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Mating Preferences and Sexual Isolation Within and Between the Incipient Species of *Drosophila paulistorum*

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ABSTRACT: The "male choice" experimental method was used to test mating preferences of six races of *Drosophila paulistorum*. The races (number of strains in parentheses) are: Centro-American (3); Amazonian (4); Orinocan (5); Andean-South Brazilian (6); Transitional (4); and Guianan (1).

Strains of the same race often showed significant preferences for homogamic matings, but strains of different races showed such preferences to a much greater extent. On the average, sexual isolation was lower in matings between the Transitional race strains and strains of other races than it was in matings between strains of the other five races. The degree of sexual isolation showed only a weak positive correlation with fertility or sterility of the hybrids between the strains crossed.

An addendum contains additions and corrections to the data reported (1959) on *D. paulistorum* by Dobzhansky and Spassky with regard to the production of sterile and fertile F₁ hybrids in various crosses between strains.

Drosophila paulistorum Dobzhansky and Pavan is a taxon which contains an extraordinary complex of geographic races or incipient species. Five of them have almost reached the status of reproductively isolated but morphologically indistinguishable species. These are the Centro-American, Orinocan, Amazonian, Andean-South Brazilian, and Guianan races. They are mostly allopatric, but in some places their geographic ranges overlap, and two incipient species may coexist sympatrically without interbreeding. When placed together in laboratory experiments, females of one and males of another race exhibit a pronounced and in some instances nearly complete, sexual isolation. If hybrids are produced, the females are fertile but the males are sterile. The sixth, or Transitional, race occurs in Colombia; all strains of this race can be crossed and will produce fertile hybrids of both sexes with at least one of the other five races (Dobzhansky and Spassky, 1959). The two isolating mechanisms, sexual isolation and hybrid sterility, are quite different in their genetic bases. The former is determined by polygenic differences between the races; the latter involves a remarkable predetermination of the egg cytoplasm by the genotype present in the egg before meiosis and fertilization (Ehrman 1960, 1961).

It is mainly because of the existence of the Transitional race that *Drosophila paulistorum* is regarded as a single species. It still has a single, though deeply cleft, gene pool. The races (incipient species) of

D. paulistorum are among the best known examples of borderline situations bridging the gap between race and species (Dobzhansky, 1961). Analysis of such borderline situations presents a challenging problem to evolutionists. It is highly improbable that the reproductive isolation which is observed between the incipient species could have arisen simultaneously as an absolute barrier to gene exchange. More likely, it arose gradually, and is probably in the process of construction now.



Fig. 1.—The geographic origins of the strains of *Drosophila paulistorum* used in this study.

It is likely, then, that the raw material from which isolation can be built is in the populations of some or of all the races. The purpose of the present study is to test this hypothesis by exploring the variability of sexual isolation and of mating preferences within and between the incipient species.

MATERIAL AND METHODS

The geographic origin of the strains of *D. paulistorum* used in the experiment reported below is as follows (for more details see Dobzhansky and Spassky, 1959).

<i>Centro-American Race</i>	<i>Andean-South Brazilian</i>
Honduras	Llanos B, Colombia
Salvador	Santo Domingo, Ecuador
Costa Rica	Tarapoto, Peru
<i>Amazonian Race</i>	Tingo Maria, Peru
Panama A	Coroico, Bolivia
Trinidad	Santa Cruz, Bolivia
Içana, Brazil	Minas Gerais, Brazil
Belem, Brazil	Angra, Brazil
<i>Orinocan Race</i>	<i>Transitional Race</i>
Panama B	Santa Marta, Colombia
Panama C	Bucaramanga, Colombia
Llanos A, Colombia	Palmira, Colombia
Caripe, Venezuela	Buenaventura, Colombia
Guiana A, Br. Guiana	<i>Guianan Race</i>
	Guiana B, Br. Guiana

The so-called male choice experimental method has been used. (In reality the choice of the mating partner is exercised, in *Drosophila*, mainly by females.) Virgin females from two strains, marked for recognition by having either the right or the left wing clipped, were aged for 3 days or longer at 25C or at room temperature. Groups of 5 to 10 females from each of the two strains tested were then confined, in glass vials containing food, with an equal number of males of one of the strains, at the same temperatures. The length of exposure varied from 24 to 48 hours; this was adjusted after trial experiments to secure the insemination of approximately one-half of all the females exposed. The females were dissected in physiological saline, and their sperm receptacles were examined under a compound microscope.

