable differences in the proportions caught on different days.

In the case of the wild flies the first of the above causes of change does not hold, but the real population changes may be in either direction. There is no obvious trend in experiments I, III, and IV, but there is a suggestion of a rising trend in experiment II. There are also irregularities from day to day that indicate changes in the proportions caught.

The almost perfect correlation between the catch of wild flies and temperature in experiment I has been noted. The estimates for the orange flies show closely similar fluctuations. It seems reasonably certain, therefore, that the estimates for the orange flies are low on certain days, especially on the first, fourth, and fifth days of experiment I, because of exceptionally low temperatures on those days (56°, 59° and 55°, respectively). On the other hand, little significance can be attributed to differences in temperatures above this in view of the relations in the wild flies discussed above. Excluding these three days in

experiment I, the estimate for the orange flies (column 5, tables 10 and 11) indicate on the whole a downward trend. In table 12 these estimates are given on a scale on which 100 is that for the first day (second day in experiment I). Those relating to days on which the temperature was below 60° are in parentheses and are omitted in calculating the average. The figures used are those for captures in four directions where available, but two directions where not.

TABLE 12

Estimates of the relative numbers of orange flies on each day of each experiment, taking the number on the first day as 100 (second day in experiment I). These are based on the entries in column 5, table 10, as far as possible, on column 5, table 11, for the later days of experiments II, III, and IV. These are independent of the counts of wild flies. Estimates for three days in experiment I in which the temperature was below 60° F (in parentheses) were not used in calculating the unweighted average given in the last column.

DAY	I	II	III	IV	AV.
1	(30)	100	100	100	100
2	100	106	153	78	109
3	79	84	132	40	84
4	(35)	117	74	38	76
5	(17)	62	130	28	74
6	57	76	87	—	73
7	25	82	63	—	57
8	26	—	—	—	—
9	8	—	—	—	—

The regression of relative number on day is found to be 7.5 ± 1.4 for the averages from the first to seventh day (at least three experiments). This is 5.4 times the standard error which with five degrees of freedom may be considered significant. (Probability about .003 of being exceeded by accidents of sampling.) The ratio of this regression to the estimate on the middle (fourth) day indicates a rate of decrease of about 9.2 percent per day in the orange population.

Another method of attack on the problem is to use the ratio of wild per station on a given day to that on the first day as an index of relative activity by which the estimate of the number of orange flies on the same day may be divided in order to reduce the latter to comparability with the number on the first day. This is done in columns 4 and 6 of tables 10 and 11. The entries in column (6) table 10, where available, table 11 otherwise, are transformed in table 13 to a scale on which the entry for the first day becomes 100. The resulting numbers fall off more or less regularly from day to day in experiments IV and II. In experiment I the records of the first and fourth days are brought fairly well into line with the others, but there is overcorrection to an extreme extent of the figure for the fifth day. However, the catch of wild flies (35) was too small on this day to give an adequate basis for calculations. In experiment III the results are somewhat less irregular in table 13 than in table 12 but there is a much less rapid decline than in the other experiments. The unweighted averages for the first seven days, omitting nothing, yield a regression of 6.4

± 1.7. This is 3.7 times its standard error and probably significant. Taken in ratio to the value on the fourth day, it indicates a rate of decrease of population of about 8.2 percent per day instead of 9.2 percent from the actual numbers (temperatures of 60° or more).

Neither of these methods of estimating the rate of decline in the numbers of the released flies is unequivocal. Those of table 12 are entirely independent of the wild flies, but may merely reflect an average decrease in activity of the

TABLE 13

Estimates of the relative numbers of orange flies in each day of each experiment, as in table 12 but based on the entries in column 6 in tables 10 and 11 and thus supposedly corrected for differential activity on different days by use of the index (R), based on the numbers of wild flies caught. All figures are used in the unweighted average, including the highly unreliable estimate for the fifth day of experiment I. Without this the average for the fifth day becomes 58.

DAY	I	II	III	IV	AV.
1	100	100	100	100	100
2	74	89	121	82	91
3	78	70	140	48	84
4	72	66	88	46	68
5	154	43	98	32	82
6	70	51	110	—	77
7	57	33	59	—	50
8	40	—	—	—	—
9	18	—	—	—	—

flies during the four experiments. Those of table 13 should be free on the average from the effects of external conditions but may merely reflect (in reverse) an average rising trend in the wild populations of the four experiments. However, there is no apparent reason for a systematic deterioration of external conditions in all experiments nor for a systematic rising trend in the four wild populations, recalling that they were started at intervals from June 2 to July 23. The fact that both methods give approximately the same rate of decline tends to indicate that this rate, 8 or 9 percent per day, is approximately the actual rate of decline in the numbers of the released flies. The estimates for the eighth and ninth days of experiment I were not used in either case, but as far as they go indicate an even more rapid decline in numbers after seven days.

THE DENSITY OF THE WILD POPULATIONS

Another question on which estimates are of interest is the density of the wild population. We have estimated that 566K orange flies would have been caught on the first day of experiment I (column 5, table 10) if traps had been set in a grid with 20 m × 20 m spacing, extending sufficiently to cover the entire range. But 3051 flies had been released. Assuming a 9.2 percent loss per day, the number of orange flies on hand after one day should be 2770. The proportion which would have been captured under the postulated conditions is .204K(= 566K/2770). On this day 95 wild flies were caught in 34 traps. The number that would have been caught per trap in a grid with 20 m × 20 m spac-

ing may be estimated as $2.79K(=95K/34)$, assuming the same factor K as in the case of the orange flies to allow for the greater competition between traps in a grid than in single lines. The actual number of wild flies per 400 square meters may thus be estimated at $13.7(=2.79K/.204K)$ or 3.4 per 100 square meters.

