

## NOTES AND COMMENTS

THE *DROSOPHILA* OF SOUTHERN CALIFORNIA II. ISOLATIONS OF POPULATIONS IN THE DEATH VALLEY REGION

The floor of Death Valley in eastern California is one of the most stressful environments for life. It is an elongate valley with mountain ranges on the eastern and western sides. Much is below sea level and highly saline; all is excessively arid. Typical plants such as creosote bush (*Larrea tridentata*) and desert holly (*Atriplex hymenelytra*) are spaced far apart and large areas are devoid of all plants. (Photographs of the desert floor are given in Lewontin et al. [1981, figs. 25, 26].) The average yearly rainfall is about 4 cm. Temperatures are exceedingly high from May to September when the maxima are usually in the mid to high 40's C and the night temperatures drop only to the low 30's. *Drosophila* are not encountered under these conditions.

Nevertheless there are *Drosophila*. From September through April they are found in some of the oases and their numbers may be enormous in March and April. One such oasis is the Furnace Creek Ranch which has a commercial date grove occupying about 10 ha and is 60 m below sea level.

Those involved in recent studies of the *Drosophila* of the Death Valley region (Jones et al. 1981; Coyne et al. 1981) have speculated on the origins of the *D. pseudoobscura* populations in the desert oases. One possibility is that some of the flies persist in cooler microhabitats, such as beneath the ground, during the excessively high temperatures of the summer. If it is assumed that the flies cannot survive these summer temperatures, migration from other areas is an alternative hypothesis. One such source could be the forested mountains bordering Death Valley. These mountains were the site of the first studies of population genetics of *D. pseudoobscura* (Dobzhansky and Queal 1938a, 1938b; Koller 1939) and one locality, Wildrose in the Panamint Mountain range, has been studied from 1938 to the present.

The Wildrose site is at 2070–2380 m in the pinon-juniper (*Pinus monophylla* and *Juniperus osteosperma*) portion of the Upper Sonoran Life Zone (photographs in Lewontin et al. 1981, figs. 24a, 24b). The straight-line distance from Furnace Creek is 30 km. Winters are cold and there is usually a blanket of snow. The *Drosophila* appear in late April or May and disappear about September.

If the *Drosophila* become extinct in the desert oases during the hot summer

months and are then repopulated in the autumn from the surrounding mountains, the oasis populations should reflect that origin. To test this hypothesis a study was made of the species composition and of the third chromosome gene arrangements of *D. pseudoobscura* and *D. persimilis* throughout the year at Wildrose and Furnace Creek.

The general collecting plan was to sample one of the sites, Wildrose or Furnace Creek, the first afternoon and the following morning and then drive to the other site and collect that afternoon and the following morning. Ten or more buckets of freshly mashed yeasted bananas were used for bait and were left out overnight. The collected flies were placed in vials with *Drosophila* media and kept in an insulated chest with ice. Back in the laboratory, each *obscura* female was isolated and the chromosomes of a single F<sub>1</sub> larva were scored for third chromosome gene arrangements. If only a few females had been collected, the males were also used. In that case each male was crossed with a ST/ST female *pseudoobscura* and a single F<sub>1</sub> larva was scored.

The data for species collected in 1980 and 1981 are given in table 1. At Furnace Creek *pseudoobscura*, *simulans*, and *melanogaster* were common and a single *carbonaria* was taken. (This is the only locality in southern California where we have found *melanogaster* to be abundant.) At Wildrose both *persimilis* and *pseudoobscura* were present as was *pinicola*. There were no *melanogaster* or *simulans*. (Subsequently in 1982 a single *occidentalis* and a single *miranda* were collected at Wildrose.)

The data show almost no overlap in the periods of adult activity of the *Drosophila* at Wildrose and Furnace Creek (table 1, fig. 1). One cannot exclude the possibility that *pseudoobscura* repopulates Furnace Creek from sites such as Wildrose by migration in early autumn but, if so, *persimilis* does not accompany it. Moreover, Wildrose cannot be the source of the *melanogaster* and *simulans* found at Furnace Creek since they do not occur at Wildrose.

The hypothesis of recolonization is made unlikely by the data on third chromosome gene arrangements (table 2). The AR gene arrangement is the only common one in *pseudoobscura* at Furnace Creek. By contrast, ST, AR, and CH are all common at Wildrose. Thus, the gene arrangements of the Furnace Creek population cannot be explained by the hypothesis of their origin by mass migration of flies from Wildrose in the autumn. One cannot exclude all migration, but if any occurs, it is not sufficient to make the two populations identical in the frequencies of their gene arrangements.

