COURTSHIP INTERACTION IN THE SEMISPECIES OF *DROSOPHILA PAULISTORUM*

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Courtship behavior is a major component of ethological isolation, and may lead to reproductive isolation by selective mating.

Koref-Santibañez (1972) showed that the strains of each species of the *Drosophila paulistorum* complex have a distinctive courtship pattern, due to quantitative variations in the use of the different courtship elements. The two most distinctive strains proved to be those from allopatric semispecies (Centroamerican and Andean Brazilian), although Interior, Orinocan and Amazonian ones also had characteristic patterns. The strains from the Transitional group were intermediate, as is also shown by geographic distribution and sexual isolation of this semispecies with respect to the other semispecies (Dobzhansky et al., 1969).

Differences in courtship patterns do not necessarily correlate with actual mating, as revealed by studies on insemination of females. To obtain an estimate of the mechanisms involved in mating, it was thought of interest to investigate the behavioral patterns involved in the mutual recognition of males and females of the different *D. paulistorum* semispecies. A "no choice" situation (one male and one female) was used, since it has advantages in permitting direct observation of the behavior of males and females, as compared to "male, or multiple choice" methods used elsewhere (Manning, 1967*a*).

MATERIAL AND METHODS

One strain, representing each of the six semispecies of *D. paulistorum* whose courtship behavior had been studied before (Koref-Santibañez, 1972), was employed. The strains used are given in Table 1.

Males and females from each strain were collected within four hours of hatching and aged separately for ten to fifteen days.

For the observation of courtship behavior, one male was introduced by means of an aspirator without anaesthetization, together with one female from a different semispecies, into a small courtship chamber previously described (Koref-Santibañez, 1972). The pair was kept under continuous observation for 30 minutes under a low power dissecting microscope. All courtship activity was recorded and timed. A sufficient number of couples was observed to provide a total of ten pairs exhibiting courtship activity, but when no courtship occurred, up to 20 or 25 pairs were watched.

After 30 minutes, regardless of whether the individuals courted or not, all couples were transferred, without anaesthetization, to vials with *Drosophila* food. Twenty-four hours later, the females were dissected to check whether they had been inseminated after the observation period. Twenty-five pairs of each of the 36 combinations were so studied.

Courtship rituals and elements are denoted according to Spieth's terminology (1952, 1968).

RESULTS

When a male of one of the semispecies of *D. paulistorum* is confined with a female of a different semispecies, two types of reactions are observed. The male may ignore the female altogether, walking around the chamber as if there was no other individual present, or he may go through a courtship

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TABLE 1. *The six strains, their geographic origin and date of collection.*

Strain	Geographic origin	Collection date
Orinocan (O): 0-4	Turbo, Colombia	1967
Centroamerican (C): A 54 P	Agua Fría, Costa Rica	1970
Amazonian (A): A-24	Tapuruquara, Brazil	1969
Transitional (T): T-3	Chocó, Colombia	1969
Interior (I): I-3	Mitú, Colombia	1968
Andean-Brazilian (AB): AB-10	Leticia, Colombia	1968

ritual similar to that performed towards females of his own semispecies, although certain quantitative differences appear that will be mentioned below. Only 22 matings were recorded during the 30 minutes of observation.

To clarify the intersemispecific courtship behavior of males and females, each semispecies will be considered separately.

Orinocan (*O*).—Less than one half of the males observed courted foreign females (Table 2). They did not court Andean-Brazilian females at all, and only oriented very briefly to Amazonian females. They courted Centroamerican, Interior and Transitional females, often orienting towards them more frequently than towards their own Orinocan females (Table 2), but all courtship bouts were of short duration (Table 4). During a greater part of the 30 minute observation period, the males and the foreign females walked past one another, occasionally touching with their forelegs, but the females showed few acceptance responses, and males no signs of stimulation to initiate further courtship. Two males mated with Centroamerican and one with Interior females. Table 5 shows that after 24 hours Orinocan males did not inseminate Amazonian females, and that all other foreign females were inseminated less frequently than Orinocan females. Orinocan females were courted by all males except Andean (Table 3), but were not inseminated by Andean nor by Amazonian males (Table 5).