THE STATISTICS

The data obtained in 172 different crosses, involving some 16,335 females, are enumerated in Table I. The figures reported are the absolute numbers of inseminated (+) and uninseminated (—) females; "homogamic" refers to the females of the same strain to which the males belong, and "heterogamic" to females of a strain different from the males. The isolation indices are computed according to the simple formula suggested by Stalker (1942), namely, the percentage of homogamic females inseminated minus the percentage of insemi-

TABLE I.—Frequency of insemination (+) and non-insemination (—) in “male choice” experiments with different strains of *Drosophila paulistorum*

Males and females	Females	Homogamic +	Homogamic —	Heterogamic +	Heterogamic —	Isolation index	Chi- square
<i>Centro-American Race</i>							
1. Honduras	Salvador	29	45	54	26	—0.26	12.4
2. Salvador	Honduras	43	27	28	42	+0.21	6.4
3. Salvador	Costa Rica	21	10	5	27	+0.63	17.6
4. Costa Rica	Salvador	12	20	27	8	—0.35	10.7
5. Costa Rica	Honduras	15	14	12	16	+0.09	0.5
6. Honduras	Costa Rica	20	16	17	19	+0.08	0.5
<i>Amazonian Race</i>							
7. Panama A	Trinidad	21	6	19	8	+0.05	0.4
8. Trinidad	Panama A	24	11	27	7	—0.07	1.1
9. Panama A	Içana	41	26	24	44	+0.27	9.2
10. Içana	Panama A	55	82	47	91	+0.08	1.1
11. Panama A	Belem	26	7	10	20	+0.41	13.5
12. Belem	Panama A	57	19	15	44	+0.44	19.2
13. Trinidad	Içana	23	15	15	21	+0.18	2.6
14. Içana	Trinidad	13	2	2	10	+0.68	13.4
15. Trinidad	Belem	49	22	41	33	+0.11	2.8
16. Belem	Trinidad	35	16	22	29	+0.23	6.7
17. Içana	Belem	24	25	19	29	+0.11	0.9
18. Belem	Içana	32	24	38	14	+0.12	0.9
<i>Transitional Race</i>							
19. Santa Marta	Bucaramanga	31	30	29	32	+0.04	0.1
20. Bucaramanga	Santa Marta	6	12	9	11	—0.15	0.5
21. Santa Marta	Palmira	20	26	4	39	+0.65	13.2
<i>Andean-South Brazilian Race</i>							
22. Llanos B	Santo Domingo	38	8	21	27	+0.31	15.1
23. Llanos B	Tarapoto	36	22	38	19	—0.04	0.3

TABLE I.—(continued)