The catch on this first day was poor, presumably because of the low temperature $(56°)$. It is therefore desirable to make an estimate from the second day's catch which was the largest in this experiment. It will be assumed that the original 3051 orange flies have been reduced to $2515(=3051 \times .908^2)$. The proportion of those which would be caught in a grid with 20 m $\times$ 20 m spacing is estimated at $.761K(=1914K/2515)$. On this day 437 wild flies were caught in 34 traps or 12.85 per trap. The estimated density of the wild population on the same basis as for the first day is 4.2 per 100 square meters. This is probably somewhat more accurate than the estimate of 3.4 per 100 square meters from the first day's data, because of the larger numbers, although possible errors in the estimate of the rate of decline have been compounded. For the latter reason it is not desirable to go on to estimates from later days, although these are on the whole consistent. The estimates of density, per 100 square meters, of the wild population during the first two days of each of the four experiments, calculated as above, are given below.

Day	I	II	III	IV
1	3.4	8.3	8.5	8.2
2	4.2	8.5	6.4	7.5

Since the four experiments were conducted at different places and at different times, there is no necessity for agreement. There is indeed no necessity for agreement between different days in the same experiment since the wild population might conceivably receive a great addition or loss from one day to the next. It may be noted that if the estimated rate of decline of the released flies, 9.2 percent per day, does not apply on the first and second days, the above figures would be increased by 10 percent and 21 percent, respectively. It appears safe to conclude that the density of the wild population was about four per 100 square meters in experiment I and about twice as great in the other experiments.

THE DISPERSION OF THE RELEASED FLIES

The next question concerns the way in which the dispersion of the released flies takes place. The simplest hypothesis would be that the flies scatter at random to the same extent every day. If this holds, the variance of the whole population in a direction at right angles to any line through the point of release should rise by a uniform amount each day, according to the principle that the variance of the sum of independent contributions equals the sum of the separate variances. The variance of radial distances of flies from the point of release should also increase uniformly since it should be equal on any day to the sum of the variances in two directions at right angles to each other.

The averages of the observed variances along the lines of traps and the standard errors $(\sigma^2\sqrt{2/n})$ are given in tables 14 and 15. In every case the variance is more than twice as great on the second day than on the first and continues to increase, with exceptions on particular days. The irregularities in experiment I (actual but not significant decrease in variance on 4th, 5th and 9th days) are probably due to cessation of most activity on those days on which the temperature was 60° or less, in line with the interpretation of the low

TABLE 14

The variance $(\sigma^2 = \Sigma r^2 f/n)$ of the orange flies along a single line of traps, on successive days of each experiment. The origin is the point of release. The east-west and north-south lines are combined, and the central trap is counted twice. The unit of distance is that between stations (20 meters). The standard error, $\sigma^2\sqrt{2/n}$, is given.

DAY	I			II			III			IV		
	NO.	σ^2	SE	NO.	σ^2	SE	NO.	σ^2	SE	NO.	σ^2	E
1	279	3.8±0.3		584	8.7±0.5		674	8.4±0.5		1048	11.4±0.5	
2	609	8.1±0.5		354	21.0±1.6		532	22.2±1.4		—		
3	369	13.6±1.0		238	25.8±2.4		288	42.6±3.6		—		
4	171	13.0±1.4		276	34.5±2.9		166	41.6±4.6		—		
5	94	10.4±1.5		145	37.5±4.4		—			—		
6	215	17.8±1.7		—			—			—		
7	81	21.4±3.4		—			—			—		
8	69	32.4±5.5		—			—			—		
9	27	23.3±6.4		—			—			—		

TABLE 15

The variance of the distribution of orange flies along the two arms of the cross that were continued to the end of the experiment. The unit of distance is that between stations. The standard error is given.

DAY	NO.	II′		NO.	III′		NO.	IV′	
		σ^2	SE		σ^2	SE		σ^2	SE
1	337	7.6± 0.6		295	9.0± 0.7		635	11.3± 0.6	
2	220	22.5± 2.1		236	30.5± 2.8		306	22.8± 1.9	
3	128	22.7± 2.8		133	52.2± 6.4		102	46.5± 6.5	
4	168	35.0± 3.8		69	40.3± 6.9		73	78.4±13.0	
5	90	35.7± 5.3		123	44.3± 5.7		51	73.1±14.5	
6	78	63.2±10.1		58	73.0±13.6		—		
7	79	64.5±10.3		39	90.4±20.5		—		

catches of both orange and wild flies on these days. But while there was no significant correlation between the size of catch and temperature above 60°, there is a significant correlation between the increment of variance and temperature. Excluding experiment I, this correlation was .75 based on 19 entries, and the regression of increment on temperature was 2.31±0.50 units (400m²) per degree Fahrenheit. Including experiment I, the correlation was .70. The regression was 1.17±.25. The regression is clearly not linear, there being relatively little dispersion below 70° in comparison with the large amount above.

