

**CACTOBLASTIS CACTORUM (LEPIDOPTERA: PYRALIDAE):
OBSERVATIONS OF COURTSHIP AND MATING BEHAVIORS
AT TWO LOCATIONS ON THE GULF COAST OF FLORIDA**

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ABSTRACT

Cactoblastis cactorum (Berg) has become an invasive pest of *Opuntia* spp. along the coastal areas of southeastern United States from the panhandle of Florida to South Carolina. Spread of this insect into cactus dominated natural areas of the United States and Mexico and into agricultural opuntia fields of Mexico is raising concerns within international governments and conservation organizations. Interest is growing in using the Sterile Insect Technique (SIT) to manage *C. cactorum* populations. Information on courtship and mating behaviors of this insect is important in the development and application of SIT. We conducted mating table studies and determined that this moth exhibits simple rather than elaborate mating behaviors and that courtship and mating take place briefly during morning twilight. Typically, females initiate calling, males respond to females, and copulation are complete before sunrise. Successfully mated females attract males within a short period (mean of 5.2 min), while unsuccessful females continue calling for about 40 minutes. Mating pairs remain in copula for a mean of 31.8 min. Generally, mated females are busy ovipositing the first few nights after mating, not exhibiting additional mating behaviors. A release of marked males revealed that males stay near the release site and can be recovered and identified for subsequent population estimate studies. This study on courtship/mating behavior is helpful to the ongoing *C. cactorum* research to develop a successful SIT program, identify the female calling pheromone, improve monitoring traps, and develop a technique to estimate adult moth population abundance.

Key Words: cactus moth, invasive pest, *Opuntia*, sterile insect technique

RESUMEN

Desde su accidental llegada al estado de Florida, *Cactoblastis cactorum* (Berg) se ha convertido en una especie invasora atacando especies de *Opuntia* a lo largo de áreas costeras del sureste de los Estados Unidos desde Florida hasta Carolina del Sur. La invasión de *C. cactorum* tanto en áreas naturales con predominancia de cactáceas en Estados Unidos y México como en plantaciones agrícolas de *Opuntia* en México están causando gran preocupación a gobiernos internacionales y a organizaciones que se ocupan de la conservación de recursos biológicos. Sin embargo, el interés en utilizar la Técnica del Insecto Estéril (TIE) para controlar poblaciones de *C. cactorum* está aumentando simultáneamente. Para desarrollar y aplicar la TIE de manera efectiva es importante obtener información sobre el cortejo y comportamiento de cópula de este insecto. En este estudio de campo determinamos que el comportamiento de cópula de *C. cactorum* es relativamente simple y que el apareamiento ocurre durante un periodo bastante corto, justo antes del amanecer. En general, las hembras comienzan a llamar a los machos, los machos responden y la cópula se inicia y termina antes de que salga el sol. Las hembras que logran copular típicamente llaman a los machos por corto tiempo (5.2 min), mientras que las hembras que no se aparean continúan llamando por 40 minutos. La cópula dura un tiempo promedio de 31.8 minutos. En general las hembras que copulan la primera noche se dedican a ovipositar durante la noche siguiente y no se involucran en actividades de cortejo. Realizamos una liberación de machos coloreados con polvo fluorescente que demostró que los machos permanecen en las áreas donde fueron liberados y que pueden ser identificados sin problema al copular con hembras en mesas de cortejo. Nuestros resultados son útiles para el desarrollo de la TIE y asimismo para la identificación de la feromona de cópula, para mejorar el sistema de trampeo y para desarrollar un método para calcular el tamaño de la población absoluta de esta especie.

