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Sexual Selection and Lek Behavior in the Mediterranean Fruit Fly, *Ceratitis capitata* (Diptera: Tephritidae)[1]

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ABSTRACT: Field and laboratory studies were conducted to describe the complex lek mating system of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). Results of these studies indicate that there are two phases in the mating system: (1) lek behavior and (2) courtship. In the initial lek behavior phase, males acquire and defend territories that are used as courting sites for receptive females. An aggregation of these territories that form a communal display area is known as a "lek" and once a female enters the lek and arrives at the territory of a male, a series of courtship actions are reciprocated between the pair that may result in copulation. Descriptions of other environmental parameters that appear to be important features of the lek system are also presented.

SEXUAL REPRODUCTION is one of the most important features in the life history of most higher organisms. The processes that result in the bringing together of individuals of the opposite sex and the subsequent mating of these individuals are essential to the perpetuation of the species. In polygamous populations, there is often differential mating success among the males. This differential mating success is a result of the sexual selection process, which ensures that individuals whose genetic combination results in high Darwinian fitness are those that will participate in the mating community.

There are two aspects to sexual selection: (1) intrasexual selection, which involves competition among individuals of the same sex (usually males), and (2) epigamic selection, which involves interaction between individuals of the opposite sex (see Thornhill and Alcock [1983] for a general review of this topic). In the former, males may form mating territories frequented by receptive females, resulting in the evolution of sexually dimorphic characteristics that would give better endowed individuals a higher success rate in defending such preferred territories. In epigamic selection, the performance of courtship displays by the male (which may involve visual, chemical, or acoustical signals) must be able to satisfy the mating requirement of the female. Those males whose courtship actions are performed in the "right" sequence and temporal pattern will satisfy the mating requirements of a higher number of females in the population, resulting in differential mating success among the males. Also, any morphological embellishment that provides males with an advantage over other males that lack such features will evolve as part of the intraspecific mate recognition system of the population.

The lek mating system, which has been observed in a wide variety of organisms (Bradbury and Gibson 1983), involves the formation of an aggregation of territories called a lek. In most lek systems, each territory within a lek is occupied by a single male to which receptive females are attracted for the sole purpose of mating. Males compete for possession of these territories and in some cases, "preferred" territories have been observed, as evidenced by the number of males competing for the territory as well as the number of fe-

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males frequenting it. However, in addition to defending and occupying a territory that provides a male with the opportunity to encounter receptive females, males must also be able to perform precise courtship displays to satisfy the receptivity threshold of those females. Thus, the dynamics of lek systems represents a highly intense form of sexual selection in natural populations where both intrasexual and epigamic selection contribute to mating success.

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), is considered one of the most damaging insect pests because of the wide variety of fruits and vegetables that serve as hosts for the developing larvae. During the past three decades, efforts to control or eradicate *C. capitata* have been initiated by many countries hoping to increase their fruit exports as well as curb their current fruit losses. One of the major control methods that has been applied to *C. capitata* is the Sterile Insect Release Method (SIRM). This technique, which was first proposed by Knipling (1955), utilizes sterilized laboratory-reared insects that are released into the field to control wild population levels, leading to the eradication of the pest from an area. The application of this technique was initially successful when used for the control of the screwworm, *Cochliomyia hominivorax* (Coquerel). However, problems with the mating competitiveness of the laboratory stock of *C. hominivorax* greatly diminished its effectiveness against wild populations in subsequent control attempts (Richardson et al. 1982).

The relatively frequent infestations of *C. capitata* in parts of southern California emphasize the need for a more comprehensive understanding of the behavioral ecology of this pest so that more efficient control programs can be developed. To avoid setbacks similar to those experienced in the screwworm programs, the genetic quality of the laboratory stock of *C. capitata* must be reestablished and maintained. Yet, one area of the ecology of this fly that is least understood but of vital importance to control programs, especially those involving the SIRM, is the mating behavior.

