



Courtship and Sexual Isolation in *Drosophila pavani* Brncic and *Drosophila gaucha* Jaeger and Salzano

Author(s): Susi Koref-Santibanez and Eduardo del Solar O

Source: *Evolution*, Vol. 15, No. 4 (Dec., 1961), pp. 401-406

Published by: Society for the Study of Evolution

Stable URL: <http://www.jstor.org/stable/2406308>

Accessed: 04/02/2010 18:54

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=ssevol>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Society for the Study of Evolution is collaborating with JSTOR to digitize, preserve and extend access to *Evolution*.

<http://www.jstor.org>

COURTSHIP AND SEXUAL ISOLATION IN *DROSOPHILA PAVANI* BRNCIC AND *DROSOPHILA GAUCHA* JAEGER AND SALZANO¹

SUSI KOREF-SANTIBAÑEZ AND EDUARDO DEL SOLAR O.²

*University of Chile*³

Received October 27, 1960

Within populations of a species, reproductive isolating mechanisms, including sexual isolation, may arise and be favored by natural selection if the populations have diverged sufficiently to make compromise genotypes unfavorable (Dobzhansky, 1944). Reproductive isolation, which may first be expressed at the sensorial level, may precede morphological differentiation (Spieth, 1952), and may manifest itself already at the racial or subspecific level. In an effort to determine the mechanisms of the establishment of reproductive isolation, several authors have studied incipient sexual isolation within species (Rendel, 1944; Dobzhansky, 1945; Patterson, Wharton and Stone, 1947; Smith, 1958; Koref-Santibañez and Waddington, 1958; Hoenigsberg and Koref-Santibañez, 1960, and others). In general, it has been shown that the rudiments of isolation within a species are genetically the same as those between species.

Courtship is the ritual which precedes mating, and the components of this ritual are so specific that they may be used as taxonomic characteristics (Spieth, 1952). Differences between groups which do not yet manifest themselves at the copulation level tend to appear as differential utilization of certain courtship elements, which may be explained by different stimuli thresholds on the part of either the male or the female (Hoenigsberg and Koref-Santibañez, 1959 a and b, 1960). Most of these studies were made on laboratory populations of cosmo-

politan and domestic species such as *D. melanogaster*, or in wide-ranging wild species which form rather continuous populations such as *D. willistoni*, *D. pseudoobscura*, etc. How do these processes express themselves in more endemic wild species which live in restricted and isolated populations? In these latter it may be expected that the courtship behavior exhibited by each population will be more differentiated. For this reason, it was decided to study courtship and sexual isolation in members of the *mesophragmatica* group (Brncic and Koref-Santibañez, 1957). *Drosophila pavani* Brncic 1957 is a species belonging to this group, which lives exclusively in Chile and on the eastern slope of the Andes Mountains in Argentina. It forms a chain of rather small colonies which may be found from Copiapó (28° lat. S) to Valdivia (40° lat. S). These colonies are isolated from one another by mountain chains and semi-desert regions, which decrease or prevent interbreeding. *D. gaucha* Jaeger and Salzano 1953, another member of the same group, lives in southern Brazil and ranges up to western Argentina, in one region (San Luis) overlapping the distribution of *D. pavani*. These are sibling species which are difficult to distinguish morphologically, and although hybrids have never been found in nature they cross in the laboratory, giving sterile hybrids (Koref-Santibañez, Casanova and Brncic, 1958). Populations of *D. pavani* differ in the polygene contents of their chromosomes (Brncic, 1961). Therefore, these species are promising for the study of the appearance of behavioral differences which arise as by-products of the genetic divergence in different populations.

MATERIALS AND METHODS

The following stocks of flies were used in our study: five populations of *D. pavani*

¹ This work was done partly under Contract Number AT (30-1)-2465 from the U. S. Atomic Energy Commission.

² During the realization of this work E. del S. had a scholarship from "Comisión Inter-Facultades de Medicina."

³ Instituto de Biología "Juan Noé," and Cátedra de Biología, Facultad de Filosofía y Educación. A. Zañartu 1042. Santiago, Chile.

