Mating Behavior of the Oriental Fruit Fly, *Dacus dorsalis* HENDEL (Diptera: Tephritidae)

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Mating behavior of the oriental fruit fly, *Dacus dorsalis* HENDEL, was studied under laboratory conditions. The precopulation period was quite variable and 29 days were needed for 50% accumulated mating. Ovaries developed with time, and mated females consisted of those with ovaries in an advanced stage of development. Courtship behavior and general pattern of the daily activity rhythm of the oriental fruit fly proved very similar to those of the melon fly, described in earlier studies. Interspecific copulation between two species was not observed.

INTRODUCTION

In Japan, there are two economically important fruit flies, the oriental fruit fly, *Dacus dorsalis* HENDEL, and the melon fly, *Dacus cucurbitae* COQUILLETT. Eradication projects for these two species have been conducted using the male annihilation method and/or the sterile insect technique in Ogasawara and Ryukyu Islands (KOYAMA, 1982). In these projects, basic information on such activities as mating behavior is indispensable to achieve successful eradication. Although some studies have been conducted on the mating behavior of the melon fly (KOBAYASHI et al., 1978; SUZUKI and KOYAMA, 1980, 1981; KUBA and KOYAMA, 1982), published information on the mating behavior of the oriental fruit fly is scant (ROAN et al., 1954; KOBAYASHI et al., 1978). In this paper, the mating behavior of the oriental fruit fly is generally described, and the possibility of interspecific copulation between this fly and the melon fly is examined.

MATERIALS AND METHODS

Insect. The oriental fruit flies tested were obtained as larvae from infested peach, *Prunus persica* BATSCH, collected on Ishigaki Is., Okinawa, Japan in June, 1982. Adult flies were sexed within a day after emergence and reared in a screen cage (30×30×45 cm) on water, sugar and protein hydrolysate. The rearing room was maintained at 27±1.5°C, 60-80% R. H., with natural daylight entering through an eastern window.

Sexual maturation. Three experiments were conducted to determine the time of sexual maturation of the flies.

In the 1st experiment, 50 males and 50 females were confined together in a screen cage from the day of emergence and were maintained for 60 days. On successive days,

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mating pairs were counted and removed from the cage about half an hour after the termination of photophase, using a red light torch as an aid.

In the 2nd experiment, 150 females were held in a screen cage from the day of emergence. Ovarian development was examined in 0, 5, 10, 15, 20, 30, and 40-day-old females by dissection of 20 samples for each age. Each female was placed in one of 5 categories, depending on the stage of the most advanced terminal ovarian follicles. The stages 1, 2, 3, and 4 represented immature ovaries with the follicles being less than 0.40, 0.40–0.60, 0.61–1.00 and more than 1.00 mm in length, respectively, while the ovaries of stage 5 contained mature eggs.

In the 3rd experiment, 50, 20-day-old male flies and 50, 0-day-old females were confined together in the screen cage. The mated females were dissected daily from the day of first mating to 6 days after mating to examine the relation between ovarian development and their mating receptivity.

Daily activity rhythm. Daily activity rhythm performed by sexually matured virgin flies was examined in the following 4 experiments. In all experiments, a transparent plastic cage (30 × 30 × 45 cm: observation cage) was used to confine the flies, and light intensity was measured by an electric photometer (Yokogawa Electric Works, type-3281®) placed in the middle of the upper surface of the observation cage.

In the 4th experiment, 10 male and 10 female 41-day-old flies were confined separately in two different observation cages provided with water and food. Observations on their daily activity rhythms of 4 types of behavior, locomotion (walking and flying), preening, feeding and wing vibration were made from 05:00 to 20:00 hr. Each set was observed twice for 1-min within a 10-min period spaced at 15 or 60 min intervals. The data were presented as the average of the two observations.

In the 5th experiment, 10, 45-day-old male flies were confined in an observation cage without food or water, and those engaging in wing vibration were counted at 5-min intervals between 18:00 and 20:00 hr. Two observations were made.

In the 6th experiment, 10, 44-day-old flies of each sex were confined together in the observation cage without food or water. Males engaged in courtship and pairs *in copulo* were counted at 5-min intervals during 18:00–20:00 hr. Two observations were conducted.

In the 7th experiment, the termination time of copulation was examined using 10 pairs *in copulo* from the 6th experiment.

Courtship behavior. Observations of the courtship behavior of the oriental fruit fly were carried out in detail. The possibility of interspecific copulation between the oriental fruit fly and the melon fly was examined also. In all the experiments, observation cages were used.

In the 8th experiment, one male and one female, 39-to 60-days-old and unmated were confined together in the cage at 17:00 hr and their courtship behavior was observed continuously until either the time copulation occurred or light intensity decreased to less than 1 lux. The observations were replicated 30 times with different flies.

