

MATING BEHAVIOR WITHIN THE  
GENUS *DROSOPHILA* (DIPTERA)

HERMAN T. SPIETH

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## INTRODUCTION

THE OCCURRENCE of a complex courtship and copulatory behavior is a widespread and diverse phenomenon within the Order Diptera (Richards, 1927). It has been known for several decades (Sturtevant, 1921) that the various species of the genus *Drosophila*, as well as members of closely related genera, engage in such courtship activities.

Sturtevant (1915) studied in detail the mating behavior of *Drosophila melanogaster* Meigen. In 1921 he presented the descriptions of the mating behavior of 22 species, including two species each of *Scaptomyza* and *Chymomyza*. He returned to the subject in 1942 and briefly described the mating characteristics of a score of species. Other investigators also have reported on the mating activities of certain species, for example: Mayr (1946), *D. pseudoobscura* and *D. persimilis*; Miller (1950), *D. affinis* and *D. algonquin*; Rendel (1945), *D. subobscura*; Stalker (1942), *D. virilis* and *D. americana americana*; Spieth (1947), the *D. willistoni* species group; Wallace and Dobzhansky (1946), *D. subobscura*, *D. persimilis* and *D. pseudoobscura*; while Wheeler (1947) and Blumel (1949) recorded the copulatory time of a number of species.

A survey of these studies clearly shows that certain elements (specific types of activity) of mating behavior are widespread throughout the various species, such as vibration of the wings, licking, and circling, but it is also obvious that qualitative as well as quantitative interspecific differences exist. Between closely related species, few, if any, qualitative differences are observable, while more distantly related species invariably display qualitative differences. The closely related species often

exhibit visible and measurable quantitative differences, and in some cases such variations are also detectable in intraspecific forms.

These considerations raised the question as to whether the mating behavior of the various species might yield data that would aid in the elucidation of the phylogeny and classification of the genus. Sturtevant (1942) stated: "In general the mating habits do not seem to furnish useful group characters. It is possible that more observations, both on additional species and more exact descriptions of those already observed, may change this situation." Such a study as that suggested by Sturtevant could also possibly yield certain data that may be pertinent to two other problems that are related to the mating behavior of the various species, i.e., (1) the nature of sexual isolation between incipient subspecies, subspecies, and species, and (2) the nature, relative value, and divisions between the sexes of the stimuli involved in the mating behavior.

Obviously these two problems can best be attacked by carefully controlled experiments performed on selected species. Nevertheless careful observations of the "normal" mating behavior of the individual species can perhaps give some clues to the various factors involved and certainly can aid in the selection of the most suitable species for use in attempting experimentally to solve these problems. It was therefore decided to make a systematic and as detailed as possible study of the mating behavior of all available species of the genus *Drosophila* and its close relatives. The resultant findings, plus a limited amount of data derived from certain supplementary experiments, are presented in this paper.

## TECHNIQUE

Virgin specimens were collected from stock cultures, separated according to sex, then isolated in shell vials containing food and allowed to age. Periodically specimens of the two sexes were introduced without etherization into the observation cell and studied under 10× magnification. A binocular microscope was used, and a flask of water was interposed as a cooling agent between the light source and the observation cell. Most

investigators have made their observations either without the aid of magnification or with the aid of a hand lens. Mayr (1946) and Spieth (1947) used low-power binocular magnification.

A separate record was made of each observation. The geographical origin of the stock, the University of Texas stock number, if any, the age of the individuals, the number of individuals of each sex, the length of time

of the observation, and all activities of the individuals, regardless of whether courtship and copulation occurred or not, and the copulatory time, if any, were recorded. The duration of the copulas was timed with a stop watch in the majority of cases, although a pocket watch possessing a second hand was used for recording the copulatory time of the *D. willistoni* and *D. obscura* species groups.

The majority of the observations were of one-half hour duration, although if the specimens showed no inclination to court they were sometimes either returned to the isolation vials or discarded at the end of 15 minutes. Some species and some stocks of certain species are extremely recalcitrant in their mating behavior, especially the females. This applies regardless of whether they are observed in the stock culture bottles or in the observation cells. Often the observations on such uncooperative stocks were of an hour's duration or longer.

Three types of observation cells were used. The first consisted of a top and bottom of thin plate glass with an interposed circular vertical wall of beeswax perforated so that the individuals could be introduced into the cell. A beeswax plug was used to close the opening (Mayr, 1946; Spieth, 1947). The second type of cell had glass walls as well as glass top and bottom, with the bottom coated with a thin layer of beeswax (Spieth, 1947). The third type of cell was a glass vial 40 by 24 mm., which was half filled with a plug of fresh food. A piece of dampened paper towel- ing 20 by 25 mm. was pressed into place

against the glass wall above the food plug and a 25 by 75 mm. microscope slide was used as a cover. The actual space available for the flies in this type of cell was a cylinder approximately 20 mm. high, with a diameter of approximately 22 mm. The volumes of the first two types of cells were much smaller. In these smaller cells only two to four individuals of each sex were introduced for each observation, but in the third type many more individuals could be and normally were used for each observation.

The disadvantage of observing numerous specimens at one time is that often two or more copulas may occur at the same time and it is difficult to note the beginning and termination of each copula; as a result (table 1), some copulas occurred that were not timed. The use of large numbers of specimens increased greatly the chance of occurrence of a copula and was especially helpful in the case of stocks the females of which were relatively reluctant to mate.

A further advantage of the large cell was that the specimens were in a more nearly "normal" habitat. At least food and liquid were available, and the problem of desiccation did not arise. In the smaller cells there was some indication that the individuals often became irritated and non-responsive after having been kept under observation for some time. No attempt was made to determine what were the causes of this behavior, but perhaps it had to do with the lack of moisture and/or food.

## TERMINOLOGY OF MATING BEHAVIOR ACTIVITIES

In a description of the mating behaviors of the various species, it is convenient to employ certain terms that serve to identify special, unique, often-repeated elements of behavior. Sturtevant, in his study of *D. melanogaster* (1915), was the first to introduce and define terms; later (1921) he amplified the definitions and added others. Since then various workers have introduced still more names for specific, repeated phases of mating behavior. The terms and their definitions as used in the present study are given below:

### VIBRATION

(Sturtevant, 1915 and 1921)

A wing movement of the male which involves extending usually one wing but in some species perhaps both wings laterally from the resting position and then the moving of the wing or wings rapidly up and down. The wing is displaced laterally from the resting position 3 degrees to 90 degrees, depending on the species; the vane of the wing is held parallel or almost parallel to the substratum and then vibrated rapidly up and down. The



extent of the vertical displacement varies from a very small movement to one of considerable amplitude. The speed of vibration is variable and within limits seems to be species-specific. Rarely a species, for example, *D. parachrogaster*, after displacing the wing laterally, turns the vane of the wing 90 degrees so that it is perpendicular to the substratum, with the posterior edge ventral, and then vibrates the wing backward and forward instead of up and down. Vibrating thus consists of two distinct components, i.e., lateral displacement and rapid, small, amplitude movements which occur while the wing is held at the point of maximum displacement. Vibrating occurs in pulses of movement, each one lasting for a fraction of a second to a few seconds. Between each burst of movement the wing is typically returned to the resting position.

#### FLICKING

A wing movement of the courting males of some species that involves a quick out-and-back movement of the wing from the resting position. The vane is typically held parallel or almost parallel to the substratum. Often the complete movement is repeated several times in quick succession. Flicking and vibrating are difficult to separate sometimes, since vibration is essentially flicking with the added vertical movement of the wing. In those species in which this vertical movement is of extremely small amplitude, it is difficult to determine under low magnification whether the wing is being "vibrated" or "flicked." As with vibrating, a few species (e.g., *D. tenebrosa*) turn the vane of the flicking wing perpendicular to the substratum, with the posterior edge of the wing directed downward.

#### WAVING

(Sturtevant, 1921)

One wing of the male is slowly spread outward from the body to 90 degrees, held in this position, then relaxed without vibration. This is a rather rare wing movement but is typically seen in *D. fumipennis*.

#### SCISSORS MOVEMENT

(Sturtevant, 1915 and 1921)

A courting male, in the interval of time between wing vibrations, sometimes engages

in opening and closing of both wings in a scissors-like movement. This is rarely seen but appears most typically in some specimens of *D. melanogaster* and its relatives. Apparently highly excited males display the motion most often, and it may be that the movement is merely a part of the readjustment of the wings to the normal resting state rather than representing a courtship action.

#### FLUTTERING

Non-receptive females of many species, and usually males of the same species when courted by a male, engage in an inconspicuous but definite and distinct action which involves both wings and serves as an effective repelling movement. The wings are slightly elevated, separated from contact with each other, and then moved laterally a tiny amount and vibrated rapidly. In some species the vibration is a vertical motion, but in others it is a horizontal movement. In most cases all movements are small, but in *D. buskii* the wings are spread about 30 degrees, and the vertical movements are of considerable amplitude.

#### TAPPING

(Rendel, 1945)

A foreleg motion of the male that initiates courtship. It is carried out by the male's partially extending and simultaneously elevating one foreleg or both forelegs and then striking downward, thus bringing the ventral surface of the tarsus in contact with the other individual. It may occur at various times in the courtship, but so far as I have been able to observe no courtship is initiated without at least one tapping movement on the part of the male. (See section on Possible Stimuli, p. 456.) Rendel, in his 1945 study of *D. subobscura*, states: "When he finds her he taps with his fore legs and she usually taps him also. This sparring with the front legs seems to be the initial method of recognition between males and females. . . ."

Some authors have used the term sparring rather than tapping. Since the former connotes gaining advantage in a hostile encounter, it seems better to use Rendel's term of tapping to denote this particular movement.

#### LICKING (Sturtevant, 1921)

The male of many species of *Drosophila* when courting another individual positions himself closely behind the courted individual, extends his proboscis and licks the genitalia of the other insect. The duration of contact may be short or prolonged but always involves the labellar surfaces of the courting individual and the genitalia of the courted specimen.

#### CIRCLING (Sturtevant, 1915 and 1921)

The male of many species, after posturing at the side or rear of a non-receptive female, will leave his posturing position and circle about the female, facing towards her as he moves. Sometimes he moves until he is in front of her and then retraces his path to the rear; at other times he moves completely about her in an arc of 360 degrees. Often the male engages in special wing or proboscis posturing movements as he circles. Males of some species pause during their circling movements in front of the female and engage in special posturing actions. Certain species, it should be noted, posture exclusively in front of the females. It is assumed that such patterns have evolved from species in which the males stopped their circling movements to engage in special posturing movements in front of the female (e.g., see section on the *obscura* species group). Circling probably originated as a maneuver to prevent non-receptive females from escaping from the male's attentions.

#### STAMPING (Spieth, 1947)

In those species, especially the *D. willistoni* species group, where the courting male makes few if any physical contacts with the female that he is courting, sexually excited males often stamp their fore feet. This is not a consistently appearing action and may simply be a "by-product" of sexual excitement.

#### EXTRUDING (Spieth, 1947)

The non-receptive female of many species appresses the vaginal plates, contracts certain of the abdominal muscles, and appar-

ently relaxes other muscles attached to the vaginal plates and also perhaps the muscles of the vagina. This causes the vaginal plates to be carried posteriorly, the displacement possibly being due to a stretching of the articulating membrane that lies between the vaginal plates and the preceding sclerites. Such a complex action results in the formation of a temporary tube-like structure. All degrees of extrusion exist, from none in some species to slender, very elongated tubes such as are seen in *D. duncani* and *D. micromelanica*. The extrusion action may also be accompanied by other movements such as directing the tip of the abdomen towards the male's head or elevating the tip of the abdomen high into the air. Rendel (1945) describes extrusion in his study of *D. subobscura* but gives no name to the action. He also observed similar activity on the part of *D. melanogaster* females. He indicates that the action was effective in repelling the males of both species.

#### DECAMPING (Spieth, 1947)

Non-receptive females often attempt to escape the male's overtures by running, jumping, or flying away from the immediate vicinity of the courting male. Such movements, when associated with courting, are lumped under the convenient term "decamping."

#### DEPRESSING

Lutz (1914) noted that non-receptive females of *D. ampelophila* (*melanogaster*) prevented mating by curling the tip of the abdomen downward towards the substratum and keeping the wings together. Some species do not curl the abdomen but merely depress the tip. Depressing, as Lutz notes, involves the wings as well as the abdomen. When species that have long wings depress the abdomen, they also depress the wings and hold them firmly in place. Courting males are often unable to get underneath the rigidly held wings when attempting to lick the female's vaginal plates.

#### IGNORING (Spieth, 1947)

The non-receptive female sometimes, when courted, simply keeps on with whatever ac-



tivity she has been engaged in and apparently ignores the male's actions. Sometimes, if feeding or preening, she ceases these actions and simply sits quietly. Such a behavior is much more common in certain species of the subgenus *Sophophora* than in other subgenera.

#### COUNTERSIGNALING (Spieth, 1947)

Most species of drosophilid males court other individuals of their own sex as well as females. If the courted individual is a male,

he may engage in a series of movements such as spinning about and facing the suitor and then striking him with the forelegs, or fluttering combined with kicking. Such movements seem to serve the function of causing cessation of the courtship. All these sundry movements are considered as constituting countersignaling. Not all males are able to countersignal, and the apparent effectiveness of the action varies considerably between individuals and especially between species that do countersignal.

#### ACKNOWLEDGMENTS

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## DESCRIPTIONS OF MATING BEHAVIOR OF INDIVIDUAL SPECIES

THE SPECIES ARE LISTED in this section in accordance with the classification of the genus as formulated by Patterson and Wheeler (1949) and by Wheeler (1949a). Except in the instances where only one member of a species group was available for study, a summary of the basic pattern of each species group, as well as comparisons with closely related groups, is given. This summary follows the descriptions of the mating behaviors of the individual species of each species group.

The descriptions of the mating behaviors represent the typical pattern displayed by each species. In most cases numerous courtships and several to many copulations were observed; these formed the basis from which the typical pattern was determined. As was to be expected, individual variation occurred, and, wherever such deviations were repeated consistently and often, they are noted in the descriptions.

Following the name of each species are given the point of geographical origin of each stock and also, in the case of stocks from the University of Texas collection, the stock number under which it is maintained in the laboratory of that institution.

### SUBGENUS *HIRTODROSOPHILA* DUDA

Of the 26 species belonging to this subgenus (Wheeler, 1949a; Patterson and Wheeler, 1949), none except *D. duncani* Sturtevant can be readily maintained in the laboratory and only it was available for study. Hsu (1949) has shown that the male genitalia of *D. duncani* are quite distinct from those of the other four species of this subgenus which he has studied. There seems to be a definite correlation between the structure of the male genitalia of *D. duncani* and its mating behavior. We therefore can expect that other members of this subgenus will probably show a quite different type (or types) of mating behavior from that displayed by *D. duncani*.

#### *Drosophila duncani* Sturtevant Itasca Park, Minnesota

The male taps and then positions himself

behind the female. In this rear position he curls the tip of the abdomen downward and spreads the large and obvious genital claspers widely apart. Then, using the abdominal-thoracic junction as a hinge, he bobs the abdomen up and down rapidly. After a short but variable period of time, he lunges at the female, usually thrusting his forelegs under the female's wings, thus grasping her body, and at the same time bringing his genitalia against those of the female.

A receptive female spreads her vaginal plates and allows the male to achieve intromission, but does not spread her wings or compress her abdomen. The female's unspread wings rest upon the dorsum of the male's head and thorax, but after he has achieved intromission he pushes the female's wings apart and climbs upon the dorsal surface of her wings. The male's assumption of a standing position upon the female results in the elongation of the tip of his abdomen which extends between the female's wings and also results in the "pulling" upwards of the tip of the female's abdomen, and at the same time the weight of his body depresses her wings so that they assume a roof-like appearance. The copulating individuals remain quiescent during coitus and are not apparently disturbed by the ebullient courting activities of other individuals. At the end of copulation, the male turns to dismount, which involves turning 360 degrees to 400 degrees in one direction, then reversing in the opposite direction, and often finally turning again in the first or original direction. Invariably the dismounting and disengaging actions take between 30 and 60 seconds.

A non-receptive female repulses the courting male by rapid, small amplitude fluttering of both wings, by extruding, by kicking, and by decamping. Rarely a female elevates the tip of the abdomen when she extrudes. The extruding action is extremely striking since it involves decided shortening of the longitudinal length of the female's abdomen. Such shortening is so great that the female's abdominal contents are compressed and the abdomen is distended laterally, giving the impression that the female is swelling or in-

flating her abdomen. The compression apparently causes extrusion, and the extruded area assumes the shape of a slender, short, white tube. Males repeatedly attempt to mount extruding females but invariably are unable to achieve coitus and are quickly dislodged by the kicking actions of the females. Often the non-receptive female flutters her wings and extrudes as soon as the male taps and assumes the rear position. The male does not discriminate between receptive and non-receptive females but mounts and attempts to achieve coitus indiscriminately. Furthermore, he is an aggressive and extremely active suitor.

Sturtevant (1942) noted the "inflation" of the female's abdomen and interpreted it as indicating sexual excitement. The presently reported observations indicate that this "inflation" is part of the extrusion act and indicates sexual non-receptivity on the part of the female. Certainly the four females that accepted the males' overtures did not "inflate" their abdomens either before or after courting males mounted.

The mating behavior pattern in both the males and females is distinct from that of any other drosophilid species studied, but to date the mating behavior of no other species of *Hirtodrosophila* has been reported.

#### SUBGENUS *PHOLADORIS* STURTEVANT

Patterson and Wheeler (1949) place nine species in this subgenus and divide these into two species groups. Two species of the *victoria* species group (*D. victoria* Sturtevant and *D. lebanonensis* Wheeler) and one of the *mirim* species group (*D. baeomyia*) have been used for the present study.

#### *Drosophila victoria* Sturtevant Stock No. 1318.A7, Prescott, Arizona

The male taps the side or rear of the female, then orients behind and close to her, slightly crouches, and curls the tip of his abdomen under and forward. From such a position, he raises himself upward and at the same time jerks his abdomen forward and attempts to accomplish intromission. The crouching male will very slightly extend and vibrate one wing rapidly as he attempts to copulate. The amplitude of these vibrations is so small that

they are difficult to see even with magnification.

A receptive female spreads her vaginal plates and allows the male to achieve coitus. This having been accomplished, she elongates her abdomen so that the tip of it extends beyond the tips of her wings. At the same time, the male mounts and grasps the female's body with his legs. Since she does not spread her wings, the male's grasp includes the female's wings as well as her body. The male thus rests upon the dorsal surface of the female's wings, a very atypical position for a drosophilid. During copulation, the pair is quiet. At the end of the period the male withdraws and then usually slides off the female without turning.

A non-receptive female refuses the male by ignoring his actions, by keeping her vaginal plates tightly appressed and kicking with her hind legs, and by extruding, which typically involves a slight lifting and directing the tip of the abdomen towards the male's head. Recently fecundated females have no difficulty in repelling the males by merely extruding. The males do not circle the females.

The males court and attempt to mount one another.

#### *Drosophila lebanonensis* Wheeler Stock No. 1733.1, Beirut, Lebanon

The mating behavior of this species appears to be identical with that of *D. victoria*. Reciprocal crosses were made between the two species and showed no signs of sexual isolation.

#### *Drosophila baeomyia* Wheeler Stock No. 1877.6, Georgetown, South Carolina

The male taps and then moves to the rear of the female, extends one wing to 90 degrees, and vibrates intermittently. At the same time, the male licks the female's ovipositor, a procedure that involves extension of the proboscis and a simultaneous slight forward lunge that causes him to strike against the female. Occasionally the male circles the female.

A receptive female spreads both wings widely, and the male licks, mounts, and then inserts. At first he is positioned well forward on the female, holding onto the base of her wings with his forelegs. At the end of approxi-

TABLE 1  
SUMMARY OF SPECIMENS OBSERVED AND COPULATORY DURATION FOR THE VARIOUS SPECIES

Subgenus and Species	No. of Observations	No. of ♂	No. of ♀	No. of Copulas	No. of Copulas Timed	Min.	Max.	Mean
<b>HIRTODROSOPHILA</b>								
<i>D. duncani</i>	9	72	83	4	3	8' 58"	15' 27"	11' 49" Ca. 15' (Wheeler, 1947)
<b>PHOLADORIS</b>								
<i>D. victoria</i>	9	23	23	9	9	19"	48"	33" Ca. 43" (Wheeler, 1947)
<i>D. lebanonensis</i>	—	—	—	—	12	19"	1' 40"	47"
<i>D. baemyia</i>	8	27	27	8	8	1' 47"	5' 04"	3' 10"
<b>DORSILOPHA</b>								
<i>D. busckii</i>	8	33	55	6	5	1' 10"	2' 00"	1' 29" Ca. 3' (Wheeler, 1947)
<b>PHLORIDOSA</b>								
<i>D. lutsii</i>	—	—	—	—	—	—	—	Ca. 1' (Sturtevant, 1921)
<b>SORDOPHILA</b>								
<i>D. acanthoptera</i>	6	26	40	6	1	1° 36' 06"	—	—
<b>SOPHOPHORA</b>								
<i>D. prosaltans</i>	10	63	122	4	3	17' 00"	25' 00"	21' 08" Ca. 18' (Wheeler, 1947)
<i>D. sellata</i>	17	115	169	—	—	—	—	—
<i>D. rectangularis</i>	3	8	20	—	—	—	—	—
<i>D. emarginata</i>	8	51	50	—	—	—	—	—
<i>D. willistoni</i>	18	—	—	14	14	9' 00"	27' 00"	14' 41"
<i>D. equinoxialis</i>	25	—	—	4	4	14' 00"	19' 00"	15' 55"
<i>D. paulistorum</i>	7	25	47	12	12	10' 00"	22' 00"	15' 25"
<i>D. tropicalis</i>	6	46	56	10	10	10' 15"	13' 20"	12' 16"
<i>D. sucinea</i>	18	—	—	10	10	15' 00"	35' 00"	20' 33"
<i>D. capricorni</i>	15	—	—	5	5	6' 30"	14' 00"	9' 55"
<i>D. fumipennis</i>	15	—	—	6	6	4' 00"	5' 30"	4' 20"
<i>D. nebulosa</i>	16	—	—	13	13	1' 10"	2' 30"	1' 37" 1 cop. 5' 30" (Wheeler, 1947) Ca. 1' 30" (Wheeler, 1947)
<i>D. melanogaster</i>	2	7	7	4	4	17' 10"	20' 01"	18' 14" Ca. 20' and 21' (Sturtevant, 1915 1920); ca. 10' (Wheeler, 1947)
<i>D. simulans</i>	7	46	70	14	4	16' 27"	17' 20"	16' 52"
<i>D. takahashii</i>	5	36	32	2	2	17' 05"	17' 55"	17' 30"
<i>D. auraria</i>	6	53	53	14	8	4' 53"	10' 05"	6' 37"
<i>D. rufa</i>	6	26	44	3	2	20' 01"	20' 28"	20' 15"
<i>D. montium</i>	3	17	22	18	11	2' 50"	6' 08"	3' 46"
<i>D. ananassae</i>	5	51	51	22	16	3' 14"	5' 55"	4' 11" Ca. 4' (Wheeler, 1947)



TABLE 1—Continued

Subgenus and Species	No. of Observations	No. of ♂	No. of ♀	No. of Copulas	No. of Copulas Timed	Min.	Max.	Mean	
<i>D. pseudoobscura</i>	20	42	67	21	9	5' 00"	8' 30"	7' 01"	Ca. 5' (Wheeler, 1947); 6' 15" (Mayr, 1946)
<i>D. persimilis</i>	9	24	28	21	11	3' 40"	8' 20"	5' 46"	
<i>D. miranda</i>	13	25	32	8	7	5' 00"	12' 50"	8' 46"	
<i>D. subobscura</i>	11	23	26	2	2	6' 30"	10' 00"	8' 15"	
<i>D. affinis</i>	16	12	18	8	8	1' 00"	3' 50"	1' 46"	1' 14" (Miller, 1950)
<i>D. asalea</i>	13	31	32	17	17	3' 00"	7' 00"	5' 17"	
<i>D. alhabasca</i>	2	5	6	5	5	7' 10"	10' 05"	7' 46"	
<i>D. algonquin</i>	12	24	35	15	13	4' 13"	7' 15"	5' 28"	5' 41" (Miller, 1950)
<i>D. nannoptera</i>	7	34	43	3	3	4' 45"	5' 20"	5' 07"	
DROSOPHILA									
<i>D. innublia</i>	4	37	25	—	—	—	—	—	1 cop. 3' (Wheeler, 1947)
<i>D. munda</i>	2	8	11	5	5	7' 32"	9' 12"	8' 47"	3' 40" (Wheeler, 1947)
<i>D. occidentalis</i>	5	19	29	3	2	7' 27"	7' 55"	7' 41"	
<i>D. suboccidentalis</i>	7	40	35	10	7	6' 48"	27' 45"	13' 44"	Ca. 6' 30" (Blumel, 1949); ca. 10' (Wheeler, 1947)
<i>D. palustris</i>	7	48	50	9	6	6' 09"	8' 00"	7' 16"	7' 30" (Blumel, 1949)
<i>D. subpalustris</i>	6	32	30	10	9	6' 32"	7' 59"	7' 11"	
<i>D. phalerata</i>	11	46	98	2	1	—	—	15' 32"	
<i>D. quinaria</i>	3	31	41	13	9	4' 02"	6' 52"	5' 30"	1 cop. 7' 30" (Wheeler, 1947)
<i>D. subquinaria</i>	9	49	70	2	2	9' 21"	10' 02"	9' 42"	Ca. 8' 45" (Wheeler, 1947)
<i>D. tenebrosa</i>	6	24	29	1	—	—	—	—	6' (Blumel, 1949)
<i>D. transversa</i>	9	72	75	21	13	5' 43"	12' 05"	7' 11"	9' 30" (Wheeler, 1947)
<i>D. polychaeta</i>	2	16	7	22	16	21"	30"	25"	
<i>D. guttifera</i>	2	20+	20+	5	5	6' 58"	8' 16"	7' 49"	Ca. 9' (Wheeler, 1947)
<i>D. tripunctata</i>	4	23	51	7	5	23' 59"	47' 01"	33' 25"	Ca. 48'; 1 cop. 82' (Wheeler, 1947)
<i>D. crocina</i>	11	82	109	2	1	41' 25"	—	—	
<i>D. funebris</i>	10	76	58	19	13	14' 33"	19' 35"	16' 52"	16' 33" (Wheeler, 1947)
<i>D. subfunebris</i>	1	8	11	4	4	31' 35"	47' 35"	37' 31"	23' 30" (Wheeler, 1947)
<i>D. macrospina macrospina</i>	4	30	48	6	6	39' 40"	53' 05"	46' 09"	35' (Wheeler, 1947)
<i>D. m. limpiensis</i>	1	11	13	3	3	36' 37"	41' 15"	38' 56"	
<i>D. m. ohioensis</i>	1	2	4	—	—	—	—	—	
<i>D. tristipina</i>	2	17	11	2	2	15' 09"	15' 25"	15' 17"	

\* One abnormally short copulation of 6' 18" not included in data.

TABLE 1—Continued

Subgenus and Species	No. of Observations	No. of ♂	No. of ♀	No. of Copulas	No. of Copulas Timed	Min.	Max.	Mean
<i>D. cardini</i>	11	53	89	—	—	—	—	23' 45" (Wheeler, 1947)
<i>D. cardinoides</i>	6	48	62	—	—	—	—	—
<i>D. neocardini</i>	16	99	169	2	2	18' 55"	23' 45"	21' 20"
<i>D. polymorpha</i>	2	2	2	1	1	33' 00"	—	—
<i>D. putrida</i>	7	34	38	—	—	—	—	Ca. 29' (Wheeler, 1947)
<i>D. virilis</i>	15	54	54	34	34	2' 25"	3' 56"	3' 11"
<i>D. americana americana</i>	36	133	137	52	52	1' 30"	3' 58"	2' 30"
<i>D. a. texana</i>	15	57	68	29	29	2' 25"	5' 11"	3' 35"
<i>D. nonamexicana</i>	15	58	59	31	31	1' 18"	3' 55"	2' 44"
<i>D. lacticola</i>	2	18	22	3	3	2' 43"	3' 30"	3' 10"
<i>D. montana</i> (1218.8d)	7	70	81	15	12	3' 00"	6' 03"	4' 17"
<i>D. montana</i> (1862.2a)	2	21	21	7	5	1' 21"	2' 18"	1' 58"
<i>D. carbonaria</i>	2	3	8	2	1	37' 26"	—	Ca. 30' (Sturtevant, 1942); ca. 26' (Wheeler, 1947)
<i>D. melanica melanica</i>	7	62	63	4	4	6' 18"	9' 20"	7' 29"
<i>D. m. paramelanica</i>	12	28	30	2	2	4' 35"	4' 50"	4' 43"
<i>D. melanura</i>	10	50	64	2	1	5' 20"	—	—
<i>D. micromelanica</i>	2	18	20	6	6	5' 03"	8' 58"	6' 45"
<i>D. nigromelanica</i>	3	12	22	—	—	—	—	—
<i>D. robusta</i>	5	76	34	5	5	29"	40"	34"
<i>D. hydei</i>	4	11	14	15	11	1' 15"	3' 44"	2' 13"
<i>D. nigrohylei</i>	3	24	16	9	7	6' 00"	9' 15"	7' 25"
<i>D. bifurca</i>	2	14	14	—	—	—	—	—
<i>D. repleta</i>	21	106	121	16	8	1' 25"	2' 17"	2' 01"
<i>D. cana palpa</i>	10	89	68	6	4	1' 58"	2' 46"	2' 18"
<i>D. fulvimacula</i>	5	39	61	—	—	—	—	—
<i>D. limensis</i>	10	70	119	—	—	—	—	—
<i>D. melanopalpa</i>	2	8	24	—	—	—	—	—
<i>D. aldrichi</i>	2	13	25	15	4	2' 35"	9' 43"	6' 06"
<i>D. arizonensis</i>	3	31	51	Many	9	44"	2' 22"	1' 37"
<i>D. buzzatii</i>	2	11	11	12	9	1' 20"	2' 28"	1' 46"



## EXPLANATION OF SYMBOLS IN TABLE 2

A blank space indicates that the particular action is not present in the mating behavior.

An asterisk (\*) shows an exceptional or aberrant type of behavior, and the reader is referred to the detailed description of the species for further information.

## COURTING POSITION OF MALE

- b Male positions himself behind female when posturing.
- s Male positions himself at side of female when posturing.
- f Male positions himself in front of female when posturing.

## COURTING ACTIONS OF MALE

## PROBOSCIS MOVEMENTS OF MALE

- L1 Male licks intermittently and each licking of brief duration.
- L2 Male licks continuously for long periods of time.