Earlier descriptions of the mating behavior of *C. capitata* focused mainly on courtship (Martelli 1910, Back and Pemberton 1918). A more complete description by Feron (1962) separated the mating behavior of *C. capitata* into three stages, which he termed: (1) the awaiting period, (2) the arrival of the female, and (3) assault and coupling. However, it was not until the work of Prokopy and Hendrichs (1979) and Arita and Kaneshiro (1983, 1985) that the lek system was proposed as an integral part of the mating behavior of this species. Other authors have researched the role of pheromones (Ohinata et al. 1972, Jacobsen et al. 1972, McDonald 1987), audio stimulation (Rolli 1976, Webb et al. 1983), and environmental parameters (Myburgh 1962, Causse and Feron 1967) as contributing factors in courtship. However, though these references present a general scheme of the mating behavior of *C. capitata*, Burk and Calkins (1983) concluded that much more information about its mating behavior was essential.

In this paper, we describe the mating behavior of *C. capitata* based on field and laboratory observations. Such a description provides a basis for subsequent research in this area, especially in our understanding of the dynamics of the sexual selection process and its influence on regulating effective population size. We hope that our results will ultimately contribute toward the development of more effective control programs for this species.

MATERIALS AND METHODS

Field Observations

Preliminary field studies were conducted in various localities within the Hawaiian Islands. From these studies, two sites were chosen for more in-depth observations of the mating behavior of *C. capitata*. The areas chosen were (1) two residential farms in Kula, Maui and (2) a coffee plantation in Kona, Hawaii.

KULA, MAUI. Over a 2-yr period, 10 field trips (2–3 days each) were made to the two farms. Observations of *C. capitata* mating

behavior activity at each of the farms were made throughout each day of the field trips.

KONA, HAWAII. Over the same 2-yr period, five trips (2–3 days each) were made to a coffee plantation on the Kona coast above Kealakekua Bay. A portion of the plantation was chosen as the study site. We surveyed a plot that contained 53 coffee trees. Each tree was individually identified by row and column. Throughout each day, each tree within the transect was monitored for mating behavior activity.

Rearing Methods of Wild Flies for Laboratory Observations

Flies used for this research were reared from two different host plants collected on the island of Hawaii. One population of flies was reared from Jerusalem cherry, *Solanum pseudocapsicum* L., collected from Kipuka Ki, Volcanoes National Park. The other population was reared from Arabian coffee, *Coffea arabica* L., collected from Kona, Hawaii.

Infested fruits from these two areas were brought into the laboratory, set into rearing containers, and maintained in separate rooms at a temperature of 22°C. The rearing containers consisted of a wooden-framed screen (26 × 37 cm) placed 10 cm deep inside a plastic container (15 × 50 × 32 cm). The fruits were placed onto the framed screen, which allowed the mature larvae emerging from the fruits to fall through the mesh onto a layer of vermiculite on the bottom of the plastic container. After 7 days, the vermiculite was sifted through a 0.1-mm mesh screen, and the collected puparia were placed into holding containers until adult emergence. Within 24 hr of emergence, sex of the flies was determined and they were placed into separate holding containers provided with food (honey, sugar, protein hydrolysate mixture) and water. The flies were then held until sexually mature (Arita 1982).

Laboratory Observations of Mating Behavior

Males reared out of the field-collected substrates were placed into individual 3-gallon (11.4-liter) aquariums when sexually mature and allowed a 24-hr acclimation period to the cage conditions. On the following morning, a female (reared from the same substrate) was placed into the cage and all courtship encounters between the pair were recorded onto 3/4-in. (19-mm) videotape with a JVC camera and a Sony recorder. This procedure was repeated for 18 pairs reared from coffee and 28 pairs reared from Jerusalem cherry. The tapes were later reviewed and analyzed for mating behavior actions.

RESULTS

Previous authors such as Feron (1962) divide the mating behavior of *C. capitata* into different stages. However, the results of our field and laboratory observations of *C. capitata* activity indicate that the mating behavior is separated into two basic phases that lead to copulation: (1) lek behavior and (2) courtship. Each phase is described below.

