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A STUDY OF SEXUAL ISOLATION BETWEEN CERTAIN STRAINS OF *DROSOPHILA PAULISTORUM*

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The superspecies *Drosophila paulistorum* Dobzhansky and Pavan consists of six races or incipient species which exhibit various degrees of reproductive isolation from each other. The two principal isolating mechanisms involved are sexual (ethological) isolation and sterility of hybrid males (Dobzhansky and Spassky, 1959; Dobzhansky *et al.*, 1964). Sexual isolation is almost certainly the more effective of the two mechanisms in preventing gene exchange between the incipient species in their natural habitats. It appears to be a general rule that where two or more of the incipient species are sympatric in the same territory, no hybrids between them are formed spontaneously, and crosses can be made in laboratory experiments only with considerable difficulty, always yielding sterile hybrids. On the other hand, so-called transitional strains are found in some territories inhabited by only one race. Thus, only the Andean-Brazilian race is found in northeastern Brazil, and some of the strains derived from the populations of that region cross to some strains of the allopatric Amazonian race and produce fertile hybrid sons (Malogolowkin, 1962, 1963; Malogolowkin *et al.*, 1964). On the other hand, various degrees of sexual isolation have been encountered in crosses between strains of the same race from geographically remote localities (Carmody *et al.*, 1962).

Much of the experimental work on sexual isolation in *D. paulistorum* has used the so-called "male choice" method. Groups of virgin females belonging to two different strains or races are confined for a certain time interval with males of one of the strains; all of the females are then

dissected and their sperm receptacles are examined for the presence of spermatozoa. One of the limitations of this method is that the order in which the inseminations occur is unknown. It is, for example, possible that the homogamic matings (i.e., matings within a race or strain) occur first, and the heterogamic matings (between the races or strains) take place later. It is also possible that when one of the two classes of females has no opportunity for mating with their own kind of males, heterogamic matings might occur more often than they would in the presence of both kinds of females and males. We have consequently utilized the technique of direct observation of the behavior of flies in the observation chambers devised by Ellens (1957). The results obtained agree rather well with those secured with the aid of the "male-choice" technique, but several additional and interesting facts are brought to light, as the account given below will show.

MATERIALS AND METHODS

Strains of the Andean-Brazilian race from Bahia, Ceara, and Rio de Janeiro used in the present work are the same as used by Malogolowkin (1963). Every experiment involved one of these tester strains and one of the following strains, named after the place they were collected. CENTRO-AMERICAN race: Guatemala; El Salvador; and Boquete C (Panama). ORINOCAN race: Madden Forest (Panama); Bucaramanga 8 (Colombia); Caripe B (Venezuela), Simla N (Trinidad), Guiana A, Georgetown G and S, and Apoteri Y (British Guiana). GUIANAN race: Guiana B (Georgetown, British Guiana). AMAZONIAN race: Panama A (Barro Colorado) and Darien A (Panama); Buca-

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TABLE 1. Percentages of the females which mated with either type of male after 15 minutes, 30 minutes, and two hours of exposure in the observation chamber. C = number of females tested.

Females of strain	15 min	30 min	2 hr	C
Ceara	77	92	97	90
Boquete	46	69	83	90
Ceara	41	61	78	550
Orinocan	38	52	64	550
Ceara	45	61	74	380
New Amazonian	21	32	46	380
Ceara	62	78	89	90
Santa Marta	56	67	90	90
Ceara	62	77	88	90
Palmira	60	77	91	90
Ceara	56	69	86	90
Bucaramanga-O	9	17	46	90
Ceara	34	48	70	90
Cucuta-C	38	56	64	90
Bahia	62	78	86	90
Boquete	31	41	49	90
Bahia	42	54	60	660
Orinocan	12	21	30	660
Bahia	43	62	78	450
Old Amazonian	26	39	55	450
Bahia	35	52	64	1,032
New Amazonian	15	26	42	1,032
Bahia	51	60	79	90
Santa Marta	31	49	66	90
Bahia	37	57	66	90
Palmira	56	76	83	90
Bahia	40	60	72	90
Bucaramanga-O	40	66	81	90
Bahia	40	60	70	90
Cucuta-C	39	53	63	90
Rio	58	78	85	60
Boquete	53	73	87	60
Rio	55	71	82	370
Orinocan	36	48	61	370
Rio	56	68	83	250
New Amazonian	25	39	59	250
Rio	33	47	62	60
Cucuta-C	35	57	65	60