Males and females	Females		Homogamic		Heterogamic		Isolation index	Chi-square
	+	—	+	—	+	—		
24. Tingo Maria		Llanos B	29	16	20	22	+0.15	2.6
25. Llanos B		Urubamba	31	16	22	16	+0.06	0.6
26. Coroico		Llanos B	33	17	21	28	+0.21	5.4
27. Llanos B		Minas Gerais	16	28	22	20	-0.18	2.2
28. Llanos B		Angra	25	23	17	27	+0.15	1.7
29. Tarapoto		Santo Domingo	28	23	29	19	-0.05	0.3
30. Santo Domingo		Tingo Maria	32	14	13	34	+0.43	16.2
31. Urubamba		Santo Domingo	34	13	7	37	+0.64	29.1
32. Santo Domingo		Coroico	13	36	23	19	-0.35	7.6
33. Minas Gerais		Santo Domingo	43	10	26	20	+0.18	6.9
34. Angra		Santo Domingo	18	32	1	46	+0.89	17.6
35. Santo Domingo		Angra	27	18	17	23	+0.17	2.6
36. Tarapoto		Tingo Maria	9	6	9	9	+0.09	0.3
37. Tingo Maria		Tarapoto	38	47	55	34	-0.16	5.1
38. Tarapoto		Urubamba	42	13	21	26	+0.17	5.9
39. Coroico		Tarapoto	24	24	36	11	-0.21	7.2
40. Tarapoto		Minas Gerais	16	38	18	32	-0.05	0.1
41. Angra		Tarapoto	40	9	17	32	+0.40	22.2
42. Tingo Maria		Urubamba	28	18	17	19	+0.13	0.2
43. Urubamba		Tingo Maria	58	39	40	51	+0.15	4.8
44. Tingo Maria		Coroico	27	16	29	17	+0.01	0.0
45. Minas Gerais		Tingo Maria	31	13	13	29	+0.39	13.5
46. Tingo Maria		Angra	24	25	16	32	+0.19	2.4
47. Coroico		Urubamba	25	21	22	20	+0.02	0.3
48. Urubamba		Minas Gerais	23	26	26	21	-0.08	0.7
49. Angra		Urubamba	22	21	12	35	+0.34	6.2
50. Minas Gerais		Coroico	39	11	28	21	+0.16	4.8
51. Coroico		Angra	32	16	17	28	+0.28	7.7

TABLE I.—(continued)

Males and females	Females	Homogamic +	—	Heterogamic +	—	Isolation index	Chi- square
52. Angra	Minas Gerais	21	28	30	18	-0.19	3.8
<i>Orinocan Race</i>							
53. Panama B	Panama C	21	26	24	19	-0.11	1.1
54. Panama C	Panama B	25	20	20	23	+0.09	0.7
55. Panama B	Llanos A	32	11	7	39	+0.66	31.8
56. Llanos A	Panama B	20	25	18	27	+0.05	0.2
57. Panama C	Llanos A	27	21	13	31	+0.31	6.6
58. Llanos A	Panama C	22	22	15	29	+0.19	2.3
59. Llanos A	Caripe	30	13	17	26	+0.28	7.9
60. Panama B	Caripe	38	12	20	29	+0.30	12.6
61. Caripe	Panama B	28	22	20	30	+0.17	2.6
62. Guiana A	Llanos A	35	15	31	26	+0.13	2.1
63. Llanos A	Guiana A	43	11	20	32	+0.35	17.0
64. Guiana A	Panama B	30	15	23	23	+0.12	1.9
65. Panama B	Guiana A	42	23	49	22	-0.03	0.1
66. Llanos A	Panama B	45	29	23	43	+0.27	8.4
67. Panama B	Llanos A	47	24	49	28	+0.02	0.0
<i>Transitional x Centro-American</i>							
68. Honduras	Santa Marta	71	29	29	72	+0.42	35.8
69. Honduras	Buenaventura	41	13	10	38	+0.57	30.8
70. Honduras	Palmira	49	1	1	45	+0.96	88.1
71. Bucaramanga	Honduras	30	19	10	47	+0.56	21.4
72. Santa Marta	Costa Rica	41	10	16	28	+0.38	19.1
73. Costa Rica	Bucaramanga	38	10	3	44	+0.85	51.4
74. Palmira	Costa Rica	43	8	1	46	+0.95	66.8
75. Costa Rica	Buenaventura	42	7	7	41	+0.71	49.4

TABLE I.—(continued)

