MORPHOLOGICAL VARIATION IN NATURAL AND EXPERIMENTAL POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA* AND *DROSOPHILA PERSIMILIS*[1]

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Drosophila pseudoobscura and its sibling *D. persimilis* are two species of fruit flies which have received considerable attention from the standpoint of population genetics. Examination of the arrangements (inversions) in the third chromosome in salivary gland cells of the larval progeny of flies derived from many geographic localities throughout the distribution of these species reveals that (1) populations within a locality are largely polymorphic; (2) populations from different altitudes and latitudes differ in the frequency of chromosomal arrangements; (3) the frequency of these arrangements varies from season to season; and (4) there are secular changes in the frequency of these inversions (see Dobzhansky, 1951, p. 138, for map showing frequency of the different inversions in *D. pseudoobscura* through most of its distribution, and Dobzhansky *et al.*, 1964, for the most recent survey of inversion frequencies in this species).

Laboratory studies showing that the frequency of these inversions is modified through natural selection and manipulation of environmental conditions are too numerous to mention (review in Strickberger, 1963). A few of these studies (for example, Beardmore *et al.*, 1960; Tantawy, 1961) have combined the use of inversions and quantitative traits to measure the relative fitness of different gene arrangements under different constant and fluctuating temperatures, and one study (Druger,

1962) has reported on the changes of chromosomal polymorphism brought about by selecting for long and short wings at two different temperatures. These studies clearly show that there is an interrelationship between chromosomal arrangements and quantitative characters. In a previous study, Sokoloff (1965) reported geographic variation of various body characters in *D. pseudoobscura* derived from nine different localities, some as close as six miles and as distant as 2000 miles. The discriminant functions derived from wing length and tibia length measurements of flies reared under uniform optimal conditions clearly indicated genetic differences in the metric traits considered, even for those populations separated by only six miles and for those collected in the same locality (Grand Canyon) but separated in time by an interval of five weeks. Attempts to correlate body size with latitude, altitude, or the type of chromosomal arrangements known to be prevalent in the third chromosome of the flies in the localities studied failed.

The purpose of the present paper is diametrically opposed to the previous one (Sokoloff, 1965). Here data are reported on the phenotypic variation of *D. pseudoobscura* derived from a number of localities throughout the distribution of this species in two consecutive years, and phenotypic variation of flies obtained by rearing two distinct genetic strains under various degrees of crowding. The rationale of this study is that natural populations, even those adjacent in one mountain range, are genetically distinct not only with regard to chromosomal arrangements, but also with regard
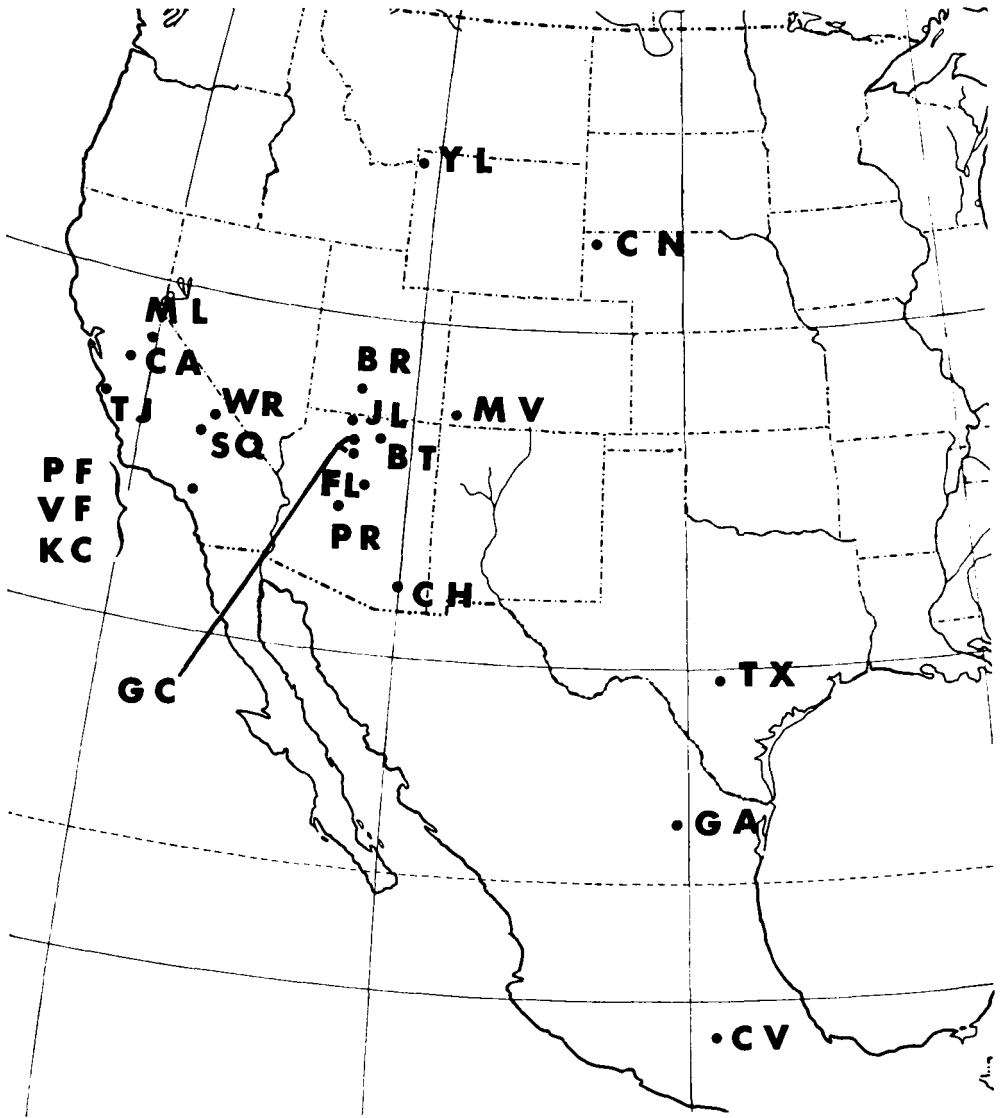
Fig. 1. Geographic location of the sites from which *Drosophila pseudoobscura* and *D. persimilis* wild flies were derived. For explanation of symbols see text.

to genes controlling the size of body characters. They must, therefore, be the product of selection for the best fit phenotype. If this is so, the populations may resemble each other phenotypically despite a variety of environments in which they are reared; any major variations would result from gross climatic differences, or perhaps because of a shortage of food. Mayr (1963)

cites *Drosophila* as being "morphologically notoriously uniform," and Sokoloff (1955, 1957, 1964), mostly from his impressions of numerous collections of wild flies of *D. pseudoobscura* and relatives, has stated that the material collected in the field generally fails to resemble in size the mean obtained when flies are reared under conditions of extreme starvation. This has led

me to conclude that these fruit flies not only manage to find enough food to complete their development, but that they do so with what appears to be the minimum of both intra- and interspecies competition under natural conditions. Thus, the data reported here are designed in part to supply some information on the degree of morphological variation primarily of natural populations of *D. pseudoobscura* (the more widespread species of the *pseudoobscura* subgroup), and to compare the results with those obtained by other investigators on other *Drosophila* species. Secondarily, but not less important, some of the data have bearing on the problem of competition, a subject much discussed in the past decade, meriting a number of reviews (see, for example, Andrewartha and Birch, 1960; Bakker, 1964; Klomp, 1964; Milne, 1961, 1962).

MATERIALS AND METHODS

Except for two samples, collected in 1956, one at Bryce Canyon, Utah, at an altitude of 8000 feet, and the other, here referred to as Mono Lake, collected 20 miles south of Leevining, California, approximately one mile south of the Big Springs campground, also at an altitude of 8000 feet, the *Drosophila* flies, from which measurements of wings, wings and legs, or body weight were obtained, were collected in 1957 and 1958 from the following areas (see Fig. 1).

In 1957 Professor Th. Dobzhansky kindly provided the writer with dead flies or live flies in excess of his needs from the following localities:

1. Tassajara Hot Springs (TJ), Monterey County, California; elevation about 1600 feet, early July.
2. Camino (CA), near Placerville, California; elevation 3000 feet, early July.
3. Wildrose (WR), Panamint Range, California, near the Thorndike Camp, between the Charcoal Kilns and Mahogany Flats; elevation 7500 feet, July 1.
4. Sequoia National Park (SQ), California, At-well Mills Campground near Mineral King; elevation 6600 feet, June 28.
5. Mesa Verde National Park (MV), Colo-

rado, exact location uncertain; elevation 7000–8000 feet, late July.
6. Grand Canyon, Arizona, North Rim (GCN); elevation over 8000 feet, late July.
7. Jacob Lake (JL), Kaibab National Forest, Arizona; elevation 7921 feet, late July.
8. Betatakin Ruin (BT), Navajo County, Arizona; this area has not been surveyed topographically, but points seven miles away are above 6000 or 7000 feet, late July.
9. Flagstaff (FL), Arizona; elevation 6895 feet, July 24.
10. Prescott (PR), Arizona; elevation 5354 feet, late July.
11. Chiricahua National Monument (CH), Arizona; elevation about 5500 feet, mid-June.
12. Aldrich Farm, near Austin, Texas (TX); elevation about 500 feet, sample collected in April.

In 1958, except where noted, the writer collected material from the following localities:

1. Yellowstone National Park (YL), Wyoming, near the west entrance; elevation 6700 feet, July 24.
2. Chadron State Park (CN), Nebraska, near the campground; elevation 3400 feet, July 26.
3. Grand Canyon, Arizona, South Rim (GCS), 14 miles east of the Visitor's Center on the East Rim Drive; elevation 7000 feet. One sample (GCS-2) collected July 4, and another (GCS-3) at the same collecting site, August 16.
4. Flagstaff (FL), Arizona. Collected in a *Pinus ponderosa* grove three miles from Highway 89A, off the road leading to Lake Mary; elevation 6895 feet, July 5.
5. Prescott (PR), Arizona. From a *P. ponderosa* grove located at the corner of the Senator's Highway and a dirt road leading to Lugar de Paz and The Pines; elevation about 5354 feet, July 6.
6. Chiricahua National Monument (CH), Arizona, five miles from monument headquarters toward Masai Point; elevation 5500 feet, July 1.
7. Vandeventer Flat (VF), in the saddle between the San Jacinto and Santa Rosa mountains, southern California (see Epling *et al.*, 1957, for map including this and the two following localities); elevation 4500 feet, early June. This material was kindly provided by Professor Carl Epling, University of California, Los Angeles, California.
8. Piñon Flat (PF), Mount San Jacinto, California, about six miles from VF; elevation 4000 feet, collected early June for Professor Carl Epling, and kindly supplied to the writer.
9. Keen Camp (KC), Mount San Jacinto, California, about 15 miles from VF and 20 or more miles from PF; elevation 4300 feet, July 7.
10. Galeana (GA) on the Sierra Madre Orien-

tal, south of Monterrey, Mexico; elevation 5425 feet, August 2.