ramanga A, and Cucuta A (Colombia); Elena L and N (Santa Elena de Uairen, Venezuela); Trinidad, and Simla A and H (Trinidad); Georgetown L and Apoteri A and D (British Guiana); and Belem A, C, and J (Brazil). TRANSITIONAL group: Santa Marta, Palmira, Bucaramanga O and Cucuta C (Colombia). Maps

and further references to the origins of these strains were given by Dobzhansky *et al* (1964). We have placed the Cucuta strain that they listed as Andean-Brazilian in the Transitional group (see below).

The "male choice" and the "observation chamber" methods were used. Flies were aged, sexes separately, for seven to 12 days. To make the flies from different strains distinguishable, the right wing was clipped in the individuals of one, and the left wing in the individuals of the other strain. For the "male choice" experiments, groups of 10 females of each of the two strains to be studied were confined for three to four hours with 20 males of one of them at 25° C. For the observation chambers, two groups of 10 females and 10 males (i.e., 40 flies in all) were placed in Ellens chambers and observed constantly for two hours at room temperature (21° C-25° C) in daylight. In a few cases more than 10 flies of each kind were used. In general, each combination of strains was replicated three times.

THE TIME FACTOR

The matings recorded in the observation chambers are reviewed in Tables 1 and 2. These tables are constructed as follows: Table 1 shows the percentages of females which have mated, whether with males of their own or of foreign strains, during the first 15 minutes, the first 30 minutes, and the entire two hours after having been placed in the observation chambers. It can be seen that with most strains, more than half of all matings that occur take place within the first 15 minutes. Very few matings occur during the second hour of observation. The strains of the Amazonian race, and to some extent of the Orinocan race, are exceptions from the above rule, since they are slow in mating, both with their own and with foreign males. The females of the Andean-Brazilian race, on the contrary, mate very quickly, with the possible exception of the Bucaramanga-O strain, which, in the test with Ceara flies, was slow in mating.

(This is the strain of the Transitional group referred to as Bucaramanga by Dobzhansky and Spassky, 1959.)

Table 2 gives the isolation indices (see below) for the flies recorded in Table 1. As expected, they vary greatly. The relative isolation of the different strains will be discussed below; here we are only interested in the effect of time. Table 2 shows that the degree of isolation does not show any tendency to change with time. In fact, regardless of whether the isolation is high or low, the isolation index is about the same immediately after the flies are introduced into the observation chamber as when most of the available females have already mated. This observation serves to confirm the conclusion of Levene and Dobzhansky (1945), that the probability of mating between females and males of a given pair of strains is independent of the numbers of other potential mates present.

Some interesting details of the relationship between time and occurrence of homogamic and heterogamic matings in the observation chambers can be seen in Fig. 1.

TABLE 2. *Isolation indices after 15 minutes, 30 minutes, and two hours in the observation chamber. Number of flies (C) the same as in Table 1.*

Strain 1	Strain 2	15 min	30 min	2 hr
Ceara	Boquete	0.36	0.37	0.37
"	Orinocan	0.59	0.67	0.69
"	New Amazonian	0.992	0.983	0.987
"	Santa Marta	0.40	0.42	0.40
"	Palmira	0.27	0.25	0.19
"	Bucamaranga-O	0.96	0.92	0.90
"	Cucuta-C	0.15	0.16	0.21
Bahia	Boquete	0.48	0.50	0.50
"	Orinocan	0.476	0.460	0.490
"	Old Amazonian	0.901	0.908	0.909
"	New Amazonian	1.000	0.979	0.970
"	Santa Marta	0.49	0.51	0.54
"	Palmira	0.64	0.63	0.66
"	Bucamaranga-O	0.83	0.84	0.85
"	Cucuta-C	0.72	0.67	0.72
Rio	Boquete	0.49	0.58	0.57
"	Orinocan	0.376	0.388	0.406
"	New Amazonian	0.960	0.970	0.966
"	Cucuta-C	0.85	0.90	0.87