Lek Behavior

The first phase in the mating behavior of *C. capitata* involves the acquisition of a territory by the male. In *C. capitata*, aggregations of these territories, which are referred to as leks or lek sites (Wilson 1975), were formed within a section of a host tree. In Kealakekua, Kona, host trees were coffee trees and in Kula, Maui, the host trees were lemon and plum trees. Each male attempted to secure a territory within the lek, which he utilized as a courting site for receptive females cueing into this communal display area.

The territories chosen by males both in the field and in the laboratory shared similar characteristics (Figure 1). A territory was identified as a leaf of a host tree that was partially shaded by the overlying canopy of the tree. Males were consistently observed occupying the portion of the leaves that was in direct sunlight. Another distinct feature of a territory was that only the underside of the leaf constituted the male's domain.

Depending on favorable environmental parameters, the lek begins to form in the morning at about 0900 hours. At that time,

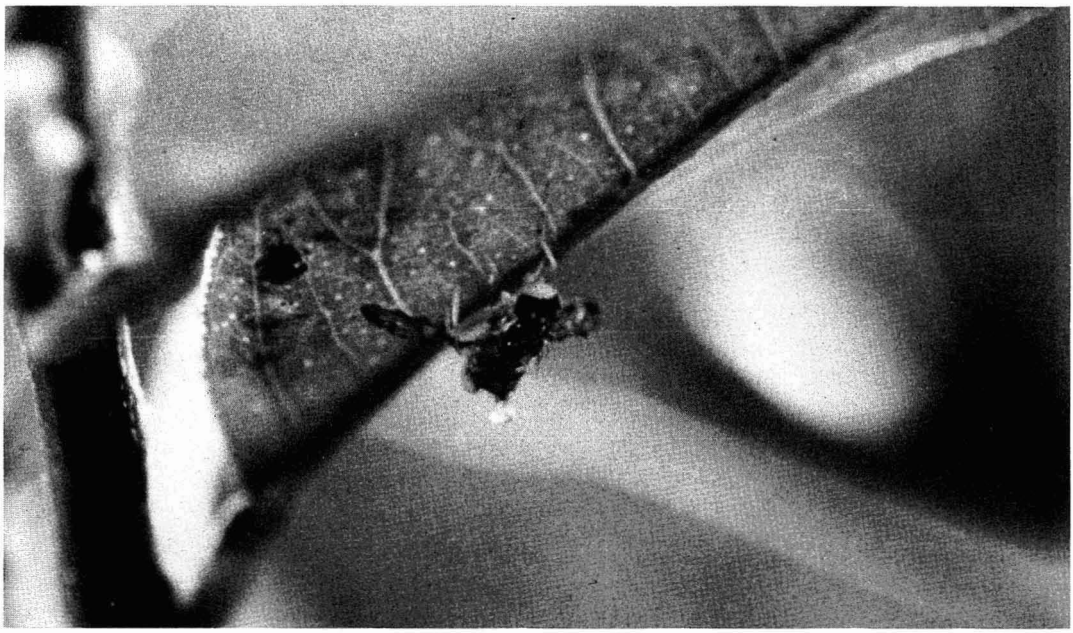

FIGURE 1. *C. capitata* male in pheromone calling position on a territory within the lek.

one or two males arrive and occupy territories. Within the next 10–15 min, other males begin to arrive at the lek. The number of males that occupied territories within the leks varied from as few as 2 males to as many as 12 males in the field. This abrupt gathering of males at specific sites on the host tree leads to numerous encounters between the males as they jockey for territorial position. These males remained on their territories until about 1500 hours, at which time they disbanded.

There appeared to be two important environmental parameters that influence lek formation. The first parameter was wind direction. On Maui, the leks were always located on the host tree with reference to the tradewinds. These tradewinds are prevalent 80 to 95% of the time, generally blowing from the east-northeasterly direction (Blumenstock and Price 1972). The leks were usually located upwind of the tradewinds so that the chemical cues (pheromones) being dispensed by the lek-king males would be dispersed through the tree rather than away from the tree. This orientation may serve not only to attract females to the lek site within the tree, but may also be important in attracting females to the specific trees on which the leks are formed. The effect of wind direction was also clearly evident in Kona where, because of the land–sea breeze system, the wind blows onto shore from the sea. Thus, the leks were always located on the south side of the trees.