11. Cuernavaca (CU), Mexico, 54 kilometers south of Mexico City; elevation about 9000 feet, August 4.

A detailed description of the ecological conditions of each locality is not necessary, but an idea may be given of the range of habitats by comparing some of the localities in Arizona and in California. In Arizona, Betatakin is in an arid belt high on the Colorado plateau, receiving a precipitation of nine inches per year. Chiricahua, in southern Arizona, is also relatively arid but receives greater moisture, about 18 inches of precipitation per year on the average. Prescott compares with Chiricahua in elevation and aridity. Greater precipitation is recorded in Flagstaff, in the south and north rims of the Grand Canyon, and in Jacob Lake. The amount of precipitation increases more or less in the order given.

In California, the localities sampled also contrast sharply: Piñon Flat, facing the Sonoran desert, has a flora characteristic of semidesert conditions (details in Epling et al., 1957). Other localities, such as Keen Camp, Wildrose, and others are in the transitional life zone. Finally, Tassajara is under the influence of the coastal climate, with winter and spring rainfalls, and morning and evening fogs during much of the year.

Flies arriving dead, and live flies in excess of other needs, were simply preserved in 70 per cent alcohol. Subsequently, if they derived from Rocky Mountain sites, both wings and hind legs of flies of both sexes were mounted. If they originated from the Sierra Nevada, or other areas where flies of the *pseudoobscura* and *affinis* subgroups coexist, only males were mounted, since these can be classified readily to subgroup by the presence of one tarsal comb for the *affinis* subgroup and two for the *pseudoobscura* subgroup; but there is no way to classify females to these subgroups except by examining the tarsal combs in their sons, or by cytological examination of the salivary glands in the larvae.

From areas where *D. pseudoobscura* and *D. persimilis* are known to coexist, only males were used, and, in addition to wings and hind legs, the genital plate was also removed and mounted in paraffin oil. Subsequently these flies were classified to their respective species by the methods outlined by Rizki (1951) and Spassky (1957).

Live males from TJ, CA, PR, FL, GCN, JL, MV, and BT were lightly etherized and weighed individually on a Misco Quartz Helix Balance, on which a load of 5 mg. caused an extension of 67 mm. from zero (read to one-half of a millimeter). After coding, they were isolated and their wings were detached for measurements. In addition to wings, the genital plates of males derived from CA, SQ, TJ, and WR were also mounted to aid in their classification to species. The information thus obtained served to compute the correlations between body weight and wing length.

Strains from two localities, Mono Lake (ML), California, and the south rim of the Grand Canyon (GCS), Arizona, were used in the intraspecies larval competition studies. The ML flies were collected in 1956, and the GCS flies in 1958. From each of these localities single non-virgin females were introduced into bottles containing cornmeal–molasses–agar medium, and from the successful cultures 10 were retained and kept in an incubator set at 16° C. (in the case of ML for over two years, but in the case of GCS for only two generations before the experiments were set up).

In carrying out the competition studies, the following procedure was followed: virgin females were collected from all the 10 stocks available for each locality. Females from half of the stocks were introduced into one oviposition bottle and females from the other stocks into another oviposition bottle. Equal numbers of males as there were females (but derived from the opposite half of the stocks) were introduced into these oviposition bottles. In this manner, brother–sister matings were prevented and a high degree of genetic variability was assured.

Into each oviposition bottle two cardboard spoons filled with cornmeal–molasses–agar medium, heavily seeded with dry Fleischmann's yeast, were introduced. The adults were transferred to new oviposition bottles daily and the egg-laden spoons returned to their original bottles. Both sets of bottles were kept in an incubator set at 16° C.

The competition experiments were carried out at 16° C. and 24° C. First instar larvae not more than 24 hours old were introduced in densities of 1, 2, 3, 4, 5, 6, 8, 10, 12, 16, 20, 24, 32, 40, 48, 64, and 80 larvae per vial into shell vials containing 4 cc. of freshly prepared Kalmus medium (Kalmus, 1943), just after seeding the medium with 0.05 cc. of a freshly prepared 20 per cent suspension of dry active Fleischmann's yeast. For a given temperature and strain, densities 1 and 2 were replicated 50 times, densities 3, 4, and 5 replicated 25 times, while densities 6 through 80 were replicated only 20 times. The number of vials set up at any one time varied, but in any one day the number of replicates for the various densities was so planned as to introduce half of them into the 16° C. and half into the 24° C. incubators.

Finally, to obtain some data on flies which developed under extreme conditions of competition in another medium, a sample of adult flies was obtained from a population cage. The population in this cage was initiated with flies originally from Piñon Flats, Mt. San Jacinto, California. Arrowhead (AR) and Chiricahua (CH), inversions in the third chromosome of *D. pseudoobscura*, were introduced as AR/CH heterozygotes. The cage was maintained at 22° C. The food supplied to these flies was the Spassky medium, consisting of Cream of Wheat inoculated with live bakers' yeast. The food cups were supplied with paper strips. The sample was obtained four months after the cage had been started, and the population had presumably achieved an equilibrium in regard to natality and mortality. The population cage was heavily infested with a non-parasitic mite. Hence, the flies had to compete not only with each other but also with the mites for the available food supply. The cage contained large numbers of adults (over 2000) which congregated, several layers deep, whenever a fresh food cup was introduced. Few eggs were laid in these cups. (For further details see Van Valen *et al.*, 1962.)

Flies from this cage and from the competition vials were fully aged so the exoskeleton was fully hardened before the flies were preserved in alcohol. The wings and legs of these flies were mounted in paraffin oil according to the method outlined by Sokoloff (1958).

The wings and legs from the various sources were measured with a dissecting microscope, with an ocular micrometer inserted into a 15× ocular, in combination with a 3× objective. Two millimeters were equivalent to 53 ocular micrometer units.

Wing length was measured from the point of bifurcation of the second and third longitudinal veins to the distal tip of the wing, along the third longitudinal vein. Wing width was determined by placing the ocular micrometer perpendicular to the long axis of the wing. The measurement was made from the tip of the fifth longitudinal vein to the first longitudinal vein.

The length of the tibia was determined from the tibiotarsal to the tibiofemoral joints, with the micrometer scale placed over the posterior surface of the tibia.

RESULTS

The data will be presented in the following order: (1) analysis of correlation between wing length and body weight in *D. pseudoobscura* and *D. persimilis*; (2) effect of density on body size of *D. pseudoobscura* as reflected by wing and leg measurements obtained from flies reared at various densities and at two temperatures in vials containing defined amounts of medium; (3) body measurements of *D. pseudoobscura* reared in a population cage where intense competition conditions prevailed; and (4) range in size of body char-

TABLE 1. *Body weight and/or wing length and wing width of* Drosophila pseudoobscura *and* D. persimilis *males collected in various localities.*

Locality	N	Body weight (mg) $\overline{m} \pm$ S.E.	Wing length (ocular units) $\overline{m} \pm$ S.E.	Wing width (ocular units) $\overline{m} \pm$ S.E.
		Drosophila pseudoobscura		
California				
Camino	18	1.056 ± 0.058	52.00 ± 1.04	27.14 ± 0.53
Mono Lake	9	1.011 ± 0.057	— —	— —
Sequoia	23	1.049 ± 0.040	55.79 ± 0.83	28.17 ± 0.38
Tassajara	27	1.077 ± 0.047	53.59 ± 0.77	27.90 ± 0.40
Wildrose	95	— —	54.74 ± 0.34	28.84 ± 0.22
Arizona				
Betatakin	47	0.871 ± 0.026	51.87 ± 0.53	26.89 ± 0.28
Chiricahua	92	0.966 ± 0.024	— —	— —
Flagstaff	20	1.059 ± 0.034	54.53 ± 0.64	28.55 ± 0.32
Grand Canyon	39	1.063 ± 0.030	53.77 ± 0.51	27.91 ± 0.27
Grand Canyon	13	1.092 ± 0.072	— —	— —
Jacob Lake	29	1.070 ± 0.040	54.12 ± 0.79	28.30 ± 0.41
Prescott	31	0.919 ± 0.028	52.28 ± 0.52	27.09 ± 0.31
Colorado				
Mesa Verde	50	0.923 ± 0.039	52.06 ± 0.51	27.05 ± 0.25
		Drosophila persimilis		
California				
Camino	14	0.801 ± 0.066	49.35 ± 0.58	26.10 ± 0.71
Mono Lake	5	— —	54.48 ± 0.23	27.76 ± 0.12
Sequoia	16	0.987 ± 0.045	55.46 ± 1.02	28.85 ± 0.46
Tassajara	8	0.981 ± 0.059	52.55 ± 1.13	27.22 ± 0.64
Wildrose	35	— —	54.07 ± 0.70	28.16 ± 0.34

acters of *D. pseudoobscura* captured in the field in two successive years.

1. *Correlation Between Wing Length and Body Weight*

The wings of Diptera and particularly of *Drosophila* have been used repeatedly as a criterion for body size (see, for example, Stalker and Carson, 1947, 1948, 1949; Prevosti, 1954, 1955a, 1955b, 1961; Teissier, 1957, 1958; Pantelouris, 1957; Tantawy and Mallah, 1961; McFarquhar and Robertson, 1963; and Misra and Reeve, 1964) since the wing veins provide accurate unchangeable landmarks, the intervals between which can be easily measured. The present study is an attempt to determine to what degree wing length and body weight are correlated in *D. pseudoobscura* and *D. persimilis*. The study has been confined to the male sex, since the weight of females

varies depending on age, the size of the ovaries, and the degree of egg-laying activity. When females are at the peak of egg-laying activity they take in large amounts of yeast and/or fluids altering their weight. To minimize the differences in feeding among males, only flies stored in culture bottles in a constant room temperature at 18° C. for a number of days (to enable any starved flies to achieve a certain degree of stability between food intake and metabolic activities) have been used. Since no attempts were made to examine the size and pigmentation of the testis, which can give a rough approximation of the age of the flies (Dobzhansky and Epling, 1944), this factor remains unknown.

