

of 0.25 microgram of *l*(-)-tryptophane gives a development of 10^8 cells in 24 hours.

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² The asparagine medium consisted of: *l*-asparagine 0.2 per cent, dextrose 0.4 per cent, Na_2HPO_4 (anhydrous) 0.6 per cent, KH_2PO_4 0.3 per cent, MgSO_4 0.005 per cent, NaCl 0.005 per cent, glass distilled water.

³ The ammonium medium consisted of: NH_4Cl 0.1 per cent, dextrose 0.4 per cent NaH_2PO_4 (anhydrous) 0.6 per cent, KH_2PO_4 0.3 per cent, MgSO_4 0.02 per cent, NaCl 0.05 per cent, glass distilled water.

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EXPERIMENTS ON SEXUAL ISOLATION IN DROSOPHILA. VII. THE NATURE OF THE ISOLATING MECHANISMS BE- TWEEN DROSOPHILA PSEUDOOBSCURA AND DROSOPHILA PERSIMILIS

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An ever increasing number of cases is being described in the current literature of pairs of exceedingly similar species that coexist at the same locality. The morphological similarity sometimes reaches the point of virtual identity, in other cases very minor differences exist in regard to the characters of eggs, larvae or adults. Adherents of a strictly morphological species concept interpret such findings as intraspecific differentiation and apply the term "physiological races" to the members of such pairs of extremely similar species. However, it has been found in all well-studied

cases that partial or complete reproductive isolation exists between the members of these pairs of populations and that no hybrids are found in nature in the regions of distributional overlap, even in the cases where hybrids can be obtained experimentally. The adherent of a biological species concept is forced to regard as species sympatric populations that are reproductively completely isolated. The two species *Drosophila pseudoobscura* and *D. persimilis* are such a pair of species. Although the morphological differences between these species¹ are very slight, still not a single hybrid has yet been found in the wide area of overlap in western America. In the laboratory the two species can be crossed fairly easily, and the hybrid females are fertile and can be backcrossed. Hybrid F_1 males, however, are completely sterile.²

Sex Behavior in Intraspecific Crosses.—A study of the normal sex behavior of the two species would seem a necessary prerequisite of a study of their mutual incompatibilities and isolating mechanisms. Unfortunately, however, the sex physiology of the two species is by no means exhaustively known.

Some data are presented in the following sections on the sexual physiology and the isolating mechanisms of an orange-eyed strain of *D. pseudoobscura* Frolova descended from flies collected at Piñon Flats, San Jacinto Mountains, California, and a wild strain of *D. persimilis* Dobzhansky and Epling from Stony Creek, north of the Sequoia National Park, California. Only these two strains of the two species were studied. Courtship in *D. melanogaster* and many other species has been described by Sturtevant^{3, 4, 5} and in *D. virilis* by Stalker.⁶ For *D. pseudoobscura* and relatives data were presented by several authors.^{2, 7, 8}

Age at Sexual Maturity.—Flies of the species *D. pseudoobscura* become sexually mature earlier than flies of the closely related species *persimilis* and *miranda*. Dobzhansky and Koller⁷ found that in a strain of *D. pseudoobscura* kept at 24.5°C. about 36% of the females were fertilized after 1½ days, 62% after 2 days, 82% after 3 days. In a strain of *D. miranda* only 4% of the females were fertilized after 2 days, 56% after 3 days, 66% after 4 days. *D. persimilis* seems to be still slower. Even 3-day-old flies are rarely fertilized and flies at least 5 days old (preferably 6 or 7) have to be used, to be sure that they are sexually mature. This poses the awkward problem that flies of different chronological age must be used to be sure that they are approximately of the same physiological age. Therefore the females of *D. pseudoobscura* used for most of the experiments were 5 or 6 days old and those of *persimilis* 7 days old.

Sexual Activity.—Both males and females of the orange-eyed strain of *D. pseudoobscura* were sexually much more active than flies of the *D. persimilis* strain. It did not prove feasible to measure this difference quantitatively, but if the following arbitrary point values are given to the sex drives:

♂ *pseudoobscura* 120, ♀ *pseudoobscura* 80, ♂ *persimilis* 50, ♀ *persimilis* 10, and a value of -110 to the isolating mechanisms in the interspecific matings, we obtain the following combined values:

$$\textit{persimilis} \text{ } \sigma \text{ with } \textit{persimilis} \text{ } \text{f} : 50 + 10 = 60$$

$$\textit{persimilis} \text{ } \sigma \text{ with } \textit{pseudoobscura} \text{ } \text{f} : 50 + 80 - 110 = 20$$

$$\textit{pseudoobscura} \text{ } \sigma \text{ with } \textit{pseudoobscura} \text{ } \text{f} : 120 + 80 = 200$$

$$\textit{pseudoobscura} \text{ } \sigma \text{ with } \textit{persimilis} \text{ } \text{f} : 120 + 10 - 110 = 20$$

