



Direct Observation of Sexual Isolation between Allopatric and between Sympatric Strains of the Different *Drosophila paulistorum* Races

Author(s): Lee Ehrman

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DIRECT OBSERVATION OF SEXUAL ISOLATION BETWEEN
ALLOPATRIC AND BETWEEN SYMPATRIC STRAINS OF
THE DIFFERENT *DROSOPHILA PAULISTORUM* RACES

LEE EHRMAN¹

The Rockefeller University, New York

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Dobzhansky and Spassky (1959) first suggested that *Drosophila paulistorum* was a cluster of species *in statu nascendi*, a borderline case of uncompleted speciation. Their suggestion has been borne out by much laboratory work since then. It is indeed a superspecies composed of six races or subspecies or incipient species. This situation is of interest precisely because these six may be considered about equally legitimately as very distinct races or as very closely related species. Each race inhabits a geographic area different from the others, but the distributions of some of the races do overlap. Where two or more races share a common territory (four is the maximum number of races occurring sympatrically), they seem not to interbreed, and thus they behave like full-fledged species (Dobzhansky *et al.*, 1964).

Sexual (or ethological or behavioral) isolation wherein potential mates meet but do not mate, is a most efficient isolating mechanism; it does away with the wastage of gametes, food and space for developing hybrids, etc. This sexual isolation which makes matings between the females and males of different *D. paulistorum* races much less likely to occur than matings within the races, is due to polygenes scattered in every one of the three pairs of chromosomes which the species possesses. These polygenes efficiently control the sexual preferences of their carriers. Their effects seem to be simply cumulative (Ehrman, 1961). A female of hybrid origin which carries a majority of the chromosomal material derived from a given race

is most likely to accept a male of that race. And conversely, a hybrid male is most likely to be accepted by females whose chromosomal constitution is closest to his. This clearly is not at all comparable with the genetic basis of the hybrid male sterility, where the properties of an egg are determined, as far as the sterility of the back-cross males is concerned, by the genotype present in it before meiosis, and not by that formed following fertilization. Thus, while the hybrid sterility depends solely on the genetic constitution and the source of the cytoplasm contributed by the mother, the sexual isolation certainly does not.

The experiments reported here were undertaken to test the degree of sexual isolation for its strength between *sympatric* and between *allopatric* strains of the *same pairs of D. paulistorum* races since different populations are exposed to the risk of hybridization when they share the same territory. There is no doubt that hybridization, in this particular case, will result in the production of reproductively inferior individuals so that those individuals which do not engage in interracial matings will contribute more to the gene pool of subsequent generations than those that do engage in interracial matings. In this way, natural selection favors genotypes which hinder or prevent hybridization altogether.

MATERIAL

There are six *Drosophila paulistorum* races, and 15 interracial crosses can be made. Since each cross might be tested with sympatric and with allopatric strains, 30 crosses are conceivable. However, only the following races occur *both* sympatri-

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cally and allopatrically and obviously only they could be used in this analysis. The strains employed and the numbers given them follow the names of the races (see Dobzhansky *et al.*, 1964, and Dobzhansky and Spassky, 1959, for further identification):

Centro-American × *Amazonian*

Allopatric

- Boquete, Panama (27) × Georgetown, British Guiana N (77)
 Cerro Campana C, Panama (32) × Georgetown, British Guiana N (77)
 Goofy Lake C, Panama (81) × Simla D, Trinidad (58)
 Cerro Campana C, Panama (32) × Simla D, Trinidad (58)
 Lancetilla, Honduras (2) × Apoteri C, British Guiana (68)
 Tikal, Guatemala (1) × Belem A, Brazil (11)

Sympatric

- Goofy Lake C, Panama (81) × Goofy Lake A, Panama (80)
 Boquete, Panama (27) × Barro Colorado A, Panama (33)
 Boquete, Panama (27) × Goofy Lake A, Panama (80)
 Cerro Campana C, Panama (32) × Cerro Campana A, Panama (31)
 Boquete, Panama (27) × Cerro Campana A, Panama (31)

Amazonian × *Orinocan*

Allopatric

- Bucaramanga A, Colombia (26) × Georgetown, British Guiana C (42)
 Georgetown, British Guiana X (78) × Tuy, Venezuela (41)
 Simla D, Trinidad (58) × Bucaramanga 8, Colombia (28)
 Piña, Panama (29) × Georgetown, British Guiana C (42)
 Goofy Lake A, Panama (80) × Georgetown, British Guiana C (42)
 Belem A, Brazil (11) × Apoteri Y, British Guiana (74)
 Barro Colorado A, Panama (33) × Georgetown, British Guiana (42)