The preliminary data on body weight and/or wing length and wing width obtained from *D. pseudoobscura* and *D. persimilis* males collected in the field in 1956 and 1957 are summarized in Table 1. As ex-

pected, the males of the former species are generally larger, as indicated both by the mean values for body weight and wing measurements. Coefficients of variation computed from these data range from 14.20 per cent for body weight of the Flagstaff (FL) sample to 30.05 per cent for the Mesa Verde (MV) sample of *D. pseudoobscura*. The smaller samples of *D. persimilis* males available give comparable coefficients of variation for body weight (17.01 per cent for Tassajara (TJ) and 30.93 per cent for the Camino (CA) sample).

Wing measurements give smaller coefficients of variation: for *D. pseudoobscura* these coefficients range from 5.29 per cent for FL to 8.52 per cent for CA for wing length, and from 5.09 per cent for FL to 8.32 per cent for CA for wing width. For *D. persimilis* these coefficients vary from 4.40 per cent for the CA sample to 7.62 for Wildrose (the Mono Lake sample actually gives a larger coefficient of variation, but the sample is small). Wing width coefficients of variation range from 6.41 per cent for Sequoia to 10.18 per cent for CA.

Although there is a fair correlation between wing length and wing width, it has been found that the latter measurement is less reliable: the bristles on the anterior margin of the wing, when mounted in paraffin oil, tend to fold back (Sokoloff, 1958), introducing a fairly large error. This measurement has therefore been omitted, and the correlation coefficients have been computed using only the wing length and body weight measurements.

Visual inspection of the means for body weight and wing length in Table 1 indicates

TABLE 2. *Correlation coefficients between body weight and wing length measurements of* Drosophila pseudoobscura *and* D. persimilis *derived from various localities.*

Locality	D. pseudoobscura	D. persimilis
Camino	+0.817	+0.867
Sequoia	+0.718	+0.772
Tassajara	+0.838	+0.852
Betatakin	+0.828	
Flagstaff	+0.665	
Grand Canyon	+0.552	
Jacob Lake	+0.885	
Prescott	+0.778	
Mesa Verde	+0.842	
Total	+0.777	+0.842

that, overall, the heavier flies have longer wings. The correlations, summarized for the individual samples and the total in Table 2, fall short of being perfect ($r = +0.777$ for *D. pseudoobscura* and $r = +0.842$ for *D. persimilis* when the total numbers of individuals are considered). This may result from a number of causes including genetic differences (since flies with intermediate wing lengths may be as heavy as those with the longest wings) and the age of flies. That these are not spurious correlations is indicated by the data given in Table 3. Here the analyses of variance and covariance are given for the nine geographic strains of *D. pseudoobscura*. The fact that the correlation coefficients and the regression values between and within strains are of comparable magnitude leads to the conclusion that the various strains studied, although variable, have comparable variations.

The regression lines of wing length on body weight for the samples of *D. pseudo-*

TABLE 3. *Analysis of variance and covariance of wing length and body weight of nine different geographic strains of* D. pseudoobscura.

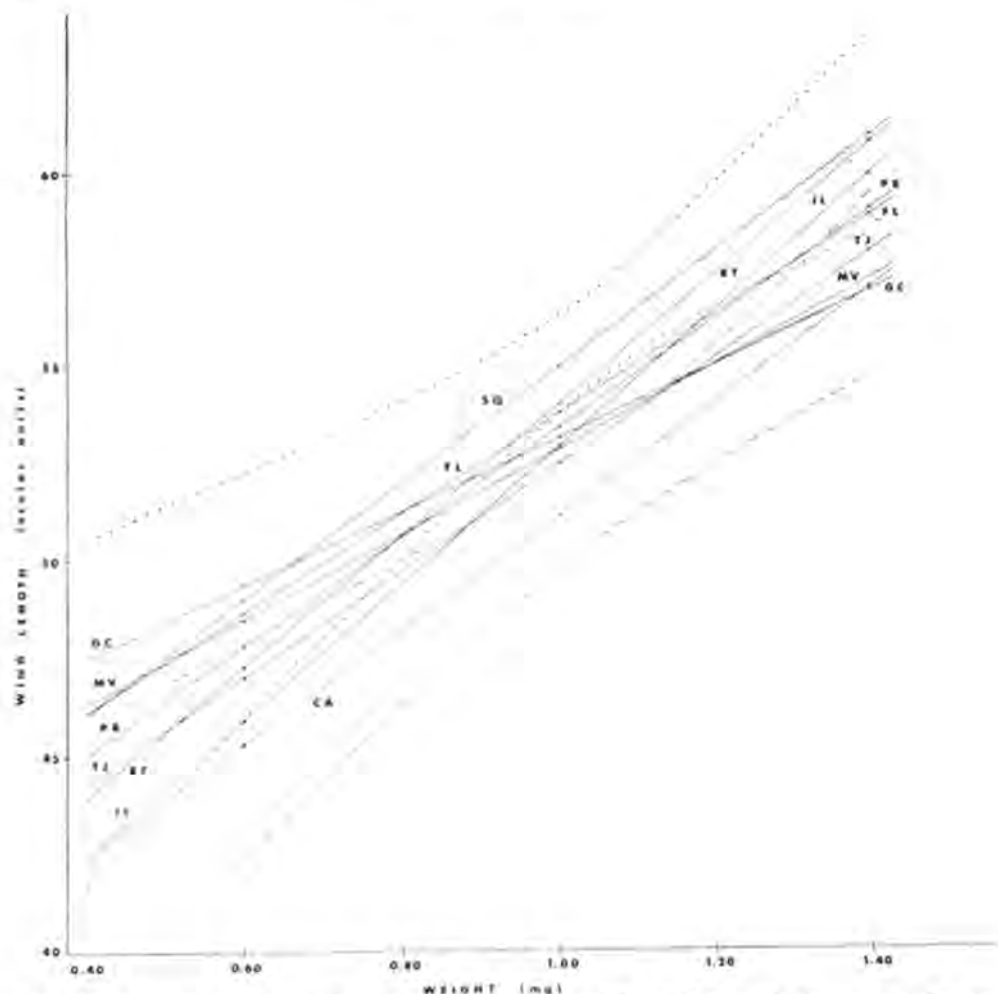| Source of variation	df	Wing length		Body weight		Covariance		
		Sums of squares	Mean square	Sums of squares	Mean square	Sum of products	Correlation coefficient	Regression
Total	283	4,085.89	2,845.74	14.33	1.036	188.09		
Between	8	429.69	61.38	1.89	0.236	21.91	0.7693	0.051
Within	275	3,656.20	2,784.36	12.44	0.800	166.18	0.779	0.045

FIG. 2. Regression lines of wing length on body weight of *Drosophila pseudoobscura* wild flies derived from nine localities. The formulae for the lines are: BT (Betatakin) $\hat{Y} = 37.289 + 16.738X$; CA (Camino) $\hat{Y} = 36.467 + 14.709X$; FL (Flagstaff) $\hat{Y} = 41.024 + 12.754X$; GC (Grand Canyon, north rim) $\hat{Y} = 43.701 + 9.476X$; JL (Jacob Lake) $\hat{Y} = 35.439 + 17.463X$; MV (Mesa Verde) $\hat{Y} = 41.881 + 11.032X$; PR (Prescott) $\hat{Y} = 39.201 + 14.228X$; SQ (Sequoia) $\hat{Y} = 40.180 + 14.881X$; TJ (Tassajara) $\hat{Y} = 38.785 + 13.742X$. The dotted and dashed curves represent the 95 per cent confidence limits for SQ and CA, respectively.

obscura and *D. persimilis* available have been computed, and diagrams of the regression lines derived therefrom are shown in Figs. 2 and 3.

It is clear from these analyses that either body weight or wing length is a good criterion for body size of these flies. The latter has the advantage that it is derived