Unfortunately the observed variance cannot be taken as representative of the variance of the whole population in an east-west or north-south direction because of the wide departures from normality in the first few days. We must return to the model of a distribution in which the ordinates at a given distance from the center in any direction are equal to the average catch at that distance from the point of release, in order to obtain less biased estimates. In such a distribution, the mean squared radial distance is $\int_0^{2\pi}\int_0^\infty r^3 dr d\theta / \int_0^{2\pi}\int_0^\infty r dr d\theta$. The expression $\Sigma r^3 \bar{f}/(\Sigma r \bar{f} + c/2\pi)$ may be used as an approximation. The estimates for each day in each experiment are given in table 16. These figures should be halved to give the variances of the population in one direction at right angles to a line through the center and thus most nearly comparable with the observed variances as given in tables 14 and 15. The latter, however, are very much less than half the corresponding entries in table 16 during the first days of each

TABLE 16

The estimated mean square distance from the point of release of orange flies on successive days of each experiment ($\Sigma r^3 \bar{f}/(\Sigma r \bar{f} + c/2\pi$). The figures under I, II, III and IV are based on all four arms of the cross, those under II', III', and IV' on the two arms that were continued to the end in each case. The unit of distance is that between trap stations (20 meters).

DAY	I	II	II'	III	III'	IV	IV'
1	15.2	36.7	27.9	42.5	46.8	52.9	51.3
2	25.0	63.8	65.8	63.8	78.6	—	75.8
3	36.8	67.9	61.9	88.1	94.1	—	119.3
4	36.0	80.1	85.6	88.3	84.4	—	197.2
5	30.4	95.1	96.5	—	86.5	—	142.8
6	40.2	—	149.7	—	107.3		
7	43.6	—	127.2	—	142.4		
8	59.5						
9	52.5						

experiment when the forms of the distributions are farthest from normal. In the revised estimates the variance on the second day is on the average only 50 percent greater than on the first (I, II, III, IV') compared with 130 percent greater in the case of the observed variances. After the second day the variance rises at an approximately uniform rate (regression 4.51 ± 0.75 units for nine days) of experiment I, 16.80 ± 2.90 for seven days of experiment II, 13.75 ± 2.23 for seven days of experiment III, and 30.12 ± 11.13 for five days of experiment IV. The figure for experiment I is probably low because of low temperature. The unweighted average for the other three is 20.2

The correlation between the increment of variance and temperature is .47 based on 27 entries (regression $1.91 \pm .71$) and is not so great as in the original data. These are less reliable, however, than those based directly on the data. The revised estimates are designed to correct a systematic bias in the data as collected, but the variation in the increments become less reliable. The conclusions that seem warranted are that the flies scatter more widely on the first day than later but that there is a fairly uniform rate of dispersion after the

first day except as affected by temperature. The rate is relatively slow below 70° but increases greatly above this.

The actual average distances reached by the flies is a matter of interest. The average radial distance in the model adopted for the distribution is $\int_0^{2\pi}\int_0^\infty r^2 dr d\theta / \int_0^{2\pi}\int_0^\infty r dr d\theta$. The figures in table 17 were obtained by using the approximate formula $20\Sigma r^2 f/[\Sigma r f + c/2\pi]$. It is to be noted that distance is

TABLE 17

The estimated average distance of orange flies from the point of release on successive days of each experiment. ($\Sigma r^2 f/(\Sigma r f + c/2\pi)$). The figures under I, II, III, IV are based on all four arms of the cross, those under II′, III′ and IV′ on the two arms that were continued to the ends of the experiments. The distances in this table are in meters.

DAY	I	II	II′	III	III′	IV	IV′
1	59	98	85	101	107	118	114
2	81	135	136	138	158	—	144
3	104	139	128	167	179	—	189
4	103	156	158	167	163	—	243
5	95	167	165	—	169	—	211
6	111	—	213	—	196		
7	116	—	204	—	225		
8	141						
9	123						

here expressed in meters instead of station intervals. In experiments II, III, IV the flies reached average distances of more than 200 meters in a week or less. Individual flies were found at 220 meters from the point of release after one day in experiment I in spite of the low temperature (56°) on this day and the same or greater distance (up to 300 meters) after one day in the other experiments. The maximum distance reported was 500 meters on the third, fourth, and fifth days of experiment IV. Individual flies were found in or near the outermost traps in so many cases, as may be seen from tables 1 to 5, that it is extremely probable a few would have been found at still greater distances if the lines of traps had been extended indefinitely. Such flies would tend to increase the various estimates that have been made.

SECONDARY EXPERIMENTS

Most of the experiments made at Keen Camp in the summer of 1941 suffer from the disability that the experimental fields were so small that some of the flies passed beyond their confines in one day after the release. Only the middle portions of the resulting distribution curves, therefore, have been observed. Variances calculated from these data are evidently much lower than they should be on the basis of the 1942 data, and this regardless of whether orange-eyed flies or flies marked with nail polish are concerned. Only a single experiment, started on July 12, 1941, by the release of 1696 wild flies caught in the same locality and marked with nail polish, appears to be free from the above disability. On July 13, 70 marked flies were recaptured on a cross-shaped experimental field consisting of 45 traps. The variances observed on the two

axes are 6.2 ± 1.3 and 3.6 ± 0.8 in terms of the units used in tables 15 and 16 (namely, 400 m²). The temperature was recorded only after the observed maximum of the activity of the flies, but by analogy with other temperature curves it should have been approximately 67°–68°F at the time of the maximum. Hence, the observed variances are somewhat lower than after one day in experiments II (8.7), III (8.4), and IV (11.4) at temperatures 70°, 70°, and 71°F, respectively, but higher than after one day in experiment I (3.8) at 56°F. On July 14, variances of 13.4 ± 3.0 and 17.7 ± 3.8 units were recorded. The temperature at the time of the maximum activity on that day was probably close to 69°F. The observed increment of variance is therefore of the right magnitude.