## LEG MOVEMENTS OF MALE

- d Male rubs or caresses dorsum of female's abdomen.
- l Male rubs or caresses lateral surfaces of female's abdomen.
- t Male taps female while posturing.
- v Male rubs or caresses venter of female's abdomen.

## WING MOVEMENTS OF MALE

- V 0°-90° Male vibrates wing while posturing; number indicates degree the vibrated wing is extended from resting position.
- F 0°-90° Male flicks wing while posturing; number indicates degree wing is flicked outward from resting position.
- W 0°-90° Male waves wing while posturing; number indicates degree wing is waved outward from resting position.

## ACCEPTANCE RESPONSES OF FEMALE

- S Female spreads vaginal plates as acceptance response.
- Y 0°-90° Female spreads wings as part of acceptance response; degree to which wings are spread indicated by numbers.

## COPULATORY ACTIONS OF MALE

- Mr Male regularly attempts to mount non-receptive females.
  - Mi Male rarely or infrequently attempts to mount non-receptive females.
  - N Male never attempts to mount non-receptive females.
  - 1 Male mounts in "forward" position, grasping female's thorax or wing bases with his fore tarsal claws.
  - 2 Male mounts in "rearward" position, grasping female's abdomen or wing tips with his fore tarsal claws.
  - 3 Male stands or rests upon female.
  - a Attached to 1, 2, or 3 indicates male achieves intromission before he mounts.
  - b Attached to 1, 2, or 3 indicates male achieves intromission after he mounts.
- No letter indicates that intromission is accomplished as the male mounts.

## DISMOUNTING ACTIONS OF MALE

- A Male dismounts and then withdraws; number indicates degree male turns before withdrawing.
- Bs Male withdraws and then slides off backward to dismount.
- Bj Male withdraws and then jumps off female.
- Bt Male withdraws and then turns to dismount.
- / Represents "or."

## CIRCLING ACTIONS OF MALE

- C Male circles female; number in degrees shows extent to which male circles about female before returning to posturing position; + indicates posturing movements are engaged in by male as he circles; - indicates that such posturing movements are not exhibited by circling male.

## REPELLING ACTIONS OF FEMALE

Decamping is a universal method of avoiding male and is not listed by symbol.

- K Kicking.
- F Fluttering wings.
- E Extruding.
- L Elevating tip of abdomen.
- D Depressing tip of abdomen.

## MALE-TO-MALE ACTIONS

- H Males court one another in typical fashion. This means that they proceed beyond just tapping one another and actually posture.
- x Males display definite, specific actions termed countersignaling.
- P Males fight with one another.



TABLE 2  
CONDENSED SUMMARY OF MATING BEHAVIOR OF *Drosophila*  
(See p. 412 for explanation of symbols.)

	Courting Position of ♂	Proboscis	Leg	Wing	Courting Actions of ♂	Acceptance Responses of ♀	Copulatory Actions of ♂	Dismounting Actions of ♂	Circling Actions of ♂	Repelling Actions of ♀	♂ to ♂ Actions
<b>HIRTODROSOPHILA</b>											
<i>D. duncani</i>	b	*				S	Mr 2-3	A400		KF E L	
<b>PHOLADORIS</b>											
<i>D. victoria</i>	b	*		V3-5		S	Mr 3a*	Bs		K E	H
<i>D. lebanonensis</i>	b	*		V3-5		S	Mr 3a*	Bs		K E	H
<i>D. baomyia</i>	b	L1		V90		S Y90	Mi 1b-2b	Bt	- C360	K E	x
<b>DORSILOPHA</b>											
<i>D. busckii</i>	b	L1	t	V90		S	N 1	A180	- C360	KF E D	xP
<b>SORDOPHILA</b>											
<i>D. acanthoptera</i>	f	L1	t	V75		S	N 2	Bj	- C180	KF	Hx
<b>SOPHOPHORA</b>											
<i>D. prosaltans</i>	b	L1	t	V20-40		S Y?	N 3-1	A180	+ C360	KF E D	xP
<i>D. sellata</i>	b	L1	t	V70-90		? ?	N ?	?	+ C360	KF E D	xP
<i>D. rectangularis</i>	b	L1	t	V20-40		? ?	N ?	?	+ C360	KF E D	xP
<i>D. emarginata</i>	b	L1	t	V or F90		? ?	N ?	?	+ C360	KF E LD	xP
<i>D. willistoni</i>	b	L1	t	V70-90		S Y90	N 1	A180	- C360	K E L	xP
<i>D. equinoxialis</i>	b	L1	t	V70-90		S Y45	N 1-2	A180	- C360	K E L	xP
<i>D. paulistorum</i>	b	L1	t	V70-90		S Y90	N 2	A180	- C360	K E L	xP
<i>D. tropicalis</i>	b	L1	t	V70-90		S Y90	N 2	A180	- C360	K E L	xP
<i>D. sucinea</i>	b	L1	t	V70-90		S Y90	N 1-2	A180	- C360	K E L	x
<i>D. capricorni</i>	b	L1	t	V70-90*		S Y45	N 1	A180	- C360	K E L	x
<i>D. fumipennis</i>	f	L1	t	W90*		S Y45	N 1	A180	- C180	K E L	x
<i>D. nebulosa</i>	f	L1	t	W90*		S Y45-90	N 1-2	A180	- C180	K E L	xP
<i>D. melanogaster</i>	b	L1	t	V90		S	Mi 1a	A180	- C360	KF E LD	HxP
<i>D. simulans</i>	b	L1	t	V90		S Y10	Mi 1a	A180	+ C360	KF E LD	Hx
<i>D. takahashii</i>	b			V90		S	Mi 1a	A180	+ C360	KF	Hx
<i>D. auraria</i>	b			V90		S	Mr 2b	Bt		K E LD	Hx
<i>D. rufa</i>	b			V90		S	Mr 2b-3b	Bt		K D	Hx
<i>D. montium</i>	b			V90		S Y70*	Mr 2b-3b	Bt	+ C360	KF E LD	Hx
<i>E. ananassae</i>	b					S Y70	Mr 2b-1b	A180 or B180	+ C360	KF E LD	Hx
<i>D. pseudoobscura</i>	sb			V90		S	Mr 1a	Bt/A180	*	KF E LD	HxP
<i>D. persimilis</i>	sb			V90		S	Mr 1a	Bt/A180	*	KF E LD	HxP
<i>D. miranda</i>	sb			V90		S	Mr 1a	Bt/A180	*	KF E LD	HxP
<i>D. subobscura</i>	f	*		W45-90		S	Mr 1a	Bt/A180	*	KF E LD	Hx?
<i>D. affinis</i>	sb			V90		S	Mr 1a	Bt/A180	- C360	KF E LD	HxP
<i>D. azteca</i>	sb			V90		S	Mr 1a	Bt/A180	+ C360	KF E LD	HxP
<i>D. aithabasca</i>	sb			V90		S	Mr 1a	Bt/A180	+ C360	KF E LD	HxP
<i>D. algonquin</i>	sb			W20-V90		S	Mr 1a	Bt/A180	+ C360	KF E LD	HxP
<i>D. nannoptera</i>	b	L2	v	V20-30		S Y15	2	Bs		KF E L	Hx
<b>DROSOPHILA</b>											
<i>D. innublia</i>	b		d	F90		? ?	Mr ?	?		KF	D H
<i>D. munda</i>	b	L2	d-v			S Y75	N 2b	Bs		KF	Hx
<i>D. occidentalis</i>	b	L2	d	F90		S Y90	Mi 2b	A180		KF L	H
<i>D. suboccidentalis</i>	b	L2	d	F90		S Y90	Mi 2b	A180		KF L	H
<i>D. palustris</i>	b	L2	d	F90		S	Mi 2b	Bs or Bt		KF	D H P
<i>D. subpalustris</i>	b	*	d			S *	Mi 2b	Bt/A180	- C360	KF	D H
<i>D. phalerata</i>	b			F90		S	Mr 2b-1b	A180	- C360	KF	D H
<i>D. quinaria</i>	b		d			S Y75	Mr 2b	Bs		KF	D H
<i>D. subquinaria</i>	b	L2	v	F90		S *	Mi 2b	Bs	- C360	KF	D Hx
<i>D. tenebrosa</i>	b	L2	l	F90-120		? ?	Mi 2b	Bs		KF	H
<i>D. transversa</i>	b			V20-30		S	Mr 2b or 1b		+ C360	KF	D H
<i>D. polychaeta</i>	b	L1	t			S?	Mr 2b	Bs			H*
<i>D. guttifera</i>	b	L2	l			S Y75	N 1b	Bs		K	H
<i>D. tripunctata</i>	s-b	L2	t	F90 to V75-90		S Y75	N 2b	Bs or Bj	- C360	K	H P
<i>D. crocina</i>	b	L2	t	V15-20		S Y75	N 2b	Bs	- C360	KF	D Hx

TABLE 2—Continued

	Courting Position of ♂	Proboscis	Leg	Wing	Courting Actions of ♂	Acceptance Responses of ♀	Copulatory Actions of ♂	Dismounting Actions of ♂	Circling Actions of ♂	Repelling Actions of ♀	♂ to ♂ Actions
<i>D. funebris</i>	b	L2		F90	S Y90	Mi 1b	Bs	— C360	KF		HxP
<i>D. subfunebris</i>	b	L2			S Y90	N 1b	Bs	+ C90	KF	L	HxP
<i>D. macrospina</i>	b	L2			S Y90	N 1b	Bs	+ C360	KF	D	HxP
<i>D. m. limpiensis</i>	b	L2			S Y90	N 1b	Bs	+ C360	KF	D	HxP
<i>D. m. ohioensis</i>	b	L2			? ?	N ?	?	+ C360	KF	D	HxP
<i>D. trispina</i>	b	L2		F90	S Y90	N 1b	Bs	— C90	KF	D	HxP
<i>D. cardini</i>	f	L2	1*		? ?	N ?	?	+ C180	KF		
<i>D. cardinoides</i>	b	L2		F90	? ?	N ?	?		KF		
<i>D. neocardini</i>	b	L2	*	F90*	S	N 2b	Bs	+ C360	KF		Hx
<i>D. polymorpha</i>	f	L2			?*	N ?	?	+ C180	? ?		??
<i>D. putrida</i>	b	L2		F90	? ?	N ?	?	— C360	KF		HxP
<i>D. virilis</i>	b	L2	v	V10-15	S Y45	Mi 1b	Bs or Bt	— C360	KF*E*	D	H P
<i>D. americana</i>	b	L2	v	V10-15	S Y45	Mi 1b	Bs or Bt	— C360	KF*E*	D	H P
<i>D. a. texana</i>	b	L2	v	V10-15	S Y45	Mi 1b	Bs or Bt	— C360	KF*E*	D	H P
<i>D. novamexicana</i>	b	L2	v	V10-15	S Y45	Mi 1b	Bs or Bt	— C360	KF*E*	D	H P
<i>D. laticola</i>	b	L2	v	V10-15	S Y45	Mi 1b	Bs or Bt	— C360	KF*E*	D	H P
<i>D. montana</i>	b	L2	v	V10-15	S Y45	Mi 1b	Bs or Bt	— C360	KF*E*	D	H P
<i>D. carbonaria</i>	b	L2	v	F90	S Y45	N 2b	A180	+ C360	KF E L		HxP
<i>D. melanica</i>	b	L2	v or l	V5-10	S Y0-75	Mi 1b	Bs	— C360	KF E L		HxP
<i>D. m. paramelanica</i>	b	L2	v or l	V5-10	S ?	Mi 1b	Bs	— C360	KF E L		HxP
<i>D. melanura</i>	b	L2	v or l	V5-10	S Y45	Mi 1b	Bs	— C360	KF E L		HxP
<i>D. micromelanica</i>	b	L2		V5-10	S Y5-90	N 3b	Bs	— C360	KF E L		HxP
<i>D. nigromelanica</i>	b	L2	v or l	V5-10	? ?	Mi ?	?	— C360	KF L		HxP
<i>D. robusta</i>	b	L2	t	V10-15	S	Mi 2b	Bs		KF	D	HxP
<i>D. hydei</i>	b	L2	v	V15	S Y30	N 2b	Bs		KF E LD		H
<i>D. nigrohydei</i>	b	L2		V15	S Y30	N 2b	Bs		KF	D	H
<i>D. repleta</i>	b	L2	v or l	V15	S Y30	N 1b	Bs or Bj		KF	D	H P
<i>D. canapalpa</i>	b	L2	l	V15	S Y0-90	N 1b	Bs		KF	D	H
<i>D. fulvimacula</i>	b	L2	v or l	V15	? ?	N 1b	Bs		KF	D	
<i>D. limensis</i>	b	L2	l	V15	? ?	N ?	?		KF	D	
<i>D. aldrichi</i>	b	L2	v	V15	S Y5-15	N 2b	Bs		KF E*	D	x
<i>D. arizonensis</i>	b	L2	v	V15	S Y5-15	N 2b	Bs		KF E*	D	x
<i>D. buzzatii</i>	b	L2	v or l	V15	S Y5-15	N 2b	Bs		KF E*	D	xP
<i>D. hamatofila</i>	b	L2	1*	V15	S Y30	N 1b*	Bs		KF E L*D	???	
<i>D. longicornis</i>	b	L2	v	V30	S Y5-15	N 1b*	Bs		KF E*	D	x
<i>D. meridiana</i>	b	L2	v	V15*	S Y5-15	N 2b	Bs	— C360	KF E*	D	x
<i>D. mojaviensis</i>	b	L2	v	V15	S Y5-15	N 2b	Bs		KF E*	D	x
<i>D. mulleri</i>	b	L2	v	V15	S Y5-15	N 2b	Bs		KF E*	D	x
<i>D. peninsularis</i>	b	L2	l	V15	S Y5-15	N 1b*	Bs		KF E*	D	xP
<i>D. ritae</i>	b	L2	1*	V15	S Y5-15	N 2b	Bs		KF E LD	???	
<i>D. anceps</i>	b	L2	1*	V15	S Y30	N 1b*	Bs	+ C360	KF		???
<i>D. mercatorum</i>	b	L2	v	V15	S Y5-15	N 2b	Bs		KF E*	D	x
<i>D. m. pararepleta</i>	b	L2	v	V15	? ?	N ?	?		KF E*	D	x
<i>D. nigricruria</i>	b	L2	v	V15	? ?	N ?	?		KF E LD		HxP
<i>D. gibberosa</i>	b	L2	t	V5	S Y45	N 2b	Bs or Bj	+ C90	KF E*		Hx
<i>D. immigrans</i>	b		t	F90	S*	Mr 2b	Bj or A180	+ C360	KF E LD		
<i>D. spinofemora</i>	b			W90	? ?	N ?	?	+ C360		L	HxP
<i>D. subbadia</i>	b	L2	v	V5	? ?	N*?	?	— C360	KF	D	x
UNCLASSIFIED											
<i>D. castanea</i>	b	L2	v	V5	S	N 1b	Bs	— C360	KF	D	x
<i>D. parachrogaster</i>	bs	L1	t	V90	? Y?	N 1*-2	Bs	— C360	KF	D	Hx
<i>D. tumidiarsus</i>	b				S Y	Mi 1b*	Bs			D	

mately the first minute of copulation, the male can be distinctly seen to slide backward, and the resultant position is held until the termination of copulation. The copulating pairs are quiet until the end of copula, when the male typically withdraws and then dismounts, usually by turning to one side.

A non-receptive female refuses a suitor by extruding and simultaneously turning the tip of her abdomen towards the head of the male, by kicking, by ignoring, and by decamping. Rarely does a male attempt to mount a non-receptive female. The males tap one another and countersignal but do not attempt to mount other males.

#### SUMMARY OF SUBGENUS *Pholadoris*

The species studied show that considerable differences exist in the mating behavior of the species of the subgenus *Pholadoris*. There are few resemblances between the two types described. Probably the *D. victoria* type of mating behavior represents a specialized condition in which certain elements (such as licking and circling on the part of the male and wing spreading on the part of the female) have been lost. Even wing vibration has been almost lost in *D. victoria* and *D. lebanonensis*, and the peculiar habit of the male's mounting on top of the female's wings is distinct from the more usual type displayed by *D. baeomyia*. *D. baeomyia* presents a mating behavior similar to that shown by the *saltans* and *willistoni* species groups of the subgenus *Sophophora*.

#### SUBGENUS *DORSILOPHA* STURTEVANT

The monotypic subgenus *Dorsilopha* Sturtevant is represented only by the unique and cosmopolitan *Drosophila busckii* Coquillett.

##### *Drosophila busckii* Coquillett

St. Paul, Minnesota, and Hearne, Texas

The male taps, goes to the rear of the female, intermittently extends one wing laterally to 90 degrees, and vibrates rapidly. Simultaneously the male licks and taps the sides of the female's abdomen. When vibrating, the male's body is slightly crouched and twisted towards the side of the moving wing. Occasionally the male circles to restimulate the female.

A receptive female accepts by spreading

her vaginal plates and drooping the tip of the abdomen. The male responds by licking, mounting (grasping the female's abdomen and shoving her wings apart and upward), and at the same time achieves coitus, the tip of his abdomen having been brought forward. After mounting, he typically grasps the female's thorax with his fore tarsal claws and at the same time rubs the region of genital union with his hind legs for *ca.* 30 seconds. At the end of the copulatory period, the male turns, withdraws, and dismounts in one coordinated movement.

A non-receptive female repulses the male by kicking, decamping, occasionally depressing the abdomen, and extruding. Extrusion is usually accompanied by a spreading of her wings (about 30 degrees) and then fluttering them rapidly and vertically.

The males court one another and countersignal by spreading and vibrating the wings vertically, and also by spinning and slashing with their forelegs at the suitors. The males are ardent suitors; both the non-receptive females and the other males are aggressive in repelling the courting males.

Sturtevant (1921) records the mating of this species. His observations agree with these, except that he records copulas of 3 minutes' duration, whereas the present observations give a range of 1 minute and 10 seconds to 2 minutes.

#### SUMMARY OF SUBGENUS *Dorsilopha*

The combination of the elements of the mating behavior of this unique species of the subgenus indicates, on this type of evidence, that this species is quite distinct from the species of other subgenera.

#### SUBGENUS *PHLORIDOSA* STURTEVANT

Five species are placed in this subgenus by Sturtevant (1942) and Patterson and Wheeler (1949a). All five species apparently are restricted to flowers, the larvae depending chiefly on pollen for food. None was available for study. Sturtevant (1921) has described the unique mating behavior of *D. lutzii* Sturtevant. His description is as follows: "*Drosophila lutzii*: No scissors movement, vibration, or circling seen. The male stands behind the female, with his head under her wings, and often stays thus quietly for some

time. Then he pushes up against her wings jerkily with his head, at the same time bending his abdomen around to one side. During this act his long axis is not quite parallel to that of the female, and the abdomen comes around the shortest way. The female spreads her wings, and the genitalia come together at almost the same time. The male then mounts, his final position being that which is usual for the genus. Two copulations timed, each lasting about 1 minute."

The short copulation period and the lack of wing vibration and circling on the part of the male suggest relationship to the *victoria* species group of *Pholadoris*. The unique method of the male in achieving coitus by bending his abdomen laterally has not been observed in any other species of *Drosophila* and is certainly atypical for the genus.

SUBGENUS **SIPHLODORA** PATTERSON AND  
MAINLAND

Three species are considered to belong to this subgenus (Patterson and Wheeler, 1949) and, like the species that belong to *Phloridosa*, cannot be maintained in the laboratory. The mating behavior of none of the three species has been recorded.

SUBGENUS **SORDOPHILA** WHEELER

This subgenus is represented by a single species, *D. acanthoptera* Wheeler.

***Drosophila acanthoptera* Wheeler**  
Stock No. 1808.21, Oaxaca, Oaxaca, Mexico

The male taps, then places himself diagonally in front of one of the female's eyes, extends one wing about 75 degrees and vibrates rapidly, the wing moving through a large arc. At the same time the male slightly curls the abdomen and bends it laterally towards the female's head. After posturing, the male rushes to the rear of the female, licks and rubs the sides of her abdomen with his forelegs.

A receptive female responds to the male by slightly lifting the tip of the abdomen and spreading the vaginal plates. The male grasps her abdomen with his forelegs and middle legs, mounts and inserts, forcing the female's wings apart. The pair is then very quiet, with the male holding onto the female's abdomen, never to the thorax or wings. At the end of copula the male dismounts quickly in a man-

ner that can best be described as jumping. There are no preliminary movements to indicate his intention of dismounting.

A non-receptive female refuses by fluttering, kicking, and especially by decamping. This occurs as the male moves from the forward-posturing position to the rear of the female. Males circle rapidly to stop such decamping females.

The males court one another and countersignal by spreading and raising both wings and then fluttering the wings rapidly. The males do not attempt to mount non-receptive females but return to the forward posturing position.

Six copulas were observed, of which only one was accurately timed for a duration of 1 hour, 36 minutes, and 6 seconds. Two other copulas were partially timed and each lasted more than 1 hour and 20 minutes. This species has the longest copulatory period known and is approached only by *D. immigrans*.

SUMMARY OF THE SUBGENUS *Sordophila*

Some elements of the mating behavior (e.g., the posturing in front of the female's eye, the method of licking and countersignaling in front of the female's eye, the method of licking and countersignaling on the part of the male) are similar to the actions of some species of the subgenus *Sophophora*. The long copulatory period, the method of dismounting, and the male's method of holding onto the female during copula are considerably different from the behavior displayed by species of *Sophophora* and seem to indicate a distinct line of evolution.

SUBGENUS **SOPHOPHORA** STURTEVANT

Patterson and Wheeler (1949) divide this subgenus into six species groups: *saltans*, *willistoni*, *melanogaster*, *obscura*, *nannoptera*, and *alagitans*. Species representing all these groups, except the *alagitans* group, were available for this study. Each species group is considered separately in the following section of this paper.

*Drosophila saltans* SPECIES GROUP

Three species of this species group were studied. In addition, a stock of *D. sellata* Sturtevant, which Patterson and Wheeler (1949) consider to be a synonym of *D. pro-*



*saltans*, was used. The mating behavior of all these species seems similar. That of *D. prosaltans* is used as the type and the others are compared to it.

***Drosophila prosaltans* Duda**

Stock No. 1911.6, Iporanga, São Paulo, Brazil

The male taps, goes to the rear of the female, and positions himself close behind her. He then extends one wing about 20 degrees to 40 degrees laterally and vibrates, occasionally extending the wing sharply to 90 degrees. At the same time he occasionally taps with his forelegs and licks the female. The licking involves a forward, lunge-like movement of the male so that his head butts against the female. He circles to restimulate her, raising and lowering both wings as he moves about her. Occasionally a circling male pauses momentarily in front of the female and vibrates one wing.

The acceptance reaction is rapid and was not observed in detail. Apparently the female widely spreads her wings and vaginal plates. The male mounts and inserts as he mounts; he then stands erect upon the female's back, with his forelegs upon her thorax and the middle legs upon her abdomen, and briefly rubs the region of genitalic union with his hind legs. Such a position pulls the tip of the female's abdomen up and forward so that she appears "saddle-backed." After 1 to 3 minutes, the male drops down and backward, assuming the normal drosophilid mating position with his forelegs holding onto the female's thorax or wing bases. Near the end of copula, the female kicks and moves about, and the male terminates copula by turning, dismounting, and withdrawing.

A non-receptive female repels (1) by decamping, accompanied usually by small-amplitude, rapid fluttering of the wings; (2) by extruding and fluttering; (3) by curling the tip of the abdomen down and preening the dorsal surface with her hind legs. Such preening almost invariably occurs when the male attempts to lick and not only prevents the male from reaching the female's genitalia, but also the movements involved in preening cause the female's hind legs to strike the male's face. The males do not attempt to mount non-receptive females.

Countersignaling occurs between males in

the form of fluttering. The individuals are pugnacious towards one another, both males and females striking at each other with their forelegs and then grasping some part of the other's body between the folded fore tibia and femur.

Ten experiments involving 6 hours and 35 minutes of observations were conducted, but only four copulas resulted.

***Drosophila sellata* Sturtevant**

Stock No. 1401.4, Huichihuayan, Mexico

The mating behavior of this stock differs from the preceding in that (1) the individuals of *sellata* are much more pugnacious; (2) the male extends his wings 90 degrees, or almost that far, and then vibrates; (3) the female often repels the male by turning upon and slashing at him with both forelegs.

No copulas occurred during 17 observations, utilizing 115 males and 169 females and involving 7 hours and 15 minutes of watching.

***Drosophila rectangularis* Sturtevant**

Stock No. 1383.18, Barranca Mital, Vera Cruz, Mexico

No copulas occurred during three observations, conducted for a total of 1 hour and 5 minutes. The male's courting behavior and the responses of the non-receptive female were identical with those of *D. prosaltans*. Sturtevant (1942) records that the female of this species spreads her wings before the male mounts.

***Drosophila emarginata* Sturtevant**

"Quirigua, C. D."

No copulas occurred during eight observations, covering 3 hours of watching. Observed differences between this species and *D. prosaltans* are: (1) the male often does not vibrate one wing, but merely flicks it outward; (2) in circling the male flicks both wings (or only one wing) outward but does not raise them at the same time; (3) the female in extruding often elevates the tip of the abdomen so much that she appears to be standing on her head; (4) the individuals are less pugnacious. Sturtevant (1942) reports that females of *D. emarginata*, as well as those of two other species of the *saltans* group (*D. elliptica* Sturtevant and *D. cordata* Sturtevant),

give a characteristic "switching" reaction during copulation.

The species so far studied indicate a uniform type of mating behavior for the *saltans* group, a behavior that seems to be typically like the basic mating behavior of the whole subgenus *Sophophora* (see summary of the subgenus).

#### *Drosophila willistoni* SPECIES GROUP

As now known, this group consists of nine species (Patterson and Wheeler, 1949; Burla *et al.*, 1950). The mating behavior of six of these species (*D. willistoni* Sturtevant, *D. equinoxialis* Dobzhansky, *D. sucinea* Patterson and Mainland, *D. nebulosa* Sturtevant, *D. fumipennis* Duda, and *D. capricorni* Dobzhansky and Pavan) have previously been described in detail by Spieth (1947). *D. paulistorum* Dobzhansky and Pavan and *D. tropicalis* Burla and da Cunha were observed in the course of the present study. A stock of *D. bocainensis* Pavan and da Cunha was made available through the kindness of Prof. Th. Dobzhansky but was lost before it could be utilized since the females were sterile.

The mating behavior of *D. willistoni* which is described below is also used to elucidate the basic pattern of the entire *willistoni* species group.

#### *Drosophila willistoni* Sturtevant Belem, Para, Brazil

The male taps, goes to the rear of the female, and assumes a slightly crouched position with the tip of his abdomen somewhat curled. Having positioned himself, he extends one wing 70 degrees to 90 degrees and vibrates it periodically, twisting his body on the longitudinal axis as he vibrates, taps (uppercuts), and occasionally licks or attempts to lick the female. Sexually excited, non-posturing males often flutter their wings vertically, usually with movements of small amplitude but sometimes the uppermost wing vane is snapped almost to a vertical position. Males also circle non-receptive females but do not display wing movements as they move about the females.

A receptive female responds by spreading her wings to 90 degrees, slightly drooping the tip of her abdomen and spreading the vaginal plates. The male then licks, mounts,

and inserts, all of these actions forming a complex coordinated movement. After the male has mounted, the female folds her wings back against the male who grasps the base of her wings with his fore tarsi while the female kicks, and he strokes the area of genitalic union.

Near the end of copula the female kicks vigorously, causing the male to lose his grasp and slide backward, but he determines the time of breaking when he turns 180 degrees, dismounts, and withdraws.

A non-receptive female signifies refusal by decamping, kicking, extruding, elevating, and ignoring. Males court one another and countersignal by spinning and facing the suitor and slashing with their forelegs.

#### *Drosophila equinoxialis* Dobzhansky Teffe, Amazonas, Brazil

Basically the mating behavior of this species is similar to that of *D. willistoni* except in the following respects: (1) *D. equinoxialis* displays less sexual drive; (2) the female spreads her wings at acceptance to about 45 degrees and elongates and droops the tip of her abdomen greatly; (3) during the first minute of copula the female extends her abdomen and depresses the tip, pulling the male backward; (4) the female switches as well as kicks just before the termination of copula.

#### *Drosophila paulistorum* Dobzhansky and Pavan Belem, Para, and Pirassununga, São Paulo, Brazil

This species is very similar to *D. willistoni*. The males seem identical in their behavior, but the *D. paulistorum* female differs from the *willistoni* female in that when she accepts (1) she elongates her abdomen so much that it almost touches the substratum, and she spreads her wings between 45 degrees and 90 degrees; (2) the female's abdomen remains elongated after copula starts and the male is thus unable to pull himself forward into a higher and more anterior position; (3) during the last half of copula, the kicking and switching of the female usually dislodge the male to the extent that he loses his grasp on her wings and rests in an almost vertical position with his wing tips on the substratum.

***Drosophila tropicalis*** Burla and da Cunha  
Belem, Para, Brazil

The mating behavior of this species seems identical with that of *D. paulistorum*. All copulas occurred when the individuals were three days old. Observations were also made on specimens whose ages varied from four to 15 days, but none of these females accepted, although the males courted vigorously.

***Drosophila sucinea*** Patterson and Mainland  
Jalapa, Mexico

This species acts much like *D. willistoni* in its mating behavior. The differences are mainly that (1) as soon as coitus is achieved, the male rubs the region of genitalic union with his hind legs; (2) about a minute after copula has commenced, the female elongates her abdomen and forces the male backward from the relatively "high and forward" position he assumed at first; (3) the length of the copular period is longer; (4) the males are pugnacious towards one another when countersignaling.

***Drosophila capricorni*** Dobzhansky and Pavan  
Jacarepagus, Federal District, Brazil

In most respects this species is similar to *D. sucinea* in its mating behavior but varies in that (1) the male, when posturing, not only vibrates one wing but at the same time stretches and extends the middle leg of the same side outward and forward towards the female and vibrates it; (2) the copular period is much shorter; (3) the male is not displaced backward during copula.

***Drosophila fumipennis*** Dobzhansky and Pavan  
Cantareira, São Paulo, Brazil

The *D. fumipennis* male, after tapping, positions himself either directly in front of the female or in front of one of her eyes. He then extends one wing to 90 degrees and, holding it at this angle, depresses the wing tip at the same time that he curves his body slightly laterally, especially the abdomen. The tip of the abdomen is also slightly depressed. Then the foreleg of the same side as the extended wing is straightened full length and raised about 40 degrees. The rigidly extended leg is slowly depressed and moved from side to side until it touches the female's body. After posturing thus for one to several

seconds, the male rushes to the rear of the female where he halts in a position similar to that displayed by the other species of the group. If the female does not accept, the male typically circles to the forward-posturing position. The female's acceptance response is similar to that of *D. willistoni*.