This is based on the combination of the Andean-Brazilian strains from Bahia and the Orinocan strains from various localities, recorded also in Tables 1 and 2. Fig. 1 is constructed so that the abscissa gives the mating number; i.e., the first mating occurring in each chamber, the second mating in each chamber, etc. The ordinate gives the percentage of any particular type of mating to the cumulative total number of matings that have occurred up to that time. The numbers on the top of the figure are these cumulative total numbers of matings. The increments become smaller as time goes on since not all chambers have e.g., as many as ten matings. It can be seen that the percentage of matings that involve Bahia females decreases with time, while the reverse is true for the Orinocan females. This is true both for the homogamic and for the heterogamic matings.

MEASURES OF SEXUAL ISOLATION

In a "male choice" experiment, let there be n_1 females of strain 1 and n_2 females of strain 2 present with males of strain 1, and let x_1 be the number of strain 1 females inseminated and x_2 be the number of strain 2 females inseminated. Also let $p_1 = x_1/n_1$, $p_2 = x_2/n_2$, $q_1 = 1 - p_1$, and $q_2 = 1 - p_2$. Stalker (1942) proposed the isolation index, which is equal to $(p_1 - p_2)/(p_1 + p_2)$, and which is equal to zero for no isolation, to 1 for complete sexual isolation (only homogamic matings) and to -1 if there are only heterogamic matings. Levene (1949) proposed the isolation coefficient, which has the same limiting values and is denoted by

$$K = \frac{\log q_1 - \log q_2}{\log q_1 + \log q_2}.$$

The standard error of K is

$$\sigma_K = \left\{ \frac{(1+K)^2}{4(\ln q_1)^2} \times \left[(1-K)^2 \frac{p_1}{n_1 q_1} + (1+K)^2 \frac{p_2}{n_2 q_2} \right] \right\}^{1/2}.$$

The isolation index has the disadvantage in "male choice" experiments that when the flies are kept together for a long time,

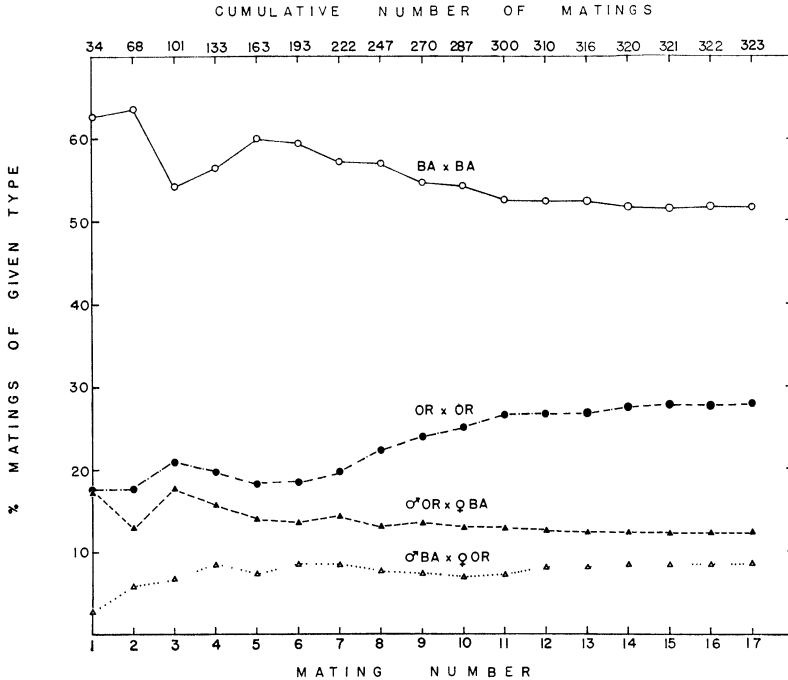


FIG. 1. Total number of first, first plus second, first plus second plus third, etc. matings observed in experiments with Bahia (BA) and Orinocan (OR) flies, and the percentage of these matings that are of each of the four types.