On July 16, 1942, 3493 orange-eyed flies were released at Pinon Flats. On July 17, 34 marked flies were recaptured on a cross-shaped field of 61 traps. This is an abnormally small proportion of recovery of marked flies, to be accounted for probably by the extreme aridity prevailing in the locality at that season. The variances on the two axes were 20.4 ± 4.1 and 23.0 ± 5.0 units. The temperature at the time of maximum activity was between 73° and 74°F. The observed variances are slightly higher than expected for the temperature, but not significantly so. It is possible that under unfavorable conditions the flies, seeking an escape, move more extensively than under favorable ones.

We have assumed throughout that the flies released at a given point spread uniformly in the surrounding territory. Yet, it is possible that the daily exposure of a series of baited traps might cause the flies to be drawn to the vicinity of the places where food is located. On a cross-shaped experimental field this would mean that the flies might move chiefly along the arms of the cross and not into the territory between the arms. The following test was arranged. The second of the four main experiments was run for seven days, and the numbers of the orange and of wild flies which were coming to the traps on the arms of the cross at different distances from the point of the release were therefore known (table 2). On June 24, 49 traps were exposed in the territory between the southern and the western arms of the cross. They attracted 1509 wild and 26 orange flies, which is about what is expected in a similar number of traps on the arms of the cross. Other evidence is provided by the numbers of wild flies captured on successive days on experimental fields. If flies were attracted to the traps from the surrounding territory and stayed near the traps till the next day, the numbers of flies caught on the experimental field would gradually increase with time. Our two years' experience shows that this is not so, although the numbers of flies visiting the traps on successive days are so greatly influenced by the temperature that the observations within any one experiment may be misleading (table 2–5).

In July and August of 1941 an attempt was made to depopulate a territory by systematic trapping and destruction of the flies within it. On a square shaped field 120×120 meters in size, 49 traps were set checkerboard fashion at 20 meters from each other. For 17 consecutive days all the flies which came to the traps on this field were caught and destroyed. About 300 meters away from the experimental field a control field with 10 traps was set; the flies

which came to these traps were counted and released at the end of the collecting time each evening. The flies caught on the experimental field on the second and the following days were either remnants of the original population which failed to enter the traps on the first day, or immigrants from the surrounding territory, or newly hatched ones within the territory. If the flies move only short distances, the ratios of the numbers of flies per trap on the experimental and the control fields should wane in the course of time. Furthermore, the numbers of flies in traps located close to the center of the experimental field should dwindle more rapidly than in traps at the periphery of the field. For about the first week, the figures seemed to indicate that the above expectations were on the way to fulfillment, but thereafter and till the end of the experiment the destruction of the flies had no effect whatever on the population density on the experimental field. This result, puzzling at the time, seems clear now. The experiment was started during relatively cool weather ($62°-72°F$ at the time of maximum activity of the flies), but from the second week on weather turned warm ($71°-78°$, except on the 16th day). The distances traveled by the flies at temperatures of $70°F$ and up are so great that an experimental field 120×120 meters in size is not at all isolated from the surrounding territory. That wild flies move extensively at these temperatures has been shown also in another way. On July 19, 1941, a forest fire destroyed the vegetation, and presumably all the flies, in a large territory at Keen Camp. Eight days thereafter MR. H. LEWIS collected flies at a distance 260 meters inside from the margin of the burned area—the farthest distance tried.

AN EXPERIMENT ON DROSOPHILA MELANOGASTER

The migration rates found in *Drosophila pseudoobscura* appear to be of a greater order of magnitude than those recorded by the TIMOFEEFF-RESSOV-SKYS (1940b, c) in *D. funebris* and *D. melanogaster*. Unfortunately, the TIMO-FEEFF-RESSOVSKYS have published their data chiefly in the form of total numbers of flies found in each trap of an experimental field during the duration of the experiment; no temperature data have been published. However, figures 1 and 2 in the 1940c paper give the results of collecting on the fourth day of experiments involving *D. funebris* and *D. melanogaster*, respectively. The variances observed on the two axes drawn through the point of release on the *D. funebris* field turn out to be 127 and 44 m² (based on 11 and 9 flies). The average, 86 m² corresponds to only 0.21 of the unit used for *D. pseudoobscura*. This would indicate daily increment of variance 22 m², and hence an average distance after a day of only about 4 meters. The data for *D. melanogaster* show that the flies migrated entirely in one direction from the point of release—something never observed in *D. pseudoobscura* even in those (fortunately, very rare) instances when some days during an experiment happened to be windy ones.

On August 4, 1942, 3083 wild type *D. melanogaster* flies were released on the same cross-shaped field which had been used previously for the first experiment with *D. pseudoobscura* (p. 308). The flies were F_1 hybrids of two wild type strains raised in the laboratory. No mutant was used as a marker since the particular

experimental field chosen was free of an indigenous population of *D. melano-gaster*. On August 5, 38 flies, and on August 6, 21 flies were recaptured. This is a smaller proportion of recapture of released flies than is customary in experiments with *D. pseudoobscura*. The variance on the first day was 256 m² (0.6 units) on one of the two axes (only two flies were recorded on the other axis outside of the point of release). On the second day the variance rose to 536 m² on the first and 118 m² on the second axis. The temperatures on both days declined from 77° to 68–67°F during the times when the flies were entering the traps. In view of the small number of the flies, it is difficult to tell the temperature at the time of maximum of their activity, although it was probably closer to the higher than to the lower of the two values just indicated. The daily increments of variance observed by us in *D. melanogaster* are about ten times as high as those found by the TIMOFEEFF-RESSOVSKYS in *D. funebris* (at temperatures which, however, might have been different), and about 20 times lower than found in *D. pseudoobscura* at similar temperatures.