It is interesting to compare the *obscura* species found at Wildrose with earlier studies (there are no long-term data for Furnace Creek). Dobzhansky (1973) obtained *pseudoobscura* in all the years he collected at Wildrose from 1937 to 1972. Although *persimilis* had been taken earlier at another locality in the Panamints, he did not encounter it until 1957. A single *miranda* was taken in 1972. Wildrose remained the easternmost locality for *persimilis* until 1972 when, for the first time, it was encountered in the Charleston Mountains in southwest Nevada. Wildrose is still the easternmost locality for *miranda*. Thus the huge area of the Basin and Range Province, to the east of Death Valley, is almost entirely *pseudoobscura* country. One of Dobzhansky's main points was that both *per-*

TABLE 1

*Drosophila* OF DEATH VALLEY

	1980	Temp. Range	% Relative Humidity	Total <i>Drosophila</i>	Total obscuras	<i>pseudo</i> . larvae	<i>persimilis</i> larvae	<i>pinicola</i>	<i>mel-sim</i> ♀	<i>melano- gaster</i> ♂	<i>simulans</i> ♂
FC	March 1 PM	21°	29	294	238	81	0	0	28	14	14
WR	March 2 PM	3°	rain	0	0	0	0	0	0	0	0
FC	May 21 AM	32-35°	19-14	1	0	0	0	0	1	0	0
WR	May 20 PM	21-16°	17-37	182	133	67	6	49	0	0	0
FC	July 17 PM	43-41°	12-14	0	0	0	0	0	0	0	0
FC	July 18 AM	34°	20	1*	0	0	0	0	0	0	0
WR	July 16 PM	27-20°	21-23	96	69	27	3	27	0	0	0
WR	July 17 AM	16-24°	35-27	102	83	35	3	19	0	0	0
FC	Sept. 3 PM	43-29°	6-17	0	0	0	0	0	0	0	0
FC	Sept. 4 AM	25-28°	16-23	9	1	0	0	0	7	1	0
WR	Sept. 2 PM	20-18°	24-33	2	2	1	0	0	0	0	0
WR	Sept. 3 AM	12-19°	35-22	5	5	2	0	0	0	0	0
FC	Nov. 12	19-25°	42-25	842	40	34	0	0	324	289	189
FC	Nov. 13 AM	16-21°	32-24	65	20	14	0	0	16	25	4
WR	Nov. 11 PM	12-10°	48-54	0	0	0	0	0	0	0	0
FC ..... 1980 totals				1212	299	133	0	0	376	329	207
WR ..... 1980 totals				387	292	132	12	95	0	0	0
1981											
FC	Jan. 16-17	20-14°	48-56	196	97	79	0	0	37	54	8
WR	Jan. 17	5°	79	0	0	0	0	0	0	0	0
FC	Mar. 13-14	18-15°	32-58	731	703	111	0	0	9	17	2
WR	March 14	7°	47	0	0	0	0	0	0	0	0
FC	June 19	—	—	0	0	0	0	0	0	0	0
WR	June 19-20	27-15°	11-35	210	151	55	18	59	0	0	0
FC	July 23	—	—	0	0	0	0	0	0	0	0
WR	July 23-24	25-15°	14-34	15	15	6	5	0	0	0	0
FC ..... 1981 totals				927	800	190	0	0	46	17	2
WR ..... 1981 totals				225	166	61	23	59	0	0	0

NOTE.—FC = Furnace Creek, WR = Wildrose. The temperatures at FC June 19 and July 23, 1981 were more than 10°C above the highest at which *Drosophila* can be collected and no buckets were put out.

\* *D. carbonaria*. The temperatures and humidities are for the period when *Drosophila* were captured. If none were captured, the data are for periods when attempts at collecting were made.