	Males and females	Females	Homogamic	Heterogamic	Isolation index	Chi-square
			+	—		square
<i>Transitional x Amazonian</i>						
76.	Santa Marta	Panama A	42	11	+0.34	17.3
77.	Panama A	Buenaventura	25	22	+0.36	7.9
78.	Palmira	Panama A	41	2	+0.95	64.0
79.	Panama A	Buenaventura	23	18	+0.82	23.1
80.	Içana	Santa Marta	30	24	+0.50	15.9
81.	Santa Marta	Içana	19	6	+0.68	17.5
82.	Bucaramanga	Içana	33	51	+0.34	9.3
83.	Içana	Palmira	46	38	+0.71	43.0
84.	Buenaventura	Içana	21	21	+0.49	11.7
<i>Transitional x Andean-South Brazilian</i>						
85.	Santa Marta	Tingo Maria	9	9	-0.10	0.4
86.	Tingo Maria	Santa Marta	12	4	+0.71	12.7
87.	Bucaramanga	Tingo Maria	11	8	+0.18	1.3
88.	Tingo Maria	Bucaramanga	10	0	+0.50	10.0
89.	Santa Marta	Angra	40	17	+0.14	3.1
90.	Angra	Santa Marta	25	23	+1.00	35.2
91.	Angra	Bucaramanga	42	7	+0.87	63.3
92.	Angra	Buenaventura	29	21	+0.94	38.6
93.	Palmira	Angra	55	49	+0.62	36.0
94.	Angra	Palmira	29	19	+1.00	38.1
95.	Santa Cruz	Palmira	28	16	+0.08	0.7
96.	Buenaventura	Llanos B	37	12	+0.22	8.6
97.	Buenaventura	Santa Cruz	29	19	+0.19	3.8
98.	Bucaramanga	Santa Cruz	40	10	+0.32	14.9
99.	Santa Cruz	Santa Marta	36	13	+0.45	17.8
100.	Santo Domingo	Santa Marta	38	12	+0.42	18.8
101.	Palmira	Santo Domingo	93	4	+0.24	37.0

TABLE I.—(continued)

	Males and females	Females	Homogamic +	Heterogamic +	Heterogamic —	Isolation index	Chi- square
<i>Transitional x Orinocan</i>							
102.	Llanos A	Bucaramanga	24	24	45	+1.00	30.3
103.	Bucaramanga	Caripe	42	8	43	+1.00	65.7
104.	Palмира	Llanos A	51	3	41	+0.95	80.3
105.	Llanos A	Buenaventura	36	12	49	+0.90	48.7
106.	Santa Marta	Panama B	26	16	39	+0.85	30.0
107.	Santa Marta	Llanos A	57	42	30	+0.30	14.0
108.	Santa Marta	Guiana A	33	15	9	+0.55	22.2
109.	Santo Domingo	Llanos A	26	43	7	+0.59	15.8
110.	Guiana A	Bucaramanga	27	17	0	+1.00	39.0
111.	Caripe	Santa Marta	68	10	2	+0.94	114.9
112.	Caripe	Santo Domingo	80	18	7	+0.84	112.29
113.	Santo Domingo	Caripe	26	3	2	+0.86	41.9
114.	Caripe	Palмира	87	10	25	+0.53	74.8
115.	Palмира	Caripe	34	16	0	+1.00	59.1
116.	Buenaventura	Caripe	32	6	10	+0.54	27.3
117.	Llanos A	Palмира	5	5	0	+1.00	6.7
118.	Palмира	Llanos A	24	26	0	+1.00	31.6
119.	Palмира	Panama B	56	31	4	+0.88	74.3
120.	Panama B	Buenaventura	50	2	2	+0.92	87.2
121.	Panama B	Bucaramanga	47	6	4	+0.84	66.0
122.	Guiana B	Santa Marta	24	14	4	+0.67	18.6
123.	Guiana B	Bucaramanga	35	16	2	+0.88	41.1
<i>Centro American x Amazonian</i>							
124.	Costa Rica	Panama A	15	4	0	+1.00	25.7
125.	Panama A	Costa Rica	16	2	0	+1.00	30.5
126.	Costa Rica	Trinidad	17	3	0	+1.00	28.8
127.	Costa Rica	Belem	20	0	0	+1.00	38.6

TABLE I.—(continued)