Centroamerican (*C*).—These males were the most active of all the semispecies (Table 2). This was also noted previously in studying their intrasemispecific behavior (Koref-Santibañez, 1972). This great activity (high sexual drive) may be the reason why they courted females from all the other five semispecies, although again they did so less persistently than with their own females (Table 4). One to two matings were recorded with all except Amazonian females. Centroamerican males courted Orinocan and Transitional females more often and longer than the others, and Centroamerican females accepted the courtship of only the Orinocan and Transitional males (Table 3). They were inseminated also by Interior males, by a few Andean-Brazilian, but not by Amazonian males (Table 5).

Amazonian (*A*).—Both males and females of this semispecies were inactive towards the opposite sex of the other five semispecies. Males courted Orinocan, Interior and Andean-Brazilian females (Tables 2 and 4), although most activity was directed towards this latter. Amazonian females accepted the courtship of Centroamerican and Andean males very passively (Table 3). Amazonian males inseminated very few Andean females, and a small number of Amazonian females were inseminated by Centroamerican, Interior or Andean-Brazilian males (Table 5).

Transitional (*T*).—Males courted all other females except Amazonian. The frequency with which courtship elements were used was similar to that for females of the same semispecies (Table 2). One Interior, three Orinocan and six Interior females were inseminated by Transitional males during the 30 minutes. Transitional fe-

TABLE 2. *Mean number and standard error of male courtship elements and mean courtship time in seconds, when males of each of the six* D. paulistorum *semispecies are confronted with females of their own or of another semispecies (30 minutes observation period per pair).*