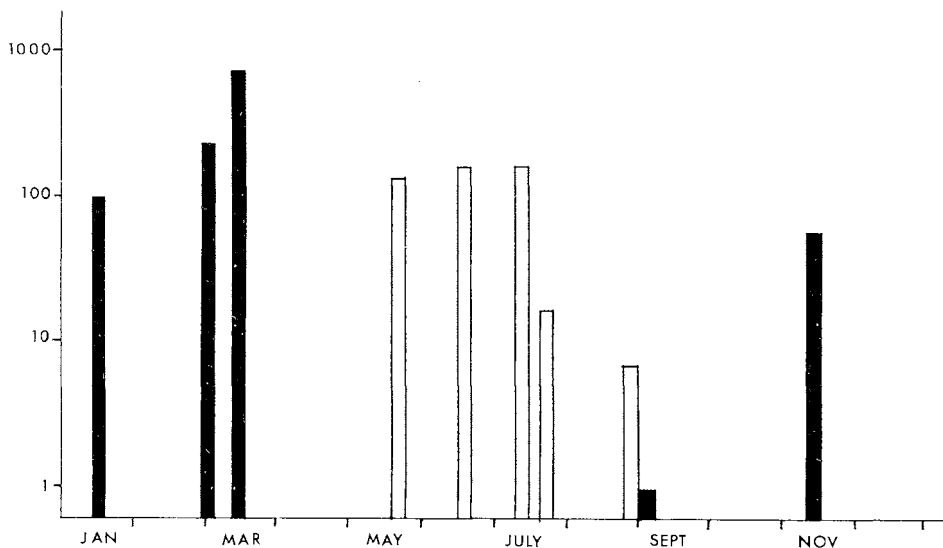


FIG. 1.—Semilog plot showing the numbers of obscuras collected at Furnace Creek (solid rectangles) and Wildrose (open rectangles) during different times of the year.

*similis* and *miranda* were extending their ranges. This is still the case and both species are extending their ranges in Southern California (Moore et al. 1979).

Dobzhansky also noted that as the years went by, *persimilis* and *miranda* became the dominant obscura species on the eastern slopes of the Sierra Nevada; this continues to be so. In June 1981 we found 70% *persimilis*, 28% *miranda*, and 2% *pseudoobscura* at Dobzhansky's long-established locality of Lone Pine Canyon. The following month at Kennedy Meadows, about 70 km to the south, we found 97% *persimilis*, 3% *miranda*, and no *pseudoobscura*.

There are other important differences between Wildrose and Furnace Creek suggesting that Wildrose populations have more in common with those of the Sierra Nevada to the west and Furnace Creek populations more in common with those of the Basin and Range province to the east. Figure 2 shows the geographic distribution of four common third chromosome gene arrangements. The data are from Dobzhansky et al. (1964, 1966), Anderson et al. (1975), plus some of our recent observations. The Wildrose-Furnace Creek break, indicated by the dashed lines, is a boundary for AR, ST, and CH, but not for PP.

The tentative conclusion that there was no appreciable movement of obscuras between Furnace Creek and Wildrose in 1980 and 1981 would appear to be in contradiction to the observations of Jones et al. (1981) and Coyne et al. (1982). Both of these studies showed that *pseudoobscura*, *simulans*, and *melanogaster* can move considerable distances across the floor of Death Valley in a very short time. We fully support those findings, having participated in making them.

One must not conclude, however, that just because the individuals of a species can move, they will move. Most animals, especially those with legs, wings, or fins, have the capacity for wide dispersal. Nevertheless, we find most species

TABLE 2

THIRD CHROMOSOME INVERSIONS OF *D. pseudoobscura* AND *D. persimilis* (numbers and percents)

WILDROSE														
1980	<i>Drosophila pseudoobscura</i>									<i>Drosophila persimilis</i>				
	N	ST	AR	CH	PP	TL	SC	OL	EP	N	ST	WT	MD	KL
May 20 .....	134	36	53	32	5	6	0	1	1	12	5	7	0	0
July 16 .....	124	60	38	21	1	4	0	0	0	12	5	6	0	1
Sept. 2 .....	6	2	2	1	0	0	1	0	0	0				
Percent .....	264	37.1	35.2	20.5	2.3	3.8	.4	.4	.4	24	41.7	54.2	0	4.1
1981														
June 19-20 ...	110*	38	36	23	4	7	0	1	1	36	12	21	1	3
July 23-24 ...	8	2	3	3	0	0	0	0	0	6	3	3	0	0
Percent .....	118	33.9	33.1	22.0	3.4	5.9	0	.9	.9	42	35.7	57.1	2.4	4.8
1980-1981 %	382	36.1	34.6	20.9	2.6	4.5	.3	.5	.5	66	37.9	56.1	1.5	4.6
FURNACE CREEK														
1980	<i>Drosophila pseudoobscura</i>													
	N	ST	AR	CH	PP	TL	SC	OL	EP					
March 1 .....	162	12	131	15	1	2	0	0	1					
Nov. 13-14 ...	69	6	59	2	2	0	0	0	0					
Percent .....	231	7.8	82.3	7.4	1.3	.9	0	0	.4					
1981														
Jan. 16-17 ...	121	7	95	9	3	7	0	0	0					
Mar. 13-14 ...	222	19	174	10	1	18	0	0	0					
Percent .....	343	7.6	78.4	5.5	1.2	7.3	0	0	0					
1980-1981 %	574	7.7	80.0	6.3	1.2	4.7	0	0	0.2					

\* Two *pseudoobscura* × *persimilis* hybrids not included.