In the 9th experiment, one virgin oriental fruit fly male, 45-to 62-days-old, together with one virgin melon fly female, 37-to 60-days-old, or one virgin melon fly male, 37-to 60-days, and one virgin oriental fruit fly female, 45-to 62-days-old were confined in separate cages at 17:00 hr. Their courtship behavior was observed continuously until light intensity decreased to less than 1 lux. The melon flies used in this experiment were obtained as larvae from infested bitter cucumber, *Mormordica charantia* var. *pavel*

CRANTZ, on Ishigaki Is. and adults were reared in the same manner as the oriental fruit fly. The observations were replicated 15 times with different flies in each combination.

RESULTS

Sexual maturation

The results of the 1st experiment, in which the same number of males and females were confined in a cage from the day of emergence, are shown in Fig. 1. The first mated pair was observed on the 11th day after the day of emergence, and successive copulations occurred very slowly. Twenty-nine days were needed for 50% accumulated mating, and 80% accumulated mating occurred on the 51st day. No subsequent copulation was observed through the end of the experiment.

Data concerning the dissection of ovaries in virgin females in the 2nd experiment are presented in Table 1. Ovaries developed with age: 20% of the females had mature eggs on the 15th day and 70% had mature eggs on the 40th day. The results of the 3rd experiment, in which the relation of ovarian development to mating receptivity of

Fig. 1. Accumulated percentage of flies which mated. Cage contained 50, 0-day-old flies of each sex at the start of the experiment. Two males died on the 1st and 46th days, and one female on the 39th day.

Table 1. Relation between the age of adult females and stage of ovary development

Stage ^a	Days after emergence						
	0	5	10	15	20	30	40
1	20	12	2	0	0	0	0
2	0	8	11	7	1	1	0
3	0	0	6	6	9	4	3
4	0	0	1	3	3	4	3
5	0	0	0	4	7	11	14

^a Stages 1 to 4 represent immature ovaries with terminal follicles less than 0.40, 0.40–0.60, 0.61–1.00, and more than 1.00 mm in length, respectively; stage 5 ovaries contain mature eggs.

Table 2. Relation between stages of ovarian development and mating receptivity of females

Stage ^a	Days after emergence						Total
	11	12	13	14	15	16	
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0
3	1	2	0	0	0	0	3
4	0	0	0	0	1	1	2
5	1	0	2	3	0	1	7
Total	2	2	2	3	1	2	12

^a For explanation see Table 1.

Fig. 2. Daily activity rhythms of locomotion (B), preening (C), feeding (D), and wing vibration (E), and frequency of physical contact per min per 10 individuals (F) at different times of day in batches containing 10 males or 10 females. Solid and dotted lines represent male and female activities, respectively. Change in light intensity (A) is also shown.

females was examined, are shown in Table 2. Copulations did not occur in females of stages 1 and 2, but were observed in females after stage 3, and occurred frequently in females of stage 5.

Daily activity rhythm

Records on the daily activity rhythms for the 4 types of behavior in the 4th experiment are shown in Fig. 2. Two definite peaks, early in the morning and at dusk, were observed in locomotion and preening activity of both males and females. Feeding occurred mainly in the morning. Only males engaged in wing vibration, which was restricted to dusk. First peak of locomotion in the morning coincided with the peak of feeding, because flies often tried to expel one another from the food dish by head-on collision. The peak of locomotion at dusk coincided with the mating behavior.

Light intensity and wing vibration frequency of males confined without females at dusk in the 5th experiment are shown in Fig. 3. Wing vibration started when light intensity decreased to 360 lux. The highest frequency occurred at 190 lux, and wing vibration stopped at 20 lux.

Figure 4 shows the light intensity and copulation frequency at dusk in the 6th experiment. First copulation was observed at 280 lux and the last at 23 lux; 50% of the flies copulated. As males did not engage in wing vibration after copulation, the wing vibration frequency was lower than in the 5th experiment, in which only males were confined in the cage.

In the 7th experiment, 10 pairs *in copulo* continued copulation until daybreak. They parted from one another when light intensity became 0–13 lux (Fig. 5). The duration *in copulo* was 10 hr 14 min on average.

Courtship behavior

Table 3 shows the light intensity at which mating behavior occurred in the 8th

Fig. 3. Percentage of males engaged in wing vibration, and the light intensity at different times between 18:00 and 19:40 hr in batches of 10 males. Averages of the two replicates are presented.

experiment. As light intensity decreased to less than 1,000 lux, male and female flies increased their locomotive activities. The first exhibitions of wing vibration and mounting by males were observed under average light intensities of 141.8 and 82.3 lux, respectively. Copulation occurred at an average light intensity of 57.8 lux.