and many of both kinds of females are inseminated, the index becomes lower. The isolation coefficient is more nearly constant, and is equal to the isolation index we would get if only a very small proportion of the females were allowed to be inseminated. On the other hand, in female choice or multiple choice experiments, the value of the corresponding isolation index is not so much affected when the flies are left together for longer periods of time, since even if all females are mated, we still have data on how many of each type of mating occurred.

The formula for the joint isolation index for multiple choice experiments follows Bateman (1949) and Merrell (1950) and is as follows. We now let C be the number of couples or females of each strain present in the chamber. The mathematics is so much simpler when the number of females of each strain is the same, that only that case will be described. We let x_{11} , x_{22} , x_{12} ,

and x_{21} be the number of matings observed between males and females of strain 1, males and females of strain 2, males of strain 1 with females of strain 2, and males of strain 2 with females of strain 1, respectively, and let $N = x_{11} + x_{22} + x_{12} + x_{21}$ be the total number of matings. Then the isolation index is $I = (x_{11} + x_{22} - x_{12} - x_{21})/N$ which is equal to $1 - 2(x_{12} + x_{21})/N$. Hence the variance of I is four times the variance of the proportion of matings that are heterogamic, or

$$\sigma_I = \sqrt{4 \left(\frac{x_{12} + x_{21}}{N} \right) \left(\frac{x_{11} + x_{22}}{N} \right) / N}$$

$$= \sqrt{(1 - I^2)/N}$$

For other types of experiment the joint isolation index, or coefficient is the mean of the two one way coefficients. Finally, the chamber experiments can give two kinds of "male choice" indices, $I_1 = (x_{11} - x_{12})/(x_{11} + x_{12})$ with variance $(1 - I_1^2)/$

TABLE 3. Comparison of isolation coefficients for "male choice" dissection experiments and isolation indices for "male choice" in observation chambers (see text) for Bahia (strain 1) and various other (strain 2).

			Bahia ♂	Other ♂	Joint
Guatemala	(C.-Am.)	Dissection	0.32 ± 0.09	0.58 ± 0.08	0.45 ± 0.06
Salvador	(C.-Am.)	Dissection	0.31 ± 0.09	0.27 ± 0.09	0.29 ± 0.06
Guiana A	(Orin.)	Dissection	0.73 ± 0.06	0.12 ± 0.10	0.42 ± 0.06
Guiana B	(Guiana)	Dissection	1.00 —	0.97 —	0.98 —
Panama A	(Amaz.)	Dissection	1.00 —	1.00 —	1.00 —
"	"	Chamber	1.00 —	1.00 —	1.00 —
Trinidad	(Amaz.)	Dissection	0.99 —	0.88 ± 0.09	0.94 ± 0.03
"	"	Chamber	0.89 ± 0.05	0.92 ± 0.05	0.91 ± 0.04
Belem A	(Amaz.)	Dissection	0.99 —	0.57 ± 0.06	0.80 ± 0.04
"	"	Chamber	0.97 —	0.75 ± 0.08	0.87 ± 0.04
Belem C	(Amaz.)	Dissection	0.98 —	0.70 ± 0.05	0.85 ± 0.03
"	"	Chamber	0.94 —	0.88 0.07	0.91 ± 0.04
Belem J	(Amaz.)	Dissection	0.99 —	0.73 ± 0.05	0.82 ± 0.03
"	"	Chamber	0.97 —	0.77 ± 0.09	0.88 ± 0.04
Combined Data	(Amaz.)	Dissection	0.99 —	0.76 ± 0.02	0.87 ± 0.02
"	"	Chamber	0.96 ± 0.05	0.85 ± 0.03	0.91 ± 0.08
Sta. Marta	(Trans.)	Dissection	0.30 ± 0.08	0.13 ± 0.10	0.22 ± 0.07
"	"	Chamber	0.58 ± 0.10	0.49 ± 0.11	0.54 ± 0.07
Palmira	(Trans.)	Dissection	0.68 ± 0.06	0.43 ± 0.07	0.56 ± 0.05
"	"	Chamber	0.60 ± 0.10	0.70 ± 0.08	0.66 ± 0.07
Bucaramango-O	(Trans.)	Dissection	0.91 ± 0.04	0.96 —	0.93 ± 0.03
"	"	Chamber	0.77 ± 0.07	0.94 —	0.86 ± 0.04
Buenaventura	(Trans.)	Dissection	1.00 —	0.69 ± 0.06	0.84 ± 0.04

