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Behavior Paradigms in the Mediterranean Fruit Fly, *Ceratitis capitata* (Weidemann)

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Abstract: The Medfly, *Ceratitis capitata* Weidemann (Diptera: Tephritidae) is one of the most important fruit fly pests in the world. Several different behavior patterns have been reported including courtship behavior, mating behavior, oviposition behavior, feeding behavior and resting behavior. Courtship behavior described for wild males usually followed a predictable sequence of: male calling → females approach → male wing vibrating → female standing → male wing fanning → copulation. In contrast, these transitions were generally absent in the courtship of mass-reared males. Mating behavior can be classified as two different tactics, lekking and fruit guarding by males. Lekking, defined as participating in a male aggregation where at least one male is emitting pheromone from the anal gland. Fruit guarding by males is the alternative-mating tactic in which a male is stationed on a host and accosts females who alight on it to oviposit. In addition, some synthetic compounds, e.g., trimedlure, can affect mating behavior of medfly males. In the ultimate stage of oviposition behavior, the Medfly lays eggs underneath the skin of host fruit. This describes as a blanket term covering pre-and post-oviposition behavior, which may change based on host and host plant variety or the availability of the host plants containing resources such as fruit and protein food stimuli. Feeding behavior of the adult medflies includes acquiring carbohydrates, primarily from feeding on the juices of ripe fruit and honeydew, protein from bird feces and decomposing fruit, whereas the immature stages develop better on diets containing higher concentrations of glucose and sucrose than containing high starch concentration or maltose. Resting behavior patterns differed between males and females, location on the host plant and temperature. Understanding these can be very important to its control on crops. Research concerning Medfly behavior could improve methods to control this important pest.

Key words: Mediterranean fruit fly, *Ceratitis capitata* Weidemann, (Diptera: Tephritidae); its behaviors

INTRODUCTION

The Mediterranean fruit fly, *Ceratitis capitata* (Weidemann) (Diptera: Tephritidae) is one of the most important fruit flies throughout the world (Borror *et al*., 1989; Smith *et al*., 1992; Pedigo, 1999). The medfly is recorded as developing in and around 300 species of fruits, nuts and vegetables, of which the majorities are of tropical origin (Borror *et al*., 1989; Liquido *et al*., 1991; Pedigo, 1999). A native of South Africa, the Medfly has spread to Europe, South and Central America, Oceania and Australia (Smith *et al*., 1992; Metcalf and Metcalf, 1992). They overwinter as pupa or adults (Metcalf and Metcalf, 1992). However, in the tropics and subtropics, reproductive activity is continuous throughout the year (Metcalf and Metcalf, 1992). The adult medfly is about the size of a housefly with a glistering black thorax with a characteristic mosaic of yellowish white lines (Smith *et al*., 1992; Metcalf and Metcalf, 1992). The abdomen is yellowish with two silvery crossbands and the wings are banded and blotched with yellow, brown and black (Metcalf and Metcalf, 1992).

Several different Medfly behavior patterns have been reported that consist of courtship behavior, mating behavior, oviposition behavior, feeding behavior and resting behavior. Courtship behavior described for wild males usually followed a predictable sequence of: male calling → females approach → male wing vibrating → female standing → male wing fanning → copulation. In contrast, these transitions were generally absent in the courtship of mass-reared males (Liimatainen *et al*., 1997). Mating behavior can be classified into two different tactics, lekking and fruit guarding by males (Liimatainen *et al*., 1997; Warburg and Yuval, 1997; Yuval *et al*., 1998). Oviposition behavior of the Medfly is a blanket term that covers pre-and post-oviposition behavior. Changes are based on host and host plant variety or the availability of the host plants containing resources such as fruit and protein food stimuli (Averill *et al*., 1996; Prokopy *et al*., 1996; Bravo and Zucoloto, 1998).

Feeding behavior of the medfly differ between adult and immature stages. Adult Medflies acquire carbohydrates, primarily from feeding on the juices of ripe fruit and honeydew, protein from bird feces and decomposing fruit (Hendrichs *et al*., 1991; Canato and Zucoloto, 1993; Fernandes-Da-Silva and Zucoloto, 1993; Bravo and Zucoloto, 1998). However immature stages develop better on diets containing higher concentrations of glucose and sucrose than those containing high starch concentration or maltose (Zucoloto, 1993). Resting behavior patterns differed between males and females when accompanied by shifts of location within and between hosts that were affected by temperature (Warburg and Yuval, 1997).