The ratios 60:20 (= 3:1) and 200:20 (= 10:1) are fairly close to the observed ones in double choice experiments.⁸ They are not entirely exact, however, since the actual values of the isolating mechanisms are fairly different in reciprocal crosses (above listed always as -110). The incompatibility between *pseudoobscura* ♂ and *persimilis* ♀ is much greater than that between *persimilis* ♂ and *pseudoobscura* ♀.

Sexual activity in *Drosophila*, unfortunately, happens to be a somewhat unpredictable factor, particularly in well-aged flies. It was high on certain days, low on others even though all experimental conditions including temperature were seemingly identical. The time of day seemed to play some rôle: sexual activity is apparently higher in the morning and evening than during the middle of the day. Quantitative experiments, to be strictly comparable, should be conducted not only at the same temperatures but also at the same hour of the day.

Mating Behavior of Males.—It has been shown by Sturtevant^{3, 4, 5} that the following elements are the most frequent components of the mating behavior of *Drosophila* males. In various combinations they are found in most species of the large genus *Drosophila*.

"*Vibrating.*"—The male faces the female (usually from the side), extends one wing at about right angles to his body, and vibrates it for a few seconds. The wing is then returned to the normal position. The vibrated wing is usually the one nearer the head of the female. Both wings are rarely vibrated simultaneously and only in a few species.

"*Waving.*"—The wing is also extended laterally, but is not vibrated.

"*Scissors Movements.*"—Both wings are rapidly opened and closed like a pair of scissors.

"*Licking.*"—The male licks with his proboscis the ovipositor of the female.

"*Circling.*"—A rapid sideways movement of the male from a frontal or lateral position to one behind the female (usually followed immediately by copulation).

Of these five elements only *vibrating* and *circling* were found in *D. pseudoobscura* and *persimilis*. It was not possible to discover any difference between the two species, either in the qualitative or quantitative aspects of the courtship.

Copulation in the two species proceeds as described by Sturtevant³ for *D. melanogaster*. The male, standing behind the female, bends up his abdomen underneath, until its tip faces forward. The phallus is then thrust into the female ovipositor, and after its intromission the male parts the wings of the female and mounts. In some other species the female opens her wings spontaneously and in still others the male mounts the back of the female before intromission of the phallus.

Termination of a normal copula is apparently always initiated by the male by extracting his phallus. Usually he succeeds in doing this in 20 or 30 seconds, but it may require 3 or 4 minutes in exceptional cases. Males of the observed strain of *D. persimilis* were usually rather inactive after completed copulation and spent much of their time in preening. No second copulation was recorded during the observation periods. Males of the observed strain of *D. pseudoobscura* sometimes engaged in a second copulation within 30 or 40 seconds after completion of the first, and in a third copulation after completing the second. If no receptive females are available, males may become completely quiescent within about 20 minutes after a period of great excitement and much displaying.

Female Behavior.—Receptive females stand still, turn the tip of the abdomen toward the male, lift it and partly extrude the ovipositor (“invitation display”). With ready males this will result in almost instantaneous copulation, other males—particularly young males and males of other species—may pay no attention to the female’s overtures. Many males copulate without a preceding invitation display by the female. Copulating females ward off other males by stretching the middle pair of legs sideways. Non-receptivity is indicated by the following actions of females: walking away rapidly, wing-flicking, depressing the tip of the abdomen toward the ground, or a combination of these methods. Females of *D. pseudoobscura* and *D. persimilis*, which had just completed copulation, were non-receptive at least for one hour. They were receptive when tested again 24 hours later. Sturtevant⁴ found that in *D. repleta* and *affinis* the same pair may copulate twice within 10 minutes. Repeated copulations were also found in other species.

Length of Copulation.—Sturtevant^{4,5} reports that the length of copulation of various species of *Drosophila* may vary between 1 minute (*lutzii*, *hydei*) and 55 minutes (*immigrans*).