♂	♀	No. obs.	No. count	Orient.	Tapping	Vibration	Scissor	Circle	Lick	Court time
O	O	10	10	4.6 ± 1.2	31.0 ± 8.7	16.7 ± 3.5	16.9 ± 5.7	9.2 ± 3.7	11.1 ± 2.2	265.5 ± 72.1
	C	29	10	5.3 ± 0.6	21.3 ± 3.3	11.3 ± 3.0	4.6 ± 1.7	1.1 ± 0.4	8.2 ± 2.8	105.4 ± 35.1
	A	20	0	–	–	–	–	–	–	–
	T	25	10	4.4 ± 0.8	13.0 ± 3.5	7.4 ± 2.2	9.6 ± 4.8	1.6 ± 0.9	4.7 ± 0.9	94.0 ± 29.2
	I	15	10	4.8 ± 1.5	21.7 ± 6.6	7.6 ± 1.9	9.9 ± 4.6	3.8 ± 1.7	6.5 ± 1.9	136.1 ± 36.6
	AB	23	0	–	–	–	–	–	–	–
C	C	10	10	5.1 ± 1.0	30.9 ± 6.5	31.9 ± 6.6	21.5 ± 6.0	1.7 ± 0.3	16.0 ± 2.3	344.0 ± 62.6
	O	11	10	7.4 ± 1.1	35.8 ± 6.7	23.5 ± 4.7	21.9 ± 6.9	0	12.6 ± 4.7	286.1 ± 59.4
	A	14	10	5.3 ± 1.2	11.4 ± 2.0	9.3 ± 2.8	2.7 ± 1.1	0	5.1 ± 2.6	65.1 ± 17.4
	T	13	10	5.3 ± 1.8	25.0 ± 4.4	18.9 ± 3.8	9.6 ± 3.2	0	7.3 ± 1.8	231.2 ± 55.0
	I	14	10	6.6 ± 1.4	28.8 ± 7.7	20.3 ± 9.0	7.9 ± 4.0	0	6.9 ± 2.6	197.8 ± 70.4
	AB	21	10	5.3 ± 0.6	13.7 ± 1.8	11.1 ± 2.0	0	0	6.0 ± 0.9	73.6 ± 13.7
A	A	10	10	4.0 ± 0.8	16.0 ± 2.7	6.9 ± 1.9	2.9 ± 1.9	7	6.5 ± 1.6	130.8 ± 43.6
	O	22	10	4.6 ± 0.7	12.0 ± 1.6	1.7 ± 0.7	7	0	2	25.0 ± 3.9
	C	20	0	–	–	–	–	–	–	–
	T	23	0	–	–	–	–	–	–	–
	I	13	10	5.5 ± 0.6	16.2 ± 3.4	3.6 ± 1.5	11	0	2	40.6 ± 10.3
	AB	15	10	7.2 ± 1.0	29.9 ± 7.6	15.3 ± 3.3	5.1 ± 1.2	3.1 ± 1.4	12.8 ± 7.0	157.9 ± 28.3
T	T	10	10	5.1 ± 1.1	11.1 ± 2.7	23.3 ± 5.1	9.3 ± 2.2	2.8 ± 1.4	9.9 ± 2.1	231.5 ± 42.8
	O	21	10	6.1 ± 1.2	18.2 ± 4.0	14.8 ± 5.1	8.3 ± 3.6	3	5.4 ± 2.0	148.6 ± 49.3
	C	14	10	8.5 ± 1.3	33.2 ± 7.0	18.5 ± 4.0	7.7 ± 3.6	2.3 ± 1.0	4.9 ± 1.2	168.8 ± 37.6
	A	20	0	–	–	–	–	–	–	–
	I	14	10	4.1 ± 1.2	11.8 ± 3.9	15.2 ± 4.7	7.4 ± 3.4	2.9 ± 1.3	7.7 ± 2.0	178.8 ± 57.4
	AB	16	10	7.9 ± 1.5	19.3 ± 2.9	15.7 ± 6.3	6.1 ± 2.4	0	7.2 ± 4.3	172.6 ± 62.0
I	I	10	10	2.2 ± 0.4	7.8 ± 3.5	10.3 ± 5.7	2.0 ± 0.8	2.2 ± 0.7	7.2 ± 3.2	130.9 ± 54.4
	O	18	10	5.7 ± 1.1	39.8 ± 8.3	22.5 ± 7.7	10.4 ± 2.6	3.3 ± 1.5	19.1 ± 5.9	242.8 ± 60.3
	C	21	0	–	–	–	–	–	–	–
	A	28	0	–	–	–	–	–	–	–
	T	12	10	6.5 ± 0.7	29.5 ± 5.2	21.3 ± 4.5	9.9 ± 4.0	2.2 ± 0.8	8.5 ± 2.3	233.4 ± 46.6
	AB	21	0	–	–	–	–	–	–	–
AB	AB	10	10	9.2 ± 0.8	30.8 ± 5.2	22.6 ± 5.5	5.5 ± 1.8	4.5 ± 1.3	2.2 ± 0.9	285.0 ± 39.8
	O	20	0	–	–	–	–	–	–	–
	C	21	0	–	–	–	–	–	–	–
	A	12	10	5.6 ± 1.0	23.8 ± 6.7	12.6 ± 2.9	2.3 ± 1.2	2.9 ± 1.6	7.7 ± 1.7	125.0 ± 41.1
	T	20	0	–	–	–	–	–	–	–
	I	22	0	–	–	–	–	–	–	–

males were not courted by Amazonian or Andean-Brazilian males during the observation (Table 3); nevertheless they were inseminated by these males in low frequencies (Table 5). No Transitional males or females mated with Amazonian.