$(x_{11} + x_{12})$ and the reverse index, $I_2 = (x_{22} - x_{21}) / (x_{22} + x_{21})$. While these can be compared with the results of true male choice experiments, and are so compared in Table 3, it should be remembered that the biological situation in the chamber, with two kinds of males present, is quite different from that in the dissection experiments, where only one kind of male is present.

As a control on the performance in the chambers, two different Bahia strains were placed in the chamber with the following results: Bahia 2 and 4, $I = -0.24$; Bahia 2 and 6, $I = -0.12$; Bahia 4 and 6, $I = -0.08$; all data combined, $I = -0.15 \pm 0.09$. As expected, the isolation between these sympatric strains of the same race is not significantly different from zero.

Since each cross in the chambers was done in replicate, often on different days, a test of heterogeneity is possible. For this purpose the isolation index between the three Bahia strains and seven Orinocan strains was used, because isolation was in

the midrange of values. Using three replicates for each of the 21 combinations the chi-square value for the total number of females mated is 78 with 42 degrees of freedom, which has a probability of less than 0.001, and shows significant variation in sexual activity. In spite of this, the corresponding chi square for the values of the isolation index is 42 with 42 degrees of freedom, which has a probability close to one half. Hence the isolation indices are consistent, and it is valid to use their theoretical standard errors.

Where there are small numbers of females and high isolation, it may happen that there are zero, or one, or two heterogamic matings. In such cases the theoretical standard error is not reliable and has been omitted, as for many of the entries in Table 3.

SEXUAL ISOLATION BETWEEN STRAINS

Table 3 gives the isolation coefficient for male choice dissection experiments between the Bahia tester strains (Andean-

TABLE 4. *Numbers of matings in the observation chambers. T = total number of females of the two strains combined; X₁₁ = number of matings of strain 1 ♀ × 1 ♂; X₂₂ = number of matings of strain 2 ♀ × 2 ♂; X₁₂ = number of matings of strain 2 ♀ × strain 1 ♂; X₂₁ = number of matings of strain 1 ♀ × strain 2 ♂; I = isolation index.*

Strain 2	Number of strains	T	X ₁₁	X ₂₂	X ₁₂	X ₂₁	I
<i>Strain 1 Ceara</i>							
Boquete C (C.-Am.)	1	180	54	57	18	33	0.370 ± 0.073
Orinocan	7	1,100	342	229	18	85	0.694 ± 0.028
Amazonian (new)	4	760	280	173	1	2	0.987 ± 0.008
Santa Marta (Trans.)	1	180	59	54	27	21	0.404 ± 0.072
Palmira (Trans.)	1	180	49	47	35	30	0.193 ± 0.077
Bucaramanga-O (Trans.)	1	180	74	38	3	3	0.898 ± 0.041
Cucuta-C (Trans.)	1	180	40	33	25	23	0.207 ± 0.089
<i>Strain 1 Bahia</i>							
Boquete C (C.-Am.)	1	180	54	37	7	23	0.504 ± 0.079
Orinocan	7	1,320	286	155	42	109	0.490 ± 0.036
Amazonian (old)	5	900	330	239	7	20	0.909 ± 0.017
Amazonian (new)	10	2,064	649	421	8	9	0.969 ± 0.007
Santa Marta (Trans.)	1	180	56	44	15	15	0.538 ± 0.074
Palmira (Trans.)	1	180	48	63	12	11	0.657 ± 0.065
Bucaramanga-O (Trans.)	1	180	63	65	8	2	0.855 ± 0.044
Cucuta-C (Trans.)	1	180	56	47	10	7	0.717 ± 0.064
<i>Strain 1 Rio</i>							
Boquete C (C.-Am.)	1	120	38	43	9	13	0.573 ± 0.081
Orinocan	7	740	200	172	52	105	0.406 ± 0.041
Amazonian (new)	4	500	202	147	0	6	0.966 ± 0.041
Cucuta-C (Trans.)	1	120	33	38	1	4	0.868 ± 0.057