Sympatric

- Caripe G, Venezuela (38G) × Caripe L, Venezuela (38L)
 Georgetown, British Guiana N (77) × Georgetown, British Guiana C (42)

Amazonian × *Andean*

Allopatric

- Elena N, Venezuela (48) × Apoteri O, British Guiana (72)

- Georgetown, British Guiana N (77) × Elena A, Venezuela (49)
 Goofy Lake A, Panama (80) × Simla M, Trinidad (54)
 Goofy Lake A, Panama (80) × Elena A, Venezuela (49)
 Apoteri C, British Guiana (68) × Cucuta C, Colombia (90)
 Belem A, Brazil (11) × Elena A, Venezuela (49)
 Belem A, Brazil (11) × Cucuta C, Colombia (90)

Sympatric

- Simla D, Trinidad (58) × Simla M, Trinidad (54)
 Cucuta A, Colombia (88) × Cucuta C, Colombia (90)
 Apoteri C, British Guiana (68) × Apoteri N, British Guiana (71)

Amazonian × *Guianan*

Allopatric

- Georgetown, British Guiana (77) × Apoteri X, British Guiana (73)
 Barro Colorado A, Panama (33) × Apoteri X, British Guiana (73)
 Simla D, Trinidad (58) × Apoteri X, British Guiana (73)
 Belem A, Brazil (11) × Georgetown, British Guiana B (10B)
 Belem A, Brazil (11) × Apoteri X, British Guiana (73)
 Apoteri C, British Guiana (68) × Georgetown, British Guiana B (10B)

Sympatric

- Georgetown, British Guiana N (77) × Georgetown, British Guiana B (10B)
 Apoteri A, British Guiana (66) × Apoteri X, British Guiana (73)
 Apoteri C, British Guiana (68) × Apoteri X, British Guiana (73)

Orinocan × *Guianan*

Allopatric

- Georgetown, British Guiana C (42) × Apoteri X, British Guiana (73)
 Bucaramanga 8, Colombia (28) × Georgetown, British Guiana B (10B)

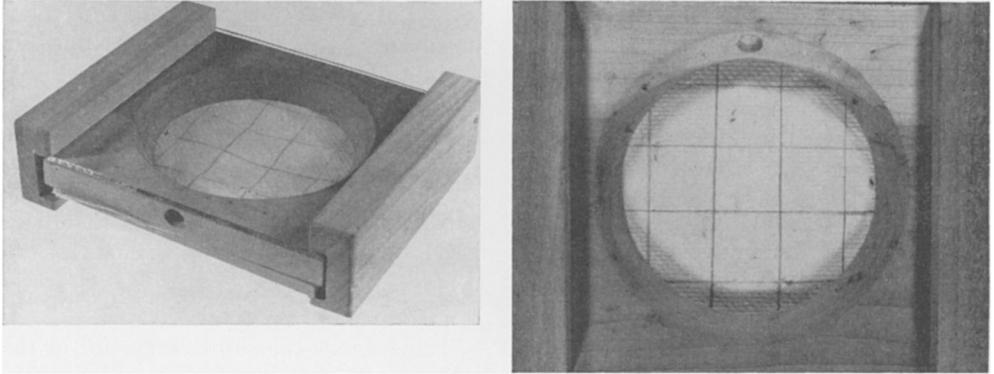
Sympatric

- Apoteri Y, British Guiana (74) × Apoteri X, British Guiana (73)
 Georgetown, British Guiana C (42) × Georgetown, British Guiana B (10B)

Orinocan × *Andean*

Allopatric

- Georgetown, British Guiana C (42) × Apoteri O, British Guiana (72)
 Apoteri Y, British Guiana (74) × Elena A, Venezuela (49)



FIGS. 1 and 2. Two views of the Elens-Wattiaux chamber used for the direct observation of mating behavior; see the Method section for an explanation of its operation.