First copulations of *D. pseudoobscura* males lasted 4’30”, 4’35”, 4’55”, 5’55”, 6’10”, 6’15”, 6’15”, 7’0”, 7’10”, 8’0”, 9’15”, 10’5”, 11’15” in homogamic matings (median 6’15”). No copulations with *D. persimilis* ♀ were timed. Second and third successive copulations usually last shorter than the first. The duration of successive copulations was: 4’30”, 3’26”, 2’20”; —4’55”, 3’10”, 4’15”, —7’10”, 4’40”; —8’0”, 5’20”. Temperatures were about 21–24°C., but unfortunately were not accurately recorded.

First copulations of *D. persimilis* males lasted 4'40", 5'0", 5'35", 5'40", 6'10", 6'10", 6'10", 6'25", 6'35", 6'40", 7'0", 7'20", 7'20", 8'20", 8'30", 9'25" in homogamic matings (median 6'30"). One copulation with a *pseudoobscura* female lasted 7'35". There is thus no striking difference between the two species. Stalker⁶ likewise found no significant difference in length of copulation between the closely related species *D. virilis* and *D. americana*.

Species Recognition and Psychological Isolating Mechanisms.—Most modern authors assume that "psychological barriers" ("species recognition") prevent or reduce the frequency of matings between members of closely related species of insects. These terms signify a crude concept of the interplay between male and female, which has no reality. The term "recognition" implies consciousness and the ability of making judgments, for which no evidence exists in *Drosophila*. Rather it must be assumed that the male stimulates the female by specific pre-copulatory displays and that the female reacts by specific responses indicating a state of receptiveness. This interpretation assumes that successful copulation is the result of a chain of interactions between specific stimuli produced by the male and adequate responses of the female which in turn stimulate the male.

If the reproductive isolation between *D. pseudoobscura* and *D. persimilis* is partly or entirely due to psychological isolating mechanisms, an analysis of the pre-copulatory display of males and females should reveal differences. The above-described observations indicate that there are no visible differences in the courtship behavior of the two species. This is, in a way, not surprising since the major elements of the courtship, vibrating, circling, scissors movement, and licking in various combinations are widespread in the genus *Drosophila*.

The possibility remains that auditory, olfactory or other factors provide the stimulation necessary to limit copulation to encounters between conspecific individuals. To test this possibility a series of multiple choice experiments were undertaken.⁸

Multiple Choice Experiments.—Males of one species were given the opportunity to mate under varying conditions with females of two species. When an equal number of females of *D. pseudoobscura* and *D. persimilis* was placed in a vial with food together with males of *D. pseudoobscura*, it was found⁸ that about 11 times as many *pseudoobscura* females were inseminated as *persimilis* females. Males of *persimilis* fertilized about 3 times as many of their own as *pseudoobscura* females. These control experiments, as well as those of earlier authors,^{2, 7} permit three conclusions. First, that sexual isolation between the two species is not nearly as complete under experimental conditions (only one kind of male present) as in nature. Second, that mating between the flies is not random, but indicative of highly developed discrimination. Third, that conspecific matings are much more

frequent than heterogamic matings. The experiments, however, do not elucidate the reason for the higher frequency of conspecific pairings.

Questions that need to be answered are the following: Is a fly stimulated by an individual of the opposite sex regardless of the species to which it belongs? If there is a difference between species in stimulation, how large is it and to what extent is it responsible for the reproductive isolation of the species concerned? Are male and female equally involved in the difference which seems to exist between conspecific and non-specific pre-copulatory stimuli? Which sense organs are important as receptory mechanisms for these stimuli?

Methods.—Different techniques were employed in the attempt to elucidate these questions. In mass experiments 10 females of each of two species were placed in a vial of food with several males of one of these species. The females were dissected after an interval sufficient to permit fertilization of about 50 per cent of them, and the percentage of fertilized females in the lots of the two species determined. This indirect method was supplemented by direct observation. A special observation chamber was constructed which consisted of a wax ring between two parallel glass plates. The size of the ring was adjusted not to exceed the field of vision of a low-power binocular microscope. The flies were introduced into the wax ring through a funnel-like opening which could be closed by a stopper. In this chamber flies remained in good physical condition for hours, but most observation periods were terminated after 30 minutes and the flies replaced by new ones. This observation chamber permitted the observation at a 7-fold magnification of every detail of the movements of 4–8 flies, all of them at all times completely in focus.

A different observation technique was employed where numerical counts were more important than a study of the details of behavior. Batteries of ten glass vials without food were used, each one of them containing the same combination of flies. The ten vials were observed simultaneously and the number and sequence of events recorded. All transfers of aged flies were made without etherization. All tested flies were virgin at the beginning of the observation periods.

