

Mating Choice in Crosses between Geographic Populations of *Drosophila pseudoobscura*

WYATT W. ANDERSON and LEE EHRMAN

*Department of Biology, Yale University, New Haven, Connecticut 06520 and
The Rockefeller University, New York, New York 10021*

ABSTRACT: Data are presented for mating choices in crosses between five geographically distant populations of *Drosophila pseudoobscura*. There is no indication of mating preferences between these strains. In contrast, mating preferences are frequent among geographic strains in many other species of *Drosophila* and may serve as a basis for later ethological isolation should the strains diverge to form separate species.

INTRODUCTION

Reproductive isolating mechanisms between populations probably originate in two stages. The first stage involves geographic separation and the accumulation of genetic differences in the course of adjustment to different environments. The second stage involves selection for stronger isolation should the populations become sympatric (see Grant, 1966 for a review). The populations must become sufficiently different while allopatric so that crosses between them are less frequent or less successful than crosses within each population. The most efficient mechanisms of isolation are those, such as sexual preference, which act before mating; they lessen the wastage of gametes in unsuccessful matings or lower the production of less fit hybrids. It is of interest to know how often mating preferences arise through genetic divergence in allopatric populations. Only in the genus *Drosophila* have a substantial number of species been tested. The tests of mating preference are made in the laboratory, of course, and do not represent fully what occurs in nature. However, laboratory experiments do provide an indication of the situation in nature, and with this in mind, we have reviewed the literature to find tests of mating behavior in crosses between allopatric strains of *Drosophila* species. The review was intended to be representative, not exhaustive. Crosses between subspecies were excluded, since in *Drosophila*, unlike many other animal groups, named subspecies are likely to be well advanced toward full speciation. We are interested in mating preferences among populations at the *beginning* of possible speciation. The data from the literature are summarized in Table 1.

There was statistically significant non-random mating between the geographic strains in 19 of the 21 species for which data are available. Not all of these experiments are comparable, since a variety of different techniques was employed to measure sexual isolation. There was a variety of deviations from random mating. Both preferences for mating with flies from the same strain (homogamic preference) and preferences for mating with flies from different strains (heterogamic preference) were encountered. Sometimes the preferences were "one-sided"; that is, the males of one race were to some

extent isolated from the females of another, but mating in the reciprocal cross was random. The evolutionary consequences of these various types of mating preference are very different. This diversity of non-random mating behavior is what we should expect if the preferences arise as accidental by-products of genetic divergence. In only a portion of the cases—but a sizable portion from the evidence in *Drosophila*—should we expect to find the homogamic mating preferences which could speed further divergence.

The selection of cases in Table 1 may be biased, because negative results from such studies are less likely to be published, and because significant isolation is more likely to attract the attention of a reviewer. With all these qualifications in mind, it still seems clear that a rather large number of species of *Drosophila* have, in the course of genetic divergence among different geographic strains, undergone some divergence for mating preferences. In some cases the rudiments of the efficient sexual isolation will be present should the strains become sympatric and should they further diverge to become separate species.

No data are available for *Drosophila pseudoobscura*, although Dobzhansky (1963) mentioned some unpublished observations on crosses between strains from Mexico and the western United States; he found no sexual isolation. The purpose of the present experiments is

TABLE 1.—Tests of mating preference between geographic strains of various species of *Drosophila*