Mounting and the ensuing copula are similar to those actions of the other species, but it is to be noted that the male strokes the area of genitalic union and that he is never displaced backward by the female's elongating her abdomen after copula is under way. The male, unlike all other species of the group, will not court immediately after termination of copula. The duration of copula is relatively short.

***Drosophila nebulosa*** Sturtevant  
Belem, Para, Brazil

Individuals of both sexes display the habit of spreading, raising, and dropping the wings intermittently as a normal (not mating) activity which distinguishes them from the other species except for *D. bocainensis* which displays similar wing actions. Like *D. fumipennis*, the male of this species postures in front of the female, but the posturing consists of curving the body, especially the abdomen, on the horizontal plane, extruding a small sphere of liquid from the anus and flicking (waving) one wing to 90 degrees. After posturing, the male races to the rear and positions himself in the typical "*willistoni*" position. Mounting is typical except that the male grasps the middle of the costal margin of the female's wings with his fore tarsal claws, and at once the female folds her wings against her sides, with the vanes in a vertical position, the costa uppermost, and elongates her abdomen. These combined movements cause the male to slip backward, and the female then rotates her wings to the normal mating position. The copulatory period is short.

SUMMARY OF *Drosophila willistoni*  
SPECIES GROUP

The basic pattern for this group involves posturing in the rear position, with the male vibrating one wing at 70 degrees to 90 degrees, accompanied by infrequent tapping and licking. Circling seems to be typical, and the

specialized posturing in front of the female as shown by *D. fumipennis* and *D. nebulosa* probably evolved as a modification of circling. The female's acceptance response always involved spreading the genitalia and wings. Mounting and coitus are achieved simultaneously, with the male assuming a position well forward (except in *D. paulistorum* and *D. tropicalis*) and holding onto the wings. While copula is in progress, the males of *D. nebulosa*, *D. sucinea*, and *D. equinoxialis* are invariably displaced backward to some extent by the actions of the females. Copula is terminated by the male's turning 180 degrees and withdrawing.

#### *Drosophila melanogaster* SPECIES GROUP

This large group consists of 18 species (Patterson and Wheeler, 1949). The *saltans* and *willistoni* groups are both confined to the Western Hemisphere, and both appear to be of Neotropical origin. In comparison the *melanogaster* group is scattered throughout the world, with three of the species being cosmopolitan. Patterson and Wheeler (1949) think that the *melanogaster* group must have evolved in Asia and then spread to other parts of the world. Wheeler (1949a) has placed 13 species of the group in five subgroups, with the remaining five of the 18 species unclassified as to subgroup. For this study, seven species representing four subgroups were available, i.e., *D. melanogaster* Meigen and *D. simulans* Sturtevant (subgroup A), *D. takahashii* Sturtevant (subgroup B), *D. auraria* Peng, *D. rufa* Kikkawa and Peng, and *D. montium* de Meijere (subgroup C), and *D. ananassae* Doleschall (subgroup C). Spieth and Hsu (1950) have reported on the effect of light on the mating behavior of these seven species and discussed some of the elements of the mating behavior. No two of these seven species have identical mating behaviors, but two basic patterns are observable, with *D. ananassae* displaying a behavior that appears intermediate between the two major types. The mating behavior of *D. melanogaster* and *D. auraria* are used to illustrate the two basic types.

#### *Drosophila melanogaster* Meigen Stephenville Wild

The male taps, circles to the rear, and posi-

tions himself close behind the female. He then curls the tip of the abdomen under and forward, vibrates intermittently one wing at 90 degrees, and licks the female. These actions may or may not be synchronous but are always intermittent in nature. Between bursts of action, the wings and proboscis are returned to the resting position. The male also may tap with his forelegs while posturing.

Receptive females spread the vaginal plates apart, and the male brings the tip of his abdomen forward and against the female, and then he lunges upward and forward, grasping the female and also pushing her wings apart. Apparently his head, forelegs, and middle legs are used for grasping the female and for pushing the wings apart. Having achieved coitus and having spread the female's wings, he then mounts still farther forward and grasps the dorsal surface of the basal area of the female's wings with his fore tarsal claws. During copula the female vibrates her wings intermittently (every 30 seconds to 2 minutes). The vibrations are of small amplitude but distinct, and occasionally she kicks with her hind legs. Near the end of copula, the male pushes backward and upward, the movement resulting in a distinct elongation of his abdomen. He then turns 180 degrees and withdraws.

A non-receptive female repels (1) by fluttering her wings, kicking with her hind legs, and extruding; (2) by depressing the tip of the abdomen; (3) by decamping; (4) if feeding, by elevating the tip of the abdomen above the male's "reach" and extruding.

Males are aggressive and persistent suitors and, in addition to the usual posturing procedures, often circle the females and repeatedly try (unsuccessfully) to mount non-receptive females. Between copulas the sexually excited male scissors his wings. The males court one another, attempt to mount other males, and countersignal by fluttering and by spinning about and slashing at the suitors with their forelegs.

#### *Drosophila simulans* Sturtevant Stock No. 1339.1a, Carron de Zapilata, Acahuizotla, Mexico

The mating behavior of this species is similar to that of *D. melanogaster*, except (1)

when the male is in the act of circling the female, he often stops either directly in front of her or in front of one of her eyes and rapidly scissors both wings, gradually increasing the amplitude of the wings until they are extended 70 degrees to 90 degrees and then holds them briefly in this position, after which he drops the wings to the normal position and continues with his circling; (2) the female spreads her wings slightly (10 degrees to 15 degrees) when giving the acceptance response; (3) the female does not vibrate her wings during copula, but the male does rub the sides of the female's thorax with his middle and hind legs. These movements occur intermittently and in sharp, rapid bursts of movement; (4) a male when courted countersignals by elevating and arching the abdomen and at the same time raising and spreading both wings about 15 degrees.

*Drosophila takahashii* Sturtevant  
Stock No. 1736.2, Hangchow, China

This species differs from *D. melanogaster* in that (1) the circling male stops in front of the female and waves his wings outward and upward to 45 degrees, holding them in this position briefly before dropping them to the normal position; (2) the male apparently never licks or strikes the female's abdomen when posturing; (3) the female appears not to extrude, but wing fluttering is an effective action for repelling the male.

*Drosophila auraria* Peng  
Stock No. 1736.1, Hangchow, China

The male sights a female, approaches and taps, moves to the rear and carefully positions himself several millimeters away from, and directly behind, the female. He crouches slightly, curls the tip of his abdomen under, and makes a running lunge at the female, propelling his body under her wings and grasping the abdomen with his legs, especially the forelegs. Having mounted and grasped the female, the male then extends one wing to 90 degrees and vibrates, at the same time attempting by abdominal movements to achieve coitus.

The male tarsi bear on the two basal joints sturdy sex combs, each consisting of 10

or more teeth the axes of which are at right angles to those of the tarsal joints and with the tips of the teeth pointing medially. Further, the tarsal segments are so formed that the tarsus is concave on its inner surface, thus giving a bow-legged appearance to the males. The fore tarsi are primarily responsible for grasping the female's abdomen, and sufficient force is exerted by the male to compress the female's abdomen.

A receptive female droops and extends her abdomen, spreading the vaginal plates. Copulation then proceeds, with the male retaining his original position without any modification. During copula the pair is quiet until near the end of the period, when the female typically spins about rapidly and vibrates both wings. The male withdraws and then dismounts.

A non-receptive female repels the male's overtures (1) by spinning about and constantly facing the male as he attempts to take up a position behind her; (2) by spreading her wings slightly and raising her abdomen high into the air and at the same time curling the tip of her abdomen down, her body assuming an almost vertical position, thus making it impossible for the male to mount; (3) by decamping very rapidly; (4) by extruding, especially in the case of recently fecundated individuals; (5) by dislodging any male that succeeds in mounting. The last method involves kicking, vibrating both wings, shaking the entire body vigorously, and keeping the tip of the abdomen close to the substratum with the vaginal plates closely appressed. Often males succeed in mounting non-receptive females, but invariably they are dislodged in a short time, and, even if the male succeeds in correctly positioning the tip of his abdomen, he is unable to achieve coitus. Having dislodged the male, the female then shows no signs of irritation as an after effect and in this respect is quite different from the females of most species. The males do not circle non-receptive females.

Males court one another, and the courted insect countersignals by elevating the abdomen and curling the tip down, assuming a position much like that of the non-receptive female. Males often mount one another, and courting individuals show no discrimination



between males and females. A male always starts courting by tapping, but after he is sexually excited he may omit the tapping when starting the courting sequence.

Sturtevant (1942) reports briefly on the mating behavior of this species and notes that the sex combs are involved in the male's grasping the female during copula.

***Drosophila rufa* Kikkawa and Peng**  
Stock No. 1736.3, Hangchow, China

*Drosophila rufa* displays a mating behavior similar to that of *D. auraria* but differs in that (1) 1 to 2 minutes after the start of copula the male releases his grasp upon the female's abdomen and pushes his way forward and upward, thus spreading the female's wings, and assumes a standing position upon the female's dorsum. The hind and middle legs are used normally, but the fore tarsal segments are all relaxed except for the basal segment of each leg; (2) repelling females and males never elevate the abdomen but do flutter their wings; (3) males that mount non-receptive individuals sometimes maintain their grasp for as long as 5 minutes before being dislodged. If a female has been mounted, the male often appears to have achieved coitus but apparently only a pseudo-copulation, lasting for 15 to 20 seconds, occurs. The males court one another and occasionally try to mount one another. Countersignaling is accomplished by fluttering rather than by elevating the abdomen as in *D. auraria*.

***Drosophila montium* de Meijere**  
Stock No. 1736.4, Japan

*Drosophila montium* behaves during mating much as *D. auraria* and *D. rufa* behave, but differs from *D. auraria* in that (1) often the male, when he lunges to mount the female, grasps her wings as well as her abdomen; (2) when the male vibrates one wing, receptive females typically spread both wings about 70 degrees; (3) after copula has started, the male typically releases his grasp upon the female's abdomen and pushes himself into a standing position upon the female's dorsum; (4) the male circles a non-receptive female, spreading and lifting both

wings to 45 degrees as he moves about her; (5) in addition to the repelling actions shown by *D. auraria*, the females of *D. montium* also flutter. In all other respects, the mating behavior seems identical with that of *D. auraria*.

***Drosophila ananassae* Doleschall**  
Stock No. 1836.3, Monterrey, Mexico

The male taps, moves to the rear of the female, and positions himself close behind her. He then curls the tip of his abdomen under, slightly crouches, sometimes slightly twists his abdomen on the longitudinal axis but does not vibrate. After pausing in this position, he lunges onto the female, grasping her abdomen with his legs and pushing her wings upward with his head. Receptive females then spread their wings and vaginal plates, the male inserts and then climbs forward between her wings and holds on in the same manner as *D. melanogaster*. During copula the pair is quiet until about 1 to 1½ minutes before termination, when the male releases his tarsal grasp and pushes himself backward. At the same time, the female places the ends of her hind tibia against the region of genitalic union and pushes vigorously. At the end of copula, the male turns 180 degrees and withdraws, or withdraws and then turns to dismount.

A non-receptive female dislodges the male that has lunged upon her by curling the tip of her abdomen down and under, simultaneously kicking and fluttering. Some females, especially those that have been recently fecundated, elevate their abdomens and extrude when tapped.

Males circle non-receptive females, scissoring their wings as they move about them.

Males court one another, attempt to copulate with other males, and countersignal by fluttering, depressing, and kicking.

*Drosophila caribbea* Sturtevant is now considered a synonym of *D. ananassae*. Sturtevant (1921) briefly describes the mating behavior of *D. caribbea*, and his description agrees well with my observations except that he lists the duration of the copula as about 10 minutes, whereas the present study showed an average of 4 minutes and 11 seconds for the *D. ananassae* stock employed.

### SUMMARY OF *Drosophila melanogaster* SPECIES GROUP

On the basis of the seven species representing four subgroups that have been studied, two major lines of evolution in the mating behavior seem clear. *D. auraria*, *D. rufa*, and *D. montium* represent one line in which mounting precedes wing vibration and coitus, in which licking does not occur, in which the male holds onto the female's abdomen part or all of the time with his forelegs, and in which the male typically withdraws before dismounting. *D. melanogaster*, *D. simulans*, and *D. takahashii* represent a second major evolutionary line in which wing vibration precedes mounting and coitus is accomplished either before or as the male mounts. After coitus is accomplished, the male pushes his way forward and upward, spreading the female's wings and eventually holding onto the female's wing bases with his fore tarsal claws. The male typically turns 180 degrees to dismount and then withdraws.

The behavior of *D. ananassae* is clearly intermediate between the two major lines. The backward movement of the male 1 to 1½ minutes before the termination of copulation, and the pushing actions of the female are similar to phases of behavior of the *willistoni* group. It is interesting in this connection that *D. ananassae* males lack the sex combs of the type that are characteristic of the males of the *melanogaster* group, and that the males of the *willistoni* group also all lack sex combs.

### *Drosophila obscura* SPECIES GROUP<sup>1</sup>

This is the largest group of the subgenus *Sophophora* and at present consists of 21 species distributed primarily in the Nearctic and the European area of the Palearctic. In addition, two species from the Neotropical region and one from the Ethiopian region are recorded (Patterson and Wheeler, 1949).

The group is divided into two subgroups (Sturtevant, 1942; Wheeler, 1949a), i.e., the *obscura* and *affinis* subgroups. Of the *obscura*

subgroup, three Nearctic species (i.e., *D. pseudoobscura* Frolova, *D. persimilis* Dobzhansky and Epling, and *D. miranda* Dobzhansky) and one European species (i.e., *D. subobscura* Collin) were used in the present study. Of the *affinis* subgroup, four Nearctic species (i.e., *D. affinis* Sturtevant, *D. algonquin* Sturtevant and Dobzhansky, *D. athabasca* Sturtevant and Dobzhansky, and *D. azteca* Sturtevant and Dobzhansky) were observed.

***Drosophila pseudoobscura* Frolova**  
Santa Barbara, Chihuahua, Mexico; Pinon  
Flats, San Jacinto Mountains, California

The male taps and then, standing at the side of the female, extends one wing to 90 degrees and vibrates intermittently the wing nearest the female's head. After a short time the male may then move to the rear of the female and continue with the vibrating. Sometimes he goes to the rear position immediately after tapping. While vibrating, the male crouches slightly and curls the tip of his abdomen down and forward. Occasionally the male extends and vibrates both wings, and, if in the side position, may rarely extend his proboscis.

A receptive female slightly raises and extends the abdomen, spreading the vaginal plates. At this time the dorsal surface of the female's abdomen forms a straight line that is parallel to the surface of the substratum. The male then lunges forward and upward, grasps the dorsolateral surface of the female's abdomen with his forelegs, brings his genitalia against those of the female, and achieves intromission. The female does not spread her wings, and as soon as intromission is achieved the male raises his forelegs to spread the female's wings. The sex combs are thus involved first in grasping the female's abdomen and then in spreading her wings. This entire series of actions is accomplished in less than one second. Having achieved intromission and having mounted, the male grasps the base of the female's wings with his fore tarsal claws and the legs are so held that the sex combs are turned upward and not in contact with the female's body. For the first 1 to 3 minutes of copula, definite peristaltic pulsations pass along the male's abdomen. The

<sup>1</sup> Milani (1950a, 1950b, 1951a, 1951b) has published on the mating behavior of five European species of this group: *Drosophila subobscura*, *D. ambigua*, *D. bifasciata*, *D. tristis*, and *D. obscuroides*. His publications were not available in time for consideration in the present paper.

pair is then quiet until shortly before termination of copula when the male first pulls himself slightly backward and downward and then upward and backward, assuming an arched position. Concurrently he places the ends of his hind tibia against the area of genitalic union and pushes vigorously. After a short interval, he either withdraws and dismounts or turns 180 degrees and withdraws.

A non-receptive female repels the male by kicking, by decamping, by depressing the abdomen, by extruding and fluttering, and at the same time either directing the tip of the abdomen towards the male's face or elevating it. Males repeatedly try to copulate with non-receptive females, but despite the fact that the genitalia are often brought into contact the males never succeed in achieving intromission and are quickly dislodged by the kicking and fluttering actions of the females.

Often, especially when three to five days old, the males stop their posturing, move backward a very short distance, and rapidly flick both wings back and forth to 90 degrees. This motion appears almost as a double wing vibration, but there is no vertical motion of the wing vanes involved. Furthermore, three- to five-day old males often sit alone in the observation cell and engage in such wing movements. The movement is not part of the posturing action but seems to appear in sexually excited individuals.

Normally the male postures only at the side or rear of the female and never in front of her. Only rarely does a courting male ever get in front of a female. When a courting male, usually owing to accidental movements of the female, does get in front of a female, he often assumes a striking posture, which involves extending the proboscis full length and parallel to the ground, extending the forelegs forward and upward and parallel to each other, depressing the thorax so that it comes almost against or against the substratum, elevating the abdomen and elevating and spreading both wings to 45 degrees. Often the female responds to this posturing by moving forward between the male's outstretched legs, simultaneously extending her proboscis forward and placing the labellar surface against the labellar surface of the male. In such a position the pair moves the

apposed proboscises backward and forward for 5 to 10 seconds. The male then moves quickly to the rear of the female and attempts to mount.

Males also court one another. Typically when a male is courted, he spins about and faces the suitor and taps or slashes with his forelegs, sometimes elevating the body before starting the downward motion. Also the male scissors his wings rapidly, sometimes laterally and sometimes vertically.

Males of this species, with those of *D. persimilis* and *D. miranda*, are unique in displaying two distinct types of posturing behavior. The atypical and rarely observed method of posturing in front of the female is almost identical with the normal method of posturing of *D. subobscura* (see below).

Mayr (1946a), for his original description of the mating behavior of this species, used a stock derived from wild flies collected at Pinon Flats, San Jacinto Mountains, California. He timed the copulations of 13 pairs and the average duration of copulas was 7 minutes and 2 seconds. The present study gave an average of 7 minutes and 1 second. Mayr (1946) also showed that second and third copulas by the same male (within a single observational period) were typically shorter than the first copula.

***Drosophila persimilis* Dobzhansky and Epling  
Aspen, California<sup>1</sup>**

The mating behavior of this species appears to be identical with that of *D. pseudoobscura* except that, as shown by Mayr (1946), the sexual drive of the species (at least under laboratory conditions) is lower for both the males and females than it is for *D. pseudoobscura*. These differences are quantitative and difficult to detect in intra-species crosses.

Mayr (1946) timed 16 copulas, which resulted in an average time of 7 minutes and 19 seconds, in comparison to the average of 5 minutes and 46 seconds of this study. His stock was originally collected at Stony Creek, north of Sequoia National Park, California.

<sup>1</sup> Another stock, supplied through the kindness of Prof. Th. Dobzhansky, was also used, but I lost the locality data for this stock.

***Drosophila miranda* Dobzhansky**  
Olympic, Puget Sound, Washington

The mating behavior of this species is identical with that of *D. pseudoobscura* and *D. persimilis*. The individuals are larger, appear more lethargic in their general activity, but courting males are aggressive, persistent suitors.

***Drosophila subobscura* Collin**  
England

The male taps, positions himself at the side of the female, crouches slightly, pauses, taps again, and then repeats the tapping motion several times before he moves to a position in front of the female. A movement of the female, especially a decamping movement, appears to be the stimulus that often causes the male to move to the forward position. When positioned in front of the female, the male extends his proboscis, places all his feet widely apart, depresses his thorax, elevates his abdomen, and at the same time raises and spreads both of his wings to 45 degrees to 75 degrees. Occasionally, but not often, the female responds by extending her proboscis, the labellar surfaces of the two individuals are brought into contact, and while thus joined the proboscises are moved alternately back and forth for about 5 seconds. Having thus postured, the male then circles rapidly to the rear and usually attempts to mount. A receptive female accepts in exactly the same manner as does *D. pseudoobscura*, and copula proceeds in a fashion similar to that displayed by *D. pseudoobscura*.

A non-receptive female reacts exactly as does a non-receptive *D. pseudoobscura* female. The male courts such a non-receptive female by returning to her side and often, but not always, while crouching beside the female, he lifts his middle legs, straightens them out and extends them towards the female and then waves them slowly for a short period. The male then returns to the forward position and postures. Males also court and posture before one another but show few indications of countersignaling.

Rendel (1945) first described the courtship of this species. His descriptions agree well

with the present observations, except that he reports wing flicking on the part of the male, a phenomenon that I saw only very rarely. Rendel timed 10 courtships that ranged from 7 minutes to 13 minutes in length and averaged 10 minutes and 42 seconds.

***Drosophila affinis* Sturtevant**  
Stock No. 1888.1, Ipswich, Massachusetts

This species is similar to *D. pseudoobscura* in most respects, for example, the male's actions in tapping, vibrating, mounting, and in attempting to mount non-receptive females; the female's actions in accepting and in refusing; and, finally, the behavior of the pair during and at the termination of copula.

It differs from *D. pseudoobscura* in that (1) the male often circles a non-receptive female but never postures in front of her; (2) the males countersignal by spreading both wings to 90 degrees and then, while facing each other, slash with their forelegs.

Sturtevant (1921) first reported the mating behavior and observed copulas of 2 minutes and 3 minutes. Miller (1950), using flies from a strain collected in southeastern Nebraska, derived an average copulatory period of 1 minute and 14 seconds as compared to the 1 minute and 46 seconds of the present study. Miller also states that he did not observe tapping on the part of the male. The stocks used in the present study definitely displayed tapping.

***Drosophila azteca* Sturtevant and Dobzhansky**  
Guatemala; Durango, Mexico; Deer Creek,  
California

Except for two differences, the mating behavior of this species is identical with that of *D. affinis*. The two variations are (1) that the male when circling the female usually flicks one wing to 90 degrees while moving past the female's head, and (2) that when a non-receptive female extrudes, the genital plates are not carried posteriorly as a whole, but rather the ventral ends of the plates are carried backward and upward while the dorsal ends remain stationary. This action also pushes the anal tubercle upward and a double papilla-like structure is formed, the appearance of which is quite distinctive.

***Drosophila athabasca* Sturtevant  
and Dobzhansky  
Sundance, Wyoming**

This species exhibits similar mating behavior to that of *D. affinis*, except that the male, when circling, stops in front of the female, extends one wing to about 75 degrees, and holds this position. When he continues with the circling action, he often still holds this wing outward and, on reaching the rear position, extends it to 90 degrees and then vibrates.

***Drosophila algonquin* Sturtevant and Dobzhansky  
Stock No. 1886.1b, Putnam, Connecticut**

*Drosophila algonquin* is similar to *D. affinis* in the method of vibration. A male of *D. algonquin* extends one wing to about 15 degrees or 20 degrees and holds it in this position, then extends it to 90 degrees for vibration. The vibrations are short in duration and almost represent a combination of vibration and waving movements.

Miller (1950) reports an average copular time of 5 minutes and 41 seconds as compared to the average of 5 minutes and 28 seconds in the present study. His specimens were from southeastern Nebraska.

**SUMMARY OF *Drosophila obscura*  
SPECIES GROUP**

All species of the *obscura* group studied show a common basic mating behavior, which consists of the male's tapping, followed by posturing at the side, front, or rear of the female, but never involves licking at any time. The female accepts by spreading the vaginal plates but not the wings. The male achieves intromission by grasping the dorso-lateral surfaces of the female's abdomen with his forelegs and bringing the tip of his abdomen forward and under; he then immediately mounts and spreads the female's wings with his forelegs, aided by the sex combs. The male assumes a "forward" copulatory position, holding onto the bases of the female's wings with his fore tarsal claws. Rhythmical pulsations of the male's abdomen occur during the early phases of copula, near the end of which the male arches back and away from the female, then withdraws and dismounts or turns 180 degrees and withdraws.

Differences in the male's posturing and circling behavior clearly divide the species studied into two sections, which correspond with the taxonomic subgroups that have been established by various workers (see Patterson and Wheeler, 1949).

*Drosophila affinis*, *D. athabasca*, *D. azteca*, and *D. algonquin* males all *circle* the females in typical drosophilid fashion. When in front of the female, males of the last three species normally engage in wing movements of some sort.

*Drosophila pseudoobscura*, *D. persimilis*, and *D. miranda* males normally posture at the side or rear of the female and *never circle in the typical manner*. *D. subobscura* males commence posturing at the side of the female, but the movements are restricted to tapping and occasionally middle-leg waving but never include wing vibrations. Invariably the males of *D. subobscura* then move to the front of the females and engage in a unique and distinctive posturing action. If the courting males of *D. pseudoobscura*, *D. persimilis*, and *D. miranda*, which normally never move into a position in front of a female, do accidentally find themselves there they may engage in a posturing movement that is almost identical with the normal posture of *D. subobscura*. This movement is so distinct and so similar in all four species that it seems logical to conclude that this element of the mating behavior was possessed by an ancestor common to all four species.

As noted above, the males of most of the species of the *affinis* subgroup engage in wing motions when circling in front of the females. Thus the peculiar posture in front of the female that is assumed by the *pseudoobscura* subgroup would appear to represent a hypertrophy of the wing movement which the *affinis* group male engages in while circling the female. Since *D. pseudoobscura*, *D. persimilis*, and *D. miranda* have lost the circling behavior, this posture occurs very infrequently in these species. In comparison, *D. subobscura* uses this type of posture almost exclusively and has lost certain of the typical posturing actions which are common to the members of this species group, i.e., wing vibrations.

As shown by Philip, Rendel, Spurway, and

Haldane (1944), Rendel (1945), and Wallace and Dobzhansky (1946), *D. subobscura* is the single example in this species group that cannot mate in the absence of light. Since *D. subobscura* males do not vibrate but *D. pseudoobscura* and the other species do, these data circumstantially indicate that probably the stimuli from males' wing vibrations are not received by the females of this group via the visual paths.

#### *Drosophila nannoptera* SPECIES GROUP

This species group consists of only one species, *D. nannoptera* (Wheeler, 1949a).

#### *Drosophila nannoptera* Wheeler

Stock No. 1808.1, Oaxaca, Oaxaca, Mexico

The male taps, positions himself at the rear of the female, then licks her ovipositor for protracted periods, simultaneously extends one wing about 20 degrees to 30 degrees from the body and vibrates it rapidly in small amplitude and at the same time rubs the under side of the female's abdomen with both forelegs. The male's body is twisted along the longitudinal axis while wing vibrations are in progress.

A receptive female spreads her wings about 15 degrees and straightens her abdomen, spreading the genital plates. The male mounts, inserting as he mounts, and grasps the female's abdomen with all his legs; his head is extended between the female's wings and his body assumes an almost vertical position. The pair is quiet during copula, at the end of which the male withdraws and then slides off the female.

A non-receptive female refuses by decamping, extruding, and kicking, fluttering, and elevating the abdomen. The extrusion is similar to that found in the *repleta* group (see below).

Males court one another and counter-signal by turning and striking the suitor with their forelegs. Sexually excited males scissor their wings rapidly.

Wheeler (1949a) described this species and, on the basis of egg, pupal, and adult characteristics, places it in the subgenus *Sophophora* where it forms a species group of its own. On the basis of its mating behavior it would seem to belong not to *Sophophora* but rather to the subgenus *Drosophila*.

#### SUMMARY OF THE SUBGENUS *Sophophora*

Excluding *D. nannoptera*, all the species of this subgenus so far studied uniformly display certain elements in their mating behavior that distinguish them from the species of other subgenera:

1. When the male licks the female ovipositor, the duration of time involved for each "licking period" is always extremely short.

2. When the male uses his legs in posturing, he always strikes downward and never rubs the ventral surface of the female's abdomen. The leg motion is always a sharp quick action and never involves prolonged contact with the female's body.

3. The usual position assumed by the male in copula is well forward so that his forelegs grasp, or are in contact with, the female's thorax or the base of the female's wings. Within the *D. melanogaster* group there are exceptions to this (*D. auraria* and its relatives), but this is clearly a modification involving the use of the unique sex combs in grasping the female. Also some members of the *willistoni* group assume a somewhat "rearward" copulatory position.

4. Intromission is typically achieved by the male either before or simultaneously with mounting, but again the same specialized species within the *melanogaster* group are exceptional in that they accomplish intromission after lunging onto the female.

5. The females of many species spread their wings widely (70 degrees to 90 degrees) as part of the acceptance response. Others do not, but invariably such females have males that possess sex combs.

6. Dismounting normally involves the male arching upward and backward just before the termination of copula and then turning 180 degrees and withdrawing.

This combination of mating-behavior actions seems restricted to species that have been placed in the subgenus *Sophophora*, and the present findings give support to the classification as it is now constructed with the exception of the unique *D. nannoptera*.

In general, distance stimuli seem to play a major part in the mating behavior, on the part of both the female and the male. This is substantiated by the relatively small

amount of actual physical contact between the sexes (again excepting *D. auraria*, *D. montium*, *D. rufa*, and *D. ananassae*) and also indirectly by the fact that the only known species that are "light dependent" in their mating behavior are to be found in this subgenus.

#### SUBGENUS *DROSOPHILA* FALLÉN

This is the largest of all the subgenera. Wheeler (1949a) and Patterson and Wheeler (1949) have divided the subgenus into 20 species groups which range in size from one to 47 species. Their arrangement of classification has been followed in the present study, since it serves as a convenient form for the discussion of the groups.

#### *Drosophila quinaria* SPECIES GROUP

This group consists of 16 species distributed primarily in the Nearctic, with a few in the Palearctic and one from the Oriental region. Eleven of these species have been used in the present study.

#### *Drosophila innublia* Spencer

Stock No. 1324.6, Lincoln National Park,  
Lincoln County, New Mexico

The male taps, goes to the rear, taps, flicks one wing outward to 90 degrees, with the wing vane horizontal, occasionally taps the dorsum of the female's abdomen, then lunges onto the female, thrusting outstretched forelegs under her wings and above the dorsum of her abdomen. At the same time he jerks the tip of his abdomen forward and against the female's ovipositor.

A non-receptive female depresses her abdomen, flutters her wings, kicks, and keeps the vaginal plates appressed. Such a female has little difficulty in repelling the courting male, and often the fluttering of the wings prevents the male from lunging, thus breaking off the courtship.

Males court and attempt to copulate with one another but appear to have no counter-signaling action.

No acceptances resulted, although the males courted vigorously, during four observations, in which 37 males and 25 females were used. Wheeler (1947) reports one copula for this species, with a duration of 3 minutes.