The purpose of the review was to understand Medfly behaviors that can be very important to its control on crops.

RESULTS AND DISCUSSION

Mediterranean fruit fly behavior can be classified as having courtship behavior, mating behavior, oviposition behavior, feeding behavior and resting behavior in the daily periodic movements.

Courtship Behavior

Males visually display this behavior while perching on the underside of a leaf by curling the abdomen upward and averting the rectal epithelium, thus releasing a pheromone attractive to females (Hendrichs and Hendrichs, 1990). Upon seeing a female, the male orients toward her, tucks his abdomen under his body and begins to vibrate his wings, which are held perpendicular to the body. When the female approaches to within 3-5 mm of the male, the male begins a second type of wing movement termed fanning in which the wings are moved rapidly forward and backward in a rhythmic manner apparently to direct the phenomenal emission at the female more precisely. In addition, the male begins a series of side-to side movements with its head. The male then moves closer to the female and if the female remains motionless, leaps onto the female back and attempts to mate. Courtship activities occur throughout most of the day. Male calling is bimodal, with a main peak in the morning before the hottest part of the day and a smaller one during the afternoon hours.

Courtship behaviors by wild males usually follow a predictable sequence of male and female behaviors: male calling → females approach → male wing vibrating → female standing → male wing fanning → copulation. In contrast, these transitions were generally absent in the courtship of mass-reared males (Liimatainen *et al*., 1997).

Mating Behavior

The mating behavior activities of males combine different tactics that are primarily lekking and fruit guarding (Warburg and Yuval, 1997). The mating behavior of Mediterranean fruit flies is based on male leks that form on the foliage of trees, which females visit for the purpose of copulation (Warburg and Yuval, 1997; Yuval *et al*., 1998). Definitions of leks are non-resource based male

aggregations, visited by females only for copulation (Shelly and Whittier, 1997). Once a male has established a territory, he engages in the performance of pheromone release, visual displays and acoustical signals to attract a female for reproduction. There was no evidence of a significant size difference between lekking and resting males, yet lekking males were significantly heavier and contained significantly more sugars and protein than resting males (Yuval *et al*., 1998).

The main environmental factor regulating mating behavior is temperature. Observations on the activity patterns of the Medfly in the field indicated that lekking activities take place from mid-morning to late afternoon (Hendrichs and Hendrichs, 1990; Whittier *et al*., 1992). In Egypt, where relatively high temperatures prevail, very little activity was seen during the middle of the day, resulting in a bimodal pattern of male lekking, female oviposition and for both male and female feeding (Hendrichs and Hendrichs, 1990).

Some synthetic compounds can affect mating behavior of medfly males. Trimedlure, a synthetic formulation (1,1-dimethylethyl 4 (and 5) chloro-2 methylcyclohexane-1-carboxylate) appears to be the strongest attractant and consequently is widely used in detection and eradication programs (Shelly *et al*., 1996). Under laboratory conditions, exposure to trimedlure confers a short-term (<24 h) mating advantage to male Medfly. Male attraction to trimedlure may reflect the resemblance between trimedlure and male sex pheromone with subsequent orientation to perceive lek sites.

Mating induced changes in olfactory mediated behavior of laboratory reared normal, sterile and wild female Medfly mated to nonspecific males (Jang, 1995; Jang *et al*., 1998). Changes in behavior have been shown to be associated with the transfer of accessory gland fluid from males to females during copulation (Jang, 1995). Understanding changes in female behavior as a result of mating may support the development of semiochemical attractants such as a host-odor food based volatile and ovipositional attractants that act on specific behavior (Jang, 1995; Jang *et al*., 1998). Physiological control of female olfactory behavior has several important implications for the use of sterile males in a sterile insect technique. Even though searching ability and mating for males are clearly important factors to be considered in developing improved strains for the sterile insect technique. Other physiological factors such as ability of males to alter female behavior should be carefully considered as part of any mass-rearing quality control program.