Translation provided by author

The control of invasive cacti in the genus *Opuntia* by the cactus moth, *Cactoblastis cactorum* (Berg), is often cited as the most famous example of successful classical biological control of weeds (Dodd 1940; Moran & Zimmermann 1984). However, the unintentional arrival of *C. cactorum* into Florida in 1989 (Habeck & Bennett 1990) has raised concerns for the survival of rare native *Opuntia* in the Florida Keys (Johnson & Stiling 1996). Of even greater concern is the potential westward spread of *C. cactorum* into areas of the United States and Mexico that are rich in *Opuntia* diversity (Soberón et al. 2001; Zimmermann et al. 2000; Stiling 2002). Recently, Hight et al. (2002) reported on the expanding range of *C. cactorum* in North America. By summer 2002, the moth had spread as far north as Folly Island near Charleston, South Carolina and as far west as St. George Island, Florida (Hight et al. 2002). In a 2003 survey of the western Florida panhandle, we found the new western limit of *C. cactorum* at Pensacola Beach, Florida, near the border with Alabama.

Even though the worldwide successes of *C. cactorum* as a biological control agent of weedy *Opuntia* have been carefully documented (Sweetman 1936; Dodd 1940; Pettey 1948; Julien & Grifiths 1998), little information on the insects' mating habits is available. Dodd (1940) reported that mating of *C. cactorum* in Australia took place during the early morning hours, from daylight until about 0730 hours, and that copulation was never observed at night or after 2100 hours. He also stated that adults of *C. cactorum* usually remained inactive during daylight hours and sat motionless in vegetation near their host plants. Pettey (1948) reported that *C. cactorum* mating at Uitenhage, South Africa only occurred early in the morning, during daylight of the first and second days after adult emergence. He reported that moths were active only after sunset until a little after sunrise, except in areas where temperatures were high.

The purpose of the present study was to document the courtship and mating behaviors of *C. cactorum* in Florida. In particular, we were interested in precisely documenting the field behaviors associated with mating, as we are investigating the possibility of using the Sterile Insect Technique (SIT) to manage populations of *C. cactorum* in the United States (Carpenter et al. 2001a). This technique relies on the ability of mass reared, irradiated, and released insects to effectively compete and mate with a feral population. Knowledge of the targeted species mating behavior is of crucial importance to the development and successful application of the SIT. We also are developing trapping technology that would allow more extensive and efficient surveys to be conducted for *C. cactorum*. An improved understanding of courtship and mating behaviors would be useful in improving trap design and in identifying

pheromones associated with the sexual communication of this species.

MATERIALS AND METHODS

Test Insects

Cactoblastis cactorum used in these experiments were reared in laboratory colonies at the USDA-ARS laboratories in Tallahassee, FL and Tifton, GA. Rearing procedures generally followed those described in Carpenter et al. (2001b). Cocoons were collected every 2-3 days from colony containers. Pupae were extracted from the cocoons and sorted by gender. Sorted pupae were placed in a screen cage (30.5 × 30.5 × 30.5 cm) or individually into 0.3 ml plastic cups with cardboard lids and allowed to emerge inside growth chambers at 26°C, a photoperiod of 14:10 (L:D), and 60% relative humidity. Virgin females (<24 h post emergence) were placed individually in small plastic cups and kept in a refrigerator (5°C) to slow their physiological ageing and activity. In the laboratory, two-thirds of one anterior wing of each female was excised with small scissors to prevent flight. Each female was returned to its plastic cup and transported to the field in an open cooler under natural light. Newly emerged males were collected and placed as a group in a 475 ml plastic container. Males were chilled, colored with fluorescent powder (Day Glo® Corp., Cleveland, OH), and transported to the field under natural light in a small cooler.

Mating Tables

Individual mating tables were similar to the ones described by McBrien & Judd (1996) with the following exceptions: the diameter of the mating arena was 17.5 cm to accommodate the larger sized female *C. cactorum*, the height of the Teflon® tape barrier was 5 cm, the Teflon® tape barrier was lightly dusted with talc, and the tables did not have roofs (Fig. 1). Communal mating tables were constructed on a base of plywood (61 × 61 × 1.5 cm) that was painted gray (Valspar American Tradition, oil based paint, light gray, #48220). A circular Teflon® tape barrier (50 cm diameter × 5 cm high) was glued to the arena and dusted with talc. Four metal legs (0.5 m high) were attached to the plywood base with metal brackets (Fig. 2).