TABLE 1. *Main courtship elements used by Drosophila pavani males from Chile with females of their own and of various other populations. The figures indicate numbers of times males used each element toward females of their choice.*

♂ <i>pavani</i> Chile	a ♀ <i>pavani</i> Chile + ♀ <i>pavani</i> Chile n = 430			b ♀ <i>pavani</i> Chile + ♀ <i>pavani</i> Mendoza n = 109			c ♀ <i>pavani</i> Chile + ♀ <i>gaucha</i> n = 228		
	Homo- gamic ¹	Hetero- gamic ²	Chi- square	Homo- gamic ¹	Hetero- gamic ²	Chi- square	Homo- gamic ¹	Hetero- gamic ²	Chi- square
Orientation	696	536	20.76 ³	173	146	2.28	339	270	7.82 ³
Vibration	2,001	1,090	268.48 ³	416	352	5.34	767	670	97.00 ³
Circle	812	408	133.78 ³	161	133	2.66	250	242	0.12
Tap	1,375	694	125.44 ³	290	230	6.92 ³	527	416	12.06 ³
Lick	1,185	511	266.84 ³	232	194	3.38	400	430	1.08
Antennae	218	91	52.20 ³	36	29	0.76	76	55	3.36
Copulation	78	56	3.62	24	29	0.48	34	63	8.66 ³
Courtship time (minutes)	25,222	14,035	111.87 ³	5,546	5,417	1.28 ³	11,453	8,778	353.70 ³

n = number of males.

¹ = females of same population as males.

² = females of different population than males.

³ = $p < 0.01$ with 1 degree of freedom.

from Chile: Copiapó (in the northern part of the country), Arayañ and Viña (in the central part), Los Queñes and Chillán (in the southern part of the country); one population of *D. pavani* from Mendoza, Argentina; and two populations of *D. gaucha*, one from Taimbas, Brazil, and the other from Córdoba, Argentina. All these populations had been maintained in the laboratory for from two to four years.

Flies were taken within a few hours of hatching, so males and females had not mated. They were kept separately at a constant temperature of 25° C for about 10 days, a period after which the sexual activity is at its maximum.

To detect courtship discrimination between populations, the male choice method (Dobzhansky and Mayr, 1944) was used. One male from each population was placed in an empty vial together with two females, one from the same strain as the male and the other from a different strain. Twenty-four hours before the observation one of the females was marked with a spot of silver paint on her thorax, to distinguish her from the other female in the same vial. Direct observations were made of courtship behavior in empty 1 × 3 cm vials, over a period of 30 minutes. The experiments were

carried out during the morning hours, at room temperatures of about 22°–23° C. Courtship behavior was analyzed and recorded according to the nomenclature and methods described by Spieth (1952) and Hoenigsberg and Koref-Santibañez (1960).

RESULTS

Courtship rituals in *D. pavani* and *D. gaucha* are in general very similar to those in other species of the subgenus *Drosophila* (Spieth, 1952), with perhaps a greater utilization of contact stimuli such as tapping and licking, although vibration is also used quite profusely. A more detailed analysis of the courtship behavior will be presented elsewhere. In about 40% of the observations no courtship activity was seen during the 30-minute observations. These were discarded, and the data involving a total of 1,240 males were analyzed.

Although there are individual variations in the activity of each population, the overall tendency may be summarized in the results shown in tables 1, 2, and 3.

The behavior of *D. pavani* males from Chile is recorded in table 1. Tapping, vibration, and licking were most frequent; these males are also the most discriminating, more frequently courting females of their

TABLE 2. Main courtship elements used by *Drosophila pavani* males from Mendoza (Argentina) with females of their own and of various other populations. The figures indicate numbers of times males used each element toward female of their choice.