Males and females	Females	Homogamic +	Homogamic —	Heterogamic +	Heterogamic —	Isolation index	Chi- square
128. Belem	Honduras	17	3	0	20	+1.00	29.6
129. Costa Rica	Içana	18	2	0	20	+1.00	32.7
130. Honduras	Içana	18	1	0	18	+1.00	33.5
<i>Centro-American x Andean-South Brazilian</i>							
131. Honduras	Llanos A	35	11	5	41	+0.75	39.8
132. Llanos A	Honduras	21	23	14	31	+0.21	2.6
133. Honduras	Santo Domingo	34	16	1	46	+0.94	45.5
134. Honduras	Tarapoto	19	1	0	20	+1.00	36.2
135. Honduras	Angra	15	5	2	18	+0.76	17.3
136. Angra	Honduras	43	3	7	41	+0.73	58.5
137. Llanos A	Costa Rica	20	0	1	18	+0.90	35.0
138. Costa Rica	Llanos A	18	2	2	18	+0.80	25.6
139. Costa Rica	Angra	20	0	1	18	+0.90	35.0
<i>Centro-American x Orinocan</i>							
140. Caripe	Honduras	43	7	1	49	+0.96	71.6
141. Honduras	Caripe	34	16	3	47	+0.84	41.2
142. Honduras	Guiana A	18	1	6	14	+0.52	17.2
143. Honduras	Llanos A	20	0	2	18	+0.82	32.7
<i>Centro-American x Guianan</i>							
144. Honduras	Guiana B	19	0	0	17	+1.00	36.2
145. Guiana B	Honduras	18	1	0	20	+1.00	35.0
<i>Orinocan x Amazonian</i>							
146. Panama A	Guiana A	48	8	2	51	+0.92	70.4
147. Guiana A	Panama A	46	16	2	52	+0.90	51.6
148. Panama A	Llanos A	59	26	9	67	+0.71	76.8
149. Llanos A	Panama A	36	12	0	44	+1.00	51.1
150. Panama A	Panama B	42	17	6	57	+0.77	46.1
151. Panama B	Panama A	31	2	0	32	+1.00	53.1

TABLE I.—(continued)

Males and females	Females	Homogamic +	Heterogamic +	Isolation index	Chi-square
<i>Orinocan x Andean-South Brazilian</i>					
152. Panama B	Llanos B	48	22	+0.46	23.0
153. Llanos B	Panama B	44	13	+0.84	48.4
154. Llanos B	Guiana A	36	8	+0.96	66.0
155. Guiana A	Llanos B	57	15	+0.66	52.9
156. Llanos A	Llanos B	32	13	+1.00	41.9
157. Llanos B	Llanos A	34	7	+0.94	48.3
158. Llanos A	Angra	19	0	+1.00	39.1
<i>Orinocan x Guianan</i>					
159. Guiana A	Guiana B	32	14	+0.94	41.8
160. Guiana B	Guiana A	44	11	+0.86	55.1
161. Llanos A	Guiana B	39	6	+0.89	54.3
162. Guiana B	Llanos A	28	14	+0.73	24.6
163. Panama B	Guiana B	32	6	+0.89	46.6
164. Guiana B	Panama B	31	11	+0.94	42.5
<i>Amazonian x Andean-South Brazilian</i>					
165. Panama A	Llanos B	45	16	+0.89	64.8
166. Llanos B	Panama A	28	9	+0.95	46.3
167. Trinidad	Belém	34	16	+0.94	45.5
168. Trinidad	Angra	14	1	+1.00	27.9
<i>Amazonian x Guianan</i>					
169. Panama A	Guiana B	30	14	+0.86	34.4
170. Guiana B	Panama A	43	7	+0.86	63.2
<i>Andean-South Brazilian x Guianan</i>					
171. Llanos B	Guiana B	52	4	+0.84	71.8
172. Guiana B	Llanos B	42	6	+0.95	63.5

nated heterogamic females, divided by the sum of these percentages. An isolation index of +1 indicates that only homogamic matings have taken place, an index 0 that the matings take place at random, while negative isolation indices suggest a preference for matings between unlikes. The chi-squares are computed from simple two-by-two contingency tables, and each chi-square has one degree of freedom.