Patches of cactus plants between 0.50-1.50 m in height were selected for placement of both individual and communal mating tables. Individual mating tables were attached to hollow metal stakes placed in the ground at a height of approximately 0.75 m and located at the edge of the cactus patches. Communal mating tables (mounted on their legs) were also placed next to cactus patches.



Fig. 1. Small mating table used in determining courtship and mating behaviors at St. Marks National Wildlife Refuge (7 July 2003) and Alligator Point, FL (8 July 2003), and determining precise timing of mating events at Alligator Point (15-18 July 2003).

Mating tables were set-up in the same fashion for each set of observations. A small (2×2 cm) section of *O. stricta* was placed in the middle of the mating arena of each individual table. One, clipped-wing, virgin female *C. cactorum* was released into each arena. In communal tables, several cladodes of fresh *O. stricta* were placed inside the arena and 7-12 clipped-wing females were placed in the center of each mating arena. Time of female deployment varied for each experiment. All times reported are in Eastern Daylight Savings Time on a 24-hour atomic clock.

Study Sites

Experiments were conducted in July 2003 at two locations in Florida along the Gulf of Mexico—St. Marks National Wildlife Refuge (N30°04', W84°10') and Alligator Point (N29°54', W84°23'). Abundant naturally occurring patches of native *Opuntia stricta* (Haworth) Haworth heavily damaged by *C. cactorum* are present at both locations. Infested *O. ficus-indica* (L.) Miller is also common among houses at Alligator Point as a planted and naturalized species. At St. Marks, the plants are located along a dike that

separates the Gulf of Mexico and a salt marsh estuary. Twenty individual mating tables and two communal mating tables were established at St. Marks, each separated by no less than 10 m from one another.

At Alligator Point, plants of *O. stricta* and *O. ficus-indica* are distributed along open (un-fenced) front-yards of beach houses along the Gulf of Mexico. For the first set of observations (morning of 8 July), 12 individual mating tables and a single communal table were placed near infested cactus patches. Each table was separated from one another by no less than 3 m. For the second set of observations (mornings of 15-18 July), 15 mating tables were placed in groups of five around three heavily infested cactus patches in the same vicinity as those used for the first observations. Tables within a group were separated from each other by about 1 m.

Mating Behavior

At St. Marks, 47 marked male *C. cactorum* were released along the dike on the opposing side of mating tables. Releases were made at 1730 hours on 6 July 2003 to insure that males would