♂ <i>pavani</i> Mendoza	a			b		
	♀ <i>pavani</i> Mendoza + ♀ <i>pavani</i> Chile n = 110			♀ <i>pavani</i> Mendoza + ♀ <i>gaucha</i> Cordoba and Taimbas n = 51		
	Homogamic	Heterogamic	Chi-square	Homogamic	Heterogamic	Chi-square
Orientation	152	91	15.32 ¹	74	52	3.84
Vibration	358	182	57.38 ¹	124	86	6.88 ¹
Circle	157	40	69.48 ¹	42	35	0.64
Tap	256	90	79.64 ¹	102	41	26.02 ¹
Lick	228	91	58.84 ¹	64	38	6.62 ¹
Antennae	48	8	14.29 ¹	13	4	5.76
Copulation	35	12	11.26	16	9	1.96
Courtship time (minutes)	3,585	1,368	2,758.3 ¹	1,415	711	233.12 ¹

n = number of males.

¹ = P < 0.01 with 1 degree of freedom.

own population (homogamic column) than foreign females (heterogamic column). Although *D. pavani* males spent significantly more time courting females from their own group, they did not mate with them more frequently (section a, table 1). *D. pavani* males from Chile, when confronted with females from Chile and Mendoza (section b, table 1), showed practically no discrimination. Only tapping was used slightly more towards their own females. *D. pavani* males (section c), although courting preferentially the homogamic females, inseminated more *D. gaucha* females than *D. pavani* females.

Table 2 shows that *D. pavani* males from Mendoza discriminate quite intensely against *D. pavani* females from Chile (section a). These males use all the elements of courtship significantly more toward their own females. With *D. gaucha* females, on the other hand, the preferential tendency is less marked, although present. In copulation, in contrast to what is observed with Chilean males, there is only a slight tendency for heterogamic mating.

Table 3 summarizes the observations on the activity of *D. gaucha* males. These exhibit practically no interpopulational preferences (sec. a), nor do they show any preferences between females of their own

population and *pavani* females from Mendoza (sec. c). On the other hand, when confronted with *D. pavani* females from Chile these males direct the greater part of their activity toward their own females, also mating with them in a significantly higher proportion.

Although *D. gaucha* males use most of the elements of courtship in a fashion similar to *D. pavani* males, they make less use of the act of antennae touching.

In both species, the copulatory periods last about 50–60 minutes, and although, in general, this process is shorter in heterogamic copulations, their difference is not significant.

DISCUSSION

The results briefly analyzed above indicate that in *D. pavani* certain variations have arisen which express themselves as courtship preference of males toward females of their own population, although this preference does not reach the mating level. This is especially clear in the behavior of individual populations: the more distant ones, as for instance Copiapó and Los Queñes or Chillán, separated by strong mountain barriers, show the highest discrimination. Therefore, these populations, geographically isolated, with different ge-

TABLE 3. Main courtship elements used by *Drosophila gaucha* males with females of their own and of various other populations. The figures indicate numbers of times males used each element toward females of their choice.

♂ <i>gaucha</i>	a ♀ <i>gaucha</i> + ♀ <i>gaucha</i> n = 42			b ♀ <i>gaucha</i> + ♀ <i>pavani</i> Chile n = 230			c ♀ <i>gaucha</i> + ♀ <i>pavani</i> Mendoza n = 228		
	Homo- gamic ¹	Hetero- gamic ²	Chi- square	Homo- gamic ¹	Hetero- gamic ²	Chi- square	Homo- gamic ¹	Hetero- gamic ²	Chi- square
Orientation	47	46	0.010	374	219	40.52 ³	55	60	0.22
Vibration	110	86	2.94	644	343	91.80 ³	84	106	2.54
Circle	18	29	2.58	204	138	12.74 ³	29	38	1.20
Tap	72	46	5.72	426	239	52.58 ³	58	43	2.22
Lick	62	40	4.74	417	163	111.24 ³	47	55	0.58
Antennae	4	4	—	30	22	1.22	5	3	0.50
Copulation	9	15	1.5	94	18	51.56 ³	7	10	0.52
Courtship time (minutes)	904	702	29.92 ³	6,324	3,403	877.16 ³	951	853	5.32

n = number of males.