Interior (I).—The males of this semispecies displayed very little courtship activity towards their own females, although they did inseminate all of them (Table 5). When they courted foreign females (Orinocan and Transitional), they did so with

TABLE 3. *Mean number and standard error of courtship responses of females to males of their own and of each of the other five* D. paulistorum *semispecies (30 minutes observation time per pair).*

♀	♂	No. observed	No. court.	Running	Standing	Rubbing	Extruding
O	O	10	10	46.5 ± 14.3	22.8 ± 6.0	5.2 ± 2.1	9.6 ± 2.3
	C	11	10	67.8 ± 17.1	18.1 ± 6.0	13.7 ± 4.5	4.3 ± 1.6
	A	22	10	3.9 ± 1.1	1.6 ± 0.5	8	1
	T	21	10	33.2 ± 13.7	9.1 ± 2.9	5.3 ± 1.9	4.2 ± 2.7
	I	18	10	42.2 ± 8.8	12.8 ± 3.2	18.8 ± 7.1	5.7 ± 2.2
	AB	20	0	–	–	–	–
C	C	10	10	82.1 ± 19.0	26.7 ± 5.9	39.2 ± 9.8	7.5 ± 2.7
	O	29	10	22.5 ± 9.3	4.8 ± 0.9	3.7 ± 1.3	2.8 ± 0.7
	A	20	0	–	–	–	–
	T	14	10	42.5 ± 13.8	10.7 ± 2.3	7.5 ± 3.1	4.4 ± 1.5
	I	21	0	–	–	–	–
	AB	21	0	–	–	–	–
A	A	10	10	18.2 ± 7.1	12.5 ± 2.3	7.0 ± 2.3	8.0 ± 1.1
	O	20	0	–	–	–	–
	C	14	10	8.2 ± 3.1	4.9 ± 1.2	5.2 ± 2.2	0
	T	20	0	–	–	–	–
	I	28	0	–	–	–	–
	AB	12	10	16.8 ± 6.6	8.2 ± 2.7	11.6 ± 4.8	18
T	T	10	10	38.2 ± 7.7	25.6 ± 6.4	20.0 ± 5.7	4.9 ± 2.0
	O	25	10	20.9 ± 8.8	5.2 ± 1.9	2.5 ± 1.2	3.0 ± 1.5
	C	13	10	62.4 ± 15.9	11.3 ± 2.3	11.5 ± 2.2	4.1 ± 1.1
	A	23	0	–	–	–	–
	I	12	10	50.1 ± 12.3	14.5 ± 3.3	16.1 ± 3.7	4.7 ± 1.5
	AB	20	0	–	–	–	–
I	I	10	10	15.2 ± 5.3	16.0 ± 7.3	6.8 ± 3.8	8
	O	15	10	22.7 ± 8.0	7.2 ± 2.3	5.7 ± 2.4	4.5 ± 2.5
	C	14	10	55.2 ± 24.6	6.6 ± 2.2	5.1 ± 2.1	4.6 ± 1.6
	A	13	10	6.2 ± 2.7	3.1 ± 0.7	1.5 ± 0.5	7
	T	14	10	37.1 ± 16.3	12.1 ± 3.5	6.1 ± 2.0	9.5 ± 4.03
	AB	22	0	–	–	–	–
AB	AB	10	10	67.8 ± 13.0	16.0 ± 1.8	3.5 ± 1.0	7.2 ± 1.4
	O	23	0	–	–	–	–
	C	21	10	12.2 ± 2.9	4.1 ± 1.0	2.4 ± 0.8	2.5 ± 0.8
	A	15	10	30.2 ± 4.3	9.9 ± 1.5	9.6 ± 1.9	2.7 ± 1.5
	T	16	10	40.7 ± 15.3	9.4 ± 3.4	5.2 ± 1.8	7.0 ± 3.1
	I	21	0	–	–	–	–

greater intensity and for a longer time than their own. (Table 2); however, the duration of each courtship bout was shorter when they courted foreign females than when they courted Interior females (Table 4). During the 30 minutes of observation one Interior male inseminated an Orinocan female, but after 24 hours Interior males inseminated females of the other five semispecies, although Amazonian were inseminated at very low frequencies. Interior females were courted by all males except