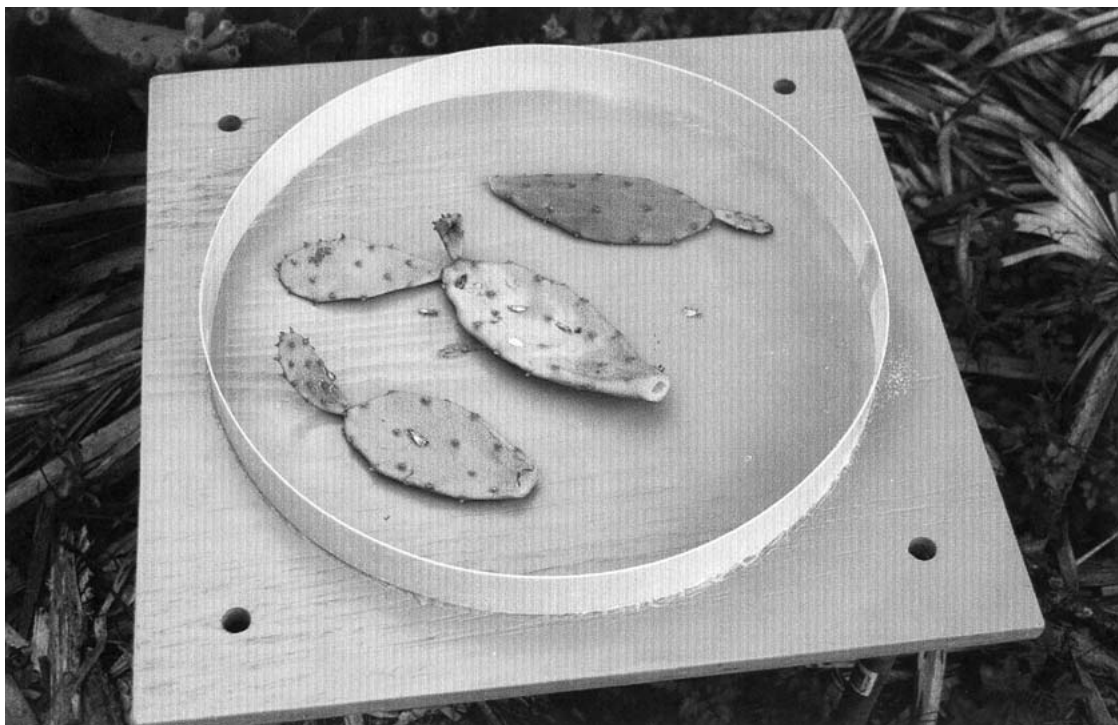


Fig. 2. Communal mating table used in determining courtship and mating behaviors at St. Marks National Wildlife Refuge (7 July 2003) and Alligator Point, FL (8 July 2003).

be present in the area. The minimum distance between male release points and the location of the mating tables was 10 m. Females were placed in individual and communal mating tables at 2000 hours and tables were observed every hour from 2100 hours until 0700 hours on 7 July 2003. Moth activity was observed using flashlights with red lenses. Moths found in copula were collected into small plastic cups and the hour noted during which each mating pair was collected. Insects were transported back to the laboratory and the type of each male (i.e., marked or wild) captured in copula was identified using ultraviolet light to detect the presence or absence of the Day Glo® dye. The total number of mating pairs recorded from individual and communal mating tables and the type of male involved in each mating (feral or released) was determined. Female mating status was confirmed by determining the presence or absence of a spermatophore in the bursa copulatrix as suggested by Ferro & Akre (1975).

After the first night of observations at St. Marks, the general timing of mating activities for *C. cactorum* was determined. Observations at Alligator Point were modified to take advantage of these findings. Forty-one marked males were released at Alligator Point at 2200 hours on 7 July 2003. Twelve females were placed in individual mating tables and 12 additional females were

placed in the communal table at 2130 hours. Mating tables were checked every 5-10 minutes between 0500-0700 hours on 8 July 2003 and all mating activities observed were recorded. Pairs in copula were collected in plastic cups and taken to the laboratory where male type and female mating status were confirmed.

Precise Timing of Mating Events

Fifteen individual mating tables were set-up as described above on four consecutive nights (14 to 17 July 2003) at Alligator Point to more accurately document the duration of all events associated with *C. cactorum* mating. Newly emerged, clipped-wing virgin females were prepared each day and placed in the mating arenas between 2200-2400 hours. Observations began at 0500 hours each morning and continued uninterrupted until all mating activities ceased. The following mating behavior events were recorded: time female initiated calling posture, time female terminated calling posture, time first male responded to calling female, time last male responded to calling female, time copula was initiated, and time copula was terminated. Verification of successful copula was confirmed in the laboratory by the presence of a spermatophore in the female upon dissection. Light intensity was measured in

the early morning hours of 18 July with a HOBO data logger (Onset Computer Corp., Pocasset, MA).

Female Refractory Period

Females that successfully mated at Alligator Point during the precise timing experiments were observed on subsequent mornings to determine whether they produced an eggstick, resumed a calling posture, and/or were attractive to males. The five females that mated on the morning of 15 July 2003 were placed on individual mating tables at the same time and in the same manner as each group of 15 new females on evenings of 15-17 July 2003. Three females that mated on the morning of 16 July 2003 and six females that mated on the morning of 17 July 2003 were observed on the morning of 18 July 2003. Any eggsticks that were produced were collected, the time of oviposition noted, and the number of eggs counted.