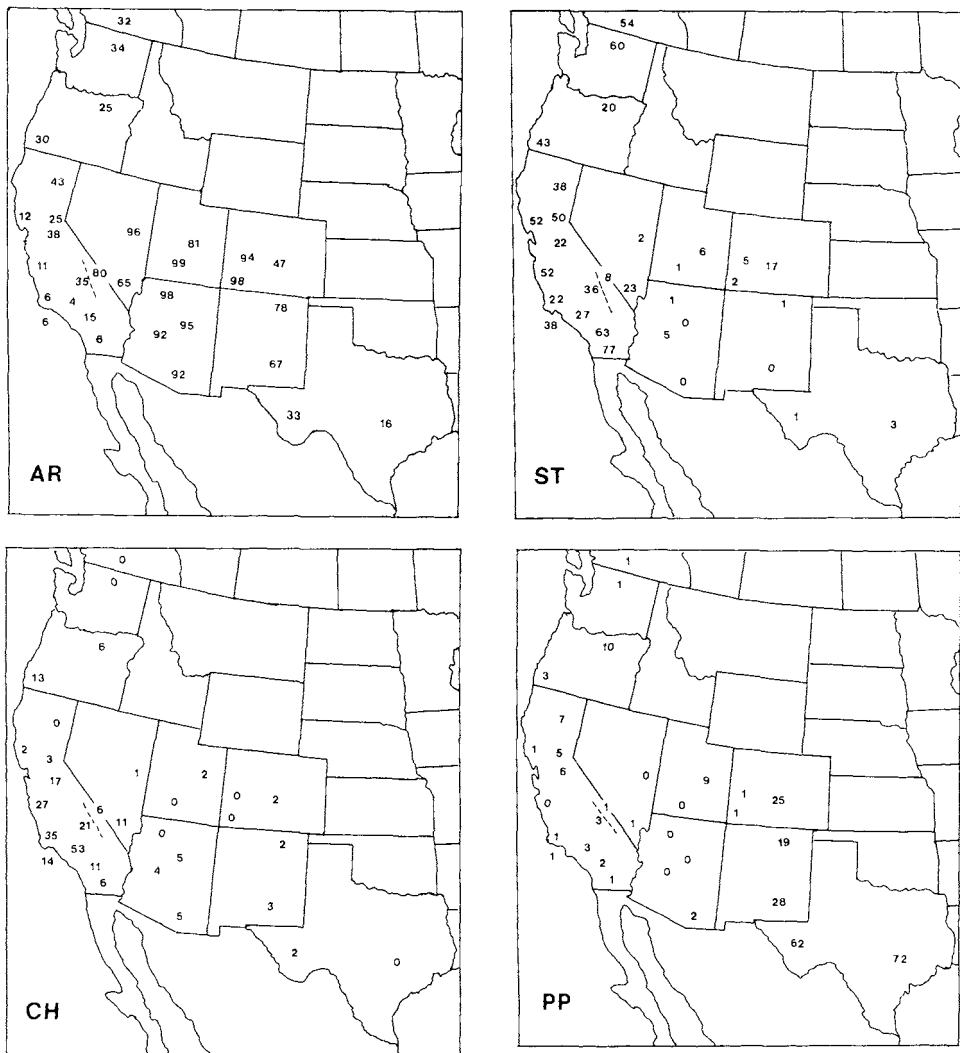


FIG. 2.—Percentages of four third chromosome gene arrangements of *Drosophila pseudoobscura* in the western United States. The dotted line separates Wildrose (west) and Furnace Creek (east).

drastically restricted in their distributions for reasons that are rarely known. This is a classic problem. Charles Darwin was much puzzled by the restriction of some of the unique Galapagos birds to single islands (1859, pp. 401–402). The islands could be “in sight of each other” yet some of the birds “though so well adapted for flying from island to island, are distinct on each.”

Jones et al. (1981) have interpreted their allozyme data as suggesting extensive gene flow among local populations of *pseudoobscura*. They reported similar frequencies of *Est-5*<sup>0.85</sup> in paired lowland and montane localities, as well as the

general lack of geographic differentiation. The uniformly low frequencies of the allele, however, make interpretation difficult. Thus the frequency of the allele was 2 in 258 at Furnace Creek and 1 in 74 at Wildrose. One must be careful in drawing conclusions from such data.

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