#### *Drosophila munda* Spencer

Stock No. 929.8, Cave Creek, Chiricahua,  
Arizona

The male taps, moves to the rear, rubs the dorsum of the female's abdomen with his forelegs, and licks the female's ovipositor. The forelegs of the male are drawn backward and forward along the female's dorsum, and each leg is used alternately, i.e., while one leg is being drawn backward the other leg is moving forward. This alternating type of motion is typical of all species of the *quinaria* group, as well as of most of the other species of the subgenus *Drosophila*. The male then changes the position of his forelegs from the dorsal to the ventral surface of the female's abdomen and proceeds to rub the ventral surface.

The female accepts by spreading her wings outward and upward to 75 degrees, at the same time drooping the tip of her abdomen and spreading the vaginal plates. The male mounts and accomplishes intromission after mounting. The female spins about for 2 to 3 minutes, and then the pair remains quiet, except that the male occasionally rubs the side of the female's abdomen. The male holds onto the female's abdomen exclusively, grasping the anterodorsal surface of her abdomen with his fore tarsal claws. At the end of copula, the male withdraws and slides off.

A non-receptive female repels by kicking, fluttering, and decamping. Males court one another and repel (countersignal) by means of fluttering.

Wheeler (1947) observed two copulas which averaged 3 minutes and 40 seconds, considerably less than the average of 8 minutes and 47 seconds observed in the present study.

#### *Drosophila occidentalis* Spencer

Stock No. 1974.5, Dark Canyon, California

The male taps, goes to the rear, extends his forelegs under the female's wings and rubs (claws) the dorsum of her abdomen, moving his legs alternately. At the same time the male flicks one wing to 90 degrees and licks the female's ovipositor.

The female accepts by spreading her wings to 90 degrees, drooping the tip of her abdomen, and spreading her vaginal plates.



The male mounts and then inserts, holding on as in *D. munda* but not rubbing the female's side. The pair is quiet during copula; at the end, the male turns 180 degrees and withdraws.

The non-receptive female repels by kicking, fluttering, and elevating her abdomen, but not by extruding. Males court one another but do not countersignal. Occasionally the males attempt to mount non-receptive females.

***Drosophila suboccidentalis* Spencer**  
Stock No. 1942.5, Reno, Nevada

The mating behavior of this species is identical with that of *D. occidentalis*. The average time of copula obtained in this study was 13 minutes and 44 seconds. Wheeler (1947) reports about 10 minutes for several copulas, and Blumel (1949) records about 6 minutes and 30 seconds as the average time for the species. Blumel used Stock No. 1763.5 from Glacier National Park, Montana.

***Drosophila palustris* Spencer**  
Stock No. 1757.13, Bemidji, Minnesota

The male taps, goes to the rear, rubs the dorsal surface of the female's abdomen with his forelegs, flicks one wing to 90 degrees, and tries to lick the female's ovipositor.

A receptive female shortens and raises her abdomen and spreads the vaginal plates, allowing the male to lick, but she does not spread her wings. The male mounts well forward, spreading the female's wings with his body and grasping the base of her wings with his fore tarsi. After mounting, the male achieves intromission. The pair is quiet during copula, and at the end the male withdraws, then either slides off or turns 90 degrees to dismount.

The non-receptive female repels by kicking, fluttering, decamping, or by holding the tip of her abdomen close to the substratum. Males occasionally attempt to mount such females.

Males court one another, often facing one another, posturing and attempting to mount. The males apparently have no method of countersignaling but do slash at one another with their forelegs.

Blumel (1949) reports on the mating time of four pairs of this species which averaged about 7 minutes and 30 seconds. This compares closely with the 7 minutes and 16 seconds of the present study.

***Drosophila subpalustris* Spencer**  
Stock No. 1877.9, Santee River, Georgetown, South Carolina

The male taps, goes to the rear of the female, rubs the dorsum of her abdomen with his legs, occasionally extends his proboscis but does not lick nor does he engage in wing movements.

A receptive female slightly elevates her abdomen and spreads the vaginal plates. The male curls his abdomen under, lunges onto the female, grasps the anterodorsal surface of her abdomen, and achieves intromission. Usually the female spreads her wings just after the male has mounted. The pair is quiet during copula, at the end of which the male turns 180 degrees and dismounts.

A non-receptive female kicks, flutters, depresses, and decamps. The male circles a non-receptive female. Males court one another as freely as they do females, but display no effective countersignaling mechanism. Infrequently the males attempt to mount non-receptive females.

***Drosophila phalerata* Meigen**  
Stock No. 1915.1, Beirut, Lebanon

The male taps, positions himself close behind the female, flicks one wing to 90 degrees, and then lunges onto the female, grasping her abdomen with his legs, spreading her wings with his head, and bringing the tip of his abdomen against her genitalia. At the same time he continues to flick one wing.

A receptive female shortens and compresses her abdomen, spreads the vaginal plates, and allows the male to achieve intromission. The male then pushes his way between the female's wings and grasps the base of her wings. The pair is quiet until termination of copula when the male turns 180 degrees and withdraws.

A non-receptive female kicks, decamps, flutters, depresses, turns and faces the courting male, or, if the male does mount,

quickly dislodges him in 4 to 10 seconds by kicking and fluttering. These unsuccessful mountings appear like copulas in that the male accurately places his genitalia in contact with the female genitalia, but is not able to achieve intromission. Males circle non-receptive females and also court and try to copulate with one another.

***Drosophila quinaria* Loew**

Stock No. 1753.7, Lake Shetek, Currie,  
Minnesota

The male taps, positions himself close behind the female, lunges towards her, extending and thrusting his forelegs under her wings, and then claws the dorsum of her abdomen. At the same time he thrusts himself upward and brings the tip of his abdomen sharply forward and against the female's ovipositor.

A receptive female spreads her wings about 75 degrees, as the male claws. The male grasps her abdomen with his legs and, having mounted, then achieves intromission. During copula the pair is quiet, with the male holding onto the female's abdomen. At the termination, the male withdraws and slides off.

A non-receptive female decamps, kicks, flutters, and depresses her abdomen and wings. Often a male will lunge at a non-receptive female, his extended forelegs will fail to get under the female's wings, he will "overrun" her, and end standing upon her thorax and head. Males court and try to mount one another. The courted male then depresses his abdomen and wings.

***Drosophila subquinaria* Spencer**

Stock No. 1902.9, Clare, Michigan

The male taps, goes to the rear, positions himself close behind the female, with his head under her wings, proceeds to lick and simultaneously rub the ventral abdominal region surrounding the female's ovipositor with his forelegs. Occasionally he scissors one wing very rapidly.

The female accepts by spreading the vaginal plates. The male grasps the antero-dorsal surface of her abdomen with his forelegs and then achieves intromission. Just after the male mounts, the female spreads

her wings, and thus wing spreading is not part of the acceptance response. During the early part of copula, the female is restless, vibrates her wings, and kicks; then the pair is quiet until termination when the male turns 180 degrees and withdraws.

A non-receptive female repels by kicking, fluttering, and decamping. Occasionally a male circles such a female and also tries to mount.

Males court one another and countersignal by fluttering.

Wheeler (1947) reports 8 minutes and 45 seconds as the average copulatory time for this species, which compares well with the average of 9 minutes and 42 seconds for the present study.

***Drosophila tenebrosa* Spencer**

Stock No. 1958.7b, Pojwache, New Mexico

The male taps, goes to the rear of the female, licks her ovipositor, and taps the sides of her abdomen with his forelegs. The tapping motion is atypical for the *quinaria* species group in that both legs are moved up and down synchronously and not alternately. Furthermore, the sides of the female's abdomen rather than the dorsum are struck. At the same time the male flicks one wing rapidly and vigorously, carrying the vane of the wing forward in a *vertical* position. Often his flicking is so vigorous that the tip of the wing is carried beyond the male's head.

One copula was incompletely recorded, since the observation started after the male had mounted. The male holds onto the female's abdomen, and at termination withdraws and slides off.

A non-receptive female flutters, kicks, and decamps. Occasionally a male will try unsuccessfully to mount. Males infrequently court one another.

Blumel (1949) reports that three copulas averaged about 6 minutes.

***Drosophila transversa* Fallén**

Stock No. 1062.6, Great Smoky Mountains,  
Tennessee

The male taps, positions himself at the rear of the female, with his head under her wings, curls the tip of his abdomen under and extends one wing 20 degrees to 30 degrees

and *vibrates it in bursts* of activity. The male then lunges onto the female, grasping her with his legs, especially the forelegs, and then tries to achieve intromission.

A receptive female slightly straightens her abdomen and spreads the vaginal plates, allowing the male to insert. Usually the male grasps the anterodorsal surface of the female's abdomen, but sometimes he pushes himself forward between her wings and grasps the base of her wings with his fore tarsal claws. At the end of the copula, the male turns 180 degrees and withdraws.

A non-receptive female repels by fluttering, kicking, and depressing, and by decamping. The male circles a non-receptive female, scissoring one wing as he moves about her. Males court and try to mount one another but show no signs of countersignaling.

#### SUMMARY OF *Drosophila quinaria* SPECIES GROUP

The 10 species of this group that were studied show considerable variation. The males of some species vibrate (*D. transversa*); others scissor their wings, and some do not use their wings in posturing. Some lick, and others show no signs of such behavior. The mating behavior of *D. transversa* is reminiscent of that of *D. ananassae*, although the wing vibration is quantitatively different. At the other extreme *D. munda* is similar in many respects to the *D. funebris* species group in its mating behavior.

Some constantly recurring features, however, are displayed by the species studied, for example: (1) none of the females extrudes either before or after copulation; (2) posturing always occurs at the rear of the female; (3) the males all rub, tap, or grab the dorsum of the female's abdomen with their forelegs sometime during courting and mounting; (4) no effective method of countersignaling exists between the males except in the instance of *D. munda* and *D. subquinaria*.

#### *Drosophila polychaeta* SPECIES GROUP

Sturtevant (1942) placed three species in this group, and Patterson and Wheeler (1949) follow this classification. Of the three, only one, *D. polychaeta*, was studied.

#### *Drosophila polychaeta* Patterson and Wheeler Stock No. 119.62, Galveston, Texas

The male taps, moves to the rear position, "ducks" under the wings of the courted individual, and licks quickly and briefly the genitalia, tapping the abdomen at the same time with the forelegs. If a male is being courted, courtship is broken at this point, but if a female is being courted the male quickly raises his forelegs outward and upward, thus moving the legs around and above the female's wings, and then grasps either the costal margin or the dorsal surface of the female's wings with his fore tarsal claws. At the same time the abdomen is curled forward and genitalic contact is quickly made. These movements force the tips of the male's wings against the substratum and spread each about 15 degrees from the midline. The male thus rests his weight on his hind legs and wing tips.

No acceptance response of any sort was evinced by the female other than that she did not decamp. Often the female would not accept the male that mounted, and such males were unable to achieve intromission. Perhaps receptive females spread their vaginal plates as the males attempt to achieve copula.

During the short copulatory period, the pair is quiet, and at the end of copula the male withdraws and dismounts by a backward-sliding movement.

Non-receptive females, in addition to not allowing the males to achieve intromission, avoid the males' overtures by decamping. Otherwise, they give no indication of repelling actions.

The copula period averages 25 seconds and is the shortest of that in any known species. The females, however, will and do copulate repeatedly within a short period of time. Thus, four 10-day old females copulated 21 times with eight males during a single half-hour observation period. Perhaps normal insemination in this species requires multiple copulations. The males court other males repeatedly in a normal fashion but do not attempt to mount one another. There is no visible countersignaling of any sort, but some type must exist since the males repeatedly try to mount non-receptive as well as receptive females.

Sturtevant (1942) describes the mating behavior of this species, and his description agrees with the present one except that he observed both the forelegs and middle legs of the male were used to grasp the female's wings during copulation. Sturtevant records the average copulation time to be about 30 seconds, which agrees well with the present observation of 25 seconds.

Despite the aberrant character of the copular behavior, the courtship actions clearly indicate that *D. polychaeta* is a member of the subgenus *Drosophila*, and the tapping, licking, mounting, and methods of grasping the female's wings and the copular position indicate that *D. polychaeta* is related perhaps more closely to the *quinaria* species group than to any other group so far studied. The multiple copulas, the extremely short copulatory period, the lack of both visible accepting and repelling responses on the part of the female are unique and clearly separate *D. polychaeta* from all other known species.

#### *Drosophila guttifera* SPECIES GROUP

Only a single species is placed in this group (Wheeler, 1949a; Patterson and Wheeler, 1949).

*Drosophila guttifera* Walker  
Stock No. 1589.7, Arkansas River,  
Morrilton, Arkansas

The male taps, goes to the rear of the female, gingerly approaches her with outstretched proboscis, and licks her ovipositor. At the same time he raises and extends his forelegs, and strikes sharply downward, hitting the dorsolateral surfaces of the female's abdomen.

A receptive female spreads her wings widely, slightly elongates and elevates the tip of her abdomen, and spreads the vaginal plates. The male must lick the surface between the vaginal plate area before he will mount. If, as happens in some instances, his proboscis is in contact only with the sides of the ovipositor or even against the ventral sternites, he never mounts. He mounts well forward, holding onto the female's thorax with his fore tarsi, and she then shortens her abdomen, elevates the tip,

and allows the male to achieve intromission.

Except for pulsations of the male's abdomen during the first few minutes of copula, the pair is quiet until just before the end when the female begins to kick with her hind legs. The male terminates copula by withdrawing and then dismounting.

A non-receptive female repels by decamping and kicking. Males court one another and are attracted to courting pairs. They may form a chain of three and four individuals consisting of a female followed by males, the first one courting the female and the others courting the preceding male.

This species shows the relationship to the *quinaria* species group in the manner in which the courting male uses his forelegs. The method of licking is similar to that of the *funbris* species group, and the necessity of the male's licking the inner surfaces of the female's genitalia before mounting is typical of many species of the subgenus *Drosophila*.

#### *Drosophila tripunctata* SPECIES GROUP

Patterson and Wheeler place two Nearctic and one Neotropical species in this group. Two of these have been studied.

*Drosophila tripunctata* Loew  
Stock No. 1910.4, Dexter, Missouri

The male taps at the side and then flicks one wing to 90 degrees. The tapping and wing movement may be repeated several times. The male then goes to the rear, extends one wing 75 degrees to 90 degrees and vibrates slowly, simultaneously licking and tapping with his forelegs.

A receptive female spreads her wings widely, elevates the tip of her abdomen, and spreads the vaginal plates. She may do so when the male taps and flicks or when he is posturing at the rear. Often a female gives the acceptance response while a male is courting *another* female. The male mounts only after he has licked the female's genitalia; he inserts either after he has mounted or just as he mounts. He grasps the anterodorsal surface of the female's abdomen with his fore tarsal claws, and during copula the pair is quiet except for occasional kicking on the part of the female. Towards the end of copula, the male slides backward so that his

grasp is only on the posterior part of the female's abdomen. At termination the male withdraws and dismounts either by sliding off backward or jumping off.

Non-receptive females decamp and kick, but do not flutter or extrude. Males circle such non-receptive females.

Males court one another aggressively. They tap, face towards one another, and scissor one wing. Often they actually butt and push against one another in a "shoulder-to-shoulder" position. Fluttering appears to be absent.

Wheeler (1947) reports an average copulatory length of 48 minutes, with a maximum time of 82 minutes. This compares with 33 minutes and 25 seconds and 47 minutes and 1 second, respectively, for the present study.

***Drosophila crocina* Patterson and Mainland**  
Stock No. 1383.10, Vera Cruz, Mexico

The male taps, goes to the rear, licks, taps the dorsum of the female, and occasionally extends one wing about 15 degrees to 20 degrees and vibrates. The male twists his body slightly on the longitudinal axis while vibrating and also curls the tip of his abdomen under. He mounts and then achieves intromission. During copula he grasps the anterodorsal surface of the female's abdomen, and the pair is relatively quiet, although the female occasionally kicks with her hind legs. The male withdraws and then dismounts by sliding off backward.

Non-receptive females decamp, kick, and flutter. Males rarely circle such females. Males court one another vigorously and countersignal by fluttering.

Only two copulations were observed, and the acceptance response was not observed in either. In one case, however, observation was begun just as the male had mounted and before he had accomplished coitus. Apparently the female accepts by spreading her wings and vaginal plates.

**SUMMARY OF *Drosophila tripunctata***  
**SPECIES GROUP**

These two species (*D. tripunctata* Loew and *D. crocina* Patterson and Mainland), on the basis of their mating behavior, show relationship to the *quinaria* group on one

hand and to the *funnebris* group on the other. The long copulatory period also indicates the relationship to these two groups.

***Drosophila funnebris* SPECIES GROUP**

Four species, one cosmopolitan and three Nearctic, constitute this species group (Patterson and Wheeler, 1949). One of the species (*D. macrospina*) is made up of three geographical subspecies. All the members of the group have been studied.

***Drosophila funnebris* (Fabricius)**

Stock No. 1732.3, Ain Anub, Lebanon;

Stock No. 1767.10, New Meadows, Idaho

The male taps, goes to the rear, licks the female ovipositor, and flicks one wing to 90 degrees. A receptive female elevates the tip of her abdomen, spreads the vaginal plates, extends both wings to 90 degrees, and rotates each wing so that the vane is vertical, with the posterior edge ventral. The male mounts and inserts. Within 30 seconds the female rotates the wing vane to normal position and relaxes it against the male's body. The male holds onto her wing bases with his forelegs. The pair is quiet during copula until just before termination when the female kicks and moves about. The male terminates copula by withdrawing and then sliding off.

A non-receptive female repels by decamping, fluttering, kicking, preening, and turning the tip of her abdomen towards the male's face, although there is no visible extrusion. The male circles a non-receptive female and occasionally tries to mount. He courts other males and tries to mount them. The males countersignal by fluttering. Infrequently they fight in a manner reminiscent of *D. virilis*. A male never mounts a receptive female until he has licked, even though she gives the acceptance response at the tapping stage.

Sturtevant (1921) first described the mating behavior of this species. Wheeler (1947) gives an average copulatory time of 16 minutes and 33 seconds which agrees closely with the present findings of 16 minutes and 52 seconds. Uncourted but receptive females often give the acceptance response when a near-by male courting another female scissors his wings. The position with respect to each other seems not to have any

influence. This species is much like *D. virilis* and its relatives in this respect.

***Drosophila subfunnebris* Stalker and Spencer**  
Pasadena, California

The male taps, moves to the rear, and licks the female's ovipositor, but does not scissor or vibrate his wings.

A receptive female spreads her wings and vaginal plates and droops the tip of her abdomen. The male mounts and then inserts, grasping the female's thorax or wing bases with his fore tarsi. During copula the pair is relatively quiet and at the end the male withdraws, using his hind tibia to push against the region of genitalic union, and then dismounts. The males are similar to those of *D. funnebris* in that they refuse to mount before they have licked the female's ovipositor.

A non-receptive female kicks, flutters, elevates her abdomen, and decamps. The male does not circle such a female completely, but merely circles to her side, taps, and often places all feet widely apart and then rapidly raises his body up and down in a series of quick movements.

Males court one another, try to mount one another, and countersignal by fluttering vigorously. Often a courted male extends his wing on the side closest to a suitor and then drives against him vigorously, striking the side of his body sharply against the suitor.

Wheeler (1947) reports an average copulatory time of 23 minutes and 30 seconds which is considerably less than the 37 minutes and 31 seconds of the present study.

***Drosophila macrospina macrospina***

Stalker and Spencer

Stock No. 1897.10, Alleghany State Park,  
New York

The male taps, moves to the rear of the female, ducks under her wings, and licks. The receptive female spreads her wings, droops her abdomen, and spreads her vaginal plates. The male mounts and then inserts. During copula the male assumes a position like that of *D. subfunnebris* and at the end withdraws and then dismounts.

A non-receptive female repels by kicking, fluttering, depressing the tip of her abdomen, and decamping. The male extends the pro-

boscis when attempting to lick, and gingerly approaches the female. The slightest kicking motion on the part of the female will prevent the male from licking. He repeatedly and rapidly circles a non-receptive female, and occasionally scissors both wings to 90 degrees as he passes in front of her. The individuals of this species spar with both forelegs and middle legs, and the females usually spar with circling males.

The males court one another and countersignal by sparring and by fluttering their wings and by spinning and slashing at the suitor.

Wheeler (1947) records an average copulation time of about 35 minutes which is considerably lower than the 46 minutes and 9 seconds of the present study.

***Drosophila macrospina limpiensis***  
Mainland

Stock No. 1248.1b, San Bernardino, Arizona

The mating behavior of this subspecies is identical in all respects with that of *D. macrospina macrospina*. Two copulations were timed at 36 minutes and 37 seconds and 47 minutes and 15 seconds, respectively, while a third copulation, which appeared normal in all respects, lasted for only 6 minutes and 18 seconds.

***Drosophila macrospina ohioensis* Spencer**  
Stock No. 1035.3, Piqua, Ohio

The mating behavior of this subspecies appears to be identical with that of *D. macrospina macrospina*, but no copulations were observed.

***Drosophila trispina* Wheeler**

Stock No. 1858.5, Earp, California

The mating behavior of *D. trispina* is much like that of *D. subfunnebris* and *D. macrospina*. The following actions seem distinctive: (1) like *D. subfunnebris* the male circles mainly about the side and rear of the female; (2) while posturing at the rear, the male flicks one wing rapidly as does *D. funnebris*; (3) the courtship time appears to be relatively short and similar to that of *D. funnebris*. In all other respects *D. trispina* is similar to both *D. macrospina* and *D. subfunnebris*.

SUMMARY OF *Drosophila funebris*  
SPECIES GROUP

The mating behavior of the *funebris* group is relatively uniform and conforms to the basic pattern found in the subgenus *Drosophila*. The repelling actions of the females, the gingerly fashion in which the males ready to engage in licking approach the females, and their general courting demeanor are reminiscent of the *quinaria* group. The aggressiveness of the males, their habit of "fighting" with one another when sexually excited indicates a slight similarity to the *virilis* group.

*Drosophila cardini* SPECIES GROUP

Of the nine species that Patterson and Wheeler (1949) place in this group, four were available for the present study. The group is Neotropical in distribution, but ranges of three of the species extend into the southern edge of the Nearctic region.

*Drosophila cardini* Sturtevant  
Stock No. 1797.1, Mexico City, Mexico

The male taps, circles in front of the female, moves back and forth in front of her several times, following an arc-like path, then runs to the rear of the female, extends his proboscis, and attempts to lick the female's genitalia. Occasionally a male concurrently caresses the dorsolateral side of the abdomen with his forelegs. There are no wing movements of any type on the part of the male.

Non-receptive females decamp, kick, and flutter when the male is in the rear position but do not extrude. Occasionally a female rotates her body along the longitudinal axis, extends the middle leg of the elevated side out straight and parallel to the substratum, and fends off the courting male. The males do not attempt to mount non-receptive females nor do they court one another.

Eleven observations, utilizing 53 males and 89 females, resulted in no copulations. The specimens ranged in age from four to 19 days, with the bulk of the individuals four to eight days old. Sturtevant (1942) observed copulas of this species and reports that the female spreads her wings before the male mounts. Wheeler (1947), using flies of

four days of age, observed copulation to last "about 23' 45".

*Drosophila cardinoides* Dobzhansky and Pavan  
Stock No. 1413.3, Guatemala City,  
Guatemala

The male taps, goes to the rear position behind the female, extends his proboscis, and licks the female's genitalia. Concurrently he repeatedly flicks one wing to 90 degrees. The fore legs are not used to caress the female, and the male does not circle.

Females repulse the courting males by fluttering, kicking, and decamping, but do not extrude. The males do not attempt to mount non-receptive females.

Six observations, using 48 males and 62 females ranging in age from five to eight days, resulted in no copulations. The males courted steadily and persistently, but the females refused all overtures.

*Drosophila neocardini* Streisinger  
Stock No. 1802a, Atlitico, Mexico

The male taps, goes to the rear, extends his proboscis, and attempts to lick the female's genitalia. Concurrently he repeatedly waves (flicks) one wing to 90 degrees from the mid-line and simultaneously rotates the vane in a vertical position, with the posterior wing margin near the substratum. If the female kicks with her hind legs when the male is licking or attempting to lick, then the male brings his forelegs forward so that the fore femora are parallel along each side of the proboscis, and at the same time he curves the fore tibia and tarsi outward from the femora with these structures parallel to the substratum. The base of the tibia is at right angles to the femur, directed outward, and the combined tibia and tarsus form a smooth arc, with the tip of the tarsus directed posteriorly. This striking position of the forelegs appears to serve as an efficient guard against the kicking movements of the female's hind legs. Males circle non-receptive females, usually interrupting the circling action to stop in front of one of the female's eyes and posture briefly. Such posturing consists of extending the proboscis towards the female and simultaneously waving one wing to 90 degrees, with the vane held vertically.



A receptive female spreads the vaginal plates, but not the wings, and the male mounts and then inserts. During copula the male grasps the anterodorsal surface of the female's abdomen with his fore tarsal claws. At the end of copula, the male withdraws and dismounts by sliding off backward. During the first and last part of the copular period, the female may switch her body and vibrate her wings.

Non-receptive females refuse the males' overtures by fluttering and kicking, and by decamping, but not by extruding or depressing. Fluttering and kicking appear to be the typical methods for repelling the males. Males do not attempt to mount non-receptive females.

Males court one another and countersignal by fluttering and kicking.

Two copulas occurred during 16 observations, utilizing 99 males and 169 females. The individuals varied from three to 19 days in age, and the copulas occurred between 17-day old specimens. During every observation, regardless of age or appearance of the individuals, the males courted vigorously and persistently, but except for two individuals every female was thoroughly recalcitrant to the males' overtures.

***Drosophila polymorpha* Dobzhansky and Pavan**  
Locality unknown

The male taps, then moves to the front of the female and places himself diagonally in front of one of her eyes. In this position, he extends his proboscis, but does not touch the female, and then vibrates one or both wings. After posturing in the front of her, he then races to the rear and attempts to lick the female's vaginal plates.

A receptive female spreads her wings slightly and probably the vaginal plates (see below), and the male mounts and then inserts. During copula, the pair is mostly quiet, but occasionally the female kicks with her hind legs and the male sometimes strokes the sides of her abdomen with his middle legs.

The observations on this species were conducted in 1946, and the recorded data are incomplete. Only one copula was observed, and it was not noted whether the female

spread her vaginal plates or not, how the male dismounted, or how the non-receptive female responded other than that she decamped.

**SUMMARY OF *Drosophila cardini***  
**SPECIES GROUP**

The four species studied constitute the full complement of species which Wheeler (1947) places in subgroup b. Even though belonging to one subgroup, the species show considerable difference in mating behavior, for example: (1) *cardinoides* does not circle the female and consequently never postures in front of her, while the other three do circle and all posture in front of the female to some degree; (2) *polymorpha* males vibrate one or both wings, *cardinoides* and *neocardini* wave one wing, while the *cardini* males display no wing movements at all; (3) the female of *polymorpha* spreads her wings when giving the acceptance response, but *neocardini* females do not (females of the other two species did not accept the males' overtures).

The four species show similarity in that (1) none of the males attempts to mount a non-receptive female; (2) the males are persistent suitors but typically do not court one another; (3) the females do not seem able to extrude; (4) kicking and fluttering on the part of the female is the chief method of repelling the courting males; (5) on the basis of the data available (table 1), a relatively long copulatory period is indicated.

As a whole, the subgroup conforms to the main features of the mating pattern of the subgenus *Drosophila* and within this subgroup appears to be more closely related to the *D. funebris* and *D. tripunctata* species group than to any other.

***Drosophila testacea* SPECIES GROUP**

Two species, *D. testacea* and *D. putrida*, belong to this species group. Only one of these, *D. putrida*, was available for the present study.

***Drosophila putrida* Sturtevant**  
Stock No. 1971.2b, St. Paul, Minnesota;  
Stock No. 1773.4, Texarkana, Texas;  
Austin, Texas

The male taps, goes to the rear, scissors

one wing to 90 degrees, and gingerly approaches the female with outstretched proboscis and attempts to lick. A non-receptive female spreads her wings apart slightly, then elevates them vertically and snaps them sharply down against the abdomen. Such wing snapping, which is apparently a modified type of fluttering, is done while the male is scissoring. When the male attempts to lick, the female also kicks, easily repelling the male. The males circle such non-receptive females and also court one another. They countersignal by fluttering, and the courted individual often spins and slashes at the suitor.

No copulas were observed in this species, although four different stocks were used, two of which were collected specifically for this study. In addition, numerous observations were made on mass cultures with the hope that at least one copula might be recorded.

Wheeler (1947) gives the average length of copula as about 29 minutes for this species. On the basis of the known courting behavior and the length of the copular period, *D. putrida* seems to be closely related to the *junebris* group.

#### *Drosophila virilis* SPECIES GROUP

This group consists of seven species,<sup>1</sup> one of which is represented by the two subspecies, i.e., *D. americana americana* and *D. americana texana* (Wheeler, 1949; Patterson and Wheeler, 1949). All the species and subspecies of the group, except *D. littoralis* Meigen and *D. imeretensis* Sokolov, were available for study. *D. virilis*, a domestic species, is practically cosmopolitan, while the wild species are all Holarctic in distribution.

#### *Drosophila virilis* Sturtevant

Stock No. 1801.1, Texmelucan, Puebla,  
Mexico

The male taps, goes to the rear of the female, "ducks" under her wings, extends his

proboscis, licks the female's ovipositor, and at the same time extends his forelegs and rubs the ventral surface of the female's abdomen. Such rubbing is done rapidly, with the legs moving alternately back and forth. Considerable force is exerted by the male since his rapidly moving legs gradually slip laterally and on reaching the lateral edge of the female's abdomen slide off and upward with a sharp, quick movement that often carries them well above the level of the female's body. The male also exerts force in a forward and upward direction when licking, and thus often pushes the tip of the female's abdomen upward. Licking and rubbing typically occur together and extend over relatively long periods, with only occasional short pauses. Meanwhile either of the male's wings is singly extended from the resting position 10 degrees to 15 degrees and vibrated rapidly but intermittently.

A receptive female accepts by spreading her wings outward and upward 45 degrees, and at the same time she spreads her vaginal plates. The male mounts and typically achieves intromission after mounting, but occasionally inserts just as he mounts. Upon mounting he grasps the base of the female's wings with his fore tarsi. During copula he rubs the sides of the female's abdomen with his mesothoracic legs, doing so in intermittent and rapid bursts of movement.

The pair is quiet during copula until near the end when the female becomes restless, kicks with her hind legs, and walks about. At termination, the male withdraws and then dismounts by sliding off backward or turning to one side.