RESULTS

Weather conditions for each morning's observation were relatively similar. Skies were mostly clear, temperatures were 25-27°C, and relative humidity was 95-100%. Rain never occurred during our observation periods and winds were variable, differing most mornings in relation to speed and/or direction.

Mating Behavior—St. Marks National Wildlife Refuge

No mating activity was observed between 2100 hours on 6 July 2003 and 0500 hours on 7 July 2003. At each hourly observation, females were motionless and most were perched on host plant material. However, when observations were made during the 0600 hours check on 7 July 2003, 89% of the females (32 of 36) were found to be engaged in courtship/mating activities and males were observed flying around the mating tables. Twenty-one females (58%) were positioned in a typical calling posture (abdomen protruding upwards through the wings and held at an angle approximating 45°), eleven females (31%) were found in copula and four females (11%) were still inactive. Seven of the copulating females were in individual tables and four in the communal tables (three in one and one in the other). By 0625 hours, all mating pairs had disengaged from one another.

Mating tables were again visited at 0630 hours and the number of females observed in the calling position had decreased to 15 (42%). Males could still be seen flying around the area, but no additional mating pairs were formed. When tables were checked at 0700 hours only three females (8.33%) remained in the calling position and no males were observed flying in the vicinity of the tables. When *C. cactorum* pairs were examined under UV light, six males were identified as be-

longing to the released group while the remaining five were feral males. Dissection confirmed that all copulating females had a spermatophore in the bursa copulatrix.

Mating Behavior—Alligator Point

Even though mating tables were under almost continuous observation from 0500 hours on 8 July 2003, no courtship/mating activities were observed until 0545 hours when 6 of 22 females assumed a calling posture. Two females placed on the communal mating table became entrapped in excessive dew and were not included in the reported outcomes. In total, nine mating pairs (41% of observed females) were collected on 8 July 2003. The first mating pair was found at 0545 hours. Thereafter, mating pairs were observed at 0550 hours (2 pair), 0552 hours (1 pair), 0553 hours (2 pair), 0611 hours (1 pair), and 0612 hours (2 pairs). Females continued to call until 0647 hours. During the entire observation period, three (14%) females did not participate in courtship/mating activities. Males and females remained in copula for a short period of time. Most pairs disengaged from one another in less than 30 min (range 14-29 min). When captured pairs were examined in the laboratory, all males were determined to be feral. Dissection confirmed that eight of nine mated females retained a spermatophore in the bursa copulatrix.

Precise Timing of Mating Events

A temporal description of *C. cactorum* courtship and mating behaviors observed during the mornings of 15-18 July 2003 is summarized in Table 1. Events related to the rising sun during these mornings are also presented in Table 1. All courtship and mating activities were concentrated during a two-hour period (0528-0733 hours), beginning each day between astronomical and nautical twilight when skies had just started to lighten. Activity ended soon after sunrise. The majority of *C. cactorum* completed all measured courtship/mating events before sunrise, including initiation of female calling (100%), male response to female (100%), initiation of copula (100%), copula termination (96%), and female calling termination (77%). In fact, the mean time between the initiation of calling behavior by females and the last male seen responding to the females was only 16 min (0602-0618 hours). Light intensity measured each minute during the evening/morning of 17/18 July 2003 was negligible from 2054 to 0628 hours and did not increase until 0629 hours when the intensity was measured at 43 lum/m².

Initiation of calling posture by females was immediately followed by the response of males (flying around the mating tables, landing inside the mating arenas, and attempting copulation with

TABLE 1. TEMPORAL DESCRIPTION OF COURTSHIP AND MATING BEHAVIORS OF *Cactoblastis cactorum*, AND SUNRISE EVENTS AT ALLIGATOR POINT, FL, 15-18 JULY 2003. SUNRISE EVENTS CALCULATED FROM U.S. NAVAL OBSERVATORY WEBSITE <HTTP://AA.USNO.NAVY.MIL/>. TIMES ARE REPORTED IN EASTERN DAYLIGHT SAVINGS TIME ON 24-HOUR CLOCK.