¹ = females of same population as males.

² = females of different populations than males.

³ = $P < 0.01$ with 1 degree of freedom.

netic constitutions (Brcic, 1961), have also evolved, together with the processes of divergence of their genetic systems (Muller, 1949), incipient barriers to genetic exchange. Many of these preferences are of the "one-sided" type (Dobzhansky, 1944), in which females of a population A discriminate against males of population B, but females of population B do not discriminate against males of population A (*D. pavani* from Chile, and *D. gaucha* females, respecting *D. gaucha* males). As stated by Dobzhansky (1944) and Merrel (1949), among others, this type of preferential mating may initiate a trend towards a greater divergence.

Why is no sexual isolation observable between such "good" species as *D. gaucha* and *D. pavani*? Dobzhansky and Koller (1938) and Mayr (1946) have described the existence of less marked isolation between certain species of the *obscura* group, with increasing distance between the populations considered. Sympatric populations, on the other hand, exhibit the greatest discrimination. A similar situation seems to occur in our species, which are sympatric only in a restricted region in Argentina. Therefore, natural selection has not had an opportunity to intensify the barriers to cross-fertilization. It has only acted to

lower the stimulus-response threshold of *D. gaucha* females.

What is the situation in the populations of *D. pavani* from Argentina, relatively near the region where both sibling species overlap? Toward the Chilean populations, both males and females of Mendoza origin act in a way similar to males and females from the populations of Chile. Nevertheless, Chilean males exhibit less activity and discrimination than do males from Mendoza. With *D. gaucha*, on the other hand, the barrier is more marked, Mendoza males showing both courtship and mating preferences.

In general, there is a kind of gradient of sensory response in these populations and species, which may reflect their phylogenetic relationships. This gradient is revealed especially in the receptivity of the female, which in polygamous forms such as *Drosophila* is the real discriminative partner which ultimately decides whether mating will occur or not (Smith, 1958). *D. gaucha* females are the most receptive, with the lowest stimulus-response threshold; there follow *D. pavani* from Mendoza, and finally *D. pavani* from Chile, with a very high threshold of response. This observation confirms a previous study of Brcic (1958), which showed that *D. pavani* fe-

males are inseminated at a lower rate than *D. gaucha* females in heterogamic crosses.

Within the species studied there are elements which may lead to a reduction of the gene exchange between different geographically isolated populations. If these populations were to meet, and the hybrids were at a disadvantage, these differences could become more intense (Dobzhansky, 1941; Koopman, 1950; Knight, Robertson, and Waddington, 1956). If, on the other hand, the hybrids were to show a high fitness, the differences will eventually be swamped out. The one-sided mating preferences between *D. gaucha* and *D. pavani* from Chile are probably due to their allopatric condition, but still suggest the existence of sensory preferences (Hoenigsberg and Koref-Santibañez, 1960).

SUMMARY

An analysis by means of the male choice method was made of the courtship behavior of five populations of *D. pavani* from Chile, one population of *D. pavani* from Mendoza, Argentina, and two populations of *D. gaucha*, one from Brazil and another from Argentina.

Within the Chilean populations of *D. pavani* there are homogamic courtship preferences—greater frequencies of certain elements of courtship and longer courtship time with females of the same population as males. These homogamic courtship preferences do not result in greater frequencies of homogamic matings.

D. gaucha males exhibit one-sided mating preferences when confronted with *D. gaucha* females and *D. pavani* females from Chile.

D. pavani males from Mendoza (Argentina) discriminate more against *D. gaucha* females than do *D. pavani* males from Chile. This may be a consequence of the sympatric condition of these species in Argentina.

ACKNOWLEDGMENTS

The authors wish to thank Dr. D. Brncic for his help and encouragement during the realization of this work, and for his valuable suggestions in the preparation of the manu-

script. They wish to express their appreciation to Prof. T. Dobzhansky for his kind help in the revision of the manuscript, and to acknowledge the technical aid of Miss M. D. Pellicer.