Brazilian race) and strains from various races, as well as the isolation index for chamber experiments with some of these strains. In each case the two male choice coefficients or indices and the joint coefficient or index are given. In general there is good agreement between the results of the two types of experiment. With a few exceptions the values are either nearly equal, or the isolation is higher in the chamber. This would be expected if females were more likely to mate with males of another race when no males of their own race were present. To the extent that this were true it would contradict the inference from Table 2 that the probability of a heterogamic mating is not affected by the presence of other flies. Evidently more evidence on this point is required.

Table 4 summarizes all the data from the chambers, using Ceara, Bahia, and Rio as tester strains, and gives actual num-

bers as well as the joint isolation coefficients. These latter are the same as are given in the last column of Table 2, and are also the same as some of the values in Table 3. The total number of females involved in Table 4 is 9,424, of which 5,834 were observed to mate; 5,015 matings were homogamic, and 819 were heterogamic, giving an overall isolation index of 0.719, although this value has no real meaning.

We will now consider the sexual isolation between the tester strains and the various other strains, first dealing only with the crosses involving the Bahia tester strains. Malogolowkin (1963) listed Bahia 2 and 6 but not Bahia 4 as "transitional strains." This was verified in the comparison with Belem in Malogolowkin *et al.* (1964). However, with the present data from many other localities there seems to be no difference in behavior of

these strains with most of the strains tested. Even where a large amount of data are available most differences seem to be small and nonsignificant, or at best contradictory. Accordingly, all the data for the three strains have been combined in this paper.

It is evident from inspection of Tables 3 and 4 that the isolation is very strong between the Bahia tester strains and the Amazonian and Guianan races. In fact, Amazonian females almost never accept Bahia males, while Bahia females accept Amazonian males relatively more freely. This confirms the observations of Malogolowkin *et al.* (1964) on the relationships of these races. There is an indication that the Amazonian race strains which were kept in laboratory cultures for several years (Belem, Panama A, and Trinidad) show a weaker isolation than the new strains of the same race (Darién, Bucaramanga, Simla, Elena, Georgetown, and Apoteri). This is, however, uncertain because the geographic origins of some of these strains are different.

The seven new Orinocan strains used in the chamber experiments (Table 4) and the old strain, Guiana A, used in the dissection experiment (Table 3), agree in showing a joint isolation of 0.49 and 0.45. The isolation between the Orinocan females and the Bahia males is 0.74 ± 0.04 in the chamber, and 0.73 ± 0.06 by dissection, while for Bahia females and Orinocan males the corresponding values are 0.17 ± 0.06 and 0.12 ± 0.10 .

Three Centro-American strains give moderate isolation, similar to that of the Orinocan strains, but with no clear trend for the male choice coefficients. The two coefficients are nearly equal for Salvador, smaller for Bahia males with Guatemala, and larger for Bahia males with Boquete.

Bucaramanga-O, Buenaventura, Santa Marta, Palmira, and Cucuta-C belong to the Transitional group from Colombia. This group is really a subdivision of the Andean-Brazilian race (see Dobzhansky and Pavlovsky, 1962; Malogolowkin, 1963;

Dobzhansky *et al.*, 1964). Therefore it is surprising that the Andean-Brazilian Bahia strains show such high isolation with the first two, as well as moderate isolation with the other three. However, such high isolation between strains of the same race from remote localities was also observed by Carmody *et al.* (1963).