Non-receptive females refuse by decamping, kicking with their hind legs, and fluttering, as well as by depressing the wings and abdomen so that the male is never able to position himself correctly for posturing. Fecundated females repel by kicking but not by fluttering. When licked, they display an extrusion that appears to involve the raising and extending of the vaginal plates. Such extrusion does not repel the males from courting. Individuals of this species also often wave or scissor one wing to 90 degrees when approached by another individual. This appears to be a general repelling reaction

<sup>1</sup> Patterson (1952a) has shown that *Drosophila littoralis* Meigen belongs to the *virilis* species group. In addition, Patterson (1952b) has described *Drosophila borealis* and *D. flavomontana*, both of which he places in the *virilis* species group. These last two species have a mating behavior identical with that of *D. montana*. The mating behavior of *D. littoralis* is unknown.

and often replaces the sparring action of the middle leg which is displayed by many species of other groups.

The males are aggressive suitors and court non-receptive females persistently, often circling about the females but very rarely do they try to mount such females. They also court one another and display no effective countersignaling movements. Often chains of individuals are found consisting of a female in front being courted by a male, with the following individuals being males courting one another. Sexually excited males engage in what can best be described as fighting. Such a male extends his legs, raising his body from the normal position and at the same time arching the abdomen laterally so that the concave surface of the abdomen is facing his adversary, and then rushes and pushes the other male. Typically the two males face in opposite directions, so positioned that the tip of each abdomen is against the opponent's thorax. The ensuing rough-and-tumble activities continue for periods of a few seconds to a minute or two, and usually result in the flight of one male.

Sturtevant (1921) first described the mating behavior of *D. virilis*. Stalker (1942) observed the mating behavior of *D. virilis* and *D. americana americana*. Spieth (1951) has reported on this species and some of its relatives in detail.

***Drosophila americana americana*** Spencer  
Stock No. 1899.6b, Chagrin Falls, Ohio; Stock No. 1761.9a, Chinook, Montana; Stock No. 1760.8i, Poplar, Montana; Stock No. 1773.4i, Chadron, Nebraska; Independence No. 2, Defiance, Ohio; Smithville, Smithville, Ohio; Stock No. 1882, Millersburg, Pennsylvania

The mating behavior of this species is identical with that of *D. virilis*, except that the sexual drive is invariably lower. Furthermore, there are definite differences in sexual drive between the stocks from the western part of the species range and those from the eastern sections of the range (Spieth, 1951).

***Drosophila americana texana*** Patterson,  
Stone, and Griffen  
Stock No. 1128.10, New Orleans, Louisiana;  
Stock No. 1148.9, Lake McKethan, Florida  
The mating behavior is identical with that

of *D. americana americana*, but the males are more persistent suitors, especially when compared to those of western *D. americana americana* stocks.

***Drosophila novamexicana*** Patterson  
Stock No. 1720.7, Gila River, Gila, New Mexico;  
Stock No. 1714.4, San Antonio, New Mexico;  
Stock No. 1954.3a, White Water, Colorado

The mating behavior is similar to that of *D. virilis*. The males are aggressive and "fight" with one another more than do those of any other species.

***Drosophila lacicola*** Patterson  
Stock No. 1360.1, Fairbanks, Minnesota

This species displays a low sexual drive, but the mating behavior throughout is similar to that of *D. virilis* except that during copula the male does not rub the female with his middle legs.

***Drosophila montana*** Patterson and Wheeler  
Stock No. 1218.8d, Cottonwood Canyon, Utah; Stock No. 1862.2a, Lake Tahoe, California

This species is identical in mating behavior with its close relative *D. lacicola*. Two stocks were observed which gave quite different averages for the copular period. Stock 1218.8d ranged from 3 minutes to 6 minutes and 3 seconds, with an average of 4 minutes and 17 seconds. Stock 1862.2a was much lower, ranging from 1 minute and 21 seconds to 2 minutes and 18 seconds, with an average of 1 minute and 58 seconds. This is the only known instance where the copular time of two stocks of the same species shows no overlap between the minimum time of one stock and the maximum time of another. The averages are wide apart and indicate that a considerable difference exists in the mating physiology of these two stocks.

#### SUMMARY OF *Drosophila virilis* SPECIES GROUP

The mating behavior confirms other data that this species group forms a closely related, compact series of species and subspecies. The group can be divided, however, into two sections on the basis of mating behavior, i.e., *D. montana* and *D. lacicola* form

one section, which is clearly distinct from the other section that is comprised of the other known species of the group.

#### *Drosophila carbonaria* SPECIES GROUP

A single species, the unique *D. carbonaria*, belongs to this species group (Patterson and Wheeler, 1949). Adult specimens captured in the field were used for observation.

#### *Drosophila carbonaria* Patterson and Wheeler Austin, Texas

The male taps, moves to the rear of the female, positions himself under the tips of her wings, extends his proboscis, and licks the female's genitalia. Concurrently the male also rubs the ventral surface of the female's abdomen with his fore tarsi and repeatedly flicks one wing sharply and quickly outward to 90 degrees.

A receptive female accepts the male's overtures by spreading both wings outward and upward to 45 degrees from the mid-line and spreading the vaginal plates. The male mounts and then inserts. During copula, the pair is quiet, with the male grasping the anterodorsal surfaces of the female's abdomen with his fore tarsi. At the end of the copular period, the male turns 180 degrees to dismount and then withdraws.

A non-receptive female refuses the male's courtship by kicking, fluttering, and decamping (especially by actually flying). A fecundated female can extrude in a manner similar to that displayed by *D. virilis* but also elevates the tip of the abdomen high into the air. This does not prevent the male from courting such a female. The male circles non-receptive females, often moving back and forth in an arc in front of the female and concurrently flicking one wing repeatedly outward to 90 degrees.

The males court one another and counter-signal by fluttering. Also the sexually excited males fight with one another in a manner identical to that shown by *D. virilis*, i.e., curling the body towards the opponent, and at the same time straightening the legs and elevating the body, and then lunging sidewise at the other individual.

Two copulations were observed, one lasting between 6 and 7 minutes and the other

37 minutes and 38 seconds. Whether or not this represents the normal range of copula time is impossible to determine. *D. carbonaria* normally breeds in the wounds of the mesquite *Prosopis julifolia*, to the geographical range of which it is restricted in its distribution. The fly is difficult to rear in the laboratory, and the specimens utilized in the present studies were captured in the wild, aged for several days in the laboratory, and then used for the observations. Without the previous history (especially the age) of the specimens, it is not possible to draw valid conclusions about the copulatory period. It should be noted, however, that the specimens all appeared healthy and in good physical condition. Sturtevant (1942) records a copular period of "about 30 minutes" for this species, and Wheeler (1947) states that the average length of copulation "was about 26 minutes." Probably the 6- to 7-minute copula observed in the present study was atypically short for this species.

#### *Drosophila melanica* SPECIES GROUP

Of the eight species placed in this group by Wheeler (1949a) and Patterson and Wheeler (1949), four have been studied: *D. melanica*, *D. melanura*, *D. micromelanica*, and *D. nigromelanica*. *D. melanica* consists of two subspecies, i.e., *D. melanica melanica* and *D. melanica paramelanica*, both of which have been available for the present study.

#### *Drosophila melanica melanica* Sturtevant Stock No. 1761.2, Chinook, Montana; Stock No. 1714.4e, San Antonio, New Mexico

The male taps, goes to the rear of the female, licks her ovipositor and at the same time rubs the ventral or lateroventral surface of her abdomen with one leg, occasionally with both legs. The male also vibrates one wing intermittently while licking and rubbing. The wing is extended 5 degrees to 10 degrees from the resting position and vibrated rapidly.

A receptive female spreads her wings, moves her abdomen so that the longitudinal axis is parallel to the substratum, spreads the vaginal plates, and allows the male to lick the exposed inner area. The male mounts

and then achieves intromission. His fore tarsi grasp the base of the female's wings, and his middle and hind tarsi rest on her abdomen. Some females do not spread their wings when they give the acceptance response; others vary in the extent to which they spread their wings, with 75 degrees representing about the maximum. During copula the pair is quiet, and at the termination the male withdraws and slides off backward.

A non-receptive female repels by kicking, extruding, elevating the abdomen (thus causing the male to lick the ventral sternites instead of the vaginal area), by fluttering, and by decamping. Males occasionally attempt to mount non-receptive females and circle such individuals, often circling two or three times before posturing again.

Males also court one another and counter-signal by fluttering, striking with their forelegs, and they often give the appearance of being rather pugnacious.

Sturtevant (1921) briefly mentions the mating behavior of this species. Wheeler (1947) observed one copulation which was 4 minutes and 35 seconds in duration.

***Drosophila melanica paramelanica* Patterson**  
St. Paul, Minnesota

The mating behavior of this species is similar to that of *D. melanica melanica*. Only two copulas were observed, and in neither of these did the female spread her wings when giving the acceptance response. Also, the copular time seems shorter, since each copulation consumed less time than the shortest of *D. melanica melanica* (see table 1).

***Drosophila melanura* Miller**  
Stock No. 1891.6, Guarete, Maine

The mating behavior of this species is like that of *D. melanica melanica*. Only two copulas were observed, and in both of these the females spread their wings as well as the vaginal plates when giving acceptance responses. The single timed copula took 5 minutes and 20 seconds.

***Drosophila micromelanica* Patterson**  
Stock No. 1876.4, Kingman, Arizona

The male taps, goes to the rear of the female, "ducks" his head under her wings,

and licks her genitalia. At the same time, the male intermittently extends one wing 5 degrees to 10 degrees from the resting position and then vibrates at an extremely rapid speed.

The receptive female accepts by spreading her wings, varying with the individual from a small angle to about 90 degrees, and by dropping the tip of the abdomen and spreading the vaginal plates. The male mounts and then inserts. The mounted male assumes a standing position upon the female. This attitude causes the tip of the female's abdomen to be pulled upward, and she presents a saddle-backed appearance similar to that displayed by females of *D. prosaltans* during the early phase of the *D. prosaltans* copula. In the case of *D. micromelanica*, the position is maintained throughout the copular period, during which time the pair is quiet and at termination the male withdraws and then dismounts by backing off.

A non-receptive female repels the courting male by decamping, kicking, and extruding. The extruding action is the most spectacular of any species of the genus, and the "extrusion tube" is almost as long as the female's abdomen proper. Males circle such non-receptive females but have not been observed trying to mount uncooperative females.

Sturtevant (1942) reports that the female of this species spreads her wings before the male mounts.

***Drosophila nigromelanica* Patterson and Wheeler**  
Stock No. 1880.7, Swift Creek, Virginia

The courting behavior of the males of this species seems identical with that of *D. melanica*. The female repels in the same manner as do the females of *D. melanica* except that she was not observed to extrude. No copulas were observed.

**SUMMARY OF *Drosophila melanica***  
**SPECIES GROUP**

On the basis of mating behavior, the *melanica* species group appears to be closely related to the *virilis*, *robusta*, and *repleta* species groups. The basic elements of the mating behavior, such as licking, the type of vibration, and the foreleg caressing of the

*melanica* species group males, are similar to those of the males of the other three species groups. The acceptance response of the females of the *melanica* species group and the insertion after mounting on the part of the males agree also with the behavior of the members of the *virilis*, *robusta*, and *repleta* species groups. The ability of the females of the *melanica* species group, with the exception of *D. nigromelanica* females, effectively to repel the courting males by extrusion is, however, a type of behavior seen most typically in the subgenus *Sophophora* rather than in the subgenus *Drosophila*. In general, the mating behavior of the *melanica* species group, which is definitely a member of the subgenus *Drosophila*, is certainly more reminiscent of that of various species of the subgenus *Sophophora* than of that of any other species group of the subgenus *Drosophila* that has been used in the present study.

#### *Drosophila robusta* SPECIES GROUP

Six species, distributed in North America and eastern Asia, belong to this group (Patterson and Wheeler, 1949). Only one of these six species, i.e., *D. robusta*, was available for the present study.

*Drosophila robusta* Sturtevant  
Stock No. 1910.3, Dexter, Missouri

The male taps, moves to the rear of the female, and licks her ovipositor steadily and persistently. Simultaneously he intermittently taps the female's abdomen with his forelegs (but does not rub) and rapidly vibrates one wing in bursts of movement. The licking and vibrating movements are similar to those displayed by *D. virilis* and its relatives, but the foreleg movements are different from those of *D. virilis*.

A receptive female slightly lifts the tip of the abdomen and spreads the vaginal plates but not her wings. The male pushes his proboscis between the opened vaginal plates, holds this position for a very short time, and then mounts by raising his body upward, grasping the female's abdomen with his forelegs and middle legs, pulling the tip of his abdomen under and forward, and then achieving intromission. In copula the male's body assumes an almost vertical position.

Sometimes the mounting action of the male spreads the female's wings slightly, but at other times the wings remain together and are carried upward by the male's head. The copulatory position assumed by the pair is identical with that found in many of the *repleta* group species. At termination of copula, the male withdraws and then dismounts by backing off the female with a sliding action. The copulatory time is very short, averaging 34 seconds.

A non-receptive female repels by kicking and fluttering, decamping, depressing the abdomen, and by defecating. The males show timidity in attempting to lick non-receptive females that kick and flutter and apparently do not circle such females.

The males court one another in a manner similar to that displayed by species of the *virilis* group, but fight by slashing with their forelegs instead of the peculiar combat tactics shown by the *virilis* group males.

#### SUMMARY OF *Drosophila robusta* SPECIES GROUP

Since only a single species of this group was studied, few conclusions concerning the group as a whole can be drawn. *D. robusta* itself, on the basis of copulatory position and time, seems closely related to the *D. mulleri* section of the *repleta* species group. The courtship behavior of the males is reminiscent of the *virilis* species group except for the foreleg movements of the posturing males. The somewhat diffident actions of the courting males, especially the timid manner in which they attempt to lick the females that kick and flutter, remind the observer of the *funnebris* species group.

#### *Drosophila repleta* SPECIES GROUP

This is the largest and most complex species group of the subgenus *Drosophila*. Patterson and Wheeler (1949) and Wheeler (1949a) divide the group into three sections consisting of six *hydei*-like species, 12 *repleta*-like species, and 15 *mulleri*-like species. In addition they leave a residue of 14 species unclassified as to subgroup, since either the species are insufficiently described for purposes of subgrouping or the characters are such that they do not fit any one subgroup.

*Hydei*-LIKE SUBGROUP

Of the six species that belong to this subgroup, three (i.e., *D. hydei*, *D. nigrohydei*, and *D. bifurca*) were used for the study of mating behavior.

***Drosophila hydei* Sturtevant**  
Stock No. 1758.1a, Grand Fork, North  
Dakota; St. Paul, Minnesota

The male taps, moves to the rear, and licks the female's genitalia. At the same time he rubs the venter of the female with his forelegs and intermittently extends one wing about 15 degrees and vibrates it rapidly. Vibration of the wing involves twisting of the male's body about the longitudinal axis and elevating the wing that is vibrated.

A receptive female spreads her wings about 30 degrees, slightly elevates the tip of the abdomen, and spreads the vaginal plates. The male mounts and then inserts, the two actions occurring in close sequence. During copula the male grasps the anterodorsal surface of the female's abdomen with his fore tarsal claws. For a short period of time, during the first part of copula, the male rubs the region of genitalic union with the inner surface of the tarsi of his mesothoracic legs. At copular termination, the male withdraws, and then dismounts with a backward-sliding motion.

A non-receptive female repels by kicking and fluttering, by depressing the tip of the abdomen, by decamping; in addition, the recently fecundated female can extrude. The extruding movement is small in magnitude and involves shortening and compressing the abdomen, accompanied apparently by the relaxation of the ventral musculature of the posterior segments which results in expansion of this area. At the same time the ventral ends of the vaginal plates are rotated upward and backward. Extrusion is thus closely similar to that displayed by the *D. virilis* species group members. In recently fecundated females, in addition to extrusion, sometimes the tip of the abdomen is elevated. Neither extrusion nor the sometimes accompanying elevation seems effective in preventing the males from courting. The males do not circle non-receptive females. Males court one another but apparently have no effective

method of countersignaling.

Wheeler (1947) indicates that the copular period averages about 4 minutes, which is somewhat higher than the mean of 2 minutes and 13 seconds observed in the present study.

***Drosophila nigrohydei* Patterson and Mainland**  
Boyce Thompson Arboretum, Superior,  
Arizona

The mating behavior of this species is almost identical with that of *D. hydei* except: (1) during copula the male does not rub the region of genitalic union; (2) the recently fecundated female is apparently unable to extrude and also does not elevate the tip of the abdomen; (3) the copular period is much longer, averaging 7 minutes and 25 seconds for *D. nigrohydei* as against 2 minutes and 13 seconds for *D. hydei*.

***Drosophila bifurca* Patterson and Wheeler**  
Stocks No. 1809.2, 1797.2, 1784.13, and  
1796.7

Two observations using a breeding stock derived from mixing specimens of the above stocks were made. All these stocks were collected in Mexico. Seven individuals of each sex were employed in each observation, but no courtships were observed. During the observations the individuals moved about the observation cell and repeated physical contacts occurred, but no male ever showed any signs of even starting to court. This is a rather aberrant species of the *hydei* subgroup and is difficult to maintain in the laboratory. Perhaps this is associated with its reluctance to court under observation.

*Repleta*-LIKE SUBGROUP

Of the 12 species that are assigned to this subgroup by Patterson and Wheeler (1949), the following four were studied: *D. repleta*, *D. canapalpa*, *D. fulvimacula*, and *D. limensis*.

***Drosophila repleta* Wollaston**  
Stock No. 1574.1, Kilgore, Texas

The male taps, goes to the rear, licks the female's genitalia and at the same time intermittently rubs the venter or side of the female's abdomen with his forelegs, and vibrates one wing, extending the wing about 15 degrees for each vibration. The body of



the male twists on its longitudinal axis as he vibrates, thus rotating upward the side of the body that carries the wing being vibrated.

The female accepts by extending and slightly lifting the tip of her abdomen, spreading the vaginal plates, and at the same time spreading both of her wings about 30 degrees from the mid-line.

The male mounts and then achieves intromission. He typically grasps the female's thorax with his fore tarsal claws, and the pair is quiescent during copula. At the termination he typically withdraws and then slides off backward. Twice males were seen to withdraw and dismount by quickly jumping backward.

A non-receptive female repels by kicking and fluttering, by decamping, and by depressing the tip of the abdomen, at the same time preening the dorsal surface of the abdomen with her hind legs. This is effective in repelling males that are attempting to lick and caress. Neither fecundated nor unfecundated females seem capable of extruding.

The males court one another in typical manner, and the only countersignaling action seems to involve turning and slashing at the suitor with the forelegs. This species often forms chains of courting individuals, consisting of a single female and several males.

As was found with many species of the *D. repleta* group, the females are relatively non-receptive. The male courts vigorously and persistently but only occasionally does a female accept his overtures. Despite the recalcitrant nature of most of these females, the male does not circle to restimulate such individuals nor attempt to mount them. In 21 observations, utilizing 106 males and 121 females, only 16 females accepted. In two instances, males were observed to achieve intromission without the females' spreading their wings. In one of these two cases, just prior to the instant when the female spread the vaginal plates, the male proboscis slipped from its typical position and was not in contact with the female's genitalia. The male made no attempt to mount until he had succeeded in properly placing his proboscis and had licked the region between the spread vaginal plates. Thus licking by the

male of the female genitalia is not an absolutely necessary part of the stimulus pattern that causes the female to give the acceptance response, but it is apparently necessary in this species before the male will attempt to mount. As with the species of the *virilis* group, the male apparently receives the stimulus for mounting from the area between the vaginal plates, which is made accessible to his proboscis when the female spreads the plates.

***Drosophila canapalpa*** Patterson and Mainland  
Stock No. 1402.17, Jacala, Hidalgo, Mexico

This species behaves during courtship and copulation almost exactly as *D. repleta* does except that (1) the male typically rubs the side rather than the venter of the female's abdomen with his forelegs and (2) when the female accepts, she may spread her wings to 90 degrees from the body. Of the six copulas that were observed, in only two of these did the female spread both her wings and vaginal plates when accepting the male. Perhaps such lack of wing spreading is related to the relatively great reluctance of the females of the species to accept the males under the conditions in which the experiments were conducted.

***Drosophila fulvimacula*** Patterson and Mainland  
Stock No. 1808.37, Oaxaca, Oaxaca, Mexico

The courtship pattern of this species appears to be identical with that of *D. repleta*. No acceptances were observed, although copulating pairs were observed in small mass cultures. The copulatory position also appears similar to that of *D. repleta*. Apparently individuals of this species, when reared at a temperature of 20° C., must reach an age of seven or eight days before the males at least are sexually mature. Males of two to six days of age were completely indifferent to the females, even though numerous physical contacts were made between the individuals.

***Drosophila limensis*** Pavan and Patterson  
Stock No. 1529.2a, Lima, Peru

Only a few courtships and no copulations occurred during 10 observations utilizing 70 males and 119 females. The individuals stud-

ied ranged from two to 23 days in age. The observed courtships were identical with those of *D. canapalpa*.

***Drosophila melanopalpa*** Patterson and Wheeler  
Stock No. 1351.7, Camécuaro, Michoacán,  
Mexico

Two observations involving eight males and 24 females resulted in no courtships. The specimens for the first observation were seven days old, for the second observation 12 days old.

***Drosophila linearepleta*** Patterson and Wheeler

Sturtevant (1942) records that he observed the mating behavior of this species, but gives no details other than to say that the copulatory period was less than 5 minutes' duration.

#### *Mulleri*-LIKE SUBGROUP

Patterson and Wheeler (1949) list 15 species as belonging to this subgroup. Three of these species are atypical for the subgroup in that they fall outside the normal range of one or more of the various subgroup characteristics. None of these three was available for study, but 11 of the remaining 12 species of the subgroup were studied. In comparison to the species of the two other subgroups, the typical *mulleri*-like forms mated freely in the observation cell. Furthermore, these species can be maintained in the laboratory with relative ease.

***Drosophila aldrichi*** Patterson and Crow  
Stock No. 1781.4, San Pedro, Coahuila,  
Mexico

The male taps, goes to the rear, and positions himself behind the female, extends his proboscis and licks the female's genitalia. Simultaneously he rubs the sides of the female's vaginal plates with his fore tarsi, twists his body slightly about the longitudinal axis and curls the tip of his abdomen forward. This twisting and curling movement rolls one side of the male's body slightly dorsad, and the wing of this side is then extended about 15 degrees and vibrated. Such movements of the male are intermittent but typically occur together, although the wing vibration may be sometimes omitted.

A receptive female slightly elevates the tip of her abdomen, spreads the vaginal

plates, and typically spreads both wings about 5 degrees to 15 degrees from the midline of the body.

The male licks the exposed surface between the vaginal plates, then rises sharply upward and at the same time jerks the tip of his abdomen under and forward, meanwhile grasping the dorsal surface of the female's wings with his forelegs, placing his hind and middle legs upon the female's abdomen, and then achieves intromission. The body of the male is in an almost vertical position during copulation and is similar to the position assumed by *D. robusta*. At the end of copula the male withdraws and then dismounts by sliding backward.

A non-receptive female repels the male by kicking, fluttering, depressing the tip of the abdomen, decamping, and extruding. The extruding action, which seems restricted to females that have been recently fecundated, is not obvious and seems not especially effective, since the males continue to court such females.

If a male taps another male, the tapped individual responds by fluttering. This seems to be an effective countersignal, since males were not observed posturing behind other males.

The males do not circle the females to restimulate them, although sometimes they leave the posterior position and move as far forward as the female's thorax, and then return to the rear position. Nor do the males attempt to mount non-receptive females.

Individual females were observed to copulate two times during a single observation, usually with the same male but sometimes with a second male.

Patterson (1947b) reports a minimum of 1 minute and 50 seconds, a maximum of 5 minutes, and a mean of 3 minutes and 27 seconds for the copulation time of this species. The four timed copulations for the present study (table 1) range from 2 minutes and 35 seconds to 9 minutes and 43 seconds and possibly are atypically long.

***Drosophila arizonensis*** Patterson and Wheeler  
Stock No. 928.5, Tucson, Arizona

The mating behavior of this species is

similar to that of *D. aldrichi* except that (1) when the courting male rubs the female's abdomen, the contact between the male's tarsi and the female's body is not restricted to the area of the vaginal plates as it is in *D. aldrichi*, but rather the tips of the tibia and the bases of the tarsi of *D. arizonensis* are in the region of the vaginal plates while the distal parts of the tarsi are extended along and in contact with the venter of the female's abdomen; (2) the average copulatory period (table 1) is shorter than that of *D. aldrichi*.

As with *D. aldrichi*, some females engage in copula twice during the observation period.

Patterson (1947a) lists the copulatory period of this species as ranging from 30 seconds to 2 minutes and 10 seconds, with a mean of 1 minute and 34 seconds. These times agree closely with those of the present study (table 1).

***Drosophila buzzatii*** Patterson and Mainland  
Stock No. 190, Carpenteria, Italy

*Drosophila buzzatii* has a mating behavior much like that of *D. aldrichi* but differs in that (1) the courting male uses his forelegs when rubbing the female's abdomen in the same manner as that displayed by *D. repleta*; (2) furthermore, the males show greater excitement than do those of *D. aldrichi*, often fighting with one another. The duration of the copulatory period (table 1) is close to that of *D. arizonensis*. Likewise, some females accept the males' overtures more than once during an observation period.

Patterson (1947b) records this species as having a copulatory time that varies from 1 minute to 3 minutes and 10 seconds, with a mean of 2 minutes and 4 seconds. In the present study, the range of variation was not quite so great, i.e., 1 minute and 20 seconds to 2 minutes and 28 seconds, and the mean is somewhat lower (1 minute and 46 seconds) than that found by Patterson.

***Drosophila hamatofila*** Patterson and Wheeler  
Stock No. 1939.4, Williams, Arizona; Davis  
Mountains, Texas; Boyce Thompson  
Arboretum, Superior, Arizona

The general pattern of courtship is some-

what similar to that of *D. repleta*, but the male strikes rather than rubs the latero-ventral surface of the female's abdomen when he is posturing at the rear of the female. When she accepts, she spreads her wings much as the females of *D. repleta* do, and to a much greater degree than is typical of most species of the *mulleri* subgroup. The male mounts much farther forward than is typical of *D. mulleri* and *D. aldrichi* and grasps the base of the female's wings close to her thorax with his forelegs. The copulatory position of the male is thus intermediate between that of *D. repleta* and *D. mulleri* and its close relatives.

Non-receptive virgin females refuse the males' overtures by fluttering, kicking, depressing their abdomens, and by decamping.

Recently fecundated females, when courted, typically extrude and elevate the tip of the abdomen. The courting male persists in posturing behind such females but is unable to reach the vaginal area with his proboscis and instead licks the venter of the female's abdomen. No female was observed to copulate more than once during a single observation.

Patterson (1947b) lists the copulatory period of this species as ranging from 5 minutes to 10 minutes, with a mean of 7 minutes and 3 seconds. The data from the present study are on only two timed records, but it is to be noted that the maximum (10 minutes and 57 seconds) is longer than the maximum recorded by Patterson.

***Drosophila longicornis*** Patterson and Wheeler  
Garner State Park, Texas

The courtship of this species is similar to that of *D. aldrichi*, although the male, when posturing at the rear of the female, applies the forelegs against her abdomen in such a manner that the entire tarsal length is in contact with the female. Furthermore, the vibrated wing of the male is extended 30 degrees to 40 degrees from the body and then vibrated through a much larger arc (vertically) than is that of *D. aldrichi* and its close relatives. Finally, the male grasps the base of the female's wings with his fore tarsi when in copula.

***Drosophila meridana rioensis* Patterson**  
Stock No. 1802.4, Puebla, Mexico

The mating behavior of this species is similar to that of *D. aldrichi* except that (1) the males rarely vibrate their wings when posturing at the rear, and (2) occasionally a posturing male circles a non-responsive female.

***Drosophila mojavensis* Patterson and Crow**  
Chocolate Mountains, Colorado

This species seems identical with *D. aldrichi* in its mating behavior except that no female was observed to accept a male's overtures more than once during an observation, and the general subjective impression was that the species is less aggressive than is *D. aldrichi*.

Sturtevant (1942) records observing the mating of this species and indicates that the copulatory time was less than 5 minutes in duration, with which the present findings agree (table 1). Patterson (1947b) lists the copulatory time of the species as ranging from 1 minute and 20 seconds to 5 minutes, with a mean of 3 minutes and 27 seconds, or almost 1 minute shorter than the mean found in the present study.

***Drosophila mulleri* Sturtevant**  
Stock No. 1750.5, Lawton, Oklahoma;  
Laredo, Texas

The mating behavior of *D. mulleri* and *D. aldrichi* is identical, except that the copulatory period of *D. mulleri* is very short, while that of *D. aldrichi* is much longer (table 1). This is interesting in view of the fact that these two species, although closely related, are sympatric over much of their ranges. In the laboratory *aldrichi* males and *mulleri* females produce sterile hybrid offspring; both male and female (Patterson, 1947a) and hybrid males of this cross have been found and positively identified in collections of wild flies (Patterson and Crow, 1940; Patterson, 1947a).

Patterson (1947b) records the copulatory period of the species as varying from 30 seconds to 3 minutes, with a mean of 1 minute and 35 seconds, which is much higher than the copulatory time of the stocks used

in the present study (table 1). In this connection, it should be noted that two stocks were utilized and that they behaved similarly in that the mean of the copulatory time for the Laredo stock (nine timed copulas) was 31 seconds and that of the Lawton stock (10 timed copulas) was 26 seconds.

***Drosophila peninsularis* Patterson and Wheeler**  
Tarpon Springs, Florida

The mating behavior of this species is much like that of *D. aldrichi* except that (1) the male rubs the sides of the female's abdomen, when posturing at the rear, instead of the vaginal plate area; (2) the copulating male assumes a relatively "forward" position and grasps either the base of the female's wings or the anterodorsal surface of her abdomen with his fore tarsi; (3) the males are more aggressive than the *D. aldrichi* males in their courting behavior, often fighting with one another in the same manner as displayed by the *D. buzzatii* males.

Patterson (1947b) records the copulatory time of this species as varying from 1 minute and 20 seconds to 2 minutes and 5 seconds, with a mean of 1 minute and 58 seconds. The data of the present study show a somewhat lower mean of 1 minute and 37 seconds.