LITERATURE CITED

- BRNCIC, D. 1958. The *mesophragmatica* group as an example of the speciation phenomena in *Drosophila*. Proc. X. Int. Cong. Gen., I: 420-433.
- . 1961. Integration of the genotype in geographic populations of *Drosophila pavani*. EVOLUTION, 15:92-97.
- AND S. KOREF-SANTIBAÑEZ. 1957. The *mesophragmatica* group of species of *Drosophila*. EVOLUTION, 11: 300-310.
- DOBZHANSKY, T. 1941. Genetics and the origin of species. Columbia Univ. Press, New York.
- . 1944. Experiments on sexual isolation in *Drosophila*. III. Geographic strains of *D. sturtevantii*. Proc. Nat. Acad. Sci., 30: 335-339.
- AND P. C. KOLLER. 1938. An experimental study of sexual isolation in *Drosophila*. Biol. Zentr., 589-607.
- AND E. MAYR. 1944. Experiments on sexual isolation in *Drosophila*. I. Geographic strains of *D. willistoni*. Proc. Nat. Acad. Sci., 30: 238-244.
- HOENIGSBERG, H. F., AND S. KOREF-SANTIBAÑEZ. 1959. Courtship behavior in inbred and outbred lines of *Drosophila melanogaster*. Ist. Lomb. Sc. Lett. (Cl.Sc), 93: 3-6.
- , S. KOREF-SANTIBAÑEZ, AND G. P. SIRONI. 1959. Incipient intraspecific sexual isolation in *Drosophila prosaltans* Duda and in *Drosophila equinoxialis* Dobzhansky. Experientia, 15: 223.
- AND S. KOREF-SANTIBAÑEZ. 1960. Courtship and sensory preferences in inbred lines of *Drosophila melanogaster*. EVOLUTION, 14: 1-7.
- KNIGHT, G. R., A. ROBERTSON, AND C. H. WADDINGTON. 1956. Selection for sexual isolation within a species. EVOLUTION, 10: 14-22.
- KOOPMAN, K. F. 1950. Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. EVOLUTION, 4: 135-148.
- KOREF-SANTIBAÑEZ, S., AND C. H. WADDINGTON. 1958. The origin of sexual isolation between different lines within a species. EVOLUTION, 12: 485-493.
- , A. CASANOVA, AND D. BRNCIC. 1958. Experiments on sexual isolation in species of the *mesophragmatica* group of *Drosophila* (Diptera). Proc. R. Ent. Soc. Lond., (A) 33: 179-185.
- MAYR, E. 1946. Experiments on sexual isolation in *Drosophila*. III. The nature of the isolating mechanisms between *D. pseudoobscura* and *D. persimilis*. Proc. Nat. Acad. Sci., 32: 128-137.

- AND T. DOBZHANSKY. 1945. Experiments on sexual isolation in *Drosophila*. IV. Modification of the degree of isolation between *Drosophila pseudoobscura* and *Drosophila persimilis* and of sexual preferences in *Drosophila prosaltans*. Proc. Nat. Acad. Sci., **31**: 75–82.
- MERREL, D. J. 1949. Selective mating in *Drosophila melanogaster*. Genetics, **34**: 370–389.
- MULLER, H. J. 1949. The Darwinian and modern concept of natural selection. Proc. Amer. Phil. Soc., **93**: 459–470.
- PATTERSON, J. T., L. WHARTON McDONALD, AND W. S. STONE. 1947. Sexual isolation between members of the *virilis* group of species. Univ. Tex. Publ., **4720**: 7–31.
- RENDEL, J. M. 1944. Genetics and cytology of *Drosophila subobscura*. II. Normal and selective mating in *D. subobscura*. J. Genetics, **46**: 287–302.
- SMITH, J. M. 1958. Fertility, mating behaviour and sexual selection in *D. subobscura*. J. Genetics, **54**: 261–279.
- SPIETH, H. T. 1952. Mating behavior within the genus *Drosophila*. (Diptera). Bull. Am. Mus. Nat. Hist., **99**: 401–474.