The data are admittedly poor and not strictly comparable; nevertheless, they leave no doubt that the migration rates in different species of Drosophila are quite different. *D. funebris* and *D. melanogaster* are chiefly scavengers associated with man; *D. pseudoobscura* is rarely a scavenger. May the success of the two former species in adapting themselves to man-made environments be partly due to their relatively sedentary habits?

ESTIMATES FROM THE ALLELISM OF LETHALS

Attempts have been made in two preceding papers (DOBZHANSKY and WRIGHT 1941; WRIGHT, DOBZHANSKY, and HOVANITZ 1942) to estimate the effective size of breeding populations of *Drosophila pseudoobscura* on the basis of the frequency (p) of allelism of lethals in samples trapped at various distances apart. If the number of individuals interbreeding at random in each locality were sufficiently large, the frequency of each lethal would always be maintained at a certain equilibrium, as a consequence of opposed pressures of mutation and selection. The chance of allelism of lethals from the same local population would then be no greater than for lethals from remote populations. If, on the other hand, the number of individuals interbreeding at random is everywhere small, local differences would accumulate, causing a greater chance of allelism for pairs of lethals from the same locality than from distant localities. It turned out that in tests of 6294 pairs of lethals from regions so remote from each other that common origin is practically excluded, 26 or 0.41±.08 percent were found to be alleles. This was assumed to measure the chance of allelism due to independent mutation. For comparison with this, tests were made of 5537 pairs of lethals, which came from traps at relatively short distances apart. Of these 91 or 1.64±0.17 percent proved to be alleles. Since the difference is highly significant, it was concluded that the random breeding unit is sufficiently limited in size to permit local variations in lethal frequency to exist.

It should be said that there is an alternative interpretation of this difference —namely, that the equilibrium frequencies themselves may vary from place

to place (most plausibly as a consequence of local differences in the action of selection on heterozygotes). The results of analysis of the data, however, were not favorable to this view.

The data could be broken down in various ways. In some cases the pairs of lethals came from the same "station" (a group of traps of which the extremes were not more than 100 meters apart). In others they came from different stations of the same "locality." Thus collections were made at two stations 200 meters apart at Wildrose in the Death Valley region, at two stations 200 meters apart in Andreas Canyon on Mt. San Jacinto, and at two stations 500 meters apart on Pinon Flats, Mt. San Jacinto. The locality Keen on Mt. San Jacinto was represented by five stations from 1 to 3.5 kilometers apart, sampling an area of about six square kilometers. This locality is of primary interest as that nearest and most similar to the locale of the dispersion experiments described in the present paper.

The above three localities on Mt. Jacinto were from 16 to 21 kilometers apart. All of the above studies were based on collections made in 1939. Collections made in 1937 in 11 isolated mountain forests in the Death Valley region about 320 kilometers from Mt. San Jacinto were analyzed in the 1941 paper. In each of these localities the flies were collected in lines of traps one-quarter mile to one mile long. No distinction was made in this case between flies from the same station and different stations.

The 1939 data could also be broken down according to whether the flies which furnished two tested lethals were captured within a month or at an interval of one to 11 months.

The results, subdivided roughly according to interval in space and time, are recapitulated below (table 18). The Death Valley data of 1937 (24 allelic pairs in 772 tests or 3.11 ± 0.63 percent) are included in the class of pairs collected within a month from stations 200 meters to 500 meters apart, although some undoubtedly came from the same trap and some from traps more than 500 meters apart.

It appears from these results that particular lethals may not only be present in excess in the population directly sampled at a station at a particular time but that this excess extends to some extent over considerable distances (more than a kilometer) and persists for several generations.

In interpreting these data the sampled population was assumed to consist of a certain effective number (N) of individuals. Immigration was assumed to replace this population to a certain extent (m) by flies in which the lethals are at their equilibrium frequencies. The total frequency of lethals in the populations studied was very much less than expected on the hypothesis that the mean frequencies are determined solely by mutation at the rate observed in the laboratory, balanced by elimination of the homozygotes appearing in a random breeding population. The deficiency could be due either to departures from random mating within the population under consideration measured by the inbreeding coefficient (F), or to selection against heterozygotes (rate s). Two extreme hypotheses with respect to s and F were tried. According to one (s+F) is the same for all lethal mutations. According to the other, F is as-

sumed to be o in the populations sampled at stations, s is assumed to be so high for the great majority that are observed in the laboratory that they are very rarely found in nature, while s is assumed to be zero for those found in nature. The latter hypothesis, which increases considerably the estimated value of N, was not borne out by experiments in which lethal mutations were allowed to accumulate in heterozygotes for several generations before testing. In either case it was possible only to estimate N for given values of m.

In an area as large as that sampled at Keen (six square kilometers) it appears safe to assume that the total immigration per generation is a very small per-

TABLE 18

Recapitulation of all data on the frequency of allelism in Drosophila pseudoobscura in relation to distance in time and space.