***Drosophila ritae* Patterson and Wheeler**  
Stock No. 1796.5, Morelia, Michoacan,  
Mexico

*Drosophila ritae* displays a mating behavior much like that of *D. hamatofila* except that (1) the posturing male rubs the dorsolateral areas of the female's abdomen rather than striking the lateroventral surface with his forelegs; (2) the receptive female does not spread her wings widely but only slightly, in the manner displayed by *D. aldrichi* females; (3) the copulating male grasps the anterodorsal surface of the female's abdomen instead of the wing base with his fore tarsi; (4) the non-receptive female, in addition to the usual repelling actions of fluttering, kicking, extruding, and decamping, also elevates the tip of her abdomen but to a much greater degree than is displayed by recently fecundated *D. hamatofila* females. The *D. ritae* female spreads both wings about 45

degrees from the median line, extrudes and at the same time elevates the tip of the abdomen excessively, so that the whole body is involved in the action and the individual is literally standing on her head, with the longitudinal axis of the body almost in a vertical position. Finally (5) the females are often restless during copula, kicking with their hind legs and fluttering their wings, behavior that is atypical of the entire *repleta* group.

Patterson (1947b) records the copulatory time of this species as ranging from 6 minutes to 9 minutes and 15 seconds, with a mean of 8 minutes. The three timed copulas of the present study yield a mean of 8 minutes and 57 seconds.

***Drosophila anceps*** Patterson and Mainland  
Stock No. 1808.34, Oaxaca, Oaxaca, Mexico

The mating behavior of *D. anceps* is similar to that of *D. hamatofila* except that (1) the recently fecundated female repels by fluttering, kicking, depressing the tip of the abdomen, and decamping, but not elevating the tip of the abdomen; (2) the male circles completely about non-receptive females and in doing so typically stops briefly in front of the female, extends one or both mesothoracic legs laterally and waves them.

Wheeler (1947) reports the copulatory time derived from flies of 7, 10, and 11 days old as averaging about 5 minutes and 30 seconds. This agrees closely with the single timed copula of the present study (table 1).

***Drosophila hexastigma*** Patterson and Mainland

Wheeler (1947) observed one copula of this species to last for 6 minutes and 30 seconds but gave no details as to other phases of the mating behavior.

#### SPECIES UNCLASSIFIED ACCORDING TO SUBGROUP

Of the 14 unclassified species (Wheeler, 1949a), *D. mercatorum mercatorum* Patterson and Wheeler, *D. mercatorum pararepleta* Dobzhansky and Pavan, and *D. nigricruria* Patterson and Mainland were utilized in the present study.

***Drosophila mercatorum mercatorum***  
Patterson and Mainland  
Oahu, Hawaii

The mating behavior of this species seems identical with that of *D. aldrichi* and its close relatives, except that the posturing male rarely uses his forelegs to rub the female's abdomen and, when used, the legs are applied against the side of the female's abdomen rather than against the sides of the vaginal plates.

***Drosophila mercatorum pararepleta***  
Dobzhansky and Pavan  
Stock No. 1412.9a, Jacarapagua, Federal  
District, Brazil

No copulations of this subspecies were observed, although 10 observations using individuals varying in age from one to eight days were made. The one-day old males courted at a moderate rate, while the two- to three-day old males were quite aggressive. Seven- to eight-day old males were much more lethargic than the younger males. The courtship behavior of the males seemed identical with that displayed by *D. mercatorum mercatorum* males.

***Drosophila nigricruria***  
Patterson and Mainland  
Stock No. 1794.14, Mexico City, Mexico

No copulations occurred during 11 observations on this species. The males when eight to 11 days old courted the females as well as one another. When courting the females, they show a behavior pattern similar to that displayed by *D. repleta* or *D. hydei* males. When courting one another, they are aggressive, and the courted individuals countersignal by fluttering and also by turning towards the suitor and fighting. Non-receptive females repel the males by kicking, fluttering, extruding, elevating the abdomen, depressing, and decamping. Structurally, this species is more slender and longer legged than the other *repleta* group species, and in their fighting posture the *nigricruria* males are reminiscent of the attitude assumed by the *D. virilis* males in that they straighten their legs and elevate their bodies.

SUMMARY OF *Drosophila repleta*  
SPECIES GROUP

The mating behavior of the *D. repleta* species group, on the basis of the species studied, indicates a closely knit group. The basic wing pattern can be described as follows: The male taps, moves to the rear position, licks the female's genitalia with his outstretched proboscis, caresses the ventral or lateral surfaces of the female's abdomen with his forelegs, extends one wing 10 degrees to 15 degrees from the mid-line, and vibrates the wing intermittently. At the same time that the wing is vibrated, the body of the male is rotated on its longitudinal axis, thus slightly elevating the vibrating wing, and the tip of the abdomen is slightly curled forward. All these actions, especially the wing vibration, are intermittent in nature, and between each burst of activity the organ is returned to its normal resting position. The licking activity is the most persistent and least discontinuous of the actions.

Non-receptive females repel the courting males mainly by fluttering, kicking, depressing their abdomens, and decamping. Some can extrude only after they have been fecundated (*mulleri* subgroup), but this action is always relatively inconspicuous and does not repulse the males from courting such females. Several were observed not to extrude at any time. Females of a few species (*hamatofila*, *ritae*, and *nigricruria*) elevate their abdomens and extrude and thus repel (avoid) the males' overtures.

Although the mating behavior of the group is relatively uniform, some differences between species, so far as the mating behaviors are concerned, are evident. These are as follow:

1. The posturing male always caresses the female's abdomen with his forelegs, but the exact manner in which the forelegs are employed varies; for example, *D. mulleri* rubs the lateral margins of the vaginal plates; *D. hydei* rubs the ventral surface of the abdomen; *D. ritae* rubs the dorsolateral sides of the female's abdomen; *D. hamatofila* strikes rather than rubs the lateroventral surfaces of the female's abdomen, while other species often display actions intermediate between these four types. It should also be noted that

there is considerable variation in this particular behavior and that the descriptions as given for the individual species give the typical pattern and not the variations. Furthermore, sometimes an individual male can be observed that employs only one foreleg, partially or wholly, during posturing.

2. The wing vibrations of the posturing male vary considerably. Most species extend the wing only a few degrees (10 degrees to 15 degrees) from the mid-line, and vibrate the wing in an arc of very small amplitude, but *D. longicornis* extends the wing farther (30 degrees to 40 degrees) and vibrates it through a relatively large arc.

When the females accept the males' courting overtures, individuals of the *hydei* and *repleta* subgroups tend to droop the tips of the abdomen as they spread the vaginal plates, while the *mulleri* subgroup females typically elevate very slightly but distinctly the tips of the abdomen.

Males of *D. mulleri*, *D. aldrichi*, *D. buzzatii*, *D. arizonensis*, and *D. mojavensis*, when they mount the female, assume an almost vertical position and grasp the vane of the female's wing with their fore tarsal claws. All males of the *repleta* and *hydei* subgroup species mount much farther forward and grasp the anterodorsal surface of the female's abdomen, the base of the wings, or even the thorax of the female with their fore tarsal claws. The position assumed by the male is correlated with the size of the individuals. For example, females of *D. hydei*, *D. nigrohydei*, *D. repleta*, *D. canapalpa*, and *D. fulvimacula* range from 3.4 to 4.2 mm. in length. Females of *D. aldrichi*, *D. arizonensis*, *D. buzzatii*, *D. mojavensis*, and *D. mulleri* are much smaller, ranging from 2.4 to 2.8 mm. in length. A further evidence that size is probably involved in determining the copular position of the male is shown by *D. hamatofila*, *D. longicornis*, *D. peninsularis*, and *D. ritae*, the females of which are intermediate in size (2.9 to 3.4 mm.) and their males assume an intermediate position, grasping typically the base of the wings or the anterodorsal surface of the female's abdomen with their tarsal claws. *D. peninsularis* is particularly instructive in that its female averages 3.4 mm. and the male assumes a copulatory position

almost identical with that displayed by the *hydei-repleta* subgroup males, but on the basis of morphology as well as other phases of the mating behavior, *D. peninsularis* is much more closely related to *D. mulleri* than to any of the *hydei-repleta*-like species.

Copulatory time for the group as a whole, when compared to other groups, is relatively short. As shown by the means (see table 1), certain pairs of species differ considerably in the length of the copulatory period even though they seem to be very closely related on the basis of morphology, distribution, ecology, genetics, and sexual behavior, for example, *D. aldrichi* and *D. mulleri*; *D. mulleri*, *D. arizonensis*, and *D. mojavensis*.

On the basis of mating behavior, the *D. repleta* group seems intermediate between *robusta* and the *virilis* species groups. Within the *repleta* species group itself, two divisions can be made on the basis of mating behavior. One division is represented by the combination of the *repleta* and *hydei* subgroups and the other by the *mulleri* subgroup. The *mulleri* subgroup shows a secondary splitting, with *D. aldrichi* and its close relatives forming one unit and *D. hamatofila*, *D. anceps*, and *D. ritae* another. These last three species perhaps serve as a link between the *mulleri* group on one hand and the combined *repleta-hydei* group on the other.

Of the 14 species unplaced as to subgroup, only two (*D. mercatorum* and *D. nigricruria*) were studied, and the females of both species were recalcitrant and refused to copulate in the observation cell. On the basis solely of the male's courting, however, *D. mercatorum* would appear related to the *mulleri* subgroup and *D. nigricruria* to the *repleta* or *hydei* subgroups.

#### *Drosophila annulimana* SPECIES GROUP

Breuer and Pavan (1950) place seven species in this group. It appears to be mainly a Neotropical group, with some of the species ranging into the Nearctic. Only one species, the unique large *D. gibberosa*, was available for study.

***Drosophila gibberosa*** Patterson and Mainland  
Compound Stock, Mexico

The male taps, moves to the rear, licks the

female's genitalia, taps the dorsolateral surface of her abdomen with his forelegs, and intermittently vibrates one wing, extending the wing about 5 degrees from the mid-line and vibrating it rapidly in an arc of small amplitude. The male restimulates the female by returning to her side and tapping, and also by lifting and extending both middle legs laterally, with the tips curled upward. Once extended, the legs are waved up and down synchronously. Since the dark-colored legs are marked with white tarsal bands, this movement presents a rather spectacular appearance.

A receptive female indicates acceptance of the male's overtures by spreading the vaginal plates and by spreading both wings outward and upward to about 45 degrees. The male mounts, grasps the anterodorsal surface of the female's abdomen with his fore tarsal claws, and achieves intromission after mounting. At termination of copula, the male withdraws and then dismounts.

A non-receptive female repels by decamping, fluttering, and kicking. Recently fecundated females also are able to extrude, and sometimes this seems effective in repelling the males. Males do not attempt to mount non-receptive females.

Males court one another vigorously when their courting threshold has been lowered by contact with females. The only countersignal observed to be given by the courted male is the waving, in typical manner, of the middle legs.

Four timed copulas gave an average of 6 minutes and 43 seconds which is almost 2 minutes less than the average of 8 minutes and 28 seconds recorded by Wheeler (1947). Even the maximum of the present study (7 minutes and 6 seconds) is less than the average obtained in Wheeler's study.

The stock used in the present study is a compound stock representing the descendants of a number of specimens taken at different localities.

On the basis of mating behavior, *D. gibberosa* is closely related to the *repleta* group; in fact, the mating behavior of *D. gibberosa* except for the leg waving is almost identical with that of the larger species of the *repleta* group.



*Drosophila immigrans* SPECIES GROUP

This predominantly oriental species group contains 18 species (Patterson and Wheeler, 1949), of which only two, the cosmopolitan *D. immigrans* and the unique *D. spinofemora*, were available for the present study.

*Drosophila immigrans* Sturtevant  
Stock No. 1879.9, Williamston, North  
Carolina

The male taps, goes to the rear and continues to tap, concurrently curling the tip of his abdomen under and forward and flicking one wing rapidly. After posturing thus for a brief period, the male lunges onto the female, grabbing the anterior end of her abdomen with his forelegs. After the male has lunged onto and grasped the female, he attempts to achieve coitus.

Receptive females allow the male to achieve intromission. A few of them spread the wings after the male has mounted, but typically they merely relax the wings and allow the male to push his head between the wings. During copula, the pair is usually quiet, with the male grasping the anterolateral surface of the female's abdomen with his forelegs. Often towards the end of the period, the female kicks vigorously with her hind legs. The male dismounts either by withdrawing and then jumping off or by turning 180 degrees and then withdrawing.

Non-receptive females flutter, kick, decamp, depress the tip of their abdomens or elevate the tips of the abdomens and also extrude. Males do not persist in courting non-receptive females. The male lunges onto such a female three or four times and, if she does not accept any of these overtures, he turns away and leaves her. Between lunges, however, the male typically circles the female, scissoring one wing as he moves about her.

Recently fecundated females typically repel by extruding and also elevating the tips of their abdomens (so much so sometimes that they appear to be almost standing on their heads). This seems effective, and the males usually break contact at the tapping stage of courtship. Non-receptive virgin females typically refuse by kicking, fluttering, and curling the tips of their abdomens down against the substratum. The males

have not been observed to court one another.

Wheeler (1947) reports that the copulatory time of this species varies from 14 minutes to 63 minutes, with an average of about 30 minutes. Sturtevant (1942) lists an average of 53 minutes. The present average of 47 minutes and 47 seconds agrees well with that recorded by Sturtevant.

*Drosophila spinofemora* Patterson and Wheeler  
Stock No. 1597.3

The male taps, then either pauses and taps again, or moves to the rear and taps. After the first tapping the male may or may not extend (wave) one wing to 90 degrees.

A non-receptive female often ignores the courting male, occasionally decamps and, if feeding, slightly elevates the abdomen and directs the tip towards the male. No extrusion is visible, but the male is obviously repelled by such an action. Nor do the females kick at the males with their hind legs or flutter their wings. A male does not attempt to mount non-receptive females but circles such a female and when he reaches a point in front of her he spreads one or both wings to 90 degrees. Males do try, however, to mount one another.

Males court one another, and whenever a male is tapped by another male, he turns and faces his suitor, and then both extend one or both wings to 90 degrees. Sometimes the two individuals push against each other, placing their heads against the anterolateral corner of the thorax of the other individual and spreading the "free" or outside wing to 90 degrees.

No copulas resulted during six observations, in which 40 males and 47 females were utilized. *D. spinofemora* is known to copulate within a few minutes after eclosion from the puparium. Therefore specimens were collected and isolated at 15-minute intervals. The observations were conducted with specimens that ranged from a few hours to 13 days old, but in no case did a single female give any sign of an acceptance reaction.

SUMMARY OF *Drosophila immigrans* GROUP

Few conclusions about the group as a whole can be drawn from the limited data. One of the characteristics of the males of all species

of the group is the presence of a row of short, thick spines on the fore femur. Since these seem involved in the male's grasping of the female during mounting and copula, it is reasonable to assume that other species of the group may mount in a manner similar to that displayed by *D. immigrans*.

The courting males of *D. immigrans* and *D. spinofemora* do not try to lick the female genitalia during courtship which is atypical of the subgenus *Drosophila*. Furthermore, the general mating behavior of both the males and females seems atypical for the subgenus. In most respects the species studied behaved much like the *melanogaster* and *obscura* groups of the subgenus *Sophophora*. On the basis of present knowledge, the mating behavior of the *immigrans* group appears to be specialized as shown (1) by the very long copulatory time; (2) by the male's method of mounting and grasping the female; and (3) by the variations from the generalized pattern displayed by most of the species belonging to the subgenus *Drosophila*.

#### *Drosophila guarani* SPECIES GROUP

Of the six species constituting this Neotropical species group (Patterson and Wheeler, 1949), only one, *D. subbadia*, was available for the present study.

***Drosophila subbadia* Patterson and Mainland**  
Stock No. 1802.19, Atlitxco, Mexico

The male taps, moves to the rear, "ducks" under the female's wings, extends his proboscis, and licks her genitalia. At the same time, he intermittently extends slightly (5 degrees) and vibrates one wing with motions of small amplitude. The body is twisted sharply on the longitudinal axis concurrently with each burst of wing vibration. The male also caresses the venter of the female's abdomen with one foreleg. The posturing movements of the male are very similar to those of *D. virilis* and its relatives except that only one leg is used to caress the female's abdomen.

Non-receptive females repel the courting males by decamping, fluttering, kicking, and depressing, but not by extruding. The males circle such females. One male was once observed attempting to mount a non-recep-

tive female, but this is atypical.

Males tap one another, and the courted individual immediately turns to face his suitor and taps also, an action that seems to be a countersignaling mechanism.

Seventeen observations, employing 129 males and 163 females, resulted in no copulations. The specimens ranged in age from three to 13 days. Those less than seven days in age would not court. Apparently the males do not reach maturity, when maintained at 22° C., until the seventh day after eclosion.

On the basis of the male's courting behavior, *D. subbadia* would seem to be related to the *D. melanica-virilis-repleta* section of the subgenus *Drosophila*.

#### UNCLASSIFIED SPECIES

In addition, three species, unclassified as to species group, were studied. The descriptions of their mating behavior are given below.

***Drosophila castanea* Patterson and Mainland**  
Stock No. 1802.8, Atlitxco, Puebla, Mexico

The posturing actions of the male and the responses of the non-receptive female of this species are identical with those of *D. subbadia* (see above).

A receptive female spreads the vaginal plates but not the wings. The male mounts and then inserts, grasping the female's thorax with his fore tarsal claws, and later he grasps the base of the female's wings. His body is almost vertical in position, and his hind and middle feet rest on the female's abdomen, with his wing tips against the substratum, thus partially supporting his weight. The pair is quiet during copula, and at termination the male withdraws and then slides off backward.

On the basis of mating behavior, *D. castanea* would seem to be closely related to *D. subbadia*. The structural characteristics do not indicate such a relationship.

***Drosophila parachrogaster* Patterson and Mainland**

Stock No. 1784.7, Rio Mezquitil, Mexico

The male taps, then moves either to the rear or side of the female and postures. When posturing at the rear, he extends one

wing to 90 degrees from the mid-line; the wing vane is turned to a vertical position, with the posterior edge of the wing downward, and then is vibrated slowly. At the same time, the male occasionally licks the female's genitalia for short periods and taps her abdomen with one foreleg. When posturing at the side the male always vibrates the wing nearest the female's head and omits the licking action. He mounts between the female's spread wings and grasps her thorax with his fore tarsal claws. (One copulation was observed, but the acceptance response was not seen.) After about 3 to 4 minutes she vibrates, kicks, and curls the abdomen downward, thus displacing the male backward; he now grasps the anterodorsal surface of her abdomen. The pair is then quiet until near the end of copula, at the termination of which the male withdraws and then dismounts by sliding off backward.

Non-receptive females repel the males by kicking, fluttering, depressing the tip of the abdomen, and decamping, but not by elevating the tip of the abdomen or extruding.

Males circle non-receptive females and also court one another vigorously. Occasionally the courting male may attempt to mount another male, but the males do not attempt to mount non-receptive females.

Wheeler (1947) timed one copula between 22-day old specimens, but noted that the period was probably longer than normal since "the first part of the mating seemed to be faulty." The copula observed for the present study occurred between five-day old specimens.

Wheeler (1949a) notes that this species probably belongs to the *D. rubifrons* species group. Unfortunately no other species of this group was available for study, and thus at present it is impossible to determine whether the courtship pattern will or will not provide further support to Wheeler's conclusions. Certainly the courtship pattern of the male is somewhat aberrant for a member of the subgenus *Drosophila*.

*Drosophila tumiditarsus* Tan, Hsu, and Sheng  
Stock No. 1736.6., Hangchow, China

The male taps, races to the rear of the female, and then lunges onto the female, grasping her abdomen, sometimes including

her wings within his grasp. He then curls the tip of his abdomen downward and against the female's genitalia, and attempts to achieve coitus.

A receptive female allows the male to insert after he has lunged onto her; usually she spreads her wings just as the male lunges. If her wings are pinioned by the male, as soon as coitus is achieved he releases his grasp and allows the female to spread her wings. He grasps her thorax with his fore tarsal claws, but unlike other species his foreleg is not extended but folded, so that the femur is held against the tibia, with the distal tip of the femur directed posteriorly. This necessitates the male's assuming a copulatory position well forward upon the dorsum of the female. Achieving coitus and gaining copulatory position takes about 4 to 10 seconds, and then the male violently contracts and shortens the dorsum of his abdomen, at the same time apparently relaxing the ventral and lateral abdominal muscles. This complex action pulls the male's genitalia upward and forward, and the tip of the female's abdomen is also carried upward and forward, thus stretching her entire abdomen with the posterior part being excessively stretched and elongated. Concurrently the pressure on the lateral and ventral walls of the male's abdomen distends these areas, and the female's abdomen is still further stretched. From a side view, the female's abdomen appears as a curved structure, with the tip or region of genitalic union pulled so far upward and forward that it now faces anteriorly. This bizarre copulatory position is maintained during the remainder of copula except for rare short intervals when the male relaxes the dorsal contracted area and both the male's and female's abdomens assume normal shapes such as are displayed by most other species of the genus while in copula. At the end of copula, the male relaxes, then withdraws and finally dismounts.

Non-receptive females avoid the males, and apparently curl the tips of their abdomens downward, but other than this the virgin females seem to display no repelling actions. Only occasionally does a male mount a non-receptive female, and if he does he is unable to achieve coitus and

quickly dismounts. Recently fecundated females curl the tips of their abdomens towards a tapping (courting) male, and, although no extrusion is visible, the male is clearly repelled. The males do not court one another.

The lack of wing motion and licking on the part of the male, plus the bizarre copulatory position, distinguishes *D. timiditarsus* from all other species studied. Structurally this species is a member of the subgenus *Drosophila*, but it does not fit into any species group, and certainly the mating behavior throws no light on its relationships to the other members of the subgenus.

#### SUMMARY OF THE SUBGENUS *Drosophila*

The species of this large, complex subgenus show great diversity in their mating behavior. Some elements of the mating behavior, however, are more or less constantly displayed, and the following generalizations can be noted:

1. The males of most species lick the female genitalia while posturing.
2. The "licking period" is typically long.
3. The forelegs of the male are usually employed for caressing the female while he is posturing, and this involves prolonged contact with the female's body. Typically the venter of the female's abdomen is stroked, but in some species, especially in the *quinaria* group, the sides or dorsum of the abdomen are stroked.
4. The courting males of virtually all species do not attempt to mount until they have licked the inner areas between the vaginal plates which are exposed when the females give the acceptance response.
5. Intromission is typically achieved after the male has mounted.
6. Usually the females spread their wings as well as the vaginal plates when giving the acceptance response, but typically the wings are spread less than 45 degrees from the mid-line. In those species of which the females do not spread their wings, the males merely push the wings out of their way by means of their bodies, i.e., the males do not possess special structures such as sex combs that can be used to push the female's wings apart.

7. Once the male has achieved his normal copulatory position, the mating pair is quiet and the male's position remains unchanged.

8. At the end of copula, normally the male first withdraws his phallus and then dismounts, typically by sliding off backward but sometimes by actually jumping off.

9. Non-receptive virgin females typically show no extruding action. Recently fecundated females often can extrude, but this does not seem to deter the males from courting such females. The females of the *melanica* group are exceptions, in that extrusion is a commonly observed and effective repelling action.

In general, contact stimuli (especially for the male) seem to serve the major role in the mating behavior. This is clearly shown by the fact that the male of the great majority of the species must lick the area enclosed by the female's vaginal plates before he will attempt to mount, i.e., in such species, wing spreading alone on the part of the female will not serve to stimulate mounting. No light-dependent species are known in this subgenus, but several species in various groups have developed independently the habit of lunging onto the females, for example, the *quinaria* group (some species), the *immigrans* group (perhaps all species), and *D. timiditarsus*. The evolutionary development of the method of mounting by lunging onto the female has been accompanied by the loss of some elements of posturing which are typical for the non-lungers. Thus, the *D. timiditarsus* male displays no wing, leg, or licking movements when posturing. *D. immigrans* scissors one wing and taps but does not lick. Likewise, *D. innublia* engages in wing movements but not in licking or leg movements. *D. transversa*, *D. quinaria*, *D. phalerata*, and *D. subpalustris*, all "lungers," show other combinations of omissions of typical posturing actions. Some of the species that do not lunge, however, also apparently have either lost or never possessed some of the posturing movements. It is perhaps significant that only the males of those species that lunge onto the females do not lick the female genitalia during courtship. *D. subpalustris* is the exception to this rule in that the males of this species do lick and also do lunge.

## MATING BEHAVIOR OF SOME RELATED GENERA

Mating behavior data were collected also on three other species, relatives of the genus *Drosophila*. The species with descriptions of their behavior are given below.

***Chymomyza amoena* Loew**

Stock No. 1899.10, Chagrin Falls, Ohio

Individuals of both sexes constantly raise, spread, and lower their wings as they move about or sit in either the breeding vials or the observation cell. Sometimes the resting individuals also extend the forelegs forward and then outward in a quick movement. All individuals are wary of other specimens and constantly orient themselves so as to face, if possible, the other individuals, and if this is not possible they attempt to escape from their immediate vicinity. Occasionally males were observed to tap other individuals, but not every courtship was preceded by tapping. Perhaps after becoming sexually excited, tapping is omitted. A sexually excited male circles to the rear of another individual, curls the tip of the abdomen under slightly, and then rushes towards the specimen and grabs its wings with his forelegs, using the femora and tibiae, and at the same time jerks his abdomen sharply forward and seeks to achieve intromission.

A receptive female allows the male to achieve coitus, and then elongates her abdomen, at which time the male releases his grasp upon her wings and then positions himself so that his front legs stand upon her wings, with his middle and hind wings upon the substratum. Owing to the elongation of her abdomen, the female's wings are not spread by the male's body. During copula, the pair is quiet, and at termination the male withdraws and slides off backward.

If a non-receptive female or a male has been grabbed by the courting male, then the suitor is quickly displaced by the kicking action of the assaulted individual.

Sturtevant (1921, 1942) has briefly described the behavior of this species.

Wheeler (1947) states that the average copulatory period was about 14 minutes, somewhat shorter than the average of 20 minutes and 58 seconds of the present study.

***Chymomyza procnemis* Williston**  
Unknown locality

Like *C. amoena* this species engages in wing and foreleg motions as the individuals move about in the cell. A sexually excited male taps other individuals and, if a female has been tapped, he moves to the rear position, rushes at her, pushes her wings apart with his head and grasps them with his forelegs. This grasping of the wings is done in the following manner: the fore coxa is directed forward; the fore femur is twisted outward until it is at right angles to the sagittal plane of the male and underneath the wing vane of the female, with the distal tip of the femur extending just beyond the costal margin of the female's wing; the tibia is folded back over the dorsal surface of the female's wing so that its distal tip is directed towards the mid-line and the relaxed tarsus is folded at right angles to the tibia and directed forward. Since the legs form mirror images of each other, the distal tips of the two tibiae almost meet in the mid-line and the tarsi lie parallel to each other. The effective agents for grasping the female's wings are the femora and tibiae.

Having secured his grasp on the basal part of the female's wings, the male then curls the tip of his abdomen forward, extrudes a clasper-like structure from the genitalia, and by means of this repeatedly grasps at the female's genitalia. After about 60 seconds of such pincer-like actions, a receptive female slightly raises the tip of her abdomen, spreads the vaginal plates and allows coition to occur. During copula the pair is quiet, and at the end the male withdraws but often retains his grasp of the female's wings and may again attempt to achieve coition. He is always unsuccessful on the second attempt and eventually relaxes his grasp and slides off the female.

A non-receptive female, when grasped by the male, kicks and at the same time depresses and twists her abdomen, thus avoiding the "seeking" movements of the male. Eventually the male is dislodged. Males do not attempt to mount other males, appar-

ently breaking courtship at the tapping stage.

Sturtevant (1921, 1942) described the behavior of this species. The timed copulas ranged from 8 to 18 minutes.

***Zaprionis vittiger* Coquillett**

Stock No. 1974.4, Kumba, Africa

The male taps, moves to the rear position, lunges onto the female, pushing her wings apart, grasping her abdomen with his forelegs and middle legs, while the hind legs remain on the substratum. Having assumed this position he periodically rubs the female's abdomen with his middle legs and at the same time seeks to achieve coitus. Owing to the

mating position assumed by the male, he is unable to make contact with the female's genitalia unless she elevates the tip of her abdomen. Males maintain their positions on non-receptive females for long periods of time, and sometimes a second male mounts on the dorsum of the first male.

A non-receptive female attempts to repel males that tap by extruding, elevating the tip of the abdomen, shaking the body violently, and spinning about so that the males cannot get positioned for lunging. Even these actions are not completely effective in preventing males from mounting, but no mounted male was ever observed successfully to achieve coition.

## DISCUSSION AND SUMMARY

### POSSIBLE STIMULI INVOLVED IN COURTSHIP AND MATING

THE PROBLEM OF THE STIMULI that are involved and the role played by each in the mating process has been considered by various investigators (Sturtevant, 1915, 1921; Rendel, 1945; Mayr, 1946, 1950; Wallace and Dobzhansky, 1946; Streisinger, 1948; Merrell, 1949; Spieth, 1949; Spieth and Hsu, 1950). The observations of the present study, plus accompanying experiments, add some information to that previously accumulated.

#### CHEMICAL AND MECHANICAL STIMULI

Rendel (1945) first observed that courtship of *D. subobscura* was initiated by the male's tapping the female with his fore tarsi. Wallace and Dobzhansky (1946) and Spieth (1947, 1949) also observed this phenomenon. Miller (1950) states that he did not observe tapping in *D. algonquin* and *D. affinis* courtships. In the present study it appeared that courtship was always initiated by tapping on the part of the male. That the male receives stimulus through the tapping action is indicated by several types of evidence:

1. Sexually mature males, when isolated with other males only of the same species, assume what can be described as a sexually neutral state. Only occasionally do they tap an individual with which they accidentally or otherwise come into contact. Usually the fly extends the middle leg and fends off any other individual that is met. When introduced into the observation cell with sexually mature females, such males may for some time react as if they were still with males only; often, in fact, they fend off females as they pass and sometimes actually walk over or upon the females without showing any sexual excitement. The instant that one of these neutral males taps a female, however, his behavior immediately changes, in that he shows obvious signs of sexual excitement and begins then to court. If he should lose contact with the female he rushes about tapping other individuals until he has found another female. In species that display great sexual excitement, the tapping act is often of short duration, sometimes consisting of only one stroke with one foreleg, but it seems almost

invariably to be a part of each courting sequence. The rare exceptions when tapping is not a regular part of each courtship pertain under special conditions, for example: (a) Rendel (1945) observed that *D. subobscura* males after tapping once might omit the tapping for immediately subsequent courtships. I have also observed this behavior not only for *D. subobscura* but also in the case of *D. auraria*. It should be noted that in both cases the first courtship is invariably initiated by tapping. Males of *D. subobscura* and *D. auraria* are both light dependent and apparently both possess exceptional visual acuity. (b) Aged, vigorous males of aggressive species such as *D. melanogaster* and *D. ananassae*, after having been isolated for several days, when introduced to their females, become wildly excited as soon as they have tapped a female. Such a sexually aroused male, if his courting sequence is interrupted by the female's decamping, typically postures behind the next individual he meets without tapping.