Oviposition Behavior

The Mediterranean fruit fly damages the host plant by laying eggs underneath the epidermis producing several generations each year (Averill *et al*., 1996). Females alighting on a fruit thoroughly examine the potential host before oviposition. After oviposition, females always mark the oviposition site (Warburg and Yuval, 1997). Medflies produce eggs after feeding exclusively on carbohydrates during the adult stage, but production increases when a protein or amino acid source is also ingested (Cangussu and Zucoloto, 1992). The number of times a Medflies female oviposited dramatically increased when the host plants contained fruit and protein food stimuli rather than having food, water or foliar stimuli (Averill *et al*., 1996). The presence of a vitamin mixture did not increase egg production, whereas the presence of a salt mixture increased egg production (Cangussu and Zucoloto, 1992). Mediterranean fruit fly females probably prefer to choose a permanent host for an ovipostion site on the basis of attractive volatiles emitted from the host plant rather than temporary host plants (Light *et al*., 1992).

Selection of oviposition by the females showed no differences between the lower and upper parts of orange and papaya (Fernandes-Da-Silva and Zucoloto, 1993). However, females oviposited 66% on greenish, unripe fruit; 34% on yellowish, ripe fruit. In addition, 87% of the oviposition occurred predominantly in oranges and guavas (Hendrichs and Hendrichs, 1990). Wild populations of Mediterranean fruit fly females only oviposited on papaya with the peel on but not on peeled papaya or the artificial diet; however, laboratory populations of Mediterranean fruit fly females oviposited

indiscriminately on papaya with the peel on, peeled papaya and the artificial diet. Laboratory populations of medfly females produced eggs 5 times more than wild populations of females during the pre-ovipositing phase (Bravo and Zucoloto, 1998).

The effects of food odor on fly attraction and oviposition would be greater for relatively visually inconspicuous fruits than for relatively visually conspicuous fruits (i.e., that proximity to food odor would enhance fly discovery of inconspicuous fruit to a greater extent than conspicuous fruit) (Prokopy *et al*., 1996). Oviposition site selection in non-sticky kumquats with nearby bird feces was significantly greater than oviposition in non-sticky kumquats distant from bird feces in the field cage trials. Moreover, Mediterranean fruit flies laid significantly more eggs in the fruit of the host kumquat, the non-host hawthorn, *Crataegus mollis*, both adjacent to bird feces and synthetic food than in the fruit of these types distant from food-type stimuli. Time is a very important factor for oviposition to occur. Twenty percent of the oviposition activity occurred in early morning hours, whereas oviposition activity nearly ceased during the hot hours of the day then reached a peak (71%) in later afternoon hours (Hendrichs and Hendrichs, 1990).

Feeding Behavior

Insects require a diet containing a source of carbohydrates, protein sources, vitamins and certain mineral salts (Cangussu and Zucoloto, 1992). During the adult stage, feeding mostly affects egg production, even though in many species the stores from the larval stage also affect egg production. Thus there are species that produce eggs after feeding exclusively on carbohydrates during the adult stage by using other nutrients left over from the larval stages or using symbionts (Slansky and Scriber, 1985).

Adult tephritids acquire carbohydrate primarily from feeding on the juices of ripe honeydew, protein from bird feces and decomposing fruit (Hendrichs *et al*., 1991). Adult Mediterranean fruit flies are capable of lipid synthesis and this capability is modulated by individual and sex-specific activity patterns, which are related to age and diet (Warburg and Yuval, 1996). Adult females select nutrients at proportions that are adequate for better performance and protein deprivation for a certain period of time increase the discrimination for this nutrient (Cangussu and Zucoloto, 1995). Sugar is the most important nutrient for adult females because they succeed in producing eggs without ingesting a protein source, even though production increases with protein ingestion. Adult females should have a more efficient control in terms of sugar ingestion, whereas protein ingestion is more important for the larvae (Canato and Zucoloto, 1998). Females produce more eggs when fed diets containing glucose, fructose, or sucrose as compared to diets containing starch or maltose (Zucoloto, 1992).