from an appendage which, once hardened, is not subject to fluctuations in size, while body weight may be affected by numerous physiological factors. Hence, in the following sections, body size of the flies is expressed primarily in terms of wing length and width, and tibia length. The body weight data given in Table 1 will be con-
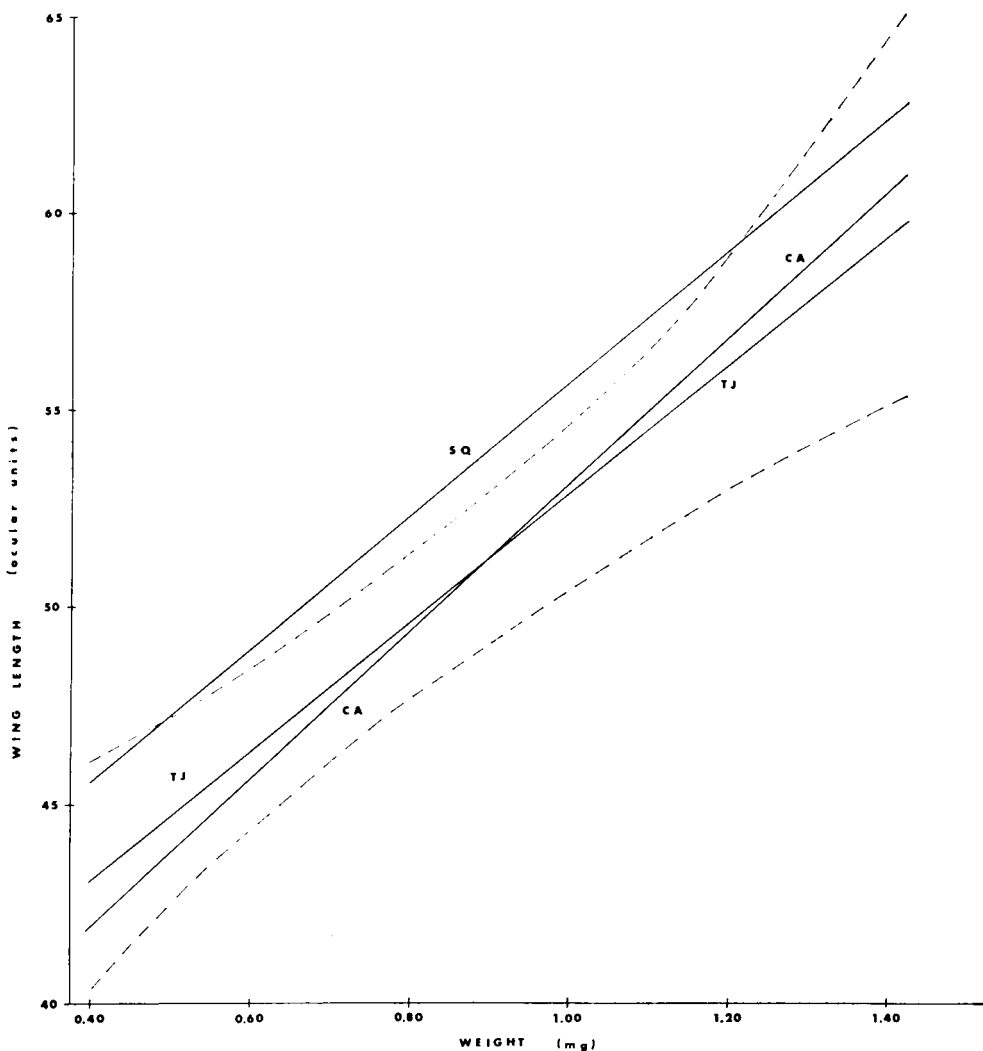
FIG. 3. Regression lines of wing length on body weight of *Drosophila persimilis* wild flies derived from three localities. The formulae for the lines are: CA (Camino) $\hat{Y} = 34.404 + 18.658X$; SQ (Sequoia) $\hat{Y} = 38.792 + 16.893X$; TJ (Tassajara) $\hat{Y} = 36.557 + 16.299X$. The dashed curves represent the 95 per cent confidence limits for CA.

sidered further in the discussion section.

2. Effect of Density on Quantitative Characters

The data obtained from flies derived from Mono Lake (ML) and Grand Canyon (GCS) reared at various competition densities (henceforth to be abbreviated as D)

at two temperatures are included in Tables 4 and 5 and they are represented graphically in Fig. 4. As expected, flies reared at low D's are larger than those reared at high D's, and they are larger when reared at low temperatures than at high temperatures in the absence of competition.

The performances of the two strains in

TABLE 4. *Wing length and width and tibia length (in ocular units) of* D. pseudoobscura *derived from the Grand Canyon, Arizona, reared at different densities.*

Density	Males				Females			
	N	Wing length $\bar{m} \pm$ S.E.	Wing width $\bar{m} \pm$ S.E.	Tibia length $\bar{m} \pm$ S.E.	N	Wing length $\bar{m} \pm$ S.E.	Wing width $\bar{m} \pm$ S.E.	Tibia length $\bar{m} \pm$ S.E.
			Flies reared at 24° C.					
1	21	54.81 ± 0.22	28.86 ± 0.15	21.41 ± 0.07	22	60.42 ± 0.35	31.05 ± 0.16	22.38 ± 0.14
2	41	54.84 ± 0.14	28.77 ± 0.15	21.39 ± 0.08	43	60.48 ± 0.17	31.14 ± 0.10	22.63 ± 0.08
3	39	54.30 ± 0.27	28.54 ± 0.16	21.20 ± 0.10	26	60.14 ± 0.23	30.71 ± 0.16	22.40 ± 0.10
4	36	54.40 ± 0.22	28.58 ± 0.15	21.19 ± 0.12	44	59.90 ± 0.20	30.59 ± 0.12	22.47 ± 0.11
5	54	54.24 ± 0.21	28.58 ± 0.11	21.12 ± 0.08	48	59.72 ± 0.22	30.63 ± 0.13	22.21 ± 0.09
6	48	54.31 ± 0.23	28.53 ± 0.14	21.27 ± 0.13	43	59.68 ± 0.26	30.79 ± 0.12	22.36 ± 0.10
8	73	53.56 ± 0.17	28.13 ± 0.10	20.88 ± 0.08	50	59.29 ± 0.24	30.57 ± 0.12	22.19 ± 0.10
10	56	53.18 ± 0.32	28.00 ± 0.17	20.70 ± 0.14	59	57.34 ± 0.42	29.47 ± 0.23	21.24 ± 0.18
12	78	51.63 ± 0.25	27.20 ± 0.13	19.85 ± 0.13	75	56.73 ± 0.32	29.22 ± 0.16	21.01 ± 0.15
16	73	50.77 ± 0.29	26.77 ± 0.16	19.48 ± 0.11	64	55.60 ± 0.39	28.78 ± 0.20	20.59 ± 0.17
20	51	49.51 ± 0.44	26.29 ± 0.26	19.05 ± 0.21	52	54.30 ± 0.54	28.28 ± 0.29	19.99 ± 0.24
24	38	47.61 ± 0.56	25.35 ± 0.30	18.10 ± 0.23	50	52.76 ± 0.30	27.64 ± 0.31	19.29 ± 0.24
32	25	48.28 ± 0.72	25.62 ± 0.34	18.49 ± 0.27	25	52.39 ± 0.87	27.14 ± 0.48	19.01 ± 0.34
40	15	48.56 ± 1.10	25.57 ± 0.58	18.28 ± 0.45	18	49.71 ± 0.82	26.02 ± 0.39	18.22 ± 0.31
48	14	46.40 ± 0.88	24.41 ± 0.45	17.86 ± 0.35	12	47.72 ± 1.03	24.82 ± 0.54	17.45 ± 0.40
64	16	47.15 ± 0.58	24.79 ± 0.32	17.88 ± 0.23	8	50.35 ± 1.28	25.73 ± 0.61	18.18 ± 0.47
80	10	47.68 ± 0.72	25.02 ± 0.40	18.36 ± 0.30	8	50.03 ± 1.31	25.90 ± 0.58	18.35 ± 0.37
			Flies reared at 16° C.					
1	25	59.67 ± 0.24	31.03 ± 0.14	22.75 ± 0.11	18	66.74 ± 0.20	33.54 ± 0.13	23.92 ± 0.15
2	40	59.96 ± 0.18	30.97 ± 0.10	22.71 ± 0.07	84	66.80 ± 0.12	33.86 ± 0.07	23.87 ± 0.05
3	34	60.21 ± 0.20	31.11 ± 0.13	22.69 ± 0.07	31	66.52 ± 0.17	33.48 ± 0.10	23.89 ± 0.07
4	96	59.74 ± 0.13	30.89 ± 0.08	22.46 ± 0.06	30	66.05 ± 0.43	33.23 ± 0.21	23.90 ± 0.09
5	93	60.09 ± 0.12	30.82 ± 0.08	22.81 ± 0.06	90	65.83 ± 0.12	33.06 ± 0.08	23.68 ± 0.05
6	97	59.63 ± 0.12	30.81 ± 0.07	22.56 ± 0.05	37	66.29 ± 0.20	33.72 ± 0.12	23.89 ± 0.08
8	113	59.69 ± 0.12	30.83 ± 0.06	22.54 ± 0.05	106	65.53 ± 0.14	33.15 ± 0.07	23.66 ± 0.06
10	120	58.73 ± 0.16	30.13 ± 0.10	22.02 ± 0.06	129	64.40 ± 0.16	32.54 ± 0.09	23.11 ± 0.06
12	125	57.67 ± 0.15	29.69 ± 0.08	21.51 ± 0.07	137	62.93 ± 0.22	31.71 ± 0.12	22.38 ± 0.09
16	127	55.05 ± 0.21	28.45 ± 0.12	20.28 ± 0.09	133	60.68 ± 0.24	30.66 ± 0.14	21.39 ± 0.10
20	143	53.58 ± 0.23	27.54 ± 0.13	19.60 ± 0.09	144	58.79 ± 0.27	29.74 ± 0.15	20.51 ± 0.10
24	113	52.00 ± 0.25	26.87 ± 0.14	19.07 ± 0.10	117	57.90 ± 0.35	29.19 ± 0.19	20.22 ± 0.13
32	103	51.39 ± 0.38	26.51 ± 0.20	18.77 ± 0.15	40	55.17 ± 0.63	27.88 ± 0.32	19.25 ± 0.23
40	113	50.41 ± 0.30	26.15 ± 0.16	18.23 ± 0.12	38	54.03 ± 0.71	27.23 ± 0.36	18.83 ± 0.24
48	34	49.84 ± 0.53	25.74 ± 0.30	18.12 ± 0.22	24	51.98 ± 0.89	26.40 ± 0.35	18.29 ± 0.29
64	35	48.61 ± 0.76	24.81 ± 0.38	17.52 ± 0.26	14	52.13 ± 1.06	26.24 ± 0.61	18.27 ± 0.41
80	24	49.30 ± 0.78	25.18 ± 0.40	17.79 ± 0.29	9	53.11 ± 1.04	26.64 ± 0.48	18.40 ± 0.34

these experiments are different depending on the temperature and sex: at 24° C. the means of all measurements of males obtained from D 1–12 are different at the five per cent level of significance (the GCS flies being larger), except for wing width, D 4, where *t* is between the one and five per cent level. For D 16–80, the means of all measurements show no significant difference at the five per cent level, except in the following cases: wing width at D 20, and wing length at D 40, with 0.01 < *t* < 0.05. For females, except for D 5, there is no difference at the five per cent level for D 1–20. At the higher D's (except for D 40 where the means of all measurements are significantly different and D 24 where wing width is significantly different), the means of all measurements show no significant difference at the five per cent level.