Table 4 shows courtship behavior of the oriental fruit fly in the 8th experiment. Of 30 males tested, 10 exhibited wing vibration but 20 did not. Physical contact occurred more frequently in wing vibrating males (80.0%) than in non-wing vibrating males (55.0%). Copulation was performed more successfully by the former (50.0%) than the latter (30.0%).

In wing vibration behavior, rapid wing vibration was accompanied by rhythmic beating of the posterior part of the abdomen by alternately moving the rear legs up and

Fig. 4. Accumulated percentage mating (solid line) and percentage males engaged in wing vibration (histogram) at different times between 18:00 and 19:40 hr, in batches of 10 males and 10 females. Averages of the two replicates are presented.

Fig. 5. Time of copulation termination and light intensity.

Table 3. Light intensity at initiation of wing vibration, mounting and copulation of single pairs

Behavior	No. observed	Light intensity (lx)	
		Mean	Range
Wing vibration	10	141.8	32-225
Mounting	20	82.3	8-176
Copulation	11	57.8	8-112

Flies tested were introduced into the experimental cage at 17:00 hr.

The experiment was replicated 30 times.

Table 4. Courtship behavior of the oriental fruit fly^a

	Yes	No
No. of males engaged in wing vibration	10 (33.3%)	20 (66.7%)
No. of pairs in physical contact	19 (63.3%)	11 (36.7%)
No. of males in physical contact of wing vibrating males	8 (80.0%)	2 (20.0%)
No. of males in physical contact of non-wing vibrating males	11 (55.0%)	9 (45.0%)
In physical contact, position of male in relation to female	<div> <div>Front</div> <div>Rear</div> <div>Other</div> </div> <div> <div>19^b(82.6%)</div> <div>2 (8.7%)</div> <div>2 (8.7%)</div> </div>	
No. of pairs engaged in head-on collision of those in physical contact	13 (68.4%)	6 (31.6%)
No. of pairs engaged in mounting	17 (56.7%)	13 (43.3%)
No. of pairs successfully copulating	11 (36.7%)	19 (63.3%)
No. of males in successful copulation of wing vibrating males	5 (50.0%)	5 (50.0%)
No. of males in successful copulation of non-wing vibrating males	6 (30.0%)	14 (70.0%)

^a The experiment was replicated 30 times.

^b Numbers include duplication of the same behavior by the same individuals.

down. During wing vibration, the male remained rather stationary, and the receptive female approached him. The male directed his attention toward the female usually in a face to face position when she had approached to within a few centimeters.

Physical contact between males and females occurred mainly in frontal positions (face to face, 82.6%) but it also occurred in some other orientations. In such cases, females crossed just in front of the males (side, 8.7%), or passed near the males (rear, 8.7%). In frontal orientation, flies usually had a head-on collision (68.4%), i.e., bumped each other with their head for a few seconds. In a few cases, however, the male jumped on the female's abdomen before any physical contact had taken place between them (31.6%). After a head-on collision, the male jumped from the frontal position over the head of the female and onto her abdomen. Seventeen males (56.7%) succeeded in mounting. As soon as he settled on the female's back, the male vibrated his wings rapidly for 1 to 20 sec and tried to insert his aedeagus into her ovipositor. A

receptive female remained stationary when a male settled on her back; however, an unreceptive female tried to dislodge the male by rapid walking, flying, or kicking with her rear legs. Eleven (36.7%) of the 30 pairs tested achieved successful copulation. After the union of genitalia, the male released his meso and rear legs from the female's abdomen and attached them to the substratum; however, his forelegs still held the female's abdomen until the copulation terminated. Copulation usually occurred on the floor of the cage and copulating pairs moved mostly toward the cage wall and stood still there until daybreak.

Interspecific courtship behavior between the oriental fruit fly and the melon fly

Table 5 shows interspecific courtship behavior between the oriental fruit fly and the melon fly in the 9th experiment. When one male oriental fruit fly and one female melon fly were confined in a cage, 4 (26.7%) of 15 males tested vibrated their wings. Eight (53.3%) and 5 (33.3%) male oriental fruit flies physically contacted and mounted, respectively, a female melon fly. As soon as a male oriental fruit fly jumped on a female melon fly's abdomen, he would depart from her. No male oriental fruit fly succeeded in copulation with a female melon fly. On the other hand, when one male melon fly and one female oriental fruit fly were confined in a cage, 12 (80%) of 15 males were observed to perform stridulation. Six pairs (40.0%) conducted physical contact but no male melon fly attempted to mount a female oriental fruit fly.