The second parameter identified as important in lek formation was light intensity. As indicated above, a territory of a male was on the underside of partially shaded leaves, with the male occupying that portion of the leaf in direct sunlight. The position of the male appears to facilitate the detection of a potential mate arriving on the top surface of the leaf by the silhouette transmitted through the leaf. To detect this silhouette, the male must be situated on the portion of the leaf receiving direct sunlight, since no silhouette is produced on the shaded portion of the leaf. It is postulated that the shaded portion of the leaf may provide an important reference for light differential that aids the male in perceiving a silhouette, thus reinforcing the notion that the relative amount of sunlight penetrating the leaf is important in selecting a territory.

In addition to its importance in territory selection, light was an important factor in the formation and location of the leks. At one of the farms in Maui two leks were observed in plum trees between 0900 and 1000 hours. Shortly after 1000 hours, the lek began to disband and within a period of 15 min from the disappearance of the last male from the plum trees, males began to arrive and form three leks on a lemon tree located approximately 20 m from the plum trees. Given that the lemon leaves were thicker than the plum leaves, it appeared that the males were relocating leks based on the amount of sunlight filtering through the leaves that served as territories. Light as an important factor in the location of the lek became even more evident in Kona, Hawaii. Although the leks were found in the same coffee trees during the investigation period, the location of the leks on the trees moved relative to the position of the sun so that the sunlight was directly on the leaves that served as territories.

The apparent influence of these two environmental parameters in lek formation was consistent over the 2-yr observation period. Leks were always located in positions that appeared to optimize the amount of sunlight penetrating leaves that served as mating territories while referencing wind direction for the facilitation of pheromone dispersal.

A distinct series of actions is performed by males in acquiring and maintaining territories within a lek. Once a male occupies a territory, he assumes a characteristic position referred to as "pheromone calling" (Prokopy and Hendrichs 1979). In this position, the male curls his abdomen upward and extrudes the terminal end of his rectal epithelium, which forms a bubble-like structure presumably for the release of pheromone (Lloste and Roche 1960, Arita and Kaneshiro 1986). In addition, there are two pouches located in the pleural region of the abdomen that are displayed only during pheromone calling and courtship (Arita and Kaneshiro 1983). The wings are extended laterally during pheromone calling with the under surface of the wings facing anteriorly. The male's legs are set in a characteristic position during pheromone calling with the forefemur positioned parallel to the substrate and perpendicular to the longitudinal aspect of the body. The tibia is positioned perpendicular to the substrate. The midfemur is also parallel to the substrate and perpendicular to the longitudinal aspect of his body with the tibia positioned such that the inner angle formed by the femur and tibia is 120°. The third pair of legs are set in the same position as the forelegs. The male remains in this pheromone calling position on the underside of the leaf until he perceives the presence of a potential mate as a silhouette through the leaf. The male then initiates courtship actions (see below) while orienting toward the approaching individual on the top surface of the leaf. As the individual reaches the edge of the leaf, walks onto the bottom side of the leaf, and approaches the courting male, the male must discern whether the individual is a potential mate or another male who is challenging the resident for territorial rights. If the approaching individual is a receptive female, the male continues his courtship actions. If the approaching individual is another male, however, the resident initiates defense actions.

The intruder male may approach the territory from any direction, landing within or near the territory. Males were observed approaching directly onto the territory (bottom surface of the leaf) or approaching from the top of the leaf and then walking to the lower surface. They were also observed hopping from bottom surface to bottom surface of neighboring leaves onto the resident's territory. When a resident male perceives an intruder male, there are two sets of actions that the resident can initiate. These defensive actions have been termed (1) aggressive defense actions and (2) passive defense actions.