Males reared at 16° C. show the following. For D 1–12, tibia length GCS > ML, but wing measurements show no significant difference (at the five per cent level) except for the following: D 2 wing length—ML > GCS; D 3 wing width—GCS > ML;

TABLE 5. *Wing length and width and tibia length (in ocular units) of* D. pseudoobscura *derived from Mono Lake, California, reared at different densities.*

Den-sity	N	Males Wing length $\bar{m} \pm$ S.E.	Wing width $\bar{m} \pm$ S.E.	Tibia length $\bar{m} \pm$ S.E.	N	Females Wing length $\bar{m} \pm$ S.E.	Wing width $\bar{m} \pm$ S.E.	Tibia length $\bar{m} \pm$ S.E.
			Flies reared at 24° C.					
1	55	53.15 ± 0.14	27.98 ± 0.09	20.37 ± 0.07	32	59.00 ± 0.22	30.25 ± 0.10	21.69 ± 0.11
2	45	52.03 ± 0.22	27.35 ± 0.12	19.96 ± 0.10	36	57.86 ± 0.20	29.66 ± 0.10	21.61 ± 0.10
3	40	51.46 ± 0.19	27.13 ± 0.10	20.01 ± 0.08	39	57.91 ± 0.20	29.75 ± 0.11	21.54 ± 0.11
4	35	52.91 ± 0.30	28.09 ± 0.19	20.32 ± 0.11	29	58.44 ± 0.28	30.07 ± 0.14	21.72 ± 0.16
5	39	52.26 ± 0.32	27.47 ± 0.21	20.08 ± 0.15	42	59.06 ± 0.18	30.40 ± 0.11	21.68 ± 0.16
6	41	52.32 ± 0.31	27.60 ± 0.19	20.02 ± 0.14	48	57.93 ± 0.30	29.89 ± 0.16	21.40 ± 0.12
8	54	51.24 ± 0.30	26.99 ± 0.15	19.81 ± 0.12	65	56.57 ± 0.36	29.23 ± 0.17	20.87 ± 0.16
10	52	49.68 ± 0.42	26.15 ± 0.22	19.18 ± 0.18	64	55.46 ± 0.36	28.63 ± 0.18	20.23 ± 0.15
12	54	48.82 ± 0.39	26.01 ± 0.20	18.78 ± 0.18	65	54.83 ± 0.36	28.32 ± 0.18	20.16 ± 0.15
16	67	50.01 ± 0.35	26.40 ± 0.18	19.17 ± 0.15	79	54.45 ± 0.38	28.14 ± 0.22	20.06 ± 0.16
20	29	48.52 ± 0.52	25.48 ± 0.27	18.51 ± 0.20	63	52.26 ± 0.46	27.04 ± 0.24	19.06 ± 0.14
24	40	48.63 ± 0.54	25.81 ± 0.29	18.68 ± 0.22	81	53.91 ± 0.35	28.07 ± 0.15	19.77 ± 0.15
32	34	47.92 ± 0.55	25.31 ± 0.30	18.29 ± 0.23	57	51.53 ± 0.57	26.88 ± 0.28	18.80 ± 0.21
40	17	45.39 ± 0.90	24.18 ± 0.42	17.24 ± 0.31	53	53.36 ± 0.34	27.72 ± 0.16	19.34 ± 0.14
48	13	44.26 ± 0.83	23.48 ± 0.46	17.08 ± 0.31	21	48.47 ± 0.62	25.24 ± 0.34	17.84 ± 0.22
64	18	47.92 ± 0.94	25.69 ± 0.46	18.37 ± 0.36	41	51.18 ± 0.56	26.35 ± 0.27	18.36 ± 0.20
80	7	47.51 ± 1.35	24.49 ± 0.78	18.03 ± 0.42	50	51.73 ± 0.48	26.55 ± 0.24	18.75 ± 0.19
			Flies reared at 16° C.					
1	20	60.51 ± 0.41	31.00 ± 0.17	21.89 ± 0.16	38	67.82 ± 0.23	33.44 ± 0.10	23.27 ± 0.10
2	33	60.90 ± 0.20	31.02 ± 0.11	22.12 ± 0.09	39	67.02 ± 0.22	33.10 ± 0.10	23.37 ± 0.09
3	23	59.98 ± 0.25	30.61 ± 0.13	21.99 ± 0.10	87	66.50 ± 0.12	32.90 ± 0.18	23.33 ± 0.05
4	24	59.63 ± 0.46	30.52 ± 0.24	21.73 ± 0.16	37	66.02 ± 0.40	33.15 ± 0.15	23.42 ± 0.11
5	84	59.68 ± 0.22	30.86 ± 0.13	21.95 ± 0.08	35	66.45 ± 0.25	33.39 ± 0.09	23.37 ± 0.08
6	89	59.64 ± 0.20	30.64 ± 0.12	21.81 ± 0.08	92	66.11 ± 0.25	33.01 ± 0.11	23.13 ± 0.10
8	123	57.80 ± 0.23	29.72 ± 0.11	21.21 ± 0.10	126	64.83 ± 0.21	32.51 ± 0.10	22.80 ± 0.08
10	113	58.62 ± 0.19	30.08 ± 0.10	21.42 ± 0.07	127	64.56 ± 0.25	32.28 ± 0.11	22.61 ± 0.10
12	130	57.72 ± 0.19	29.78 ± 0.11	21.09 ± 0.08	76	64.26 ± 0.25	32.25 ± 0.13	22.39 ± 0.11
16	66	56.29 ± 0.30	28.91 ± 0.17	20.40 ± 0.13	89	63.10 ± 0.24	31.62 ± 0.13	21.80 ± 0.12
20	56	55.68 ± 0.41	28.53 ± 0.22	20.30 ± 0.16	63	61.57 ± 0.42	30.82 ± 0.21	21.35 ± 0.16
24	70	55.65 ± 0.26	28.87 ± 0.14	20.19 ± 0.12	88	60.61 ± 0.34	30.59 ± 0.16	21.04 ± 0.14
32	72	53.73 ± 0.31	27.59 ± 0.15	19.50 ± 0.11	95	58.82 ± 0.41	29.58 ± 0.20	20.36 ± 0.15
40	50	53.40 ± 0.39	27.35 ± 0.20	19.51 ± 0.17	86	58.20 ± 0.43	29.28 ± 0.20	20.03 ± 0.16
48	35	52.01 ± 0.46	26.75 ± 0.23	18.96 ± 0.18	28	55.89 ± 0.63	27.99 ± 0.30	19.34 ± 0.23
64	14	53.31 ± 0.72	27.21 ± 0.41	19.49 ± 0.28	44	58.33 ± 0.54	28.88 ± 0.26	20.21 ± 0.19
80	20	52.44 ± 0.56	26.92 ± 0.27	19.05 ± 0.22	44	55.95 ± 0.62	27.84 ± 0.28	19.15 ± 0.23

D 8 wing length and wing width—GCS > ML. For D 20–80, means of all three characters show ML > GCS.

Females reared at this temperature can be summarized as follows. For D 1–10, tibia length GCS > ML. At these low densities no significant difference in wing length is detectable at D 2–4, 6, or 10, but ML > GCS in D 1, 5, and 8. For wing width GCS ≅ ML at D 1, 3, 4, and 10, and GCS > ML at D 2, 5, 6, and 8. At the higher densities D 12 shows no difference (five per cent level) for tibia length but wing measurements are significantly different (ML > GCS). For the remaining densities ML > GCS in the means of all three characters.

Comparing the effect of crowding for a given sex and strain at the two temperatures, we find:

1. The means of GCS male flies in D 1–24 for all three characters are significantly greater at 16° C. than at 24° C. at the one per cent level. For D 32–80 the means for tibia length are not significantly different at the five per cent level. The

differences between wing measurements show varying degrees of significance: they are not significant for wing length or wing width at D 64 or 80. Wing length is significantly different, at least at the five per cent level for D 32–48, and wing width at D 32 and D 48, but the last character fails to show any significance at D 40.

2. The means of GCS females in D 24 are significantly greater at 16° C. than at 24° C. for D 1–24 at the one per cent level (except for tibia length, D 20, which is significantly different at the five per cent level). In D 32–80 the means of tibia length are not different at the five per cent level. Differences between wing measurements show varying degrees of significance: there is no significant difference in wing length at D 64 or 80, nor in wing width at D 32, 64, or 80; the difference for wing length is significant at the five per cent level in D 32, and for wing width at D 40 and 48; the difference in wing length is significant at the one per cent level for D 40 and 48.

3. The means of ML males are significantly greater at 16° C. than those at 24° C. for all measurements at the one per cent level, except for wing width and tibia length at D 64 and tibia length at D 80 which are significantly different at the five per cent level.

4. The means of ML females in all characters are significantly greater at 16° C. than at 24° C. at all densities, except for the means of tibia length in D 80 which showed no significance even at the five per cent level.

Paired comparisons between the sexes, when the density and temperature are held constant, show the following relationships:

1. For GCS flies at 24° C., no differences at the five per cent level are observed between males and females in regard to wing length at D 40, 48, or 80; in wing width at D 40–80; in tibia length at D 32–80. The differences between the two sexes are significant at the one per cent level at D 1–32 for wing length, at D 1–24 for wing width, and at D 1–8 and 12–24 for

tibia length. Differences in wing length at D 64, wing width at D 32, and tibia length at D 10 are significant at the five per cent level.

2. For GCS flies reared at 16° C., means of wing length of females are significantly different at all densities, D 1–40 at the one per cent level, D 48–80 at the five per cent level. The means of wing width are significantly different at the one per cent level at D 1–40 and at the five per cent level at D 64. No significant difference is detected at D 48 or 80. The means of tibia length are significantly different at D 1–24 at the one per cent level, and except for D 40, which is significantly different at the five per cent level, the higher densities show no significant differences between the two sexes.

3. For ML flies reared at 24° C. the differences between the two sexes are significant at the one per cent level for wing length and wing width at all densities with one exception: D 64 wing width is not significantly different. Tibia length is significantly different at the one per cent level for D 1–16, 24, and 40, but not significantly so for D 20, 32, or 64–80.

4. For ML flies reared at 16° C. the differences between the means of males and females are also significant at the one per cent level for wing length and width at all densities except D 80 where wing width is not significantly different. Tibia length at D 1–32 differs significantly at the one per cent level, D 40 at the five per cent level, but D 48–80 are not significantly different.