TABLE 4. *Mean courtship time per orientation (in seconds) of males of each of the six* D. paulistorum *semispecies when these males were confined with females of their own or of each of the other five semispecies.*

		♀♀					
		O	C	A	T	I	AB
♂♂	O	*57.72*	19.89	0	21.36	28.35	0
	C	38.67	*67.45*	12.29	43.62	29.97	13.89
	A	5.43	0	*32.70*	0	7.38	21.93
	T	24.36	19.86	0	*45.39*	43.49	21.85
	I	42.60	0	0	35.91	*59.50*	0
	AB	0	0	27.37	0	0	*30.98*

TABLE 5. *Percentage of inseminated females of each of the* D. paulistorum *semispecies after being confined with males of their own or of each of the other five semispecies for 24 hours (25 females examined in each cross).*

		♀♀					
		O	C	A	T	I	AB
♂♂	O	*96*	60	0	56	36	24
	C	84	*72*	8	70	84	36
	A	0	0	*96*	0	0	8
	T	60	72	0	*92*	84	60
	I	80	68	4	72	*100*	24
	AB	0	12	16	16	16	*80*

by Andean-Brazilian (Table 3), but they were not inseminated by Amazonian males (Table 5).

Andean-Brazilian (AB).—Within the observation period these males only courted Amazonian females, and that, with a much lower intensity than their own females (Table 2). However, they did inseminate females from all the semispecies except Orinocan. Andean-Brazilian females were courted by Centroamerican, Amazonian and Transitional males, but they responded little to this courtship (Table 3). However, males of the other five semispecies inseminated some Andean-Brazilian females (Table 5).

In those cases where no courtship was recorded in 20–25 couples, additional observations were made. Two males from one semispecies and two females from another, or two males from one semispecies and one female from another, were confined in an observation chamber for 30 minutes. No significant heterosexual activity was observed. Males walked by each other or by the female, often touching one or the other with their forelegs. Since this touching did not elicit a response on the part of the female, no courtship would ensue. Occasionally a male would engage in a short courtship bout of one half to one second, tapping the female once or twice, and vibrating one wing a few times. Frequently the male, after touching the other male, initiated a short courtship bout, consisting of an orientation, several tappings with his forelegs, a few wing vibrations, and sometimes a "lick" of the other male's genitalia with his proboscis. During the observation period, only one or two such courtship bouts would occur. After these bouts, the males and females would remain still, preen their wings, "clean" their faces, or walk around.

These observations indicate that the *D. paulistorum* male initially needs to establish physical contact with his partner in order to receive an adequate stimulus for courtship to proceed.

Although the courtship ritual used by the male towards the foreign female was very similar to that used towards his own female, the time spent in each courtship bout was considerably shorter in the former case (Table 4).

DISCUSSION

The observations reported above confirm the conclusions of several authors (Spieth 1952, 1966; Manning 1959, 1965, and others) that *Drosophila* male discrimination is based on stimuli received when tapping the female. Males from the different *D. paulistorum* semispecies frequently "touch" (occasional contacts of individuals with their legs) or "tap" (contact with forelegs after orientation and

initiation of courtship), and only after there has been a feedback response from the female do they pursue active courtship. This acceptance response of the female enables the male to prolong his courtship until the female's stimulus threshold is lowered sufficiently for the male to mount. If the female belongs to a different semispecies, her stimulus response threshold is very high, and although the total time spent by the male in courting her may be just as long or longer than when he courts a female of his own semispecies, each courtship bout is shorter. In some cases the response threshold of the females will be lowered only after a considerable number of stimuli from the male are "summated" (Manning, 1967), and they will permit insemination long after the 30 minute observation period.