2. When males are placed with females of another species, especially females of about the same size and demeanor as their own females, they usually investigate and tap and then turn away from the females, indicating the reception of a stimulus that enables them to differentiate the foreign females from their own females.

3. When males are placed with their own females and also with females of another species, they become sexually excited as soon as they tap their own females. This lowers the excitation threshold, and the males rush about tapping the various females. If they tap a foreign female, the courtship stops at that point. Males of *D. virilis*, for example, show this behavior distinctly when placed with females of *D. virilis* and *D. americana*.

4. If males and females of the same species are placed together and subsequently the males become sexually excited, then such males often tap other males as well as the females. Males of many species, when they tap a male of their own species, stop courtship immediately. Other males, such as

TABLE 3  
EFFECT OF FORE TARSAL AMPUTATION ON MATING BEHAVIOR OF MALES  
OF TWO STRAINS OF *Drosophila virilis*

Strain	Homogamic ♀ ♀		Heterogamic ♀ ♀		Species	Geographic Origin
	Fecun- dated	Non- fecun- dated	Fecun- dated	Non- fecun- dated		
Texmelucan <sup>a</sup>						
Normal	4	0	0	4	<i>texana</i>	New Orleans, La.
♂ ♂	8	0	0	7	<i>americana</i>	Poplar, Mont.
	3	1	0	4	<i>americana</i>	Millersburg, Pa.
	4	0	0	4	<i>novamexicana</i>	San Antonio, Tex.
	—	—	—	—		
	19	1	0	19		
Amputated	4	0	0	4	<i>texana</i>	New Orleans, La.
♂ ♂	8	0	5	3	<i>americana</i>	Poplar, Mont.
	4	0	1	2	<i>americana</i>	Millersburg, Pa.
	4	0	1	3	<i>novamexicana</i>	San Antonio, Tex.
	—	—	—	—		
	20	0	7	12		
Pasadena <sup>b</sup>						
Normal	4	0	0	4	<i>texana</i>	New Orleans, La.
♂ ♂	12	0	0	11	<i>americana</i>	Poplar, Mont.
	5	1	0	8	<i>americana</i>	Millersburg, Pa.
	6	1	0	8	<i>novamexicana</i>	San Antonio, Tex.
	—	—	—	—		
	27	2	0	31		
Amputated	7	1	1	6	<i>texana</i>	New Orleans, La.
♂ ♂	5	3	0	8	<i>americana</i>	Poplar, Mont.
	0	8	0	8	<i>americana</i>	Millersburg, Pa.
	0	8	0	8	<i>novamexicana</i>	San Antonio, Tex.
	—	—	—	—		
	12	20	1	30		

<sup>a</sup> Texmelucan, Puebla, Mexico: Stock No. 1801.1.

<sup>b</sup> New York, New York: Pasadena stock.

those belonging to the *D. virilis* and *D. repleta* species groups, seem not to differentiate between males and females of their own species and continue with courting.

5. As stated above, males of *D. virilis*, when they encounter females of other species of the *virilis* group (e.g., *D. novamexicana*, *D. americana americana*, and *D. americana texana*), merely tap and then turn away from the females. If placed together with their own females and an equal number of foreign females (the so-called multiple-choice experiments), they usually quickly fecundate their

own females but not the foreign females. Occasionally, however, a male fecundates a foreign female of one of the three species or subspecies listed above. Direct observation of many individuals shows that a male of *D. virilis*, once he has passed the tapping stage, so to speak, and has begun to posture, courts such foreign females vigorously, persistently, and in typical fashion. It was therefore decided to amputate the fore tarsi of some males and by means of multiple-choice experiments determine whether such mutilated males would more frequently



fecundate foreign females or not. Males of two stocks (No. 1801.1 collected at Texmelucan, Puebla, Mexico, and the Pasadena stock originally collected in New York City, New York) were utilized. The virgin individuals, both males and females, were aged for 10 days, and then four males were placed with four of their own females (homogamic) and four foreign females (heterogamic). The 12 individuals were kept together for 26 hours, after which the females were dissected and checked for the presence of sperm.

As shown in table 3, the Texmelucan males (both operated and normal) fecundated readily and efficiently their own females, but the normal males discriminated completely against the foreign females, while the operated males (i.e., those whose fore tarsi had been removed) fecundated seven individuals, or 37 per cent of the foreign females. Only the *D. texana* females were not represented in the fecundated group.

The experiments with the Pasadena males, however, gave different results. These males, both normal and operated, discriminated against the foreign females (table 3) but, in addition, the operated males failed to fecundate many of their own females. It was not determined whether this was due to the effects of the operation and the loss of the fore tarsi, or the courting pattern was interfered with owing to the lack of reception of the appropriate stimuli. In any case, the experiments clearly indicate that stimuli are received by the male via his fore tarsi and that differences exist in this factor between strains of the same species.

It is thus safe to conclude that the male receives stimuli via receptors located on the fore tarsi and that these stimuli enable the individuals to discriminate between their own and foreign females and in some cases between their own females and males of the same species. Furthermore, the tapping action is a typical part of the courtship pattern but, in light-dependent species and some other species in which the male's excitation threshold drops to a low level, tapping is dispensed with once the males have become sexually excited owing to the presence of their own sexually mature females.

Females also receive specific stimulus from

the tapping action of the male, as is shown by the following observations:

1. Sexually non-receptive females of numerous species often respond with repelling actions as soon as they are tapped by a male. If the male strikes the female with his middle leg or some other part of his body other than the under surface of his fore tarsi, the female ignores the male or reacts to him as if he were a female or an individual of another species.

2. Sexually receptive females often respond to the male's tapping action by immediately giving the acceptance response without the male's having postured.

3. Females of *D. prosaltans* often use their forelegs to execute a striking motion against other individuals. As far as can be determined, this action is identical with the tapping action of the *D. prosaltans* males. If a non-receptive female is tapped by another female, the tapped individual ignores the action, but if she is then tapped by a male she responds with a repelling action, thus indicating that she can differentiate between the tapping of a male and that of a female.

That the fore tarsi should be capable of receiving stimuli involved in the mating behavior is not surprising, since Barrows (1907) clearly shows that chemoreceptors located on the fore tarsi of drosophilids enable them to "taste" their food.

Whether chemical or mechanical stimuli, or a combination of both, are involved in the tapping behavior, it is impossible to say. It seems plausible that the male receives chemo-tactile stimuli as well as mechano-stimuli when he taps. The female must certainly receive mechano-stimuli from the tapping action of the male, but no evidence exists to indicate whether or not she also receives chemo-stimuli.

The licking actions of the male obviously stimulate the females. Non-receptive females almost invariably respond by kicking, decamping, or with some other form of repelling action. Here again there is no evidence to indicate exactly the type of stimulus received by the female. Certainly on the part of the female, tactile stimuli must be involved, but it is possible that chemo-stimuli are also involved. On the part of the male, indirect

evidence indicates that in many species, especially those of the subgenus *Drosophila*, effective stimuli, so far as courtship is concerned, are probably chemical in nature. Males of most species of the subgenus *Drosophila* lick persistently and for considerable periods of time. The proboscis is typically placed over the vaginal plates, and when the female responds with the spreading of the vaginal plates (the acceptance reaction), it is clear that the male will not mount until he has inserted his proboscis briefly into the space between the plates.

No experimental evidence exists to indicate whether or not auditory stimuli are involved in courtship. Indirect evidence indicates that they are. As shown in the descriptions of the mating behaviors of the various species, many males vibrate their wings during courtship. At least three possible explanations of the effect of this behavior are possible, i.e., (a) that the female sees the wing action; (b) that the wing action creates air currents that disperse odoriferous substances in a directed manner towards the female; (c) that the sound produced by the wing vibrations is perceived by the female. Although it is true that no auditory receptors have ever been shown to be present on *Drosophila*, the following two types of evidence indicate that they may well be present, probably in the form of delicate tactile hairs that are stimulated by the movements of the air which are secondary to the pressure waves themselves.

1. Most drosophilids can and do mate in the absence of light. Two species, *D. subobscura* and *D. auraria*, are, however, light dependent and unable to mate in total darkness. The *D. subobscura* male postures in front of its females but does not vibrate its wings. The *D. auraria* male postures at the rear of the female, lunges onto the female, and then after he has mounted he vibrates one wing very briefly. Males of species closely related to these two species vibrate vigorously and persistently while posturing. Thus the lack of wing vibration in *D. auraria* and *D. subobscura* appears to be a secondary specialization, a condition that would scarcely be expected in light-dependent species if we assume that wing vibrations are visually perceived.

2. Males of the *Drosophila virilis* species group, when posturing, intermittently vibrate one wing and engage simultaneously in licking the genitalia and in rubbing the venter of the female's abdomen with their forelegs (see section on Descriptions of the Mating Behavior). Repeatedly it was observed that when a male and female of one of these species were engaged in courtship, another female in the observation cell that was not being courted but merely sitting near the courting pair gave the acceptance response every time the male vibrated his wing. This solitary female never gave the acceptance response to the licking and rubbing actions of the male. Sometimes the solitary female was in front of the courting pair, sometimes beside it, sometimes behind it, sometimes only a few millimeters away, and sometimes as far as 2 cm. away from the pair. Solitary females of *D. tropicalis*, *D. tripunctata*, and *D. funebris* were also observed to react in a similar fashion. All these species have males that vibrate or flick one wing vigorously when posturing. Certainly in all these cases "distance" stimuli are involved, and it seems most likely that such stimuli are of an auditory nature.

Odor unquestionably serves a role in the mating sequence. Barrows (1907) showed that olfactory perception in *Drosophila* is located in the third segment of the antennae. Flüge (1934) proved that removal of this segment deprives the insect of its sense of smell. Mayr (1950) showed that removal of the antennae from females of *D. pseudoobscura* and *D. persimilis* reduced the sexual receptivity of the females and, further, that sexual isolation between the two species almost disappeared. The olfactory receptors are located in a small pit on the third antennal segment, but it is known that this segment also carries other receptors, for example, the segment serves as an air speed indicator (Hollick, 1940; Waterman, 1950), and it is highly probable that auditory receptors, if possessed by *Drosophila*, may also be located on this segment. Males of both *D. persimilis* and *D. pseudoobscura* vibrate their wings vigorously when courting, and it is possible that antennae-less females of these species are thus deprived of auditory as well as olfactory stimuli.

*Drosophila victoria* males, however, display a very simple type of courtship (see species description), consisting simply of tapping followed by the male's lunging onto the female. The antennae were removed from five- to seven-day old virgin females of *D. victoria*, and 24 hours later the specimens were inspected and placed with males of that species. After 24 hours of exposure to the males, the females were etherized, dissected, and checked for the presence of sperm. Of 82 operated specimens, only 11, or 13.4 per cent of the females, were fecundated, while of the 19 normal control specimens, 18, or 94.5 per cent of the females, were fecundated. Direct observations showed that the antennae-less females appeared just as healthy as the normal females and that the males courted them just as vigorously, repeatedly lunging onto them and attempting to copulate. In view of the type of courtship of the males of this species, it seems most probable that antennae-less females failed to accept the males' overtures owing to their failure to receive olfactory stimuli.

Observations indicate that olfaction serves a role in the repulsion actions of the female towards the male. Often a posturing male turns sharply away when the female that he is courting suddenly extrudes. Furthermore, the extruding female often directs the tip of her abdomen towards the male's face. If the male is standing at her side, she may curve the abdomen sharply and move her position if necessary so that the tip of her abdomen is brought into close proximity to the male's antennae.

The wing movements designated as fluttering which are produced by both the males and the females of many species in connection with countersignaling or repelling may also be perceived by auditory receptors, but since they occur typically when the male's head is near the insect that he is courting, it is possible that these wing movements are involved in directing odoriferous materials towards the courting male.

Finally, it should be noted that Sturtevant (1915) found that pairs of *D. melanogaster* could be induced to copulate more quickly if the container (glass vial) in which the

individuals were placed had just previously been occupied by another pair of courting individuals. The first pair was, of course, removed before the second pair was introduced. Apparently the courting actions of the first pair resulted in the release of some substance in the vial that served as a stimulus to the second pair. The total number of copulations between parallel series of the same size was not increased by this technique, but the second series copulated much more quickly than the first series. Clearly this represents a chemical type of stimulation that affects the individuals.

#### VISUAL STIMULI

Sturtevant (1915) noted that when a female decamped from a courting male, the latter followed the female readily if she were only a few millimeters away. Observations on the mating of many hundreds of individuals clearly confirm these findings and also indicate that visual stimuli constitute one of the major factors in the initiation of courtships. Sexually mature male drosophilids have a habit of investigating any individual that comes within a few millimeters and apparently are stimulated by the ambulatory movements of the individual. If a female and male are resting near each other, the female may preen herself, move her wings about, and so on, without the male's showing any response, but if either she or the male starts to walk, then the male usually investigates the female by approaching her and tapping. Owing, of course, to the mosaic type of vision of the insects, walking on the part of either individual would serve to initiate visual stimuli.

Two species, *D. auraria* (Spieth and Hsu, 1950) and *D. subobscura* (Rendel, 1945; Wallace and Dobzhansky, 1946), do not mate in the absence of light. Both of these species display courtship patterns (see detailed descriptions) that seem to indicate that vision on the part of both the male and female plays a major role in the courtship and that the refusal to mate in the dark is not merely the result of an inhibitory effect upon the male's excitation threshold but rather that the males must see the females in order to court.

## NATURE OF THE MATING BEHAVIOR

Huxley (1938) has shown that in species lacking a family life between the sexes, and especially in the invertebrates, courtship display is almost always unilateral and devolves upon the male. *Drosophila* clearly fit the pattern so far as courtship display is concerned. In addition, drosophilids are promiscuous, for the males mate with several females when given the opportunity. With one exception (*D. fumipennis*) the males of all species that have been observed immediately court and copulate with another female as soon as they have completed copulation with a first female. Often they proceed to court the female with which they have just copulated. The females of most species do not immediately accept the male a second time, but during their life span copulate repeatedly. Huxley (1938) states that promiscuity exists in only certain birds such as the Ruff and the Blackcock which lack familial association between the sexes, and the individuals of which gather regularly in groups at special, restricted places such as the feeding grounds. At these gatherings the emotional excitement among the males is intense, and the two facets of sexual excitement, rivalry and display, are always combined. Clearly drosophilids parallel these birds in many respects. The individuals are attracted to isolated masses of food such as decaying fruit, wounds on plants, slime fluxes, and, in the case of the fungous feeders, to fungi. These materials occupy relatively small areas, and numerous individuals of various species of *Drosophila* are thus gathered together in close proximity.

As many observations have clearly shown, individual drosophilids are not able by visual or other sense receptors to determine at a distance whether another individual is of the same or the opposite sex. Thus sexual recognition is by the trial and error method of investigating each individual. Not only can the sex of another individual of the same species not be determined at a distance, but individuals of another species usually cannot be discriminated without physical contact between the specimens. Observations show that a sexually mature drosophilid male

usually investigates, by approaching and tapping, any moving individual that presents about the same demeanor and is approximately of the same size as his own females.

Males do not engage in this investigatory behavior before they are sexually mature, i.e., before they possess a sexual drive. Such sexual drive, owing to internal factors as yet unknown, causes the male to respond to the presence of another individual, and tapping results. As has been shown (Spieth, 1949) tapping is mostly a function of the male, but some females of various species also engage in the same type of action.

If a male taps a female of his own species, he receives a stimulus to which he responds by posturing; if he taps a male of his own species he may receive a stimulus which causes a cessation of action due apparently entirely to the stimulus received by tapping; but, more typically, the tapped individual responds with a countersignaling response which causes the suitor to break off the action. In some species, however, males, after tapping, proceed to court one another by posturing and even attempt to copulate. Usually these courtships are much shorter than the heterosexual ones.

If the male taps an individual of another species, observations to date show that the male can differentiate individuals that are evolutionally distantly related with certainty, but they have difficulty in discriminating closely related species. There are exceptions known in the few groups that have been carefully observed. Thus in the *willistoni* species group (Spieth, 1949) males of *D. fumipennis* and *D. equinoxialis*, two widely separated species, respond to each other's females exactly as they do to their own females, thereby showing that they cannot differentiate females of a distantly related species from their own females. Males of both of these species acutely discriminate, however, between the females of species that are closely related to them.

*Drosophila virilis* males clearly discriminate by tapping the females of their close relatives, *D. americana americana*, *D. americana texana*, and *D. novamexicana*. Although these males

are sexually very aggressive, even under the artificial conditions of no-choice experiments they very rarely more than tap the females of these related species. The reciprocal crosses are quite different. Males of *D. americana americana*, *D. americana texana*, and *D. novamexicana* are practically unable to discriminate, by tapping, the females of *D. virilis* from their own females.

Tapping therefore serves as the first, and perhaps the major, action on the part of the male in the trial and error determination of both sexual recognition and species recognition. That other stimuli are also involved is shown by the fact that *D. virilis*, *D. pseudoobscura*, and *D. persimilis* males that have had their fore tarsi amputated are still able to identify their own females and court and copulate with them. Tapping serves a dual purpose and enables a courting male to commence the process of discrimination as to (1) whether the individual he is investigating is a member of his own species, and (2), if it is one of his own species, whether it is another male or a female. It is not therefore surprising that tapping appears to be a universal phenomenon in the genus and is the starting action in the courting sequence. In a few species such as the light-dependent *D. auraria* and *D. subobscura* and in some very aggressive species such as *D. melanogaster* and its relatives tapping may be dispensed with for short periods, but it always occurs at least as a beginning action.

Having tapped another individual, the male reacts according to the type of stimulus he has received. If he has tapped a female of his own species, he then proceeds to posture. Posturing may vary according to the species involved, from a simple pattern such as that displayed by *D. victoria* to the complex patterns shown by most members of the subgenera *Drosophila* and *Sophophora*, where wing, leg, and proboscis movements are usually involved. In any case the actions of the male represent his response to the stimulus received when he taps the female.

The female, when courted by the posturing male, can respond in one of two ways, i.e., either by accepting the male's overtures or by rejecting them. Since drosophilids are gregarious insects, any female is normally

repeatedly courted. There have evolved a number of ways by which she can repel or refuse the male: extruding, elevating the tip of the abdomen, depressing the tip of the abdomen and the wings, kicking, simply ignoring the male, fluttering her wings, and decamping. Not all the species possess the whole gamut of refusal actions, but certainly they are widely spread through the genus, and all females possess at least more than one type of refusal response. (See table 2.) Decamping seems to be a universal method, but if the female is feeding this seriously interferes with her activities. Observations show that resting females, or females that are moving when the male courts them, are most likely to decamp. Feeding females usually extrude and elevate or depress and kick. Not all females are able to extrude, but those that can usually do so if feeding. All females therefore possess one to several ways of repelling the males which they employ when they are in a non-receptive state. Furthermore, all observations, both in the field and in the laboratory, indicate that each female normally is courted many, many times during her life span, both before and while sexually mature. Despite the fact that she will copulate more than once during her lifetime, the ratio of acceptances to rejections of the males' courting attentions must be extremely low. This, of course, is a result of the promiscuous mating behavior of *Drosophila*. The evolution in the females of a number of repelling reactions which can be employed to refuse the courting overtures of the promiscuous males has as a reciprocal development the hypertrophy of the males' various display actions. As a result, females of most species receive from the posturing males not one type of stimulus but several, some of which are tactile, some chemical, and, when courting occurs in the light, visual. Tinbergen (1948) shows that the reaction of an animal to another animal is rarely governed by a single type of stimulus, but that as a rule several stimuli act together to elicit the reaction. What is necessary is that the heterogeneous stimuli added together are sufficient to reach the threshold of reaction of the individual being stimulated. This threshold of reaction can and does vary

TABLE 4  
EFFECT OF REMOVAL OF ANTENNAE AND ABSENCE OF LIGHT ON FECUNDATION OF  
*Drosophila pseudoobscura* AND *Drosophila persimilis*

	Antennae-less		Per Cent Fecundated	Normal		Per Cent Fecundated
	+	-		+	-	
Light						
<i>D. pseudoobscura</i>	101	101	50.0%	18	1	95.0%
<i>D. persimilis</i>	11	120	8.4	76	4	95.0
Dark						
<i>D. pseudoobscura</i>	58	163	26.2	91	23	79.6
<i>D. persimilis</i>	1	121	0.8	46	20	69.6

\* A plus sign indicates inseminated individuals; a minus sign, non-inseminated individuals.

according to the state of the individual being stimulated. Mayr (1950) shows by direct observation and multiple-choice experiments that the removal of the female's antennae in *D. melanogaster*, *D. persimilis*, and *D. pseudoobscura* reduced the number of inseminations. Since, as indicated above, odor and perhaps other stimuli are perceived by the antennae, the antennae-less females are unable to receive the full effect of the heterogeneous stimuli from the male, and a number of them have a reaction threshold too high to be reached by the stimuli that they were capable of receiving. As a control against the possibility that the severity of the operation might be the causative agent in the decrease of inseminations, Mayr removed the proboscis of some females of *D. melanogaster*. This is a drastic operation that results in death of the specimens within a relatively short time, but nevertheless these severely mutilated flies accepted the males' overtures much more often (45 per cent) than did the antennae-less females (26 per cent).

The effect of heterogeneous summation is also shown by the following data, which were gathered for the present study:

Five- to 10-day old virgin females of *D. persimilis* and *D. pseudoobscura* were introduced in lots of 10 each, with five males of similar age, into a culture vial. The specimens were exposed to the males for 24 hours, and then the females were dissected and checked for insemination. Some of the vials were kept on the laboratory shelf and thus

exposed to diurnal light effects. Others were kept on the same shelves, but the vials were placed in light-tight containers. The third segment of the antennae was removed from the females on the day that they emerged, and they were thus aged as antennae-less flies. They were etherized and reexamined when introduced into the vials with the males. Controls of normal flies were run parallel, although in smaller numbers, with the operated flies. As shown in table 4 the removal of the antennae greatly reduced the per cent of fecundation of those specimens that were kept in the light. The effect was much greater on *D. persimilis* than on *D. pseudoobscura*. When the specimens were placed in total darkness, there was a further decrease in number of inseminations, and only one of 122 *D. persimilis* females was fecundated. In comparison, over one-fourth of the *D. pseudoobscura* females were fecundated. Thus, in the absence of light, the reaction threshold of antennae-less *D. persimilis* females is almost never reached by the stimuli provided by the males' courting actions. In the case of *D. pseudoobscura* a considerable number of individual females are still stimulated sufficiently under similar conditions to accept the males' overtures.

Mayr's experiments (1950) also elucidate one other highly important point in the mating behavior, i.e., the question of species discrimination. Using *D. pseudoobscura* males and females of *D. pseudoobscura* and *D. persimilis* and employing the multiple-choice experiments, he found the coefficient of

isolation (see Levene, 1949) for the normal flies to be 0.975. Since 1.0 represents total isolation, this shows that the normal *D. persimilis* females, even when exposed under artificial conditions to males of *D. pseudoobscura* only, discriminate acutely. In comparison the antennae-less females yielded a coefficient of isolation of only 0.125—in fact almost as many *D. persimilis* females (26.8 per cent) were fecundated as *D. pseudoobscura* females (33.0 per cent). Apparently in the case of these two species, the stimuli that enable the *D. persimilis* females to discriminate the males of their close relative *D. pseudoobscura* are received through the sense receptors of the antennae.

While summation of heterogeneous stimuli seems necessary for the normal mating of the species, certain of these stimuli are of differential value as far as species discrimination is concerned. Some investigators (see Merrell, 1949) have held that with related species, species discrimination is solely a function of the male. As shown by Spieth (1949, 1951) species discrimination is a function of both sexes. In some interspecific crosses, for example, those involving *D. virilis* males, the male is responsible, while in others (such as *D. fumipennis* × *D. equinoxialis*) the female is solely responsible. In most instances, both sexes are partially responsible. This, of course, applies only to closely related species. In the case of distantly related species, the male discriminates by means of the tapping action.

Receptive drosophilid females respond to the males' posturing actions by giving the acceptance response that consists in all species of the spreading apart of the vaginal plates. Often the action is accompanied by a small movement of the abdomen plus the spreading of the wings (see table 2). The spreading of the vaginal plates is a small motion that is difficult for the observer to see, but the drosophilid male seems to have no difficulty in determining its occurrence, since almost without exception he immediately responds to the stimulation he receives from the female's acceptance reaction.

The types of stimuli that the posturing male receives from the female's acceptance reaction obviously vary throughout the

genus. Probably summation of heterogeneous stimuli operates in this case also, but apparently the reactor threshold of mature, sexually excited males is low, and a single type of stimulus may be sufficient to call forth the male's response. The males of virtually all species of the subgenus *Drosophila* will not react to the females' acceptance response until they have inserted their proboscis between the spread vaginal plates of the females. If a female gives the acceptance response, which in many species consists of both wing spreading and vaginal plate opening (see table 2), but if the male is unable to lick the exposed area between the vaginal plates, he does not respond but merely continues to posture. Thus the stimulus or stimuli received via the sense receptors of the proboscis from the area between the vaginal plates seem necessary to elicit the male's response in these species.

In the subgenus *Sophophora*, olfactory and visual stimuli seem to play the major role in stimulating the male. Thus Streisinger (1948) etherized females of *D. persimilis* and *D. pseudoobscura* and exposed them simultaneously to males of *D. pseudoobscura*. In the experiment just as the females were introduced into the observation vials "the ovipositors of the females were squeezed with a pair of fine forceps so that the two halves [vaginal plates] were not tightly closed during the course of the experiment." The normal acceptance response of *D. persimilis* and *D. pseudoobscura* females consists merely of the spreading of the vaginal plates, wing spreading being completely absent. Thus each of these etherized females was giving the total acceptance response when introduced to the males. As a result 45 per cent of the etherized *D. persimilis* females and 55 per cent of the *D. pseudoobscura* females were inseminated by the males. Probably an odor given off by the female as a result of the acceptance action is the stimulus that causes the males to respond.

*Drosophila fumipennis* females spread both their wings and their vaginal plates as the acceptance response. Furthermore, the male postures in front of the female, and thus he must move from his posturing position to the

rear of the female before he can mount. If the female spreads her wings while he is posturing before her, he immediately responds by rushing to the rear and mounting. Spieth (1947) observed such a courting pair, as well as a second sexually excited but non-posturing male that was standing several millimeters behind the female. The female responded to the posturing overtures of the male that was in front of her but before he could reach her rear and mount, the second male had accepted the female's overtures and mounted. It seems probable that in this species both visual and olfactory (but primarily visual) stimuli are involved in eliciting the male's reaction.

As in the case of the promiscuous birds (Huxley, 1938), sexually aroused drosophilid males become highly excited and apparently have a low threshold of reaction. Thus the stimuli needed to effect the reaction on the part of the male can be weak and still be effective. Observation bears this out, since males of many species court not only their own females but also females of closely related species. Furthermore, if given the opportunity males of many species copulate with females of closely related species.

In comparison the reaction threshold of the females may be and usually is relatively high. Females seldom accept foreign males when courted by them and often do not accept their own males. Often the observer is unable to discover any evidence as to why a female or a group of females consistently refuses the overtures of their own males.

Richards (1927) described and discussed this reluctance of the females to accept the males' overtures, which occurs in many species of insects, and termed it "female coyness." No experimental evidence exists to indicate the value, if any, or the cause of this female coyness. Certainly in *Drosophila* the males court vigorously, persistently, and as nearly as can be determined, in a perfectly normal fashion. Often a female that has been courted for long periods of time suddenly becomes receptive and accepts the male's overtures. Some species, and stocks of certain other species, have females that under laboratory conditions are difficult to stimulate to the point of accepting the males'

overtures. For instance, in the present study no copulations have been observed of *D. sellata*, *D. rectangularis*, *D. emarginata*, *D. innublia*, *D. putrida*, *D. nigromelanica*, *D. limensis*, *D. nigricruria*, *D. cardini*, *D. cardinoides*, *D. spinafemora*, and *D. subbadia*. Numerous observations were made on these species and individuals of various ages were employed. In every case the sexually mature males courted vigorously, but the females, all virgins, steadily refused the overtures. All these species can be maintained in the laboratory, which clearly indicates that at least a number of the females must become receptive at some time or other when kept under the standard rearing conditions. Observations as well as experimental data (see Spieth and Hsu, 1950) indicate (1) that a greater percentage of copulations occurs if the individuals are placed together in a mass mating than if the same number of individuals is used for pair matings or even small mass matings (five to 10 individuals of each sex), and (2) that individuals of each species reach a peak of receptivity sometime during the early part of their normal life spans. While this varies considerably for the various species, most drosophilids reach this peak sometime between three to 10 days after eclosion. Those that take a long time to reach the peak usually do not reach sexual maturity until they are five to seven days old, thus indicating that the peak is reached three to five days after the attainment of sexual maturity. Those species that reach the peak on the third day usually reach sexual maturity during the first day and a half of their adulthood. This peak of receptivity may be very short, lasting for only a day or less, or it may taper off gradually, depending on the species. In the *D. repleta* species group apparently the females reach their peak of receptivity, and perhaps many females have actually passed the stage where they will accept the males at all, before males of the same age have reached sexual maturity.

The excessive recalcitrance on the part of females of many species is a by-product in some fashion of the artificial conditions under which the specimens are kept in the laboratory. Patterson, McDanald, and Stone



TABLE 5  
PER CENT OF INSEMINATED FEMALES  
IN WILD *Drosophila*<sup>a</sup>

Species	No. of Females	Per Cent Inseminated	Per Cent in Population
<i>D. busckii</i>	51	98.0%	1.8%
<i>D. putrida</i>	203	92.6	15.4
<i>D. melanogaster</i>	547	95.6	23.2
<i>D. simulans</i>	302	93.0	18.1
<i>D. affinis</i>	88	84.1	5.5
<i>D. pseudoobscura</i>	331	98.5	27.0
<i>D. tripunctata</i>	42	92.8	0.89
<i>D. macrospina</i>	105	86.6	4.8
<i>D. repleta</i>	152	94.0	18.7
<i>D. hydei</i>	552	90.7	23.4
<i>D. mulleri</i>	201	70.1	12.7
<i>D. longicornis</i>	130	67.7	11.6
<i>D. meridiana</i>	63	93.6	3.2

<sup>a</sup> Data from Patterson, McDanald, and Stone (1947).

(1947) collected wild specimens of 13 species and checked them for inseminations (table 5).

These species contain members of three subgenera, and seven species groups. As can be readily seen, the vast majority of the females were fecundated. *D. longicornis* and *D. mulleri* gave low values, but, interestingly, these two species mate readily in the laboratory. In comparison *D. putrida*, a copulation of which has not been observed in the laboratory, showed 92.6 per cent of the wild females inseminated. These data show conclusively that in the normal habitat the vast majority of all sexually mature drosophilid females accept the males' courting activities with sufficient frequency that they have a supply of sperm present at all times.