When the data from Ceara and Rio are added, the general picture as to isolation between the tester strains and the others is similar. However, there are interesting differences.

For the Orinocan strains the joint isolation with Ceara is significantly higher than with Bahia and Rio. For the Palmira and Cucuta-C strains of the Transitional group, Ceara gives low and Bahia high isolation, with the difference highly significant. With Cucuta-C, Rio is likewise significantly higher than Ceara.

Looking at this data from the point of view of differences between strains of the Transitional group, we find Bucaramanga strongly isolated from Ceara and from Bahia by both male choice and multiple choice experiments. Buenaventura is likewise highly isolated in the only test done. Santa Marta is moderately isolated from Ceara and Bahia in chambers, but not from Bahia by dissection, while Palmira is moderately isolated from Bahia, and Cucuta from Bahia and Rio. Both have low isolation with Ceara.

DISCUSSION

The superspecies *D. paulistorum* is broken up into nearly isolated races occupying different geographic areas with more or less overlap. It is not surprising that the overall picture of relationships should be complicated. As allopatric races diverge there may be development of hybrid sterility, sexual isolation because of different sexual behavior patterns, and changes in chromosomal morphology. For different pairs of strains any of these reproductive barriers may be the most important.

Thus when the Andean-Brazilian tester

strains are crossed with Orinocan and Amazonian races, male hybrids, if produced, are usually sterile. The cross of females of the latter two races with the tester strains shows higher sexual isolation than does the reverse cross. This may be related to the fact that the Andean-Brazilian race occupies a very extensive territory, in much of which no other races of *D. paulistorum* are found. By contrast, the Amazonian and Orinocan races are mostly sympatric with each other and with still other races.

Where two races are sympatric and where hybrids are sterile or at a disadvantage, natural selection will tend to strengthen sexual isolation. Thus Dobzhansky *et al.* (1964) found higher isolation between sympatric strains of different races than between allopatric strains of the same races. Malogolowkin *et al.* (1964) found that this relationship held even in comparing allopatric strains that are closer and farther apart. Similarly we find that the Ceara tester strain, which is nearest geographically to the Amazonian and Orinocan races, shows the highest isolation, while Rio, the farthest away, shows the lowest. There are insufficient data to show if this is also true for the Centro-American race.

Colombia represents a fairly isolated area at the boundary of the range of the Andean-Brazilian race. In Colombia this race seems to be diversifying and showing strange properties. It shows high sexual isolation with some Brazilian strains of the same race, while the incidence of fertile hybrids is unusually high when members of this group are crossed with other races (hence the name Transitional).

However, it should be pointed out that fertile hybrids have been observed in a number of interracial crosses not involving the Transitional group; this group is unique only in the frequency with which it occurs.

The Transitional group is far from homogeneous, and for this reason, as well as because it is really a part of the Andean-

Brazilian race, we refer to it as the Transitional group of strains, rather than the Transitional race. Heterogeneity appears both in the tests of crossability, and in the sexual isolation with our tester strains. Clearly, study of additional Colombian strains would be highly desirable.

SUMMARY

Sexual isolation has been tested between strains of *Drosophila paulistorum* of the Andean-Brazilian race from Brazil on the one hand, and strains of various races from other localities on the other. The method of "male choice," putting females of two strains in a vial with males of one of the strains, and then dissecting the females to see if they were inseminated, and "multiple choice" experiments, using males and females of both strains, and observing mating in observation chambers of the kind designed by Ellens, were used. The two methods give comparable results.

Females of the Amazonian, and also of the Orinocan race, mate less often than do the Andean-Brazilian females. Sexual isolation is very high between the Andean-Brazilian tester strains and the Amazonian race, and moderate with the Orinocan race. In both cases the isolation is lower for the Andean-Brazilian females than in the reverse direction. When hybrids are produced, the males are usually sterile. On the other hand, rather strong sexual isolation, not accompanied by sterility of the hybrids, is observed between strains of the Andean-Brazilian race from geographically very remote localities: Ceara, Bahia, and Rio de Janeiro on one side, and western and northern Colombia on the other.

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