Species	Number of strains tested	Pairs of strains with preferences	Reference
1. <i>americana</i>	4	5/6	Stalker, 1942
2. <i>arizonensis</i>	5	4/10	Baker, 1947
3. <i>athabasca</i>	6	6/6	Miller, 1958 and Miller and Westphal, 1967
4. <i>auraria</i>	14	11/27	Kurokawa, 1959 and 1963
5. <i>birchii</i>	6	4/6	Ayala, 1965
6. <i>crocina</i>	3	2/3	Heed, 1957
7. <i>gasici</i>	4	3/5	Brncic and Koref-Santibanez, 1965
8. <i>gaucha</i>	2	0/1	Koref-Santibanez and Del Solar, 1961
9. <i>miranda</i>	2	1/1	Dobzhansky and Koller, 1938
10. <i>montana</i>	4	3/3	Patterson, McDanald, and Stone, 1947
11. <i>nebulosa</i>	2	1/1	Dobzhansky, 1944
12. <i>paulistorum</i>	24	29/46	Carmody <i>et al.</i> , 1962
13. <i>pavani</i>	2	0/1	Koref-Santibanez and Del Solar, 1961
14. <i>peninsularis</i>	2	1/1	Paterson and Wheeler, 1947
15. <i>prosaltans</i>	7	18/21	Dobzhansky and Streisinger, 1944
16. <i>repleta</i>	6	6/15	Wharton, 1942
17. <i>serrata</i>	15	13/80	Ayala, 1965
18. <i>sturtevanti</i>	5	7/10	Dobzhansky, 1944
19. <i>texana</i>	4	2/3	Patterson, McDanald, and Stone, 1947
20. <i>virilis</i>	4	3/3	Patterson, McDanald, and Stone, 1947
21. <i>willistoni</i>	5	4/8	Dobzhansky and Mayr, 1944
TOTAL	126	123/257=.479	

to provide data on mating preferences in crosses between five geographic strains of *Drosophila pseudoobscura*.

MATERIALS AND METHODS

Experimental populations established from recent collections were the source of animals for these experiments. The populations were begun with the F_1 progeny of females inseminated in the wild and were maintained in large plastic cages for $1\frac{1}{2}$ years at 25 C before the present experiments were begun. The cages sustain large, stable populations of several thousand flies. Each population was begun with 20 female and 20 male progeny from each inseminated female taken in nature. The number of wild females whose progeny were used to begin a population ranged from 24 to 114, depending on the size of the collection. The localities are shown in Figure 1; they were chosen to allow crosses among the most widely separated populations from the available collections. These are the same populations studied by Dobzhansky *et al.* (1966), and by Anderson *et al.* (1967 a, 1967 b).

The mating preferences were measured in multiple-choice experiments with the direct observation chambers devised by Elens (see Elens and Wattiaux, 1964). Adults were raised from egg samples taken in the experimental populations. Ten virgin females and 10 virgin males from each of two strains were introduced into the chamber and all matings recorded for $1\frac{1}{2}$ hours. The left wings of



Fig. 1.—Geographic populations utilized in tests for mating preferences: Okanagan, British Columbia; Berkeley, California; Hayden Creek, Colorado; Sonora, Mexico; and Austin, Texas.

one type of female and one type of male were clipped to distinguish flies from different localities. The clipping was rotated between the two populations in the replicate chambers set up for each cross. The observations were made on coded samples, so that the observer (L.E.) had no idea what strains were being tested. The multiple-choice technique is closer to the situation in nature than is the older male-choice procedure. It permits recording of each of the four types of mating between two populations. Malogolowkin-Cohen *et al.* (1965) showed that the results of tests with Elens' observation chambers are like those obtained by the male-choice method. With one exception, all combinations of the five localities were tested. The cross Hayden \times Sonora was omitted, and the cross Hayden \times Berkeley was repeated a smaller number of times than the others, because we obtained too few flies from the bottles representing Hayden.

RESULTS AND DISCUSSION

The results are given in Table 2. Random mating was tested by chi-square and the joint isolation index =

$$\frac{(\text{homogamic matings—heterogamic matings})}{\text{total matings}}$$

was calculated for each cross (see Malogolowkin-Cohen *et al.*, 1965 for a discussion of the statistics); the number of flies of each sex which mated was tested by chi-square. A high proportion (75%) of all the flies mated; one great advantage of the mating chambers is that the data still accurately reflect the mating preferences, since each *type* of mating is recorded. As a check, isolation indices were calculated for the first half of the data alone; in every case they were like the indices calculated from all the observations. The indices in Table 2 were calculated from the total numbers of matings.

There are no indications that either heterogamic or homogamic matings are preferred. The only cross in which non-random mating was observed was that between Berkeley and Okanagan; the non-randomness involved no mating preference, but rather, a significantly increased activity of Berkeley males. An extra set of four chambers was run to verify this greater activity of Berkeley males. The results were entirely consistent with the previous ones and were therefore grouped with them.