AGGRESSIVE DEFENSE ACTIONS. Immediately upon recognition of an intruder male, the resident male terminates his calling position, returns his abdomen to a more normal position in line with his thorax, and folds his wings over his abdomen. Then in a lunging motion, the resident rushes toward the intruder and physically pushes the intruder with his head. If the push is not met with an equal challenge by the intruder, the resident will succeed in pushing the intruder off his territory. In addi-

tion to the "head butt," the resident brings his wings forward in a repetitive slashing motion in what appears to be even more forceful actions against the intruder. The intruder can also meet the resident's actions with similar actions of his own and indeed, on several occasions, the intruder male was observed to displace the resident.

PASSIVE DEFENSE ACTIONS. The resident male initiates this type of defense in the same manner as the aggressive defense actions by folding his wings over his abdomen. However, as he approaches the intruder, rather than attacking the intruder, the resident male will engage in a "face-off" where the two males contact heads without any visible force and remain in this position for as long as 5 min. Eventually, one of the two males will turn and leave the territory. As far as we have been able to detect, there does not seem to be any distinguishable pattern as to which of the two kinds of defense actions will occur during any one particular encounter.

Courtship

There is a series of actions that serve as the transitional phase between lek behavior and courtship and are essentially the initial steps in courtship. These actions are referred to as "orientation and fanning motions" (Arita and Kaneshiro 1983). During pheromone calling by the male from the underside of the leaf (territory), a visual stimulus produced by the silhouette of an individual on the top of the leaf causes the male to immediately orient toward the direction of the stimulus. As the male orients, he terminates the pheromone calling position and tucks his abdomen under his body with the rectal epithelium still everted and begins to vibrate his wings. He continues wing vibrations with his abdomen tucked under his body as long as the stimulus is present. The abdominal pouches described earlier are inflated during wing vibrations and appear to form a physical channel through which the male can direct air currents carrying the pheromone. Analysis of wing motion using a variable frequency stroboscope (Arita and Kaneshiro, unpublished observations) indicates that there is a distinct pattern during this phase of the male's mating behavior. It appears that wing vibrations may be facilitating the dispersal of the pheromone toward the direction of the approaching stimulus (silhouette) on the top surface of the leaf. The resident male is constantly reorienting his position such that when the individual on the top of the leaf walks over the edge and onto the underside of the leaf, it will be facing the resident male head-on. Given that the wing vibrations are apparently facilitating the movement of pheromone toward the female, facing her would allow for maximal reception of the chemical stimulus.

If the individual that approaches the resident male is a female, a series of signals cumulatively known as courtship will be exchanged between them. Courtship actions are performed by the male upon the arrival of the female onto his territory and when the male has discerned that she is a female. During the entire period that the female is approaching, the male has his abdomen tucked under his body with the rectal epithelium still everted. His abdominal pouches are still inflated as he continues performing wing vibrations. Should the female change direction while approaching the male, the male will make a corresponding directional change so that he is facing her. When the female is within 3–5 mm of the male, he begins a series of head movements, oscillating his head in both directions to a maximum plane of 30°. Within 1–2 sec of initiating these head movements, the male initiates a second set of wing actions that are superimposed on the wing vibrations. While continuing wing vibrations, the male simultaneously begins rhythmic wing fannings, bringing his wings from a backward position with the broad surface of the wings facing ventrally to a forward position with the wings facing anteriorly. He then moves closer to the female, who remains motionless except for some cleaning behavior. The male then leaps onto the female's back while still vibrating his wings and with his hindlegs clasps the female near the base of her wings. He then reorients himself so that he is facing in the same direction as the female and copulation ensues. At any point, the female is able to reject the

male's courtship advances simply by walking away from the male and leaving the leaf. Or, if the male has already leaped onto her back in an attempt to mount, the female can still reject the male by releasing her hold on the leaf surface.