A measure of variation of the flies emerging at the various densities can be gained by computing the coefficient of variation (CV). At the lower densities, where ample food is available, it is expected that flies will be fairly uniform, differing in size only as a result of genetic differences. Since CV values can readily be computed by the statistics given in Tables 3 and 4, they have been omitted from the body of the table, but they can be summarized briefly as follows. For the Grand Canyon data, regardless of temperature, sex, and character, the CV values are generally less than
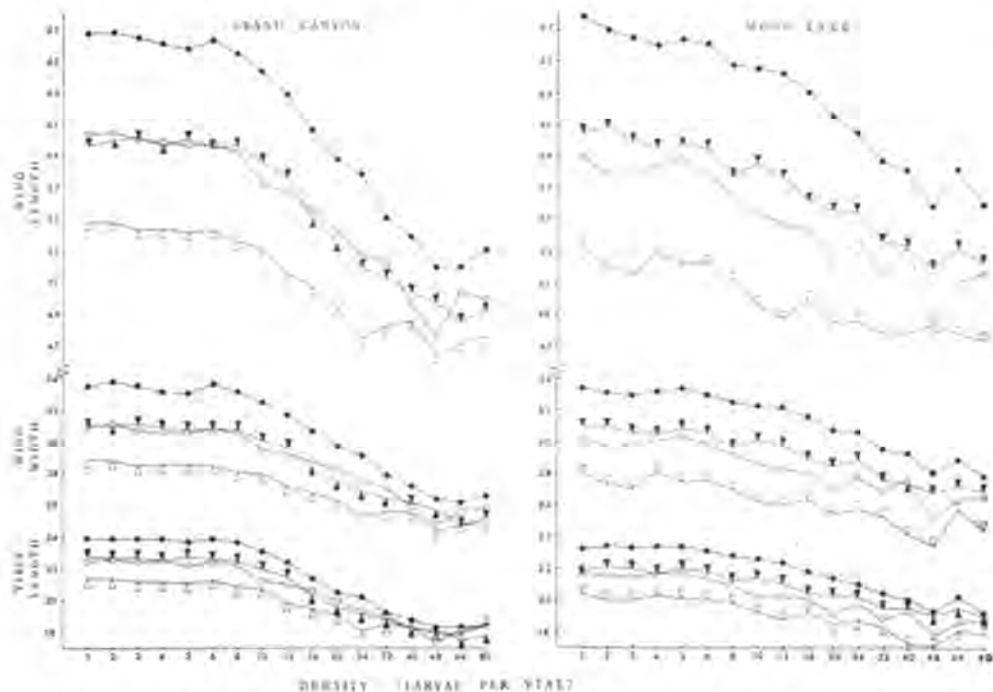
FIG. 4. Wing length (upper), wing width (middle), and tibia length (lower), in ocular units, of two strains of *Drosophila pseudoobscura* reared at different densities. Open triangles = males, at 24° C.; solid triangles = males at 16° C. Open circles = females at 24° C.; solid circles = females at 16° C.

three per cent for densities below 12. A near doubling in CV values is detected at D 10–16 at 24° C. and at D 12–24 at 16° C., the CV values exceeding six per cent. Above D 20 at 24° C. and above D 24 at 16° C., the CV values generally are again significantly higher, ranging between six and nine per cent. This is also generally true for the Mono Lake population at 24° C., but at 16° C. there seems to be a gradual increase in CV values up to D 16 for wing length and width, while there is an abrupt and significant increase in CV values for tibia length at about D 10. Above D 20 there is again a gradual but inconsistent increase in CV values varying with the character, tibia length showing a more uniform increase.

These results largely parallel the more limited study of intra- and interspecies competition in *D. pseudoobscura* and allied species (Sokoloff, 1955). In that study,

weight of flies gave fairly low CV values at the lower densities. At D 10 there was a significant increase in the value of CV, accompanying a sharp reduction in mean body weight. Regardless of the temperature conditions, as the density increased from 10 to 20 the weight of the flies dropped to a minimum, the developmental period increased, and survivorship of the flies decreased, but the CV values remained fairly stable or increased slightly.

With regard to the total numbers of males and females produced at the various densities, it may be observed that the GCS vials yielded about the same number of males and females at all densities at the two experimental temperatures. The only exceptions, D 32 and 40, gave significantly larger numbers of males than females at 16° C. Since the larvae were not sexed, it is probable that in these vials more male than female larvae were introduced by

TABLE 6. *Mean wing lengths (in ocular units) of male and female* D. pseudoobscura *derived from a population cage, infested with a non-parasitic mite, maintained at 22° C.*

Sex	$\overline{m} \pm$ S.E.	CV (per cent)	N
Males	47.72 ± 0.24	8.12	251
Females	52.98 ± 0.25	7.36	248

chance. This explanation cannot hold for the ML flies: at 24° C. females outnumber males at all densities above D 16. At 16° C., with the exception of D 40, the same phenomenon is observed for the same densities, the effect becoming pronounced above D 32. This effect was observed previously (Sokoloff, 1955) in samples of *D. pseudoobscura* and *D. persimilis* derived from the same locality.

It may be noted that these experiments differ from the previous one (Sokoloff, 1955) in that flies were obtained at all densities including D 80. It is probable that no survivors were observed at D 80 in the previous experiment because of insufficient replication.

3. Size of Flies Reared in a Population Cage Infested with Mites

The data for the flies derived from this population cage (see section on Materials and Methods for pertinent details) are restricted to one body character, wing length, and they are reported in Table 6. They fully confirm the observation of Van Valen *et al.* (1962) that extreme competition conditions existed in the mite-infested cage. A comparison may be made with the flies caught in nature in 1958 at the same locality from which flies in the population cages were derived: 22 males gave a mean wing length of 51.46 ± 1.16 ocular units; 84 females had a mean wing length of 54.12 ± 0.60 ocular units (see Table 6 for other measurements). Flies from the same locality reared under optimal conditions, 30 larvae per vial in 5 cc. of standard cornmeal–molasses–agar fly medium inoculated with brewers' yeast, reared at 16° C., produced flies whose measurements were as

follows: 45 males gave a mean wing length of 55.33 ± 0.14 ocular units and 50 females 61.35 ± 0.11 ocular units.

It may be pointed out that these values are optimal only in the standard medium. Flies from the Grand Canyon, contemporary in space and time with those used in the experiments reported in the previous section, reared in the same standard medium at 16° C., produced the following mean wing lengths (data from Sokoloff, 1965).

	$\overline{m} \pm$ S.E.	N
Males	57.19 ± 0.09	101
Females	63.14 ± 0.08	166

These values clearly are smaller than the mean values reported above (Table 4) in the low density vials for the GCS flies reared in Kalmus medium at 16° C., indicating that this medium provides certain essential mineral requirements which enable the flies to attain a larger size.

4. Comparisons Between Laboratory-reared Flies and Those Captured in Nature

Before undertaking these comparisons it will be useful to review the salient findings of the previous intraspecies competition studies. Sokoloff (1955) found that when first instar larvae of *D. pseudoobscura*, *D. persimilis*, and *D. miranda* are introduced into vials with defined amounts of food at various densities at two temperatures, all three species decrease in weight, lengthen in period of development, and the number of flies reaching the imago stage decreases as density increases. The mean weights, in milligrams, of *D. pseudoobscura* (given in more detail in Tables 4 and 5 in Sokoloff, 1955) are shown in Table 7.

Clearly, at a density of six larvae per vial there is an effect of temperature: the flies at the lower temperature are larger, and the weight of females greatly exceeds the weight of males. At D 10 the temperature effect disappears, but there is still a difference between the two sexes. At D 20 the flies are reduced to their possible mini-

TABLE 7. *Mean weights, in milligrams, of* D. pseudoobscura.

Density	24° C.				16° C.			
	Males		Females		Males		Females	
	$\overline{m} \pm$ S.E.	N	$\overline{m} \pm$ S.E.	N	$\overline{m} \pm$ S.E.	N	$\overline{m} \pm$ S.E.	N
6	1.070 ± 0.020	44	1.326 ± 0.018	57	1.232 ± 0.022	63	1.407 ± 0.034	54
10	0.927 ± 0.019	74	1.050 ± 0.024	87	0.924 ± 0.018	83	1.073 ± 0.017	77
20	0.605 ± 0.015	83	0.690 ± 0.010	122	0.634 ± 0.010	113	0.736 ± 0.011	141
40	0.580 ± 0.034	5	0.638 ± 0.046	8	0.646 ± 0.027	13	0.706 ± 0.031	18

mal size, since a further increase in density has no effect in reducing body weight.

Returning now to the data in Tables 4 and 5 (section 2, above), it was noted that tibia length in flies from GCS and ML is equal in the two sexes at D 32–80 within a given temperature. At different temperatures only GCS males and females give comparable measurements at D 32–80. ML tibiae in both sexes give distinctly larger values at nearly all densities at the lower temperature. The exceptions are D 64–80, where tibiae become the same at 16° C. and 24° C. for males, while the only density in which no differences were demonstrable for ML females at the two temperatures was D 80.

The genetic differences of the two strains with regard to wing length and width, evidenced by the fact that these characters were consistently larger for GCS than for ML at the lower densities (D 1–12 for males and D 1–20 for females), were largely eliminated at the higher densities at 24° C., since nearly all t values for these paired comparisons were not significant at the five per cent level. However, at 16° C., while the GCS male flies were larger in D 1–12 and females in D 1–10, at the higher densities the reduction in wing length and width was significantly greater for GCS than for ML.

The t values of paired comparisons of wing length and width, when density and sex are held constant, show that for both strains the two dimensions are larger at 16° C. than at 24° C. (D 64–80 for GCS representing the only notable exceptions). The two sexes are significantly different in regard to wing length when density and temperature are held constant (with the few exceptions already noted in section 3).

It would appear from these results that a highly adaptive character such as wing length and width may be among the last to be sacrificed when shortages of food modify body size. In view of this, tibia length is probably more reliable as a criterion of body size than wing measurements. It would seem that if wing measurements are used as criteria for body size, and if body size is used as a measure of food shortages or competition, then the most reasonable comparisons would be between laboratory-bred flies and wild flies from the areas from which the laboratory populations were derived. As a test case, therefore, the following comparisons of wing length, wing width, and leg length derived from flies captured at the Grand Canyon in July and August, 1958, have been made with the values obtained for flies derived from the same locality, but reared at different densities and temperatures in the laboratory (see Table 4).