The Rôle of the Sense Organs.—*Vision:* The two species *D. pseudoobscura* and *D. persimilis* are indistinguishable to the human eye. There is no significant difference in the insemination ratio of mixed cultures kept in the light and such that were kept in the dark.⁸ This indicates that vision is not essential for species discrimination. However, absolute proof for the rôle of light can be obtained only if the dark-light experiment could be repeated after the complete elimination of all other sense organs, because it is conceivable that other senses might take over the function of vision after its elimination.

Hearing: When a male of *D. pseudoobscura* or *D. persimilis* courts a

female he spreads a wing and vibrates it. Since Reed, *et al.*,⁹ have shown that the means of the wing areas are different in the two species, the possibility exists that the pitch of wing vibration is also different and may serve as a "species recognition signal." However, it was shown⁸ in experiments involving wingless males, that actually a smaller percentage of alien females was inseminated and that the total number of inseminated females had dropped. It seems on the basis of these and other observations that it is the rôle of the vibrating wings to stimulate the females and to get them into a receptive state. Furthermore, the overlap in the normal wing pitch variability of the two species is much too large for a character to be useful in species discrimination.

Smell: It is well known that specific scents play an important rôle in the courtship of many insects. It was therefore tried to test what effect on species discrimination the elimination of the olfactory sense would have. The olfactory organ of *Drosophila* is located in the terminal segment of the antennae,^{10, 11} and can be removed rather easily. Four males of *D. pseudoobscura*, each placed with ten females of *D. pseudoobscura* and *D. persimilis* one day after the complete amputation of all segments of both antennae, performed as shown in table 1.

TABLE 1
RECORDS OF *D. pseudoobscura* AND *D. persimilis* FEMALES INSEMINATED BY
D. pseudoobscura MALES WITHOUT ANTENNAE

HOMOGAMIC FEMALES		HETEROGAMIC FEMALES		ISOLATION INDEX
N	%	N	%	
38	52.7	39	10.2	0.68

N = number of females; % = percentage of inseminated females.

Although the isolation index is significantly lower than in control experiments⁸ (where it is 0.80 or higher), still five times as many conspecific as alien females were inseminated by males without antennae. If these findings could be confirmed with more extensive material, they would indicate the following facts: lack of the olfactory sense in males increases the number of heterogamic crosses, which implies that to a certain extent the olfactory sense of males is involved in species discrimination. However, species discrimination is still high even without the olfactory apparatus.

Absence of Species Discrimination in Courting Males.—The reported experiments indicate that none of the investigated sense organs and display mechanisms had a controlling influence on species discrimination. It appeared therefore advisable to record quantitative data on species discrimination by direct observation of courting males, both in the observation chamber and in the vial batteries previously described. The observations gave no indication of species discrimination by males, as documented by the following excerpts from my protocols. (The term "incomplete copula-

tions" is applied to copulations which are typical in every respect and include intromission of the male phallus and mounting, but are terminated after 1-2 seconds.)

"July 19 (10:15 A.M.). 2 ♂ *pseudoobscura* (8 days old) placed with 4 ♀ *persimilis* (6 days old). Males very active and aggressive. No less than 50 incomplete copulations observed during a 30-minute period. No sperm found in genital tract of females. Females seem to cooperate fully during the incomplete copulations. They go through the same motions as when being courted by their own males, such as stopping, lifting the abdomen and turning it slightly toward the courting male."

Males display to alien females and attempt to copulate with them even when females of their own species are available. This is particularly true when males of *D. persimilis* are placed with the very active *pseudoobscura* females together with their own rather quiet and sluggish females:

"July 20 (10:26 A.M.). 3 ♂ *persimilis* (8 days old), 3 ♀ *persimilis* (8 days old), 2 ♀ *pseudoobscura* (7 days old). 30-minute period. Male *persimilis* rather active, display both to *persimilis* and *pseudoobscura* females. After 15 minutes first and only copulation (homogamic). Males display during the last fifteen minutes almost entirely to *pseudoobscura* females."

"July 21 (8:06 A.M.). One hour. 3 ♂ *persimilis* (8 days old), 3 ♀ *persimilis* (8 days old), 3 ♀ *pseudoobscura* (8 days old). There are numerous incomplete copulations of *persimilis* males with *pseudoobscura* females. One such heterogamic copulation is successful. During the whole hour there is not a single persistent attempt of a *persimilis* ♂ to copulate with a *persimilis* ♀."