This does not mean that the females copulate each time that they are courted. Field observations clearly show that the wild males engage in many courtships, just as is observable in the laboratory, and that the females repel them by the standard repulsing techniques. It appears probable that the coyness shown by the drosophilid females is of adaptive advantage in that excess copulations do not take place, and therefore conservation of the gametes, in this case the sperm, is insured. At the same

time the courting behavior of the males insures the opportunity to the vast majority of females of being adequately supplied with sperm during the entire period of sexual maturity.

Although, under the artificial conditions of laboratory existence, many females exhibit unpredictable non-cooperation to the courting activities of their own males, some species display a breakdown of sexual isolation and mate with males that they will not accept in nature even though the species exist in the same locality (sympatric species) and can be collected at the same time. The breakdown of sexual isolation under conditions of confinement is known to exist in many groups of animals, and it is not surprising that it also occurs in *Drosophila*.

If a female accepts the courting actions of a male, the acceptance response stimulates the male to mount the female and achieve intromission of the phallus. The male mounts the female from the rear and assumes the male vertical position (Lamb, 1922; Richards, 1927) on the back of the female, with the tip of his abdomen curled downward and forward, in contact with the female's genitalia. Many species (see table 2) assume a position well forward between the spread wings of the female. In such cases, the male grasps the prothorax or the base of the wings of the female with his fore tarsi, while his middle legs rest on the side of the female's abdomen and his hind legs are either on the female's abdomen or on the substratum. Males of other species (table 2) assume a much more rearward position, grasping the anterodorsal surface of the female's abdomen or even the sides of the female's abdomen with their forelegs, while the hind legs are almost invariably upon the substratum. The bodies of such males are held in an almost vertical position. Sometimes the wings of the female are spread so that the male's head rests between them but in many cases the unsprung wings of the female are merely pushed upward and rest upon the male's head. In a few cases (*D. duncani*, *D. prosaltans*, and *D. rufa*) the male mounts and stands upon the female's dorsum for all or part of the copulatory period. *D. victoria* displays the posture of the male mounting on top of the

female's wings rather than under or between the wings, while *D. tumiditarsus* engages in a bizarre type of copulatory position totally unlike that of any other species so far studied (see detailed description, p. 452).

Intromission of the phallus may occur just before the male mounts, as he mounts, or after he mounts, although (table 2) each species is consistent in its behavior.

After intromission and mounting have been achieved, the copulation usually proceeds without any considerable action on the part of either partner. In some species, such as the *D. willistoni* species group, the male may change his position somewhat during copulation. Some individuals are restless, and the female especially may kick with her hind legs, switch her body, and move about.

Near the end of copula, the female almost invariably becomes restless and begins to kick and walk about. Often these actions cause the male to lose his fore tarsal grasp, and he is displaced backward so that his wing tips and hind legs are his main support. Sometimes the genital union is the only point of contact between the male and the female. Almost invariably the male attempts to regain his position upon the female's body, and certainly the breaking of copula is universally a function of the male. At the end of copula, the male can withdraw and then dismount either by jumping or, most commonly, by sliding backward off the female. He also can terminate copula by turning 180 degrees off the female so that he is facing in the opposite direction from the female and then withdraw. The latter method is most commonly seen in species of the subgenus *Sophophora* and in *D. duncani*, while the former type is displayed by most other species of the genus. After the male has dismounted, the individuals usually preen themselves, and the male proceeds to move about in search of food or another female.

The length of the copulatory period is fairly constant for each species (table 2) but varies enormously within the genus, from about 30 seconds (*D. polychaeta*, 25 seconds; *D. mulleri*, 29 seconds; *D. victoria*, 33 seconds) to over 1½ hours (*D. acanthoptera*). Most species, however, consume less than 20 minutes each per copula.

Males of a number of species belonging to the *melanogaster* and *obscura* species groups of the subgenus *Sophophora* possess structures known as sex combs. These are modified setae that are enlarged so that they give a peg-like appearance. They are located on the basal tarsal segment of the forelegs, and in some species also on the second tarsal segments of the forelegs. Typically a number of these heavy setae are arranged parallel to one another in a row, thus presenting the appearance of a comb. The longitudinal axis of the individual setae may be at right angles to the longitudinal axis of the tarsal segment, or in some species diagonally oriented to the tarsal segment. In all cases the combs are located on the anteromedial surface so that the tips of the setae point either inward or inward and down. Sturtevant (1942) noted that in *D. auraria*, the sex combs aided the male in grasping the female when mounting and during copulation. Spieth and Hsu (1950) found that the sex combs served a similar purpose in *D. rufa* and *D. montium*. In species of the *obscura* group as well as in *D. melanogaster* and *D. simulans*, observations show that the sex combs lying on the anteromedial surfaces of the male's fore tarsi are not in contact with the female's body after he assumes the final copulatory position. A male of the *obscura* group, however, does grasp the dorsolateral surfaces of the female's abdomen with his fore tarsi as he mounts the female, and apparently the sex combs aid at this time in grasping the female. This act occupies an extremely short period of time, and as soon as the male has achieved intromission he immediately releases his grasp and uses his forelegs to push the female's wings upward and apart as he mounts, an action that is necessary since the females do not spread their wings when they give the acceptance response. The males, however, assume a forward copulatory position between the wings and therefore must spread the wings to achieve the copulatory position. In order to test whether or not the males of *D. pseudoobscura* and *D. persimilis* use the sex combs to spread the female's wings, the following experiment was performed:

Six-day old virgin male individuals were

TABLE 6  
EFFECT OF REMOVAL OF FORE TARSI ON MATING BEHAVIOR OF  
*Drosophila pseudoobscura* AND *Drosophila persimilis*

Males	<i>D. pseudoobscura</i>		Females Per Cent	<i>D. persimilis</i>		Females Per Cent
	+ <sup>a</sup>	—		+	—	
Normal	26	0	86.6%	59	10	85.5%
Fore tarsi amputated	1	71	1.4	2	36	5.3
Fore tarsi amputated except for basal segment	28	4	87.4	39	7	84.8
Hind tarsi amputated	60	3	95.2	25	21	54.4

<sup>a</sup> A plus sign indicates inseminated individuals; a minus sign, non-inseminated individuals.

divided into four groups. Group 1 consisted of normal flies; males of group 2 had both fore tarsi amputated; males of group 3 had all segments except the basal segment of the fore tarsi amputated; males of group 4 had the hind tarsi amputated. Five males were then placed with 10 females for 24 hours, after which the females were dissected and checked for the presence of sperm. Observation on the operated specimens shows that the males suffered no serious handicap or displayed no obvious discomfort except that those lacking the hind tarsi had difficulty in balancing themselves. The data derived from this experiment (table 6) clearly show that complete amputation of the fore tarsi interferes seriously with the number of inseminations, but that those males that retain the basal tarsal segment and therefore the major sex combs (these species have in addition to the sex comb on the basal tarsal segment a single enlarged seta on the second tarsal segment) can inseminate the females as readily as the normal males. *D. pseudoobscura* males that lack the hind tarsi are as effective as normal males but *D. persimilis* males that lack the hind tarsi are somewhat handicapped.

Direct observations showed that the males that lack fore tarsi court as vigorously and persistently, and attempt repeatedly to mount the females but are unable to do so except for an occasional individual that manages to separate the female's wings with his head. The sex combs thus serve different functions in various species. Apparently they evolved first as structures for pushing the

wings of the female apart, and secondarily were converted to grasping organs in species such as *D. auraria* and its close relatives which lunge onto the females rather than climb into position as do *D. pseudoobscura* and *D. melanogaster*.

*Drosophila ananassae* males also lunge onto their females when attempting to copulate, but once they have achieved intromission they release their grasp and clamber into a position similar to that of *D. melanogaster*. The males possess transverse rows of stout bristles on the first and second tarsal segments of the forelegs as well as somewhat smaller bristles on the distal end of the fore tibia.

*Drosophila immigrans*, *D. spinofemora*, and *D. tumiditarsus* all possess heavy, peg-like setae on the distal or apical ends of the fore femora plus shortened first tarsal segments which also bear heavy setae. *D. spinofemora* was not observed in copula, but both of the other two species lunge onto the female when attempting to copulate (see detailed species descriptions) and apparently use the specialized forelegs to aid in grasping the female.

In summary we can say that the mating behavior of *Drosophila* consists of a series of actions and reactions that result in species discrimination and sexual discrimination, and at the same time insures that each female of these promiscuous insects is regularly and constantly supplied with an adequate amount of sexual products by males of her own species. The causative stimuli responsible for each reaction seem in almost every case to

be multiple in number, and therefore the principle of summation of heterogeneous stimuli is generally in operation. As a concomitant of the promiscuous nature of these insects, in the courting stage at least the males appear to have a low threshold of response, while the females may display a high threshold of response. This results in the conservation of the male gametes, since

females whose threshold of response is so high that they are non-receptive to the males' overtures are able in all instances to prevent the male from achieving copula. Finally there has evolved in the males of some species specialized structures on the forelegs in the form of modified setae that aid in the copulatory process.

## EVOLUTION OF THE MATING BEHAVIOR

The diversity of the mating behavior displayed by the various species as well as the basic similarity between some species leaves no doubt that there has been an evolution of mating behavior. The present classification of the genus is based on a great mass of evidence that has been derived not only from the external anatomy of the adults, but also from the developmental stages, the internal anatomy of the adults, the chromosomes, and even the positions of the genes themselves as well as from a vast amount of genetic, distributional, and ecological data. An analysis of the evolution of the mating behavior should add another facet of information to our knowledge of the evolution of the genus, and in a small way either confirm, or raise questions as to, the validity of the present classificatory scheme.

Of the eight subgenera now recognized, unfortunately the studies to date on the mating behavior are totally insufficient for the subgenera *Hirtodrosophila*, *Phloridosa*, and *Siphlodora*. *Hirtodrosophila* contains 26 species, of which one has been observed; *Phloridosa*, three species, of which the mating behavior of one has been recorded; while none of the three species belonging to *Siphlodora* has been investigated. Of the five other subgenera, two (*Dorsilopha* and *Sordophila*) are monotypic, and the mating behavior of both species has been studied. The remaining three subgenera (*Pholodoris*, *Sophophora*, and *Drosophila*) consist of 215 species divided into 28 species groups. Of these, 101 species and subspecies representing 21 species groups, plus four unplaced species, have been observed. Thus for five of the eight subgenera, considerable data are available for an attempt at an analysis of the evolution

of the mating behavior.

The first problem that is presented in such an analysis is the determination of the ancestral or primitive mating behavior. As shown in the descriptions of the behavior of the individual species, as well as in the section on the nature of the mating behavior, tapping by the male is, so far as now known, an invariable element in the mating sequence and therefore must be assumed to have been present in the ancestral stock. After tapping, the male then moves to a posturing position. Inspection of table 2 shows that in the great majority of cases the male moves to the rear of the female and then postures. This would seem to be the primitive posturing position. The male's posturing movements, i.e., striking or rubbing the female with the forelegs, vibrating the wings, and licking the female's genitalia with the proboscis, are so widespread throughout the entire genus that it seems reasonable that all three motions were utilized by the ancestral drosophilid male. On the part of the female, the spreading of the vaginal plates is an invariable part of the acceptance response and must have been derived from the ancestral stock. The wing-spreading action of the female, although lacking in many of the species, is widely distributed throughout the genus and probably is a primitive condition. This conclusion is supported by the fact that with rare exceptions (*D. duncani*, *D. victoria*, and *D. lebanonensis*) even in those species where the female does not spread her wings in giving the acceptance response, the male mounts under the wings and pushes them aside or upward with his body. Furthermore, in some cases (e.g., the *obscura* and *melanogaster* species groups) special structures such as

the sex combs have evolved to aid in pushing the wings apart. The ancestral female also doubtless possessed refusal or repelling actions, and it seems most probable that these consisted of decamping, depressing, kicking, extruding, and fluttering. All these actions are so widespread throughout the genus (see table 2) that it would be difficult to conceive that they arose independently within the various evolutionary divergent stems of the group. The widespread habit in modern males of attempting to mount non-receptive females, occasionally seen even in species that normally never attempt such an action, indicates that the ancestral male probably attempted to mount non-receptive females.

Circling on the part of the male is also a widespread action, probably represents the response of the ancestral male to the decamping female, and is often displayed in exactly that manner by modern species when the female starts to move away from a posturing male. Probably those species which now have males that posture in front of the females evolved the anterior front-posturing position in connection with this circling action of the male.

It seems likely that as soon as the female gave the acceptance response, the ancestral male mounted and achieved intromission. Probably intromission was accomplished just as the male mounted or immediately afterward. Certainly the method of inserting before mounting such as displayed by some modern species appears to be a specialized development.

The ancestral copulatory position appears to have been that of the male mounted well forward, grasping the bases of the female's wings with his fore tarsal claws; this is still the most common type. The more posterior type in which the male grasps the female's abdomen with his forelegs is primarily restricted to small, stout-bodied species and seems to represent an adjustment to specialized conditions.

The termination of copula is always a function of the male in modern species, and we can therefore assume that it represents an ancestral character. The ancestral method of dismounting, however, is doubtful. Perhaps, as is still shown by some modern species, the

male displayed variation in this act and could either withdraw and slide off the female or dismount and then withdraw.

The ancestral mating behavior can therefore be hypothesized to consist of the following: The male approached a female, tapped, moved to her rear, and positioned himself close behind her with his head under her wings. In this position, he postured by tapping the female with his forelegs, in the same manner as he initiated the courtship, vibrated one wing and at the same time occasionally licked the female's genitalia with his proboscis. Receptive females responded by spreading the vaginal plates and the wings; the male then mounted, achieving intromission just as he mounted or immediately afterward. He then assumed a "forward" position, grasping the female's wing bases with his fore tarsal claws. At the end of copula, the termination of which was a function of the male, he withdrew his phallus and dismounted or, alternately, dismounted and then withdrew. Non-receptive females repelled the males by kicking, fluttering, extruding, and decamping. In response to the decamping motion, the male circled in front of the female, attempting thus to halt her flight. If he succeeded in stopping her he then returned to the rear position and again postured. Occasionally he attempted to mount non-receptive females, but such females invariably were able to prevent the male from achieving intromission.

Excluding the three subgenera for which data are either insufficient or lacking, the mating behavior observations substantiate the validity of the subgenera as defined by Patterson and Wheeler (1949) and Wheeler (1949a). The members of the two major subgenera (*Sophophora* and *Drosophila*) show clear distinctions on the basis of the mating behavior. *Sophophora* has diverged from the ancestral pattern by the development of dependence on distance stimuli rather than contact stimuli, a phenomenon that is particularly evident in the male's behavior. When posturing the licking action may be completely absent, as in the *obscura* species group and most of the *melanogaster* species group. In the other species groups the licking is always of an intermittent nature, con-

sisting of quick motions of short duration. Likewise the tapping motion of the male while posturing may be omitted, or, if present, consists merely of tapping motions and never of prolonged rubbing actions. Wing vibration is an almost universal phenomenon in this subgenus and even in species such as *D. auraria* and its relatives which have developed a highly specialized courting pattern (see species descriptions) it still is present, although in an abbreviated form. Thus the females are primarily stimulated by distance stimuli. The males also do not depend on contact stimuli for perceiving the females' acceptance response. Apparently the spreading of the vaginal plates releases the main stimuli of the acceptance response, and the male probably receives these as chemical and/or visual stimuli since he immediately mounts after she has presented the acceptance position.

In contrast, the members of the subgenus *Drosophila* are primarily contact animals. When the males court, with few exceptions (table 2) they apply their probosces against the female genitalia and engage in vigorous and continuous licking for long periods of time. At the same time they caress the female with their forelegs, either in a rubbing or a scratching motion. Most of them also engage in wing motions at the same time, but these motions are often flicking movements or vibrations of smaller amplitude than those displayed by the *sophophoran* males. Thus the females are exposed to both contact and distance stimuli. The males, for their part, apparently depend on contact stimuli for the reception of the acceptance response, since with few exceptions, notably the *immigrans* subspecies group and a few of the *quinaria* group, the males do not mount until they have licked the area exposed between the spread vaginal plates of the receptive females. *D. nannoptera* apparently is a connecting link between these two large species groups.

*Drosophila acanthoptera*, the sole representative of the monotypic subgenus *Sordophila*, by virtue of its peculiar posturing position and extremely long copulatory time, in combination with its other actions, is clearly distinct from both *Sophophora* and

*Drosophila* and highly specialized. Probably it is more closely related to *Sophophora* than to *Drosophila* (see description, p. 416).

The unique *D. busckii*, the monotypic representative of the subgenus *Dorsilopha*, likewise presents a distinctive mating behavior that indicates its evolutionary separation from all other subgenera, although it appears to be rather closely related to *Sophophora*.

The subgenus *Pholadoris* presents a confused picture. It consists of two species groups, one of which is monotypic and represented by *D. baeomyia*. The latter, on the basis of its mating behavior, seems closely related to the *willistoni* and *saltans* species group of the subgenus *Sophophora*. The other species group, of which *D. victoria* and *D. lebanonensis* have been studied, shows a specialized mating behavior that clearly sets it apart from all other species groups. (See descriptions and summary of subgenus, p. 407.) Wheeler (1949b), in his detailed discussion of the subgenus, shows that great differences exist between these two species groups, and the mating behavior clearly parallels his findings.

Of the unclassified species that have been studied (i.e., *D. castanea*, *D. parachrogaster*, and *D. tumiditarsus*), the mating behavior, as indicated in the detailed descriptions of each species, gives some indication as to the relationships of these species, although in no case is the evidence sufficient to place them in any of the known species groups.

The mating behavior can also help to elucidate the relationships between the species groups within the subgenera. The two species groups of the subgenus *Pholadoris* are discussed above, and since *Dorsilopha* and *Sordophila* are monotypic we can restrict our attention to *Sophophora* and *Drosophila*.

Within *Sophophora* there are five species groups, one of which is represented by the unique *D. nannoptera* which, as shown above, seems somewhat intermediate between *Sophophora* and *Drosophila*. The other four form two lines of evolution, one represented by the *saltans* and *willistoni* species groups and the other by the *melanogaster* and *obscura* groups. Furthermore, subdivisions can be indicated within the species groups themselves. (See summaries at the end of descrip-

tive sections of the species groups.)

The large subgenus *Drosophila* with its numerous species groups presents a more complex pattern. On the basis of the mating behavior, various major groups or nuclei of related species groups seem quite obvious. One of these nuclei is composed of the *melanica*, *virilis*, *robusta*, *repleta*, *carbonaria*, and *annulimana* species groups. Of these the *melanica* species group seems to be the most primitive, with the *virilis* and the *robusta* groups somewhat more specialized, while *D. robusta*, the only species of the *robusta* species group that has been observed, falls in the center of the triangle formed by these three species groups. The *annulimana* species group is clearly derived from the *repleta* species group, while the *carbonaria* species group shows close relationship to the *virilis* group. In many ways the *melanica* species group not only appears to be the most primitive member of this nucleus of species groups but seems to be the most primitive (i.e., has a mating behavior most nearly like that of the hypothesized ancestral stock) of any species group of the subgenus *Drosophila*. On the scanty evidence derived from the observations on *D. subbadia* of the *guarani* species group, this group may also be closely related to the *melanica* group.

Another nucleus of related species groups is formed by the *guttifera*, *tripunctata*, *funnebris*, *testacea*, *polychaeta*, and *quinaria* groups. The *tripunctata* group appears to be the most primitive, with the *funnebris* group somewhat more specialized. Closely related and possibly derived from the same stock as the *funnebris* group are the *guttifera*, *testacea*, and *polychaeta* groups. The *quinaria* species group belongs to this nucleus but is clearly specialized and is probably most nearly related to the *funnebris* species group. The *cardini* species group shows in its mating behavior distinctive characteristics that set it apart from the groups just discussed but, as shown in the summary of this species group (see p. 436), it is more closely related to the *funnebris* and *tripunctata* species group

than to any other section of the subgenus. The *immigrans* species group, on the basis of the limited mating behavior observations so far recorded, is quite atypical in many respects and, as was noted in the summary of the group, shows similarities to the *melanogaster* and *obscura* groups of the subgenus *Sophophora*. These may represent the product of evolutionary parallelism. At present it is impossible on the basis of the mating behavior to indicate the relationships of this group.

On the basis of the mating behavior, it is difficult to assess the relationship of the two major nuclei of species groups. If the hypothetical ancestral mating behavior is correctly described, then the species groups that cluster about *D. tripunctata* and *D. funnebris* seem to be more specialized than the species groups that are related to *D. melanica* and its relatives.

The evolution of the mating behavior, that is, the gross mating behavior that can be observed by the investigator, seems to follow the structural evolution rather than to precede it. Thus, subspecies and very closely related species, for example, *D. americana americana*, *D. americana texana*, and *D. novamexicana*; *D. macrospina macrospina*, *D. macrospina limpiensis*, and *D. macrospina ohioensis*; *D. pseudoobscura* and *D. persimilis*<sup>1</sup>; *D. mulleri* and *D. aldrichi* seem invariably to display identical mating behavior. This phenomenon is so widespread that it seems to be the typical pattern for all such closely related species and subspecies. At present our data are incomplete, but the investigations of Mayr (1950) and Spieth (1951) indicate that all these species and subspecies possess differences at the sensory level, and thus the first stage in the evolution of the mating behavior must occur at the sensory and psychological levels rather than at the mechanical and physical action levels.

<sup>1</sup> It should be noted that Rizki (1951) has shown that the males of these two species (*D. pseudoobscura* and *D. persimilis*) can be separated by means of their genitalia.

## CONCLUSIONS

1. DESCRIPTIONS are presented of the mating behavior of 101 species and subspecies, representing 21 species groups, of the genus *Drosophila*.

2. The terms for certain regularly occurring, distinctive actions in mating behavior are defined or redefined.

3. The possible nature and action of various stimuli involved in the mating behavior of the various species are considered.

4. The nature and biological significance of the mating behavior are discussed.

5. An analysis of the mating behavior clearly shows that an evolution of mating behavior has occurred which seems to parallel the morphological evolution of the group.

6. On the basis of known mating behavior,

the ancestral mating behavior is hypothesized.

7. Evidence derived from the mating behavior is analyzed to show the probable relationships between certain of the subgenera and species groups. In general the mating behavior confirms the validity of the existing classification as presented by Patterson and Wheeler (1949).

8. Since closely related species, as well as subspecies, always present identical or almost identical visually observable mating behavior, it is believed that the divergence of the mating behavior between species occurs first at the physiological and psychological levels and that the visually observable differences arise much later.

## BIBLIOGRAPHY

- BARROWS, W. M.  
1907. The reactions of the pomace fly, *Drosophila ampelophila* Loew, to odorous substances. Jour. Exp. Zool., vol. 4, pp. 515-537.
- BLUMEL, JOHANNA  
1949. Additional tests within the *quinaria* species group of *Drosophila*. Univ. Texas Publ., no. 4920, pp. 31-38.
- BREUER, MARTHA ERPS, AND CORDOVALDO PAVAN  
1950. Genitalia maxulina de "Drosophila" (Diptera): Grupo "Annulimana." Rev. Brasileira Biol., vol. 10, no. 14, pp. 469-488.
- BURLA, H., A. BRITO DA CUNHA, A. R. CORDEIRO, TH. DOBZHANSKY, C. MALO-GOLOWKIN, AND C. PAVAN  
1950. The *willistoni* group of sibling species of *Drosophila*. Evolution, vol. 3, no. 4, pp. 300-314.
- FLÜGGE, C.  
1934. Geruchliche Raumorientierung von *Drosophila melanogaster*. Zeitschr. vergl. Physiol., vol. 20, pp. 463-500.
- HOLLICK, F. S. J.  
1940. The flight of the dipterous fly *Muscina stabulans* Fallén. Phil. Trans. Roy. Soc. London, ser. B, vol. 230, pp. 357-390.
- Hsu, T. C.  
1949. The external genital apparatus of male Drosophilidae in relation to systematics. Univ. Texas Publ., no. 4920, pp. 80-142.
- HUXLEY, J. S.  
1938. The present standing of the theory of sexual selection. In de Beer, G. R. (ed.), Evolution. Oxford, Clarendon Press, pp. 11-42.
- LAMB, C. G.  
1922. The geometry of insect pairing. Proc. Roy. Soc. London, ser. B, vol. 94, pp. 1-12.
- LEVENE, H.  
1949. A new measure of sexual isolation. Evolution, vol. 3, no. 4, pp. 315-321.
- LUTZ, F. E.  
1914. Biological notes concerning *Drosophila ampelophila*. Jour. New York Ent. Soc., vol. 22, no. 2, pp. 134-138.
- MAYR, ERNST  
1946. Experiments on sexual isolation in *Drosophila*. VII. The nature of the isolating mechanisms between *Drosophila pseudoobscura* and *Drosophila persimilis*. Proc. Natl. Acad. Sci., vol. 32, no. 5, pp. 128-137.
1950. The role of the antennae in the mating behavior of female *Drosophila*. Evolution, vol. 4, no. 2, pp. 149-154.
- MERRELL, D. J.  
1949. Selective matings in *Drosophila melanogaster*. Genetics, vol. 34, pp. 370-389.
- MILANI R.  
1950a. Release of courtship display in *subobscura* males stimulated with dummies. Dros. Information Serv., vol. 24, p. 88.



- 1950b. Sexual behavior of *D. subobscura*, *ambigua*, *bifasciata*, *tristis*, *obscuroides*. *Ibid.*, vol. 24, p. 88.
- 1951a. Osservazioni sul corteggiamento de *Drosophila subobscura* Collin. Inst. Lombardo di Sci. e Lett., vol. 84, pp. 1-12. (Pagination from reprint.)
- 1951b. Osservazioni comparativo ed esperimenti sulle modalita del corteggiamento nelle cinque species europee del gruppo "obscura." *Ibid.*, vol. 84, pp. 1-12. (Pagination from reprint.)
- MILLER, DWIGHT D.  
1950. Mating behavior in *Drosophila affinis* and *Drosophila algonquin*. *Evolution*, vol. 4, no. 2, pp. 123-134.
- PATTERSON, J. T.  
1947a. Sexual isolation in the *mulleri* subgroup. Univ. Texas Publ., no. 4720, pp. 32-40.  
1947b. The insemination reaction and its bearing on the problem of speciation in the *mulleri* subgroup. *Ibid.*, no. 4720, pp. 41-77.  
1952a. The genetic relationships of *Drosophila littoralis* Meigen to the other members of the *virilis* group. Univ. Texas Publ., no. 5204, pp. 7-19.  
1952b. Revision of the Montana complex of the *virilis* species group. *Ibid.*, no. 5204, pp. 20-34.
- PATTERSON, J. T., AND J. F. CROW  
1940. Hybridization in the *mulleri* subgroup. Univ. Texas Publ., no. 4032, pp. 251-256.
- PATTERSON, J. T., LINDA McDANALD, AND W. S. STONE  
1947. Sexual isolation between members of the *virilis* group of species. Univ. Texas Publ., no. 4720, pp. 7-31.
- PATTERSON, J. T., AND M. R. WHEELER  
1949. Catalogue of described species belonging to the genus *Drosophila*, with observations on their geographical distribution. Univ. Texas Publ., no. 4920, pp. 207-233.
- PHILIP, U., J. M. RENDEL, H. SPURWAY, AND J. B. S. HALDANE  
1944. Genetics and karyology of *Drosophila subobscura*. *Nature*, vol. 154, pp. 260-262.
- RENDEL, J. M.  
1945. Genetics and cytology of *Drosophila subobscura*. II. Normal and selective matings in *Drosophila subobscura*. *Jour. Genet.*, vol. 46, pp. 287-303.
- RICHARDS, O. W.  
1927. Sexual selection and allied problems in the insects. *Biol. Rev.*, vol. 2, pp. 298-364.
- RIZKI, M. T. M.  
1951. Morphological differences between two sibling species, *Drosophila pseudoobscura* and *Drosophila persimilis*. *Proc. Natl. Acad. Sci.*, vol. 37, no. 3, pp. 156-159.
- SPIETH, HERMAN T.  
1947. Sexual behavior and isolation in *Drosophila*. I. The mating behavior of species of the *willistoni* group. *Evolution*, vol. 1, no. 1, pp. 17-31.  
1949. Sexual behavior and isolation in *Drosophila*. II. The inter-specific mating behavior of species of the *willistoni* group. *Ibid.*, vol. 3, no. 1, pp. 67-81.  
1951. Mating behavior and sexual isolation in the *Drosophila virilis* species group. *Behaviour*, vol. 3, no. 2, pp. 105-145.
- SPIETH, HERMAN T., AND T. C. HSU  
1950. The influence of light on the mating behavior of seven species of the *Drosophila melanogaster* species group. *Evolution*, vol. 4, no. 4, pp. 316-325.
- STALKER, HARRISON D.  
1942. Sexual isolation studies in the species complex *Drosophila virilis*. *Genetics*, vol. 27, pp. 238-257.
- STREISINGER, G.  
1948. Experiments on sexual isolation in *Drosophila*. IX. Behavior of males with etherized females. *Evolution*, vol. 2, no. 2, pp. 187-188.
- STURTEVANT, A. H.  
1915. Experiments on sex recognition and the problem of sexual selection in *Drosophila*. *Jour. Animal Behavior*, vol. 5, no. 5, pp. 351-366.  
1921. The North American species of *Drosophila*. Publ. Carnegie Inst. Washington, no. 301, pp. 1-150.  
1942. The classification of the genus *Drosophila* with descriptions of nine new species. Univ. Texas Publ., no. 4213, pp. 5-66.
- TINBERGEN, N.  
1948. Social releasers and the experimental method required for their study. *Wilson Bull.*, vol. 60, no. 1, pp. 6-51.
- WALLACE, B., AND TH. DOBZHANSKY  
1946. Experiments on sexual isolation in *Drosophila*. VIII. Influence of light on the mating behavior of *Drosophila subobscura*, *D. persimilis* and *D. pseudoobscura*. *Proc. Natl. Acad. Sci.*, vol. 32, no. 8, pp. 226-234.
- WATERMAN, TALBOT C.  
1950. Flight instruments in insects. *Amer. Sci.*, vol. 38, no. 2, pp. 222-238.
- WHEELER, MARSHALL R.  
1947. The insemination reaction in intraspecific matings of *Drosophila*. Univ. Texas Publ., no. 4720, pp. 78-115.  
1949a. Taxonomic studies on the Drosophilidae. *Ibid.*, no. 4920, pp. 157-195.  
1949b. The subgenus *Pholadoris* (*Drosophila*) with descriptions of two new species. *Ibid.*, no. 4920, pp. 143-156.