The first sample of wild flies (Grand Canyon-2 in Table 8) collected in early July, consisted of nearly 200 males. The mean wing length was 52.53 ± 0.28, wing width 27.26 ± 0.14, and tibia length 19.19 ± 0.12 units. Over 450 contemporary females from the same locality had a mean wing length of 56.13 ± 0.23, wing width 28.54 ± 0.11, and tibia length 19.57 ± 0.08 units. Because of adverse weather conditions the sample collected in mid-August (Grand Canyon-3 in Table 8) consisted of 20 females whose measurements for wing length and width, and tibia length averaged 58.61 ± 0.92, 29.94 ± 0.37, and 20.83 ±

0.29, respectively. The values for males given in Table 4, which more nearly correspond to these values, are those given for D 10–12 for wing length and width, and somewhere between D 16 and D 20 for tibia length for 24° C. For 16° C., the values given for D 16 for wing length and width and those for D 20–24 for tibia length in Table 4 are the most comparable to those obtained from the wild male sample. For females collected in July, the means of D 12–20 most closely resemble the wing measurements, and D 20–24 the measurements of tibia length of laboratory-bred flies reared at 24° C.; for those reared at 16° C. all the measurements are intermediate between those obtained for D 24–32. The July sample, although smaller in number, consisted of larger individuals, approaching in size those obtained for D 20 at 16° C., or less than D 10 at 24° C. if wing measurements only are considered, or D 12–16 if tibia length is considered.

Unfortunately, no experiments were included in this study to test the effect of fluctuating temperatures. In nature, in a 24-hour period, summer temperatures over much of the distribution of *D. pseudoobscura* are cooler for a longer period. The experiments of Tantawy (1961), however, clearly show that in a fluctuating environment of high periodicity (flies were reared for 24-hour periods at 15°, 25°, and 27° C. in succession), it is the extreme high temperature which is the most influential, not only for the components of fitness but also for metric characters. If this is so for fluctuating environments of lower periodicity, and assuming that natural diets are comparable in nutritional value to bakers' yeast, it is fair to conclude that flies captured in nature closely resemble those obtained from vials in which there is no extreme shortage of food, i.e., in densities somewhere between 10 and 32 larvae per vial, and probably resemble most closely those flies obtained at 24° C. at the lower (10–12 larvae per vial) rather than at the higher densities.

Lacking body weight data and taking into consideration the more reliable tibia length as a measure of body size (see Table 8), the data for the remaining localities sampled in 1958, in general, closely resemble the values of the Grand Canyon samples. Cuernavaca (CU) constitutes a notable exception. No reasonable explanation can be given for this low value for tibia length but it is apparently not due to genetic causes, since the progeny, reared under optimal conditions, had tibia and wing measurements comparable with those obtained from other localities (Sokoloff, 1965). While the mean values of tibia length for the two sexes are certainly distinct from the other populations sampled, the wing measurements of CU flies are comparable to those of GCS flies or to those collected from other localities. Had tibiae from the flies collected in 1956 and 1957 been measured, it would be expected that the mean values would have been larger than those for 1958. It may be noted that in general the wing length and wing width data for the two sexes within a given year in the localities sampled resemble those obtained for the Grand Canyon. In certain cases, particularly Camino, Betatakin, and Chiricahua, the males are significantly smaller than males from other localities. It happens that these areas are characterized by somewhat more arid (and warmer) conditions than the other localities, but this cannot be the whole explanation for the difference in size, since contemporary females from these areas are considerably larger and comparable in size to those obtained from the remaining collecting sites.

A few remarks may be added with regard to body weights of flies captured in nature (Table 1) versus those reared in the laboratory. As was pointed out above, with an increase in density to 10 larvae per vial the differences in weight resulting from temperature and detectable at lower densities disappear: the weight of males at this density is 0.927 ± 0.019 mg. at 24° C. and 0.924 ± 0.018 at 16° C. When the larval density is increased to 20 larvae per vial, a loss of about 0.3 mg. in body weight is ob-

TABLE 8. *Quantitative measurements (in ocular units) from original flies collected in the field in successive years.*

Year and locality	Males						Females					
	Wing length $m \pm$ S.E.	N	Wing width $m \pm$ S.E.	N	Tibia length $m \pm$ S.E.	N	Wing length $m \pm$ S.E.	N	Wing width $m \pm$ S.E.	N	Tibia length $m \pm$ S.E.	N
1956												
Bryce Canyon	53.63 ± 0.64	24	26.52 ± 0.43	24								
1957												
Tassajara	53.74 ± 0.53	50	28.06 ± 0.27	50								
Wildrose	54.41 ± 0.56	34	28.18 ± 0.31	34								
Camino	51.95 ± 0.95	22	27.12 ± 0.54	22								
Sequoia	55.80 ± 0.83	23	28.53 ± 0.37	23								
Jacob Lake	54.05 ± 0.80	30	28.25 ± 0.88	30			57.98 ± 0.51	54	29.41 ± 0.38	54		
Betatakin	51.87 ± 0.66	48	26.88 ± 0.27	48			56.24 ± 0.41	89	28.40 ± 0.21	89		
Grand Canyon	53.77 ± 0.51	39	27.91 ± 0.27	39			55.82 ± 0.53	93	28.57 ± 0.25	93		
Prescott	52.28 ± 0.40	31	27.09 ± 0.32	31			56.64 ± 0.58	38	28.36 ± 0.31	38		
Flagstaff	54.53 ± 0.64	20	28.55 ± 0.32	20			56.95 ± 0.56	45	28.71 ± 0.33	45		
Chiricahua	50.28 ± 0.45	88	25.85 ± 0.24	88			56.39 ± 0.50	88	28.68 ± 0.24	88		
Texas	51.17 ± 1.14	15	26.80 ± 0.65	15			59.20 ± 0.81	10	31.06 ± 0.43	10		
Mesa Verde	52.14 ± 0.51	51	27.08 ± 0.24	51			57.00 ± 0.51	81	28.81 ± 0.27	81		
1958												
Vandeventer Flat	50.05 ± 0.69	27	25.87 ± 0.46	27	19.26 ± 0.37	27	54.25 ± 0.62	99	27.37 ± 0.25	98	19.68 ± 0.19	105
Piñon Flat	51.46 ± 1.16	22	26.10 ± 0.59	23	19.35 ± 0.38	24	54.12 ± 0.60	84	27.11 ± 0.30	81	19.51 ± 0.21	84
Keen Camp	50.85 ± 0.39	106	26.00 ± 0.21	105	19.13 ± 0.17	104	54.70 ± 0.55	92	27.57 ± 0.28	89	19.35 ± 0.21	95
Chiricahua	51.15 ± 0.36	100	26.18 ± 0.18	98	18.97 ± 0.15	100	54.79 ± 0.18	63	28.01 ± 0.31	59	19.57 ± 0.20	68
Grand Canyon-2	52.53 ± 0.28	198	27.26 ± 0.14	188	19.19 ± 0.12	186	56.13 ± 0.23	456	28.54 ± 0.11	452	19.57 ± 0.08	492
Grand Canyon-3	—	—	—	—	—	—	58.61 ± 0.92	19	29.94 ± 0.37	20	20.83 ± 0.29	19
Prescott	51.30 ± 0.21	384	26.30 ± 0.11	384	18.87 ± 0.09	386	54.98 ± 0.22	405	27.85 ± 0.11	406	19.40 ± 0.08	403
Flagstaff	52.43 ± 0.52	72	27.08 ± 0.26	75	19.09 ± 0.20	76	56.29 ± 0.48	116	28.70 ± 0.24	115	19.64 ± 0.19	116
Yellowstone	51.90 ± 0.34	24	27.20 ± 0.21	24	19.96 ± 0.14	24	56.19 ± 0.18	33	29.12 ± 0.14	33	20.73 ± 0.10	33
Chadron	52.18 ± 0.31	96	27.01 ± 0.15	99	19.61 ± 0.12	101	57.40 ± 0.30	120	29.42 ± 0.15	127	20.63 ± 0.11	131
Galeana	50.60 ± —	2	24.8 ± —	1	18.4 ± —	1	55.33 ± 1.03	9	28.29 ± 0.66	9	20.60 ± 0.54	9
Cuernavaca	52.03 ± 0.20	267	26.28 ± 0.09	264	17.16 ± 0.07	269	57.56 ± 1.07	14	28.60 ± 0.64	9	17.88 ± 0.36	18

served. Further crowding to 40 larvae per vial fails to reduce body size but mortality greatly increases.

The weight of *D. pseudoobscura* males collected in 1957 generally exceeds 1 mg. The weight of *D. persimilis*, coexisting with *D. pseudoobscura* in three localities in California, ranges from 0.801 to 0.987 mg. (Table 1). The weight of males of this species, derived from Mono Lake and reared in Kalmus medium at densities of 10, 20, and 40 larvae per vial, is 0.835 ± 0.015, 0.556 ± 0.010, and 0.488 ± 0.052 at 24° C., and 0.913 ± 0.020, 0.560 ± 0.010, and 0.550 at 16° C., respectively (data from Sokoloff, 1955).

DISCUSSION

Data from various sources including some reported above have shown that as food becomes scarce the differences in size within a given sex of flies at lower densities induced by differences in temperature during larval development are eliminated. With further crowding, the size of the flies is reduced to a minimum which, as Sang (1949) has pointed out, represents "the smallest possible survival size for both sexes." This phenomenon has been observed more recently by Sokoloff (1955), Miller and Thomas (1958), Bakker (1961), Bakker and Nelissen (1963), Sullivan and Sokal (1963), and Miller (1964). With still further crowding size is not reduced, but owing to an increase in larval mortality the number of surviving adults is greatly decreased.

In this paper the following additional data are shown: (1) there is high correlation between wing length and body weight; (2) wing length, wing width, and tibia length are reduced as density increases; (3) this response is not the same for the two strains of *D. pseudoobscura* which are clearly different in genetic makeup by virtue of the distance between localities (about 450 miles) and by the fact that the ML sample was derived from a population in which the prevailing chromosome arrangements, Arrowhead (AR) and Standard (ST), were in the frequencies AR more than 50 per cent and ST more than 25 per cent, while the GCS sample consisted of over 90 per cent AR, and ST was about five per cent; (4) within a given strain the response in reduction of the various characters as a result of starvation was not the same for all characters, the wings apparently becoming reduced in length and width only after no further reduction of other appendages is possible.