DISTANCE BE- TWEEN TRAPS	INTERVAL LESS THAN ONE MONTH				INTERVAL ONE TO 11 MONTHS				TOTAL			
	NO. TESTS	SAME LOCUS			NO. TESTS	SAME LOCUS			NO. TESTS	SAME LOCUS		
		NO.	%	S.E.		NO.	%	S.E.		NO.	%	S.E.
o to 0.1 km	777	16	2.06±.51		1474	29	1.97±.36		2251	45	2.00±.30	
0.2 to 0.5 km	1227	29	2.36±.43		690	6	0.87±.35		1917	35	1.83±.31	
Total o to 0.5 km	2004	45	2.25±.33		2164	35	1.62±.27		4168	80	1.92±.21	
1 to 3.5 km (Keen only)	466	6	1.29±.52		903	5	0.55±.25		1369	11	0.80±.24	
Total o to 3.5 km	2470	51	2.07±.29		3067	40	1.30±.20		5537	91	1.64±.17	
16 to 320 km									6294	26	0.41±.08	

centage, and effective m, measuring replacement by genes representative of the species with respect to lethal frequencies, would be still smaller. On taking the percentage of allelism (0.80±.24) at face value and assuming m=o, N comes out 20,000 by the first extreme assumption 104,000 by the other less favored assumption. If m is assumed to be .01, the estimate for N lies between 13,000 and 28,000. An estimate of 30,000 is as large as seems warranted, accepting 0.80 as the percentage of allelism. However, if the true value is less than 0.80 by the standard error (that is, p=0.56), the lower limit of the estimate for N rises to 53,000 for m=o; 34,000 for m=.01. On the other hand, a value larger than 0.80 is more probable than a smaller one, since most of the pairs of lethals from different stations at Keen were collected at intervals of a month or more. The percentage among those collected within the same month was in fact 1.29±0.52 percent but based on obviously inadequate numbers. If used, the lower limit of the estimate for N (with m=o) falls to 9000.

The estimate N=30,000 for the six square kilometers of Keen implies an effective density of 50 per 10,000 square meters, the approximate area sampled directly at a station. The percentage of allelism within stations at Keen was 2.45±0.49 percent. If N is taken as 50, m comes out about 0.50. These considerations were the basis for the final statement in the 1942 paper: "a typical station is estimated to have an effective N of only about fifty but with substantially no isolation from other stations in the locality." We believe that this is a valid deduction but the assignment of the definite value 0.50 to m is not

valid. The value 0.50 implies that deviations from equilibrium are swamped at a rate of 50 percent per generation. Obviously this would not permit any appreciable extension in space or persistence in time and is thus contrary to observation. There is in fact a certain minimum size of population, the "panmictic unit," below which the theoretical relation of m to N ceases to hold. The proper deduction is that the flies collected in traps at a station, while a direct sample of only about 10,000 square meters, are really a substantially random sample of flies from a much larger area. The 50 flies per 10,000 square meters is thus merely an estimate of effective density. The minimum interbreeding unit must be considerably larger than fifty.

<div align="center">THE PANMICTIC UNIT</div>

It is of primary importance in dealing with a continuous population to determine the effective number of individuals in the panmictic unit, the population from which the parents of any given individual may be considered to be drawn at random (WRIGHT 1943). Associated with this is the question of the area occupied by this population. Take the emergence site of individuals as origin and consider the emergence sites of parents as forming a radially symmetrical bivariate normal distribution relative to this, defined by a certain standard deviation σ in either an east-west (x) or north-south (y) direction $z = e^{-(x^2+y^2)/2\sigma^2}/(2\pi\sigma^2) = e^{-r^2/2\sigma^2}/(2\pi\sigma^2)$. If the panmictic unit is taken as the effective breeding population of a circle of radius $c\sigma$, there are two types of error to be considered in assigning a value to c. On the one hand, if c is small, an appreciable portion of the parents are excluded. The proportion included is $\int_0^{2\pi}\int_0^{c\sigma} rz\,dr\,d\theta / \int_0^{2\pi}\int_0^{\infty} rz\,dr\,d\theta = (z_0 - z_{c\sigma})/z_0$ in which z_0 and $z_{c\sigma}$ are the ordinates at $r=0$ and $r=c\sigma$. Effective N for the area inclosed by the circle of radius $c\sigma$ should be multiplied by $z_0/(z_0-z_{c\sigma})$ to compensate for the excluded parents. On the other hand, the ratio of parents to total number decreases as r increases. Effective N should be multiplied by $\int_0^{2\pi}\int_0^{c\sigma} rz\,dr\,d\theta / \int_0^{2\pi}\int_0^{c\sigma} rz_0\,dr\,d\theta = 2(z_0 - z_{c\sigma}) / c^2 z_0$ to correct for this. These two corrections compensate for each other if $c = \sqrt{2}$. As the mean square radial distance is $2\sigma^2$, effective N of the panmictic unit may be taken as equivalent to effective N of the population included in a circle, the radius of which is the square root of the mean square distance between emergence site of parent and of offspring.

In an actual circle of radius $\sqrt{2}\sigma$, the proportion 36.8 percent ($= z_{\sqrt{2}\sigma}/z_0$) of the parents of individuals at the center came originally from outside the circle. Considerably more than 50 percent of the parents of individuals near the margins came from outside. Thus there is about 50 percent replacement of the population of such a panmictic unit from the outside populations in each generation. Most of these immigrants, however, come from the immediate vicinity and may be expected to differ little in gene frequencies.

If q_i is the gene frequency of actual immigrants to the area in question, q_e that of the individuals in this area which they replace (not necessarily exactly the same as q, the mean gene frequency of the area), and q_t is the mean gene frequency of the species, the effective value of m is approximately $.50(q_e - q_i) / (q - q_t)$.