Caripe L, Venezuela (38L) × Simla M, Trinidad (54)

Bucaramanga 8, Colombia (28) × Cucuta C, Colombia (90)

Apoteri Y, British Guiana (74) × Cucuta C, Colombia (90)

Sympatric

Apoteri Y, British Guiana (74) × Apoteri O, British Guiana (72)

Apoteri Y, British Guiana (74) × Apoteri N, British Guiana (71)

Andean × *Guianan*

Allopatric

Simla M, Trinidad (54) × Georgetown, British Guiana B (10B)

Elena A, Venezuela (49) × Georgetown, British Guiana B (10B)

Cucuta C, Colombia (90) × Georgetown, British Guiana B (10B)

Cucuta C, Colombia (90) × Apoteri X, British Guiana (73)

Sympatric

Apoteri O, British Guiana (72) × Apoteri X, British Guiana (73)

Apoteri M, British Guiana (70) × Apoteri X, British Guiana (73)

Apoteri N, British Guiana (71) × Apoteri X, British Guiana (73)

Centro-American × *Orinocan*

Allopatric

Goofy Lake C, Panama (81) × Georgetown, British Guiana C (42)

Cerro Campana C, Panama (32) × Georgetown, British Guiana C (42)

Lancetilla, Honduras (2) × Apoteri Y, British Guiana (74)

Tikal, Guatemala (1) × Bucaramanga 8, Colombia (28)

Tikal, Guatemala (1) × Apoteri Y, British Guiana (74)

Lancetilla, Honduras (2) × Bucaramanga 8, Colombia (28)

Sympatric

Cerro Campana C, Panama (32) × Madden Forest, Panama (86)

The number of strains involved differ in the crosses between the races simply because different numbers of strains were or were not available; almost always, the number of sympatric strains tested was less than the number of allopatric strains tested—fewer do occur sympatrically in nature.

THE METHOD

Elens (1958) first described an apparatus for measuring the sexual isolation between different mutants of *Drosophila melanogaster* via direct observation of the individuals involved; Elens and Wattiaux (1964) extended the use of these observation chambers to other species (*e.g.*, Ehrman *et al.*, 1965, successfully used it with different inversion types in *D. pseudoobscura*) and described the apparatus more fully. It is to this later paper that the reader is referred for a thorough description of what is essentially a glass and wood sandwich, pictured in Figs. 1 and 2.

This method is superior to the older "male choice" technique for several reasons, the most important of which is that it easily permits the observation of four

types of matings, *i.e.*, $A\text{♀} \times A\text{♂}$, $A\text{♀} \times B\text{♂}$, $B\text{♀} \times A\text{♂}$, and $B\text{♀} \times B\text{♂}$ in any single experiment. Briefly, the "male choice" method (see Merrell, 1960) involves confining equal numbers of two kinds of virgin females with males of only one kind. After a certain lapse of time, the sperm receptacles of the females are dissected out and examined for the presence of spermatozoa (or, more time consuming, the inseminated females are permitted to produce offspring). Thus, only the matings $A\text{♂} \times A\text{♀}$ or $B\text{♀}$ can be recorded at one time, while $B\text{♂} \times A\text{♀}$ or $B\text{♀}$ must be experimentally analyzed separately.

In the observation chambers employed here, as soon as a mating occurs five facts about it are recorded: (1) the time it takes place, (2) its sequence among the other copulae which occur, (3) where in the chamber the couple is located (for this purpose, a grid forms the floor, see Fig. 1 and 2), (4) the type of female involved, and, (5) the type of male involved. It is also a simple matter to note the duration of each mount though this was not considered necessary here. No flies need be sacrificed for dissection with this procedure, and they may subsequently be used to breed additional generations.

A possible weakness of this technique is that it in no way prevents the scoring of a single male more than once, but then neither does the "male choice" technique; however, if a single male is successful more than once in a single experimental run, perhaps it should be recorded twice. Furthermore, data accumulate more slowly with the direct observation method. This is so because each individual mating is directly observed and a limited number of chambers can be run in one day. For the crosses tested here, four chambers per day was the maximum.

These observations were begun on October 4, 1963, and concluded on September 8, 1964; there is at least one advantage in stretching such experiments out over a rather long time (actually, it is unavoidable in the case of the direct observation

technique), since seasonal variations in behavior, etc. would be expected to occur even in the laboratory. The flies introduced into the chambers were aged while isolated from individuals of the opposite sex for about eight days and alternating strains and sexes had the margin of one wing clipped for ease of identification with a 4 \times hand lens while in the chambers.

RESULTS AND DISCUSSION

Table 1 tells the entire story; for it, the new joint isolation coefficient and its standard error were calculated according to the formula used by Malogolowkin-Cohen *et al.* (1965). Briefly, if P_{11} , P_{22} , q_{12} and q_{21} equal the proportion of matings observed between males and females of race 1, males and females of race 2, males of race 1 and females of race 2, and males of race 2 and females of race 1 respectively, then the coefficient equals:

$$P_{11} + P_{22} - q_{12} - q_{21}$$

and the variance is $\sqrt{4pq/N}$ where p = the proportion of homogamic matings, q = the proportion of heterogamic matings, and N = the total number of matings observed. Random mating results in an isolation index of zero and complete isolation produces a coefficient = 1.00.