Levene (1949) proposed a superior but much more laborious method of calculating isolation coefficients and their standard errors. The advantage of Levene's method is greatest when the insemination percentages observed deviate greatly from 50% total insemination. In planning the experiments we have tried to obtain total frequencies of insemination as close to 50% as possible, and with some exceptions this endeavor was successful. In any event, Levene's coefficients can be calculated from the figures given in Table I. Bateman (1949) and Merrell (1950, 1954) have suggested other useful statistics, most of which cannot be calculated from our data. However, in some instances we did compute an "isolation estimate," which is the sum of the heterogamic insemination percentages in the reciprocal crosses, divided by the sum of the homogamic insemination percentages in the same crosses. An isolation "estimate" (I) of unity indicates that mating occurs at random, while complete isolation gives $I = 0$. Finally, the female mating ratio, M_f , is a ratio of the sums of percentages of inseminated females of the two kinds in reciprocal crosses.

INTRARACIAL SEXUAL PREFERENCES

The first 67 entries (Nos. 1-67) in Table I report the results of matings in which all flies belonged to the same race, but usually to strains of different geographic origin. Almost one-half of the isolation indices (32 out of 67) for these matings are statistically significant (for one degree of freedom, a chi-square of 3.84 corresponds to a probability of 0.05). This very strongly suggests that random mating is, contrary to what one might have expected, by no means the general rule, even in intraracial crosses. A more detailed examination of the data shows that as many as 52 of the isolation indices have a positive, and only 15 have a negative sign; such a deviation from equality is quite unlikely to arise by chance alone. This indicates that when geographically different strains of the same race are tested together, homogamic matings are more frequent than heterogamic ones. The situation is, however, far from simple; 6 of the 15 negative, and 27 of the 52 positive isolation indices are significant statistically, being greater than 3.84, and thus showing that significant preferences for heterogamic as well as for homogamic matings are encountered, but with unequal frequency. The unweighted mean isolation indices for different races are as follows:

Centro-American	+0.07	Transitional	+0.18
Amazonian	+0.22	Andean-South	
Orinocan	+0.19	Brazilian	+0.14

The conclusion seems to be warranted that sexual attraction tends to be, on the average, stronger between females and males of similar geographic origin than between geographically alien ones. What then is the meaning of the negative isolation indices? They arise when matings between geographically foreign flies are more frequent than between representatives of the same strain. One of the possible explanations of such one-sided mating preferences lies in greater sexual excitability of some strains, which makes them more ready to mate than other strains. This can be illustrated by the following examples.

Entries Nos. 1 and 2 in Table I show what happens when a mixture of females of the Honduras and Salvador strains of the Centro-American race are exposed to males of those strains. About 39% of the Honduras females were inseminated by Honduras males and 40% by Salvador males; 67% of Salvador females were inseminated by Honduras males and 61% by Salvador males. This gives an M_f ratio (see above) of about 1.63 in favor of Salvador females which mate more readily than do Honduras females. But, there seems to be no mutual sexual isolation between these strains; the isolation estimate (I , see above) turns out to be 1.07, close to neutrality. The situation with the Salvador and Costa Rican strains (entries Nos. 3 and 4 in Table I) is quite similar. The M_f ratio in favor of Salvador females is even greater (2.73), but the I estimate is 0.88. With other combinations giving statistically significant negative isolation indices (entries Nos. 32, 37, 39, and 52), the reciprocal crosses unfortunately are not available. The one-sided mating preferences are, most likely, unrelated to the true sexual isolation.

