

Pseudomale Courtship Behavior of the Female Mediterranean Fruit Fly, *Ceratitis capitata* (Wiedemann)¹

LORNA H. ARITA and KENNETH Y. KANESHIRO²

ABSTRACT

Virgin laboratory females of the Mediterranean fruit fly perform a series of behavioral actions which closely resembles the courtship repertoire of their males. This pseudomale courtship behavior occurs when females are separated from males at eclosion and maintained beyond their optimum sexual period. It is postulated that under these conditions, females exhibit behavioral actions which may possibly enhance their chances of mating during periods when potential mates may be less frequent in the natural population.

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) has been called one of the world's most destructive fruit pests because of its wide distribution and broad host range which includes citrus and stone fruits. In recent times, the medfly has again been brought into the "limelight" when it was found infesting backyard fruits in parts of California. These outbreaks of the medfly in "fly-free" areas has led to an even greater resurgence of research on this pest which provides needed information for the development of sound control programs.

One area of basic research on this fly which has been investigated only to a limited degree is the mating behavior. The original description of the mating behavior by Martelli (1910) and Back and Pemberton (1918) provided the basis for subsequent research, the most complete of which was done by Feron (1962). However, though these previous researchers described the qualitative aspects of the mating behavior, a thorough quantitative analysis is still needed. Prokopy and Hendrichs (1979) have even stated that "To date, there has been no published cursory observational study of medfly mating behavior under semi-natural or natural conditions." Our present research is directed toward the understanding and analyses of the mating pattern for the medfly based on qualitative and quantitative data collected both in the field and in the laboratory.

In the process of conducting our mating studies, certain aberrant behaviors in these flies were observed. The observations of one such behavior, "pseudomale" courtship performed by females are presented here. This behavior strikingly resembles the mating ritual displayed by the male (Feron 1962) and although the significance of such capability is not clear at this time, we have the opportunity to study the genetic basis of the mating behavior and its coadaptation between the sexes.

MATERIALS AND METHODS

Laboratory reared medflies were obtained as puparia from the USDA-ARS Tropical Fruit and Vegetable culture (Tanaka et al. 1970). The puparia were held in containers and within 24 hours from the time of eclosion, the virgin adults were sexed

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²Department of Entomology, University of Hawaii, Honolulu, Hawaii 96822.

and placed in separate cages. All flies were provided with a yeast hydrolysate and sugar mixture (Tanaka et al. 1970) and water and aged for at least 7 days prior to experimental use to assure that they were sexually mature (Arita 1982). Females were aged for an additional 7 days prior to experimental use which enhanced the expression of the pseudomale behavior.

Three sets of four glass ($15 \times 8 \times 11$ cm) cages were prepared with each cage containing five sexually mature virgin females; no additional flies were added to the cages in set 1, five sexually immature males were added to each of the four cages in set 2, and five sexually mature males were added to each of the four cages in set 3. The actions of the individuals in each cage were videotaped using a JVC color video camera and a Sony $\frac{3}{4}$ inch VTR recorder. The tapes were later analyzed for the responses of the females in the presence of sexually immature males, sexually mature males, and in the absence of males.

RESULTS AND DISCUSSION

We have determined from our field observations that the sexual period for the medfly begins at 9:00 a.m. and continues until 3:00 p.m. During this period which may vary due to environmental conditions, a male attempts to attract and court those females that enter his territory.

Feron (1962) divided the mating behavior of this fly into three distinct stages: the waiting period, the arrival of the female, and the assault and coupling stage. However, the data from our research suggests that a different set of phases or stages more accurately describes the mating behavior.

The mating behavior of the medfly can be visualized as a series of dependent phases. Each phase in part of the overall process and therefore several actions within a phase may be performed in another phase or are prerequisites for subsequent actions. The phases which we have identified are lek behavior, courtship, and copulation. A brief description of each phase except for copulation will be presented followed by a description of the pseudomale actions performed by the female.

Phase I — Lek Behavior. The initial step in the sexual selection process in this species is the formation of leks. A medfly lek was observed as an aggregation (2-12) of courtship territories within the canopy of the tree (Fig. 1). The underside of leaves of the host tree were selected as territories by the males. Each territory (a single leaf) was occupied by only one male who defended his territory against all rival intruders. In the laboratory, males utilized the underside of leaves of potted bean plants though there appeared to be some abnormality in the male's capacity to occupy territories under laboratory conditions.

Females were not observed to exhibit this behavior in the field or in the laboratory though aggressive encounters similar to those performed by males when defending their territories were observed.

Prokopy and Hendrichs (1979) have used the phrase "pheromone calling" to describe the actions of a male as he attempts to "call" or attract females to his territory. For our research purposes, we have also adopted the term pheromone calling for particular actions in the lek behavior phase of mating and have defined it as a set of behaviors which can be repeated numerous times during the sexual activity period.