During the immature stage, feeding has a more direct effect on time of development, percentage of emergence, adult size and stored amounts of some nutrients that are present in emerging adults (Slansky and Scriber, 1985). Immature might vary in food choice depending on their age and physiological state. They develop better on diets containing low starch concentrations, glucose, fructose or sucrose than on diets containing high starch concentration or maltose (Zucoloto, 1993).

A choice test offering two diets, one with brewers' yeast and the other, whole milk powder were fed to newly hatched Medfly (Canato and Zucoloto, 1993). The larvae that preferred the milk powder diet. When the nutrition value of the milk powder diet became inadequate, the larvae chose the brewers yeast regardless of the food on which the population was being bred. When a population of larvae that preferred the brewers yeast diet was formed, the choice for this diet increased over successive generations, indicating that genetic factor may influence the preference of larvae.

Orange and papaya have more nutritive value in the lower part of both fruits (Fernandes-Da-Silva and Zucoloto, 1993). Although several factors may be influencing the nutritive value of the upper and lower part of the orange and papaya fruit, sugars can play an important role in the decision for the Mediterranean fruit fly. According to the study, comparing between two different fruits can affect the Mediterranean fruit fly size. For the orange, there was a greater percentage of emergence and a shorter

development cycle when the larvae fed on the lower part of the fruit, with no difference in adult size. For papaya, there was a greater percentage of emergence and a large adult size when the larvae fed on the lower part of the fruit, with no difference in the duration of the development cycle. As to the selection of the parts of the fruit, the preference was for the lower part in both cases. Also, larvae placed on the upper part of the fruit moved to the lower part and when placed on the lower part they remained there.

The performance of wild populations of Mediterranean fruit fly was superior when the flies fed on papaya compared to the artificial diet, except for egg population (Bravo and Zucoloto, 1998). In addition, the wild populations of the medfly showed a strong preference for papaya over the artificial diet even when fed on the artificial diet before the choice test. Flies fed on artificial diets were bigger than papaya fed flies. The largest difference between laboratory populations and wild population behavior was when the wild population does not accept the artificial diet when allowed choosing between this diet and papaya.

Feeding behavior differed among observation periods (Warburg and Yuval, 1997). Feeding on fruit occurred mainly during mid-morning and late afternoon, whereas feeding on leaf surfaces occurred primarily during the middle of the day when flies were in lower parts of the canopy. The highest percentages of feeding flies occurred during the early morning (females) and the late afternoon hours (males and females).

Resting Behavior

Daily behavior patterns differed between males and females, which were accompanied by shifts of location within and between hosts (Warburg and Yuval, 1997). At the apple and fig, both males and females rested much more in the morning, whereas at pitanga and guava, flies seemed to spend less time resting on leaves during this period. Flies moved from the upper-lighted leaf area to the lower shaded surface as the air warmed up. Females visiting on fruit increased during midday, 87% of the females were found on fruit in one site containing apple and fig fruits and 62% of the females were found on fruit in the other site containing pitanga and guava fruits. This trend continued in the evening observation period on fruit, the percentages of females resting on fruit were 92% in the site containing apple and fig fruits and 86% in the site containing pitanga and guava.

During midday, male distribution differed significantly from the female pattern. Females preferred fruit, whereas males preferred leaves, 95% of the males were recorded in the site containing leaves of pitanga and guava. Like the females, most males observed during the evening were on fruit with very similar percentages in sites; 92% in the site containing apple and fig and 83% in the site containing pitanga and guava. The diel pattern of fly presence on orange, guava and lemon peaked mainly in the morning; on fig it peaked around noon; and apple, mango and peach it peaked mainly in the afternoon (Hendrichs and Hendrichs, 1990).

In conclusion, the Mediterranean fruit fly, *Ceratitis capitata* (W.) is a significantly important pest of the world fruit crops. Important Mediterranean fruit fly behaviors can be classified with five different categories that consist of courtship, mating, oviposition, feeding and resting behavior. These behaviors might be changed wild or mass-reared species, host plants and host plant variety and hosts containing resources and environmental factors. Understanding of its behavior is very important not only to control these pests on the crops, but also getting the highest profit for the fruit crop production in the world.

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