It may now be asked whether the aversion for heterogamic matings tends to become stronger when more remote geographic strains are involved. Our data do not permit an unambiguous answer, although some tendency for aversion may exist. In the Amazonian race, the geographically most remote strains (Panama and Belem) give isolation indices close to 0.4 in both reciprocal crosses (Nos. 11 and 12 in Table I). In the Andean-South Brazilian race, the remote Santo Domingo (Ecuador) and Angra (Southern Brazil) females give a very high isolation index when tested with Angra males, but a rather low one with Santo Domingo males (Nos. 34 and 35). In the Orinocan race, the remote Panama and Guiana strains give only a weak isolation coefficient (Nos. 65 and 66).

INTERRACIAL CROSSES

The results of isolation experiments are recorded in Table I. With very few exceptions the results show female preferences for homogamic males. The isolation coefficients are positive (with one exception, No. 85), and, with few exceptions, very significant. Wherever reciprocal crosses have been made, isolation estimates are much smaller than unity. The races of *Drosophila paulistorum* are indeed becoming sexually isolated species.

Nevertheless, isolation varies from race to race and from strain to strain. The behavior of the Transitional race is of greatest interest; the race is called Transitional because its strains produce fertile male hybrids in crosses with other races (Dobzhansky and Spassky, 1959). Is this race "transitional" also with respect to sexual preferences? This information is given in Table II. Crosses of the Transitional race with the Centro-American, Amazonian, and Andean-South Brazilian races give lower isolation coefficients than interracial crosses not involving the Transitional race. Only the Transitional x Orinocan crosses show a high degree of isolation. The average isolation coefficient in crosses with the Transitional race turns out to be +0.65, but is +0.87 in crosses between the other races.

Dobzhansky and Spassky (1959) found that isolation between Amazonian and Centro-American, or Amazonian and Andean races, is much stronger than isolation between Centro-American and Orinocan races. This is confirmed by the data in Table II; the mean isolation coefficients in the former cases are +1.0 and +0.94 as compared with +0.78 and +0.79 for the latter. The Guianan race stands out, showing rather uniformly high isolation with all other races, including the Transitional. This agrees with cytological findings — gene arrangements in chromosomes of the Guianan race differ rather conspicuously from those of other races (Dobzhansky and Pavlovsky, unpublished).

TABLE II.—Mean isolation coefficients obtained in crosses between different races

Cross	Isolation coefficient
Transitional x Centro-American	+0.675
Transitional x Amazonian	+0.577
Transitional x Andean	+0.458
Transitional x Orinocan	+0.824
Transitional x Guianan	+0.775
Average with Transitional	+0.650
Amazonian x Andean	+0.945
Amazonian x Guianan	+0.860
Andean x Guianan	+0.895
Centro-American x Amazonian	+1.000
Centro-American x Andean	+0.777
Centro-American x Orinocan	+0.785
Centro-American x Guianan	+1.000
Orinocan x Amazonian	+0.883
Orinocan x Andean	+0.837
Orinocan x Guianan	+0.875
Average without Transitional	+0.874

In three localities (Barro Colorado Island, Panama; Llanos, Colombia; Georgetown, British Guiana), strains of two different races are known to coexist sympatrically (Dobzhansky and Spassky, 1959). It is interesting that these sympatric strains are highly isolated (entries Nos. 150, 151, 156, 157, 159, and 160, in Table I).

SEXUAL ISOLATION AND HYBRID STERILITY

Two reproductive isolating mechanisms are known to operate between the races of *D. paulistorum*, sexual isolation and hybrid sterility of males. The two are not interdependent, although there may be an over-all positive correlation between them.