The stations at San Jacinto could be considered to be "panmictic" units only if $(q_e - q_i) = (q - q_t)$—that is, if the immediate immigrants are characterized by the gene frequencies of the species as a whole $(q_e = q, q_i = q_t)$. Since there was clearly considerable extension of high frequencies of particular lethals to larger areas and considerable persistence, m must be considerably less than .50. If m is assumed to be .20, the percentage of allelism within stations at Keen implies a value of N of about 250 for the panmictic unit. Still accepting the estimated density of 50 per 10,000 square meters, this implies that the panmictic unit occupies some 50,000 square meters (radius 150 meters) and that there are 120 of them included in the area sampled at Keen. The smaller "localities" (Andreas, Pinon, most of those at Death Valley) would be only small multiples of the panmictic unit. This would at least partially account for the high average chance of allelism between stations of those localities. But swamping of exceptional frequencies at the rate implied by m = .20 is hardly compatible with the significantly high percentage of allelism between stations of the larger area of Keen. The values m = .05, N = 1000 would be more satisfactory. This implies an area of some 200,000 square meters (radius 250 meters) for the panmictic unit and the occurrence of about 30 in the locality of Keen.

If the panmictic unit is as large as this, it becomes a question whether one should not assume an appreciable value of m for Keen. If m = .01 for Keen, the minimum estimate for N falls to 13,000, and if m = .02, minimum N becomes 10,000. These suggest a value of N of about 15,000 for this locality, which implies an effective density of only 25 per 10,000 square meters. If these are correct, an estimate of effective N of the panmictic unit as small as 500 (but area 200,000 square meters as above) would be consistent with the observations.

These estimates are based on the chances of allelism within and between stations at Keen and include the data for collections made at intervals greater than a month as well as at shorter intervals. The best estimate for the chance of allelism within a panmictic unit is probably that obtained from stations 0 to 500 kilometers apart in all localities but restricted to tests of pairs collected within the same month. This figure is 2.25 ± 0.33. It yields the estimates m = .05, N = 1100 or m = .10, N = 570 (lower limits for the panmictic unit) in substantial agreement with those from Keen alone.

Summing up, rather extensive data indicating an excess chance of allelism of pairs of lethals from flies trapped 0 to 500 meters apart within the same month, coupled with evidence for partial persistence for longer periods and partial extension to considerably greater distances, lead to an estimate of the effective size of the panmictic unit of the order of 500 to 1000 individuals. The much less extensive data from flies trapped 1 to 3.5 kilometers apart indicate an effective density of the order 25 to 50 per 10,000 square meters. Combining these estimates gives some 200,000 square meters or a circle of radius of about 250 meters as a rough estimate of the area from which most of the parents of individuals are drawn. It is obviously highly desirable to be able to supplement these very indirect estimates by data on the actual density and the actual movements of the flies.

COMPARISON OF THE DEDUCTIONS FROM DISPERSION AND FREQUENCY OF ALLELISM

The investigations described in the present paper led to an estimate of about 400 flies per 10,000 square meters as the density of the wild population at Idyllwild at the beginning of June 1942 and of about 800 flies per 10,000 square meters from the middle of June to the end of July. The latter is 16 to 32 times the estimate of effective density based on frequency of allelism of lethals. But the direct estimates apply to the season of population maximum while the indirect estimate is theoretically the harmonic mean of the number of parents per generation throughout the year (that is,

$$1/N = \frac{1}{n} \sum_{i=1}^{n} (1/N_i)$$

for n generations per year and N_i breeding flies in the i'th generation). Effective N is thus much more closely related to the number of flies at population minimum (late winter at Keen and Idyllwild) than at population maximum. The estimates are consistent as far as present knowledge goes, but there is nothing in the estimate of summer density that forbids estimates of *effective* density several times larger or several times smaller than 25 to 50 per 10,000 square meters.

The amount of dispersion of the flies described in the present paper obviously bears on the area of the panmictic unit. There are, however, many uncertainties. The evidence indicates that the flies scatter more in warm than in cold weather. Thus the area from which parents are drawn may vary greatly from generation to generation, and the effective population number of this area may vary for this reason as well as from seasonal changes in population density. Full treatment requires a more complicated theory than has been developed. But populations that become thoroughly mixed in periods of great activity cannot drift apart much during the periods of low activity. It would appear that the unit area must be taken as that of which the radius is the square root of the mean square distance between emergence sites of parent and offspring at the period of greatest activity, although the effective population number is determined by the harmonic mean of the densities in this area in all generations (modified slightly by departures from panmixia due to splitting up in times of low activity, WRIGHT 1943). The marked deficiency in the number of lethals in comparison with the number expected on the basis of the observed mutation rate may be due more to inbreeding of this nature than to selection against the heterozygotes (see discussion WRIGHT, DOBZHANSKY, and HOVANITZ 1942, p. 359). This consideration favors acceptance of estimates of effective N close to those given by the minimal hypothesis (the assumption that s=0).

Another complication in relating the observed movements of the flies to the panmictic area comes from the likelihood of a difference in the mean square distance between emergence sites of father and offspring and that for mother and offspring. The former is compounded of the distance travelled by the male before encountering the female and that travelled by the female before laying the egg, which may be a considerable time, since females may carry sperm in

the spermatheca for weeks. The mortality curves and the curves of fertility in relation to time must also be taken into account in each case.