A survey of flies captured in nature in two consecutive years over much of the distribution of *D. pseudoobscura* reveals that within a given year, and despite the wide range of ecological conditions prevalent in the area of their capture, these flies are fairly uniform. There is, however, a distinct difference in size of flies captured in the two successive years, and this has been correlated with climatic conditions prevailing in the two years.

Comparisons of the wing and leg measurements and body weight measurements have been made between *D. pseudoobscura* and *D. persimilis* captured in nature and those reared in the laboratory under various intensities of competition for food. It is clear that the flies of both species captured in nature most closely resemble those flies which in the laboratory have been reared under relatively uncrowded conditions.

Admittedly, considerable gaps in information must be filled before the ecology of *D. pseudoobscura* and its relatives is better understood. It is known that in the Mather region of California, *D. pseudoobscura* (A) and *D. persimilis* (B) are quite abundant. Cooper and Dobzhansky (1956) collected over 40,000 *Drosophila* by exposing traps inoculated with various yeasts daily for eight days at intervals of three weeks from June to September, 1954. About 23,000 of the flies collected were species A and B, and 60 per cent of these were females. Fecundity of these flies in the laboratory is high: under optimal conditions females can lay over 1000 eggs, but the fecundity of smaller females is considerably reduced.

Species A and B are known to utilize wounds of the California black oak, *Quercus kelloggii*, which are transformed into so-called slime fluxes, because the exuding sap becomes infected with various microorganisms. In the Mather region about 20 per cent of the oak trees examined to a height of six feet above the ground had slime fluxes, some of these being suitable as feeding—and others as breeding—sites for *Drosophila* (Carson, 1951). Considering the large adult populations of A and B, the moderate size of females, and the high fecundity of these flies, it would be expected that slime fluxes would be full of *Drosophila* larvae. However, the number of eggs and larvae found in a given slime flux is very small, of the order of a few dozen (Carson, 1951, and personal observations). It has been suggested (Sokoloff, 1957, 1964) that other organisms (broadly classified as predators and associates) found at the slime fluxes are the biotic factors which prevent *Drosophila* populations from reaching high densities. These organisms kill the adult flies or prevent them from reaching the breeding and feeding sites. Further mortality occurs in the pre-adult stages when predators feed on the larvae or when the activities of other organisms at the sites of oviposition cause eggs to be buried in the slime with consequent drowning of the embryos.

What happens in other areas where *D. pseudoobscura* and *D. persimilis* are known to occur but where there are no oak trees remains an enigma.

There is some evidence for other species of *Drosophila* that these fruit flies cannot utilize the amount of food to the extent available: Carson and Stalker (1951) found that *D. robusta*, as well as a few other species of *Drosophila*, breed in slime fluxes of a number of species of trees. The slime isolated in vials and cultured in the laboratory generally tended to yield only few adults (one to 15 individuals from any one culture). It was observed that certain slime fluxes are suitable only for feeding while others are suitable only for breeding.

Size of adults collected in the field was not determined, but it was noted that the slime fluxes suitable for breeding attract chiefly females while those suitable for feeding yield a preponderance of males.

Birch and Battaglia (1957), studying *D. willistoni*, found that in the laboratory these flies could reproduce in fermenting fruit, an average of 106 flies having been obtained from 181 fruits. Fermenting fruit collected in the field and placed in isolation in containers in the laboratory yielded a maximum of less than one fly per fruit.

McFarquhar and Robertson (1963) have obtained measurements of thorax length from flies captured in nature in southern Scotland and compared them with measurements obtained from laboratory flies reared in cornmeal–molasses medium inoculated with live bakers' yeast at 18° C. Their detailed account of techniques does not make it clear whether the flies in the laboratory were reared with the minimum of crowding or whether these cultures were densely populated. The length of thorax, expressed as $3 \times \log$ thorax length $1/100$ mm. for a sample of 116 wild flies, was 14.34 ± 0.021 with $CV = 1.60$ per cent. For a sample of 533 laboratory flies the length was 14.60 ± 0.0035 with $CV = 0.55$ per cent. The difference between means is highly significant, and the distributions of the size of wild flies in their prepared histograms are highly skewed in the direction of smaller size.

While these data are of interest, they are inadequate to determine to what extent the size of wild flies compares with the size of individuals derived experimentally in vials with limited amounts of food. It may be pointed out, however, that McFarquhar and Robertson state (p. 109) that the samples of wild *D. subobscura* were collected "on several different occasions but, since average size and variability did not differ significantly, they have been combined." This may indicate that the flies collected in different seasons of the year may be fairly uniform, conforming with the limited observations for *D. pseudoobscura* col-

lected at different times in a given collecting station within a given year.

McFarquhar and Robertson, probably correctly, attribute the observed variation in body size to differences in nutrition, since the smallest *D. subobscura* flies are about one-third the size of the largest, which in turn are about the same size as those grown in the laboratory. Since the breeding sites of *D. subobscura* are partly known (Gordon, 1942), it would seem desirable to survey a number of these sites to determine the number of larvae which are present in any given breeding place and the size of adults emerging from them.

In the case of *D. pseudoobscura*, small sized flies are sometimes present in field captures, but I am of the opinion that these flies were reared in slime fluxes which dried shortly after oviposition and larval eclosion, but the larvae had fed and developed sufficiently prior to this event to enable them to pupate and emerge as imagoes. If size is taken as a criterion of competition, the present data would seem to indicate that, if competitive relationships among individuals of the same species or among larvae of different species occur in nature, they must occur but seldom for the species of *Drosophila* investigated.

The data reported in this paper largely parallel those obtained by Tantawy (1964), who found that natural populations of *D. melanogaster* and *D. simulans* are intermediate in size to those obtained in the laboratory under optimal and pessimal conditions for most of the year. During the summer, the size of wild adults of both species resembled the size of adults obtained from crowded cultures, but this reduction in size is attributed to high temperatures and not to starvation, since food is extremely abundant (Tantawy and Mallah, 1961).

In all of these drosophilids, sufficient evidence is available to conclude that, while the size of the wild flies seldom resembles that of flies reared under optimal laboratory conditions, the wild flies achieve a size which is far from the minimal size obtained under severe conditions of crowding, even though the diets in the larval stages must differ and the environmental conditions vary.

At the same time, the reported evidence quite strongly indicates that different species of *Drosophila* achieve their morphological adaptation to environmental conditions in different ways. At one extreme is *D. robusta*, where geographic, seasonal, and altitudinal differences in body size were correlated in a general way with the frequencies of chromosomal arrangements (Stalker and Carson, 1947, 1948, 1949). At the other extreme is *D. simulans*: despite the fact that this species appears to exhibit strict chromosomal monomorphism (Tantawy, 1964), a morphological cline related to its geographic distribution is detectable (Tantawy and Mallah, 1961). Populations of *D. melanogaster*, *D. subobscura*, *D. persimilis*, and *D. pseudoobscura* are polymorphic with regard to chromosomal arrangements, but correlations between morphological characters and inversions, while establishable for certain laboratory populations, are difficult to establish when considering geographic variation of quantitative characters, even though morphological clines can be obtained for most species (see, for example, Prevosti, 1954, McFarquhar and Robertson, 1963, and Misra and Reeve, 1964, for the evidence in *D. subobscura*, and Tantawy and Mallah, 1961, for *D. melanogaster*). Misra and Reeve (1964), from their partial correlation analyses and selection experiments, as well as their consideration of the clinal patterns of *D. subobscura* and *D. robusta*, conclude that two sets of genes are involved in these clines. One set causes an increase in relative wing and leg length and is responsible for a positive correlation of these dimensions with latitude in *D. robusta* and *D. subobscura*. The other set consists of general body size genes that cause correlative changes which apparently have been selected in the opposite direction in the two species so that the head and thorax dimensions increase in *D. subobscura*

but decrease in *D. robusta* as latitude increases. The ratio of wing length to thorax length has a high positive correlation with latitude in both species.

Considering the overall uniformity of *D. pseudoobscura* in the localities sampled, it must be concluded that this euryokous species has achieved an adaptation to a wide variety of environments in the manner suggested by Dobzhansky (1962): individuals belonging to the various races of this species have evolved favorable genotypes, through natural selection, which enable them to develop an optimal phenotype in the face of a wide range of environments, and at the same time there has been a selection for a genotypic variety or polymorphism, "the different genotypes making their carriers relatively fitter in different environments." It is probable that for *D. pseudoobscura* this genotypic variety with respect to body size is independent of the types of inversions which characterize the various races of this species.

SUMMARY

Samples of *Drosophila pseudoobscura* and *D. persimilis* derived from natural populations in a number of localities in two successive years have been measured with respect to body weight and/or wing length, wing width, and tibia length. There is a high correlation between body weight and body characters such as wing length.

For any given year, the flies from the various localities are exceedingly uniform, despite the wide array of ecological conditions of the areas sampled. Striking differences in body measurements of wild flies collected in successive years (and related to climatic variations) have been recorded.

Larvae of *D. pseudoobscura* derived from two localities have been reared under various degrees of crowding at two different temperatures. Size of these flies, determined by wing length and width and tibia length, is dependent on temperature at the lower densities, but at the higher densities, when food is short, the size of the flies is fairly uniform. The two strains behave differently in response to extreme crowding, at the two temperatures tested. Comparisons of laboratory and wild flies indicate that wild flies are comparable in size to those reared under mild degrees of crowding, and it is concluded, therefore, that *D. pseudoobscura*, under normal conditions, does not experience intense forms of competition. The available data for other *Drosophila* species confirm this conclusion.

Considering the overall uniformity of *D. pseudoobscura* in much of its distribution, one must conclude that this euryokous species has achieved, through natural selection, an optimal phenotype in the face of a wide spectrum of habitats. The available data seem to indicate that this phenotype, although varying as a result of climatic changes, probably is largely independent of the type of inversions which characterize the various races of this species.

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