Although the primary function of pheromone calling is directed towards "calling" females to the territories of the males, it is also believed that pheromone calling serves to "call" males to the lek. Our notion is that an aggregation of males at the lek site increases the concentration of the pheromone which in turn serves to attract females to

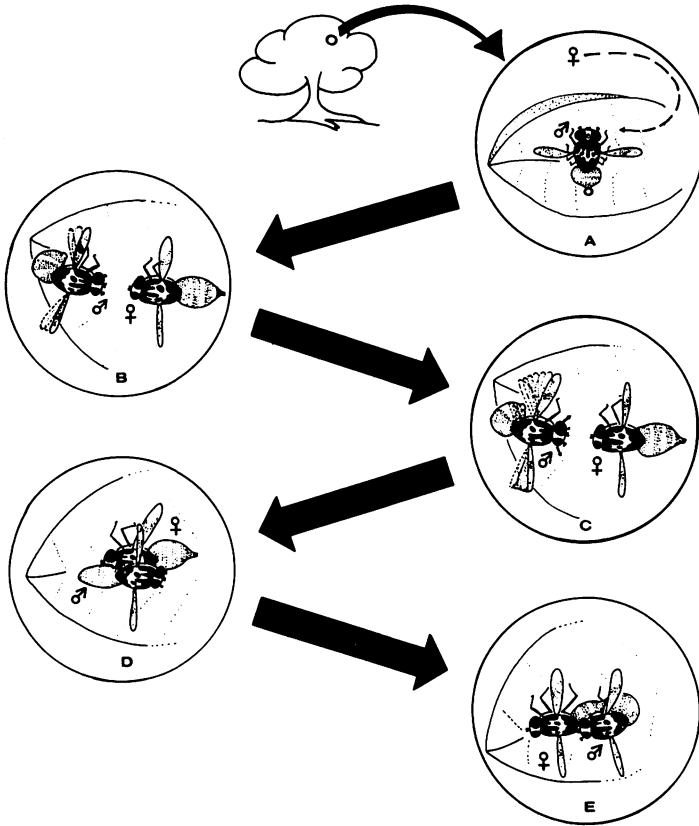


FIGURE 1. A portion of a medfly lek with two males on neighboring territories.

the mating arena. Pheromone calling therefore serves the dual function of attracting both males and females to the leks which is ultimately directed toward mating.

The male initiates pheromone calling in the "orientation position" (Fig. 2). When in this position, the male's wings are extended laterally parallel to the substrate with his legs set in a distinct stationary position. Simultaneously, the terminal end of the male's abdomen is curled dorsally with the distal end of the rectal epithelium everted from the anus. While in this position, the male releases a pheromone which is secreted by the anal glands (Lloste and Roche 1960) located within the rectal epithelium. From this position, the male can perform several actions. The male may reorient himself while performing wing lifts which are slight raises of the wings or may tuck his abdomen ventrally under his body while vibrating his wings.

Phase II — Courtship. Courtship is initiated when a female is attracted to and lands within the territory of a male (Fig. 3). The male reorients toward the female as soon as he perceives her presence. Simultaneously, the male initiates wing vibrations as the female continues to approach. When the female is within 1-2 cm of the male, she stops and remains motionless. The male will then initiate a series of head movements oscillating his head in both directions about 45° from the normal resting position. Within 1-2 seconds after the initiation of head movements, the male begins

to fan his wings. While continuing the wing and head actions, the male walks closer to the female until he is almost touching the female's antennae with his second pair of fronto-orbital bristles. If the female has not changed her position, the male will attempt to mount.

Pseudomale courtship actions performed by females. Under certain conditions, females perform all the actions of male courtship. When females were maintained as virgins several days beyond this optimum sexual maturation period, these females appear to mimic the courtship actions of the male. Such pseudomale behaviors appear to be independent of the other occupants of the cages; i.e., females in the absence of males, females in the presence of sexually immature males, or females in the presence of sexually mature males. In all cases, these older, virgin females display a certain amount of orientation posturing together with wing lifts, wing vibrations, and occasional reorientation movements. Except for the lack of an everted rectal epithelium, the posture of the female and the wing actions displayed by the females during the orientation phase of the mating pattern cannot be distinguished from those of males.

In the absence of males, females may perform all the courtship actions toward other females in the cage. Interestingly, females which are courted by pseudomale females display actions which were never observed when females were courted by sexually mature males. The females which were being courted responded with pseudomale behaviors of their own such as wing vibration and fanning and head movements. Of course, all the females in the cages were of the same age so that potentially all had developed the capability to perform the pseudomale behavior.

Pseudomale females displayed an even greater intensity of pseudomale courtship actions in the presence of males. If the males were sexually immature, the females would aggressively pursue the males while displaying head movements and wing fannings. Generally, such males would decamp or at least move away from the courting female and rarely remain in one position to receive the courtship stimuli of the female. On the other hand, if the males are sexually mature, they will orient toward the pseudomale female and then initiate his own courtship actions. At this stage, one of two alternative interactions may take place: 1) the female may cease her courtship actions, and assume a passive posture which usually results in copulation; or 2) the female may continue to display pseudomale behavior causing the male to decamp. The females have also been observed to rudely interrupt the courtship of a male toward another female by physically attacking the male. The aggressor female may then resume the courtship actions initiated by the male toward the second female.

Morris (1955a) postulated several causal factors which can regulate the expression of pseudomale and pseudofemale behavior. Though at the present time we do not know the precise causal factor for the expression of this pseudomale courtship behavior in the females of this species, the presence of the releasing stimuli for the sexual behavior of the opposite sex as proposed by Morris (1955a) would seem to be the most parsimonious. In addition, the release of this stimuli may be controlled hormonally as determined in other animals (Crews and Fitzgerald 1980; Arendash and Gorski 1982). These observations may be of even greater significance for if this behavior does indeed have a genetic basis, we may have the rare opportunity to investigate the co-adaptedness of the courtship pattern between the two sexes within a single interbreeding population (Arita et al. 1981). We intend to continue to investigate the mechanism responsible for the expression of this behavior in the female medfly as well as the potential use of this behavior to better understand the process of sexual selection.



FIGURE 2. Ventral view of a male medfly in "calling" position.



FIGURE 3. Courtship sequence in the medfly. A. male calls; female orients to site. B. male orients to female; female remains stationary. C. male wing fans and performs head movements; female remains stationary. D. male mounts; female remains stationary. E. successful copulation.

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