For an understanding of the evolutionary relationships of the *D. paulistorum* semispecies, it may be of interest to relate the present findings to previous work on sexual isolation between the semispecies. There is a certain concordance of the present observations with other analyses of sexual isolation and some of the data on the geographic distribution of the different forms (Carmody et al., 1962; Dobzhansky et al., 1964; Dobzhansky and Pavlovsky, 1967; Dobzhansky et al., 1969; Petit and Ehrman, 1969; Perez-Salas et al., 1970; Spassky et al., 1971; Perez-Salas and Ehrman, 1971). Thus, although in their general courtship pattern, strains from the geographically most remote semispecies (Centroamerican and Andean-Brazilian) are the most different (Koref-Santibañez, 1972), those of the sympatric forms (Amazonian, Orinocan and Andean-Brazilian), are the ones that show the greatest sexual and courtship discrimination in the observations presented here. There is not always a concordance between courtship and subsequent insemination, for some males, such as Amazonian, may court Orinocan and Interior females, but not inseminate them, while Andean Brazilian males, who do not court during the observation period, may subsequently inseminate Centroamerican, Transitional and Interior females. Amazonian males and females, sympatric with Orinocan, Interior, and Transitional ones, show a high isolation in reciprocal directions. Transitional males, of the semispecies that displays the least ethological isolation, court all other females except Amazonian. The Interior semispecies shows little isolation from its near relative, Orinocan, which is, as far as known, always allopatric. There is little discrimination in mating of Interior with respect to Centroamerican and Transitional, but great with respect to Amazonian and Andean-Brazilian.

Spieth (1952) claimed that in species of the subgenus *Sophophora*, males tend to rely on distance stimuli for their courtship recognition, as opposed to those of the subgenus *Drosophila*, who tend to rely mainly on contact stimuli. The observations presented above indicate that in the *D. paulistorum* complex contact stimuli are necessary because only after the males approach and tap the females do they seem to "recognize" the identity of the female and then continue or discontinue their courtship. This was also noted previously by Kessler (1962). Still, other stimuli may also be involved in the semispecific recognition. Among these visual, auditory and olfactory cues should be considered. In species of *Drosophila* such as *melanogaster*, Shorey and Bartell (1970) believe that an olfactory cue allows males to distinguish males from females. Grossfield (1966, 1968) finds that some species are light dependent in their courtship, while Bennet-Clark and Ewing (1969, 1970) and Ewing (1970) find that species such as *D. pseudoobcura* and *D. persimilis* differ in the pulse length emitted during wing vibration.

In nature, it must be important for males to establish quick recognition of their own females when semispecies coexist. The females from the same semispecies will respond by lowering their acceptance threshold after a short courtship, and the main mechanism involved here may be of a chemosensory type, both tactile and olfactory.

Summary

The courtship behavior of the six *Drosophila paulistorum* semispecies was studied when males of one semispecies were confronted with females of each of the other five, over a 30 minute observation period.

When males were confined with foreign females, if they courted at all, their general courtship pattern remained semispecies-specific. However, courtship bouts were shorter and often more frequent than those observed between males and females of the same semispecies. Tapping by males elicited adequate stimulus-response reactions for courtship to ensue, and this was the only element used more often towards foreign than towards conspecific females (tapping is the initial courtship stage). When females were not receptive, the tapping actions produced no response, therefore no courtship occurred. Although courtship was usually followed by insemination, after or during the observation period, in a few cases courted females were not inseminated. On the other hand, some females that were not courted during the observation period were inseminated within the following 24 hours.

In general, the findings reported here confirm previous studies of ethological isolation between the different *D. paulistorum* semispecies. They also indicate that direct observation of courtship cannot uncover the chemosensory stimuli that are apparently involved in heterosexual recognition.

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ANNOUNCEMENT

At the meeting of the Council in Minneapolis (August 26, 1972), it was decided that the Society would institute a system of pagination charges. Under this system a uniform charge of $30.00 per page will be made to authors. Arrangements for payment of page charges will be made after the article has been accepted. All accepted articles will be published regardless of the author's ability to pay. A portion or all of the page charges for the first 15 pages will be waived if the author indicates that funds are not available. Charges for pages in excess of the 15 page limit will not be waived. These charges will apply to all papers received after November 1, 1972.