Although it has been suggested that acoustical signals may also be important in mating success in other tephritid species (see, for example, Webb et al. 1983) and although such signals may also play a role in the courtship of *C. capitata*, we believe that they are of only secondary importance in this species. Our observations indicate that males begin to vibrate their wings, during which time airborne sounds are probably being produced, only after visual contact is made with the female (or male) that has arrived on the top of the leaf (i.e., the silhouette of the individual; see discussion above). So that at the very least, even if sounds are involved in the mating system, they do not seem to be important in *attracting* females. Recently, Kuba and Sokei (1988) reported on the emission of pheromone in the melon fly, *Dacus cucurbitae* Coquillett. Earlier studies by Keiser et al. (1973) suggested that wing vibration during courtship displays in this species, as well as in several other *Dacus* species, serve as an acoustical signal important in mating success. It was postulated that sexually dimorphic structures on the wings and abdomen of males evolved as parts of a stridulating mechanism for sound production. However, using high-speed movie photography, Kuba and Sokei (1988) convincingly showed that these structures are, in fact, used specifically for producing a "cloud" of pheromone that is dispersed toward the female during courtship. These data provide supporting evidence that, at least in some tephritid species, even if acoustical signals may have some biological significance in the mating system of the species, they are only of secondary importance. We suggest this to be the case in *C. capitata*.

DISCUSSION

Lek behavior has been well studied in bird species (e.g., Wiley 1973, Lill 1974, LeCroy 1981) as well as in a variety of other animals such as the wildebeest (Wilson 1975), fruit-eating bats (Booth 1960, Bradbury 1975), and in endemic species of Hawaiian *Drosophila* (Spieth 1968). From these studies, it is clear that the lek mating system plays an important role in regulating the effective reproductive population.

In laboratory studies of *C. capitata*, Arita and Kaneshiro (1985) showed that approximately 85% of the "census population" (total number of males in the population) acquired and defended territories and participated in the laboratory lek system. Thus, 15% of the census population was not considered as part of the viable reproductive community. They also showed that even among the males that participated in lek formation, only 70% (or 60% of the census population) actually mated with females that were introduced into the lek system. It is proposed that these males formed the "effective male population." Furthermore, even among the effective male population there was a certain percentage of males (15%) that were more proficient maters. These superior males accounted for nearly 46% of all matings. Because acquisition and successful defense of a territory only provides a male with a courting site, the ability to perform courtship actions to the satisfaction of the female is still a necessary component for mating to occur in this species. In addition, it has been observed that there are certain territories within the lek that are frequented more often in comparison to others. Consequently, it is on these territories that a majority of male battles occur. Ultimately, it is the male who can secure one of these prized territories and who can perform the courtship ritual to the satisfaction of the female who will have a larger percentage of matings. These results are strikingly similar to those of studies of other species in which only a small percentage of males are found to be responsible for most of the matings that occur in the population. What of the remaining 15% of the census population that were unable to secure a territory within the lek? These males may be prime candidates for adoption of the alternate mating strategy of approaching females at ovipositional areas that has been proposed for *C.*

capitata by Prokopy and Hendrichs (1979) and by Burk (1983) for the Caribbean fruit fly. *Anastrepha suspensa* (Loew).

Clearly, lek systems represent an intensification of the sexual selection process. Leks seem to serve as a giant "sieve" through which males are assayed for their genetic quality via sexual selection. Although intrasexual selection (i.e., male-male interaction) seems to play an important role in "sorting out" the "best" males in the population through the establishment of a dominance hierarchy (Arita and Kaneshiro 1985), female choice (i.e., epigamic selection) based on courtship ability still provides the ultimate criterion for mating success.

The importance of female choice in tephritids has apparently led to an array of courtship rituals that are performed by males, particularly among lekking species. In *Dacus tryoni* (Froggatt), though males actively defended territories and produced acoustical and chemical signals for the attraction of females, mating occurred soon after the arrival of the female, with little or no courtship display by the male before copulation (Tychesen 1977). On the other hand, *A. suspensa* appears to have a mating behavior strikingly similar to that of *C. capitata*. Males of *A. suspensa* not only defend territories and produce an airborne sex pheromone for attracting females but for successful mating to occur, females are additionally stimulated through courtship actions (Burk 1983). These studies on closely related groups of lekking species provide the foundation for understanding the role of the lek system and courtship in mating success. We are continuing our studies to determine which components are of critical importance in mating success.

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