We will assume that the flies emerging at a given place scatter in a bivariate normal distribution with the mean square distance increasing by the same amount $2h^2$ each day. The variance of the distribution in one direction may be written h^2t where t is the number of days since emergence. The ordinate of the bivariate distribution is thus $z = e^{-r^2/2h^2t}/2\pi h^2t$. The ordinate of the distribution of distances is $2\pi rz$. But the population number is falling off according to some function of time, and productivity per individual is changing according to some other function of time. Let $\phi(t)$ be the product of these two functions and thus the total productivity in terms of time. In the absence of definite information of the situation in nature, assume that total productivity falls by a constant amount per day, reaching zero in k days, $\phi(t) = (1 - t/k)$. The mean square distance from emergence site of parent to offspring may then be represented by the following.

$$\overline{r^2} = \int_0^k \int_0^\infty r^3 z(1 - t/k)drdt \Big/ \int_0^k \int_0^\infty rz(1 - t/k)drdt.$$

This may easily be evaluated, noting that

$$\int_0^\infty r^3zdr = 2h^2t \int_0^\infty rzdr = 2h^2t/2\pi.$$

$$\overline{r^2} = 2h^2k/3$$

It will be recalled that the distribution of the released flies in the experiments described here was far from the bivariate normal distribution assumed above at least on the first two days after release. There was excessive scattering of some of the flies on the first day, but after this the estimated mean square distance increased fairly uniformly. The average increment (experiments II, III, and IV) was 20.2 units per day. The conditions relating to newly emerged wild flies are so different from those relating to a large number of flies released at the same place that it seems fair to ignore the excessive dispersion of the latter on the first day and take the figure 20 units or 8000 m² as the best available estimate of $2h^2$.

No very satisfactory estimate of k is available. However it may be noted that the present data indicate that about 50 percent of a group of young flies disappear in the course of seven days. If productivity per fly is assumed to maintain the same level during this period but to fall off thereafter in such a way that total productivity continues with the same linear trend, k would be 14. The figure for males (including the period in which sperm are carried by the female) would presumably be greater. For $k = 14$, $\overline{r^2}$ is 37,300 square meters, giving 190 meters as the radius of the panmictic unit. If $k = 23$, the estimate of the radius rises to the 250 meters arrived at from consideration of the data on frequency of allelism. The estimates by the two methods are obviously in as close agreement as there is any right to expect.

The effective size of the panmictic unit in *Drosophila pseudoobscura* turns out

to be so large that but little permanent differentiation can be expected in a continuous population of this species owing to the genetic drift alone. It must, however, be pointed out that the figures obtained are valid only for the localities in which the experiments have been made and, of course, only for the species under study. Apart from species of Drosophila associated with man, *D. pseudoobscura* is the representative of the genus forming by far the densest and most widespread populations in at least the forested regions of the western United States. Furthermore, Keen Camp and Idyllwild are about as favorable localities for this species as could be found, and they were selected for experiments ·for just that reason. It is certain that the population densities in less favorable localities are much smaller than indicated above, and consequently the effective size of the panmictic unit arrived at is closer to the largest rather than to the smallest in this species. The panmictic units are probably smaller still in species that are less common or more restricted to habitats that recur only sporadically in space, especially if these species have lower dispersion rates than *D. pseudoobscura*. As shown above, *D. pseudoobscura* is certainly more mobile than *D. melanogaster* and *D. funebris*, the only two other species of the genus which have been examined in this respect.

SUMMARY

Four experiments are described in which an aggregate of 14,026 orange eyed *Drosophila pseudoobscura* were released at points near Idyllwild, California. Traps were set daily for five to nine days at intervals of 20 meters along lines crossing at right angles at the points of release (or along only one of these lines, greatly extended, in the later days), and captures of released and wild flies were recorded. Other experiments with *D. pseudoobscura* and ones with *D. melanogaster* are reported briefly.

The wild flies were uniformly distributed to the extent that some were captured in practically every trap (unless the temperature was below 60°F, under which the mean number per trap became small). However, there were marked irregularities due largely to a tendency to aggregate about old oaks and pines.

Most of the orange flies captured one day after release were still close to the point of release. Some, however, had scattered widely, causing the distribution along a line of traps to be markedly leptokurtic. Dispersion continued throughout the experiments, and the distributions became more nearly normal in the later days. Irregularities in the distributions were rather strongly correlated with the irregularities among the wild flies.

An attempt was made to estimate the relative numbers of wild flies and of orange flies that would have been captured on each day if traps had been distributed in a grid with 20 m spacing throughout the area reached by the orange flies. These estimates indicate that the orange population declined about 8 or 9 percent per day. The density of the wild population is estimated to have been 400 per 10,000 square meters in early June (1942) and 800 per 10,000 square meters in three experiments from mid-June to late July of the same year.

The dispersion of the flies was much affected by temperature, there being

very little dispersion below 60°F but increasing amounts with higher temperatures (regression 760 m² per degree). The mean squared distance travelled on the first day in three experiments in which the temperature was 70° or 71° was 17,600 m² (square root 133 meters). Dispersion increased by approximately equal increments of some 8000 m² in later days (average temperature 72°). The maximum distance recorded was 500 meters on the third (and later) days of one of the experiments.

The daily increment of the mean squared distance for *D. pseudoobscura* was more than 20 times that for *D. melanogaster* in the same locality. This in turn was nearly 10 times that observed by TIMOFEEFF-RESSOVSKY in the case of *D. funebris* in Berlin.

Analysis of population structure on the basis of the frequency of allelism of lethals in samples trapped at various distances apart had indicated an effective density of about 50 per 10,000 square meters (and reconsideration suggests reduction rather than increase). This is only one sixteenth of the density as estimated from the present data, but the latter applies to the population maximum of midsummer while effective density is more closely related to the population minimum than maximum (harmonic mean for all generations).

The data on allelism indicates that the parents of flies are typically drawn from a population of some 500 to 1000 individuals. The dispersion data indicate that the standard deviation of the distances between emergence sites of parent and offspring are of the order of 200 to 250 meters. This agrees as well as can be expected with the area of the "panmictic unit" deduced from the data on allelism.

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