Genetic modification of mating behavior in *Drosophila pseudoobscura* is well established. Tan (1946) found that several mutant genes had significant effects on mating behavior. Koopman (1950) and Kessler (1966) selected for changes in mating preference of *Drosophila pseudoobscura* with its sibling species, *Drosophila persimilis*. Del Solar (1966) observed significant isolation between strains of *Drosophila pseudoobscura* selected in different directions for phototaxis and geotaxis. The populations which we studied are known to have diverged genetically both with respect to inversion types in the chromosomes and with respect to their integrated gene pools. Thus,

while sexual isolation can clearly arise as a by-product of genetic divergence in this species, it has not done so in the natural populations which we studied. There is no apparent reason why *Drosophila pseudoobscura* differs from most of the species in Table 1 in this regard.

Acknowledgments.—We are grateful to Drs. F. Ayala, Th. Dobzhansky, D. Hagen, C. Remington, and W. Stone for critically reading the manuscript.

TABLE 2.—Mating preferences in crosses between geographic populations of *Drosophila pseudoobscura*

Cross Strain A x Strain B	Number of chambers run	Number of matings	Numbers of each type of mating				Chi-square for random mating
			A ♀ x A ♂	A ♀ x B ♂	B ♀ x A ♂	B ♀ x B ♂	
Berkeley x Okanagan	12	222	60	50	72	40	10.14*
Berkeley x Austin	8	160	37	43	42	38	0.65
Berkeley x Hayden	2	28	7	7	5	9	1.14
Berkeley x Sonora	8	103	23	22	28	30	1.74
Okanagan x Austin	8	125	27	33	33	32	0.79
Okanagan x Hayden	7	51	14	14	10	13	0.84
Okanagan x Sonora	7	114	26	29	32	27	0.74
Austin x Hayden	8	103	21	26	30	26	1.58
Austin x Sonora	8	113	36	28	27	22	3.57

* Significant at .05 level.

TABLE 2.—(continued)

Cross Strain A x Strain B	Number of flies which mated				Chi-square for numbers which mated		Isolation index ± SE
	A ♀	B ♀	A ♂	B ♂	χ^2 (♀)	χ^2 (♂)	
Berkeley x Okanagan	110	112	132	90	0.02	7.95**	-0.10 ± .07
Berkeley x Austin	80	80	79	81	0.00	0.03	0.00 ± .08
Berkeley x Hayden	14	14	12	16	0.00	0.57	0.14 ± .19
Berkeley x Sonora	45	58	51	52	1.64	0.01	0.03 ± .10
Okanagan x Austin	60	65	60	65	0.20	0.20	-0.06 ± .09
Okanagan x Hayden	28	23	24	27	0.49	0.18	0.06 ± .14
Okanagan x Sonora	55	59	58	56	0.14	0.04	-0.07 ± .09
Austin x Hayden	47	56	51	52	0.79	0.01	-0.09 ± .10
Austin x Sonora	64	49	63	50	1.99	1.50	0.03 ± .09