The Santa Marta strain of the Transitional race has been found to produce fertile F_1 male hybrids with some strains of the Centro-American race (Honduras, Salvador, and Costa Rica), but sterile hybrids are produced with the Andean-South Brazilian race. Isolation coefficients of +0.42 and +0.38 for the fertile and +0.71, +0.14, +1.00, +0.45, and +0.42 for the sterile crosses are shown in Table I. Bucaramanga and Palmira strains of the Transitional race give fertile male hybrids with most strains of the Andean-South Brazilian race and so does the cross Bucaramanga ♀ \times Costa Rica ♂. In fertile crosses, the isolation coefficients are +0.18, +0.50, +0.87, +1.00, +0.08, +0.24, +0.32, +0.85, and in the sterile ones +0.96, +0.57, and +0.71.¹

DISCUSSION

It is generally true that flies of strains belonging to the same species and race must be able to mate and produce fertile offspring. A mutant or a recombination genotype which would make carriers unable to mate with other individuals in the population would be seriously handicapped and discriminated against by natural selection. This does not mean, however, that conspecific strains must always mate at random. Many of them do not in laboratory experiments or, presumably, in nature. Such a state of things is not surprising; it is expected that strains differing in some genes will be found to differ in behavior, including sexual behavior. By and large, it would seem that behavioral differences would be greater in strains of geographically remote origin than in geographically close strains, because the former are often genetically more unlike than the latter. A close correlation between the amount of genetic differentiation and behavior, however, is neither observed nor expected; even if the genetic differences between strains increased in proportion to their geographic remoteness, the behavioral differences would not follow suit necessarily. Both geographically regular and haphazard variations in sexual preferences have been observed among species of *Drosophila* (among others, see Dobzhansky

¹ See addendum.

1944, *D. prosaltans*; Dobzhansky and Streisinger 1944, *D. sturtevanti*; Baker 1949, *D. arizonensis*; Spieth 1951, *D. virilis* group; Dobzhansky and Mather 1961, *D. serrata*; review in Patterson and Stone, 1952).

The discovery of variations in sexual preferences among strains of the same species of *Drosophila* does not automatically explain sexual isolation between full-fledged species of this genus, even though isolation is often absolute or at any rate strong enough to serve as the principal reproductive isolation barrier. Intraspecific variations are only raw materials which may be ordered into a workable isolating mechanism, and the ordering process is usually natural selection. The supposition that sexual isolation between species is an automatic product of accumulation of genetic differences, is as unlikely as the old notion that a simple aggregation of mutations eventually makes a new species. To form a new species, the mutations must be "sorted out" and "added up" by natural selection to form harmonious systems.

The seemingly haphazard sexual preferences and aversions observed among strains of *Drosophila paulistorum* add up to a biologically meaningful situation. The interest of this species lies precisely in that it contains Mendelian populations at all stages of reproductive divergence and separation, ranging from apparent identity to almost complete speciation. Two isolating mechanisms are involved in this speciation process, and they are profoundly different, genetically. One is a polygenically controlled sexual isolation, and the other is a form of hybrid sterility acting through a genically induced modification of the egg cytoplasm (Ehrman, 1960, 1961).

Much study is needed to unravel the interrelations of sexual isolation and hybrid sterility in *D. paulistorum*. Our working hypothesis has been that sterility came first in the history of the species, 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. The experiments described in the present report were designed to yield data to facilitate further testing of the above hypothesis.

ADDENDUM

We wish to record the following additions and corrections to the data of Dobzhansky and Spassky (1959). Sterile F₁ hybrid males have been obtained in the following crosses: Guatemala ♀ x Santo Domingo ♂, Honduras ♀ x Belem ♂, Honduras ♀ x Llanos A ♂, Honduras ♀ x Coroico ♂, Costa Rica ♀ x Belem ♂, Belem ♀ x Honduras ♂, Belem ♀ x Palmira ♂, Llanos A ♀ x Santo Domingo ♂, Guiana B ♀ x Santa Cruz ♂, Santa Marta ♀ x Angra ♂, Santa Marta ♀ x Bucaramanga ♂, Coroico ♀ x Honduras ♂, Angra ♀ x Guatemala ♂. The following crosses gave fertile F₁ hybrids: Honduras ♀ x Santa Marta ♂, Bucaramanga ♀ x Panama B ♂, Palmira ♀ x Buena-

ventura ♂, Buenaventura ♀ x Palmira ♂, and all crosses made between strains of the Orinocan race, as well as between Pichilingue and strains of the Andean-South Brazilian race.

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