DISCUSSION

ROAN et al. (1954) observed that adult oriental fruit flies reared on artificial diets usually copulated from 7 to 10 days after emergence in the laboratory at temperatures

Table 5. Interspecific courtship behavior between the oriental fruit fly and the melon fly^a

	Melon fly ♀ vs. oriental fruit fly ♂		Oriental fruit fly ♀ vs. melon fly ♂	
	Yes	No	Yes	No
No. of males engaged in wing vibration	4 (26.7%)	11 (73.3%)	12 (80.0%)	3 (20.0%)
No. of pairs in physical contact	8 (53.3%)	7 (46.7%)	6 (40.0%)	9 (60.0%)
In physical contact, position of male to female	Front 6 ^b (66.7%) Rear 3 (33.3%) Other 0 (0 %)		6 (100 %) 0 (0 %) 0 (0 %)	
No. of pairs in head-on collision of those in physical contact	5 (62.5%)	3 (37.5%)	6 (100 %)	0 (0 %)
No. of pairs engaged in mounting	5 (33.3%)	10 (66.7%)	0 (0 %)	15 (100 %)
No. of pairs successfully copulating	0 (0 %)	15 (100 %)	0 (0 %)	15 (100 %)

^a The experiment was replicated 15 times in each set.

^b Numbers include duplication of the same behavior by the same individuals.

ranging 23.9–29.4°C. UMEYA et al. (1973) reported that mass-produced oriental fruit flies passed 10 days before copulation at 27°C. SUZUKI and KOYAMA (1980) found that the laboratory strain of the melon fly maintained on an artificial diet for about 49 generations had a shorter pre-mating period than the wild strain. In this study, the wild oriental fruit fly had quite variable pre-copulation periods, and 29 days were needed for 50% accumulated mating (Fig. 1).

SUZUKI and KOYAMA (1980) reported a positive correlation between the stage of ovarian development and mating receptivity of females in the laboratory strain of the melon fly. Ovaries of the oriental fruit fly developed with time (Table 1), and mated females consisted of those with ovaries in an advanced stage of development (Table 2). This result coincided well with that for the melon fly.

The general patterns of daily activity of locomotion, preening, feeding, wing vibration and physical contact of the oriental fruit fly (Fig. 2) were quite similar to those of the melon fly (SUZUKI and KOYAMA, 1980). As dusk approached, locomotion activity of the oriental fruit fly increased, and physical contact frequently resulted (Fig. 2).

ROAN et al. (1954) noted that the oriental fruit fly produced a characteristic high-pitched buzzing sound associated with mating at dusk. Male flies exhibited two types of characteristic rapid wing vibration: one type was just prior to mounting, accompanied with the rhythmic beating of the abdomen by the rear legs; the second type was conducted just as the male settled on a female's back. A male fly could copulate with a female without wing vibration; however, this may have been because of the narrow space of the cage where the sexes were always close to each other. Wing vibrating males showed a higher success rate of copulation than non-wing vibrating males (Table 4).

The courtship behavior of the oriental fruit fly greatly resembled that of the melon fly (SUZUKI and KOYAMA, 1980, 1981; KUBA and KOYAMA, 1982). Namely, (A) locomotion behavior increased and physical contact was frequent at dusk, (B) the first exhibition of wing vibration by males was observed under a light intensity of a few hundred lux, (C) wing vibration of males was accompanied by a rhythmic abdominal beating behavior with the rear legs, (D) the male remained stationary when he did the wing vibration and the female moved toward him, (E) physical contact, including a head-on collision between male and female, occurred usually in a face to face position, just prior to mounting, (G) rapid wing vibration was conducted just as a male settled on a female's back, (H) copulation occurred at 8–112 lux in the oriental fruit fly, and at 1–198 lux in the melon fly (wild strain) and (I) copulation continued until daybreak.

In addition to this similar courtship behavior, these two related sympatric species have several common host plants and similar life cycles. PROKOPY and BUSH (1973) described that in combinations of *Rhagoletis pomonella* males with *R. fausta* females, or *R. fausta* males with *R. pomonella* females, copulation occurred, but mating ratio and egg hatchability were lower than in copulation within like species. KOBAYASHI et al. (1978) reported that the gland complex of the rectal sac of the male oriental fruit fly, thought to be the source of an olfactory pheromone, was highly attractive to female oriental fruit flies. They suspected that the components of the sex pheromones of the two species may be structurally related. From these facts, we wondered about the possibility of interspecific copulation between the oriental fruit fly and the melon fly. When males of the oriental fruit fly were caged without females, several attempted copulation with other males, and remained on the other male's abdomen for 1 to 30 sec. In combinations of male oriental fruit flies with female melon flies, several males engaged in head-

on collision and attempted copulation with females. But when a male jumped on a female's back, he immediately departed. In combinations of male melon flies with female oriental fruit flies, head-on collisions were frequent but copulation attempts were not observed. These results suggest that males are unable to distinguish the species until the time of tactile contact. Tactile stimulus may be one of the mechanisms involved in species discrimination.

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