"August 2 (7:42 P.M.). One hour. Ten vials each with 1 *persimilis* ♂ (7 days old), 1 *persimilis* ♀ (7 days old), 1 *pseudoobscura* ♀ (6 days old). During first 10 minutes males display almost exclusively to *pseudoobscura* females. In three vials there are very frequent incomplete copulations with *pseudoobscura* ♀. The males in two vials are entirely inactive, in six of the other vials they clearly concentrate their attention on *pseudoobscura* females. However, not a single successful heterogamic copulation occurred. The only attempted homogamic copulation was at once successful. The *persimilis* ♀ of one vial walked repeatedly past the *persimilis* ♂, who persistently displayed to *pseudoobscura* ♀ and payed no attention to his own female."

All female flies were dissected 13 hours after end of observation. Five *persimilis* ♀ and one *pseudoobscura* ♀ were found to be inseminated.

These records show clearly that males display without apparent discrimination to females of both species, and that in fact the majority of the display of *persimilis* ♂ are directed toward *pseudoobscura* ♀, which are more active than their own. However, the overwhelming majority of the

heterogamic copulations in which these displays culminate remain incomplete.

Functional Difficulties.—Entomologists have long contended that the peculiarities of the sexual armatures might and occasionally do prevent interspecific crosses. The notion of a complete fit of a lock and key mechanism of male and female genitalia in its most exaggerated form is undoubtedly not correct, as pointed out by Dobzhansky¹² and other authors. However, mechanical difficulties do exist in most interspecific matings and reduce their efficiency as indicated by Sturtevant⁴ and described in detail by Stalker⁶ for cross matings between *D. virilis* and *D. americana*. Observations of the cross matings of *D. pseudoobscura* and *D. persimilis* fully confirm this. The following protocol may be added to those recorded above.

“July 24 (9:54 A.M.). 30 minutes. 3 *pseudoobscura* ♂ (6 days old), 4 *persimilis* ♀ (7 days old). During the first 7 minutes only one male is active. At least 16 incomplete copulations are counted during this period. In the next 10 minutes all 3 males are active, attempting to copulate with 2 of the females. I count 48 genital contacts during this 10-minute period and undoubtedly overlooked several others during this frenzy of activity. None of these 70 or more contacts leads to a completed copulation. All flies are quiescent during the final 6 minutes of the observation period. The females do not run away from the males, in fact they engage in ‘invitation displays.’”

The conclusion to be drawn from these and other similar observations is inevitable. There must be some anatomical or physiological obstacle which prevents in most cases the completion of the interspecific copulations. Copulation is, of course, not entirely impossible, and if *pseudoobscura* ♂ stay sufficiently long with *persimilis* ♀ they will eventually inseminate most of them.

What the obstacle is that makes these interspecific matings so difficult has not yet been determined. A very careful study of the sexual armatures of males and females in the two species by Ferris and other workers has not yielded any apparent differences. There are obviously no “mechanical” barriers in the conventional meaning of the entomological literature. However, there may be invisible differences in the texture of the mucous membranes or in other physiological properties of the genital apparatus. Or else, the proper intromission of the phallus may require a high degree of receptivity (“coöperation”) on part of the female. It is possible that the stimulation by the combined pre-copulatory display activities of the non-conspecific male is insufficient to produce the degree of receptivity in the female necessary for successful copulation. Observations gave the hard-to-prove impression that it was the female that was mainly responsible for the incompleteness of so many of the interspecific copulations. Further observations and experiments are required to solve this problem.

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TWO TYPES OF HETEROCHROMATIN IN *DROSOPHILA NEBULOSA*

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Introduction.—Euchromatin and heterochromatin are the two principal components of plant and animal chromosomes. Heitz¹ was the first to make a study of the relative quantities and distribution of these components in the mitotic chromosomes of *Drosophila*. Working with *Drosophila funebris*, he showed that in this species the heterochromatin is concentrated mostly in the sex chromosomes, making up the entire Y and half of the length of the X-chromosome which includes the centromere. The autosomes and the other half of the X-chromosome are formed mainly of euchromatin. In another work² the same author discussed the appearance of the heterochromatin in the salivary gland chromosomes. Here the heterochromatin forms the chromocenter and the bases of some of the chromosomes. Studying the salivary gland chromosomes of *D. virilis*³ he concluded that the heterochromatin of this species is of two types, which he called, respectively, α -heterochromatin and β -heterochromatin. In the salivary gland nuclei, the α -heterochromatin forms a compact body, while