In all but one case, that entered in line 7 of Table 1, Centro-American \times Amazonian, the coefficients are higher for the sympatric than for the allopatric strains, and in this one case, the difference is not significant so that the two measures of isolation may be considered about the same. Furthermore, the average sympatric isolation coefficient is 0.85 while the average allopatric one is 0.67. It seems reasonable to conclude that any isolating mechanism which decreases the chances of the production of inferior hybrid offspring may be expected to be stronger between sympatric than between allopatric populations of the same pairs of subspecies or incipient species. This is certainly borne out by the data reported here. These data also concur with those obtained by Dobzhansky *et*

TABLE 1. Numbers of matings observed and isolation coefficient calculated for sympatric and for allopatric crosses; the total number of matings observed was 1,695.

Races	Origin	Matings	Coefficient
1. Amazonian × Andean	{ Sym	108	0.86 ± 0.049
	{ Allo	100	0.66 ± 0.074
2. Amazonian × Guianan	{ Sym	104	0.94 ± 0.033
	{ Allo	109	0.76 ± 0.061
3. Amazonian × Orinocan	{ Sym	106	0.75 ± 0.065
	{ Allo	124	0.61 ± 0.070
4. Andean × Guianan	{ Sym	109	0.96 ± 0.026
	{ Allo	102	0.74 ± 0.066
5. Orinocan × Andean	{ Sym	100	0.94 ± 0.033
	{ Allo	111	0.46 ± 0.084
6. Orinocan × Guianan	{ Sym	104	0.85 ± 0.053
	{ Allo	100	0.72 ± 0.069
7. Centro-American × Amazonian	{ Sym	102	0.68 ± 0.072
	{ Allo	103	0.71 ± 0.070
8. Centro-American × Orinocan	{ Sym	110	0.85 ± 0.052
	{ Allo	103	0.73 ± 0.069
Average (sympatric) = 0.85			
Average (allopatric) = 0.67			

al., (1964) using the traditional "male choice" method, discussed above, as applied to similar material. Malogolowkin-Cohen *et al.* (1965) found that this relationship held even when allopatric strains of *Drosophila paulistorum* that were closer or further apart in nature were compared for the strength of their behavioral isolation from one another. Indeed, one may hypothesize that the peculiar sterility of the hybrids between these races (genically induced modification of the egg cytoplasm, Ehrman, 1962, pp. 287-291), came first in the history of this species-complex, as a by-product of adaptation of allopatric races to environments of their respective distribution regions. Sexual isolation which is more effective came later, and its biological function is to limit or prevent the appearance of hybrids with reduced reproductive fitness. As a result, six races which can be considered incipient species have appeared. Alexander (1964) carefully reviewed this sort of situation (among others), *i.e.*, variation in the efficiency of reproductive isolation between sympatric and between allopatric populations, in sound-

producing insects where acoustical communication often proves to be a most dramatic isolating device. He accurately noted that: "In closely related sympatric species, very little is known about which differences developed when the species were allopatric and which developed subsequently."

Finally, we should consider time and any variation in the occurrence of interracial or intraracial matings which might be correlated with it; this was done, also with *Drosophila paulistorum*, in careful detail by Malogolowkin-Cohen *et al.* (1965) who note, ". . . regardless of whether the isolation is low or high, the isolation index is about the same immediately after the flies are introduced as when most of the available females have already mated." The data reported here certainly do confirm their conclusion. For instance, as is recorded in Table 1, a total of 1,695 matings were observed. The observation chambers were run a total of 185 separate times so that an average of 9.2 matings took place in each run (10 represents the optimal 50 per cent). 12.86 per cent or

218 of these matings were heterogamic; 103 occurred during the first half of individual runs with the observation chambers (this is, of course, just one of many possible ways of examining the time data) whereas 115 took place during the second half. The difference is not statistically significant since $\chi_1^2 = 0.66$.

To conclude, according to Grant (1963): "The relation between reproductive isolation and ecological coexistence is a reciprocal one. Not only does the formation of reproductive isolating mechanisms permit species to coexist more or less closely, but the attainment of sympatry promotes the further development of breeding barriers between species. Reproductive isolation is a cause of sympatry, and sympatry in turn can be a cause of reproductive isolation."

SUMMARY

Those races of the *Drosophila paulistorum* species-complex of six known races which occur sympatrically and retain their separate identities in nature, exhibit a greater sexual isolation than do strains of the same races which occur allopatrically. This behavioral isolation was tested by a recently developed direct observation technique and bespeaks the correctness of considering these races as incipient species.

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