** Significant at .005 level.

REFERENCES

- ANDERSON, W. W., TH. DOBZHANSKY AND C. D. KASTRITSIS. 1967a. On the relationship of structural heterozygosity in the X and third chromosomes of *Drosophila pseudoobscura*. *Amer. Natur.*, **101**:89-92.
- , ——— AND ———. 1967b. Selection and inversion polymorphism in experimental populations of *Drosophila pseudoobscura* initiated with the chromosomal constitutions of natural populations. *Evolution*, **21**:664-671.
- AYALA, F. J. 1965. Sibling species of the *Drosophila serrata* group. *Evolution*, **19**:538-545.
- BAKER, W. K. 1947. A study of the isolating mechanisms found in *Drosophila arizonensis* and *Drosophila mojavensis*. *Univ. Texas Publ.*, **4720**:126-136.
- BRNCIC, D. AND S. KOREF-SANTIBANEZ. 1965. Geographical variation of chromosomal structure in *Drosophila gasci*. *Chromosoma*, **16**:47-57.
- CARMODY, G. A., A. COLLAZO, TH. DOBZHANSKY, L. EHRMAN, I. S. JAFFREY, S. KIMBALL, S. OBRESKI, S. SILAGI, T. TIDWELL AND R. ULLRICH. 1962. Mating preferences and sexual isolation within and between the incipient species of *Drosophila paulistorum*. *Amer. Midl. Natur.*, **68**:67-82.
- DEL SOLAR, E. 1966. Sexual isolation caused by selection for positive and negative phototaxis and geotaxis in *Drosophila pseudoobscura*. *Proc. Natl. Acad. Sci.*, **56**:484-487.
- DOBZHANSKY, TH. 1944. Experiments on sexual isolation in *Drosophila*. III. Geographic strains of *Drosophila sturtevantii*. *Ibid.*, **30**:335-339.
- . 1963. Species in *Drosophila*. *Proc. Linnean Soc. London*, **174**:1-12.
- , W. W. ANDERSON AND O. PAVLOVSKY. 1966. Genetics of natural populations. XXXVIII. Continuity and change in populations of *Drosophila pseudoobscura* in western United States. *Evolution*, **20**:418-427.
- AND P. C. KOLLER. 1938. An experimental study of sexual isolation in *Drosophila*. *Biol. Zentrabl.*, **52**:589-607.
- AND E. MAYR. 1944. Experiments on sexual isolation in *Drosophila*. I. Geographic strains of *Drosophila willistoni*. *Proc. Natl. Acad. Sci.*, **30**:238-244.
- AND G. STREISINGER. 1944. Experiments on sexual isolation in *Drosophila*. II. Geographic strains of *Drosophila prosaltans*. *Ibid.*, **30**:340-345.
- ELENS, A. A. AND J. M. WATTIAUX. 1964. Direct observation of sexual isolation. *Drosophila Information Service*, **39**:118-119.
- GRANT, V. 1966. The selective origin of incompatibility barriers in the plant genus *Gilia*. *Amer. Natur.*, **100**:99-118.
- HEED, W. B. 1957. Intraspecific relationships of *Drosophila crocina* Patterson and Mainland from three localities. *Univ. Texas Publ.*, **5721**:15-16.
- KESSLER, S. 1966. Selection for and against ethological isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. *Evolution*, **20**:634-645.
- KOOPMAN, K. F. 1950. Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. *Ibid.*, **4**:135-148.
- KOREF-SANTIBANEZ, S. AND E. DEL SOLAR. 1961. Courtship and sexual isolation in *Drosophila pavani* Brncic and *Drosophila gaucha* Jaeger and Salzano. *Ibid.*, **15**:401-406.

- KUROKAWA, H. 1959. Experiments on sexual isolation between Races A and B of *Drosophila auraria*. *Annotationes Zoologicae Japonenses*, **32**:220-224.
- . 1963. Population genetics on three races of *Drosophila auraria* Peng. II. Sexual isolation among strains within a Race C. *Japanese J. Genet.*, **38**:1-5.
- MALOGOLOWKIN-COHEN, CH., A. S. SIMMONS AND H. LEVENE. 1965. A study of sexual isolation between certain strains of *Drosophila paulistorum*. *Evolution*, **19**:95-103.
- MILLER, D. D. 1958. Sexual isolation and variation in mating behavior within *Drosophila athabasca*. *Ibid.*, **12**:72-81.
- AND N. J. WESTPHAL. 1967. Further evidence on sexual isolation within *Drosophila athabasca*. *Ibid.*, **21**:479-492.
- PATTERSON, J. T., L. W. McDANALD AND W. S. STONE. 1947. Sexual isolation between members of the virilis group of species. *Univ. Texas Publ.*, **4720**:7-31.
- AND M. R. WHEELER. 1947. Two strains of *Drosophila peninsularis* with incipient reproductive isolation. *Ibid.*, **4720**:116-125.
- STALKER, H. D. 1942. Sexual isolation in the species complex *Drosophila virilis*. *Genetics*, **27**:238-257.
- TAN, C. C. 1946. Genetics of sexual isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. *Ibid.*, **31**:558-573.
- WHARTON, L. T. 1942. Analysis of the repleta group of *Drosophila*. *Univ. Texas Publ.*, **4228**:23-52.

SUBMITTED 20 OCTOBER 1967

ACCEPTED 7 DECEMBER 1967