Behaviors	n	Time (hours) or duration (min)	
		Range	Mean (\pm SD)
Initiation of ♀ calling posture	54	0528-0624	0602 (9 min)
Termination of ♀ calling posture	31	0610-0711	0644 (12 min)
Response of first ♂ to calling ♀	35	0540-0631	0603 (10 min)
Response of last ♂ to calling ♀	20	0603-0635	0618 (9 min)
Initiation of copula	25	0540-0615	0601 (10 min)
Termination of copula	23	0610-0733	0633 (16 min)
Duration of calling for ♀ that did not mate	31	12-66	40.5 (13.0)
Duration of calling for ♀ that mated	23	1-17	5.2 (4.2)
Duration of copula	23	18-113	31.8 (18.4)
Sunrise Events¹			
Sunrise	4	0646-0648	0647 (1 min)
Civil Twilight begins	4	0619-0621	0620 (1 min)
Nautical Twilight begins	4	0547-0549	0548 (1 min)
Astronomical Twilight begins	4	0512-0514	0513 (1 min)

¹Definitions of these events were derived from (Seidelman 1992): Sunrise = time when the Sun's upper edge of the disk is on the horizon; Civil Twilight = begins in the morning when the center of the Sun is geometrically 6 degrees below the horizon; Nautical Twilight = begins in the morning when the center of the sun is geometrically 12 degrees below the horizon; Astronomical Twilight = begins in the morning when the center of the Sun is geometrically 18 degrees below the horizon.

the females). We did not observe any elaborate courtship behavior by the male after landing next to the female nor prior to attempting copulation. Mating pairs were formed soon after the male landed next to the female. In a few instances, females moved away from the male. Females successful at attracting males remained in the calling posture for a short time (mean of 5.2 min). Unsuccessful females continued calling for 40 min. Mating pairs remained in copula for a short time period (mean of 31.8 min), however, one pair remained in copula for 113 min. Females that did not secure a mate remained in the calling posture beyond the time when males were seen flying near the mating tables.

Figure 3 displays the proportion of females (n = 57) involved in calling or mating activities over time. The time between 0606 and 0645 hours was when the highest proportion of females was observed to be in a calling posture. The period between 0601 through 0635 hours was when the greatest number of females was found to be in copula.

Female Refractory Period

Thirteen of the 14-mated females produced an average of 1.4 eggsticks/female their first night after mating. The eggsticks averaged 37 eggs/eggstick. Only one female exhibited calling behavior on its first morning after mating. This female did not attract a male and died by the next morning without producing an eggstick, although dissec-

tion revealed successful mating had occurred. On the second night after mating, only three of the eight mated females produced eggsticks; one eggstick/female averaging 28 eggs/eggstick. One female called for 71 min without attracting a male. This female had produced two eggsticks its first night after mating but did not produce an eggstick after its second calling event. Of the five females that mated on the morning of 15 July and followed a third night/morning, two females produced two eggsticks (mean of 19 eggs/eggstick), one female died, and two females were idle.

DISCUSSION

Behaviors associated with courtship and mating in Pyralidae vary from elaborate and interactive sequences to simple straightforward behaviors. For example, males attract females through acoustic signaling from song perches, such as in *Symmoracma minoralis* Snellen (Heller & Achmann 1995). Stationary males of *Galleria melonella* (L.) produce 0.5 to 1 s bursts of wing fanning and are approached by attracted females (Flint & Merkle 1983). *Ephestia elutella* (Hübner) males approach pheromone-producing females, engage in head-to-head posturing while positioning their abdominal scent structures in close proximity to the female antennae and attempt copulation from the head-to-head position (Phelan & Baker 1990). Other species of Pyralidae exhibit very simple courtship behaviors, with

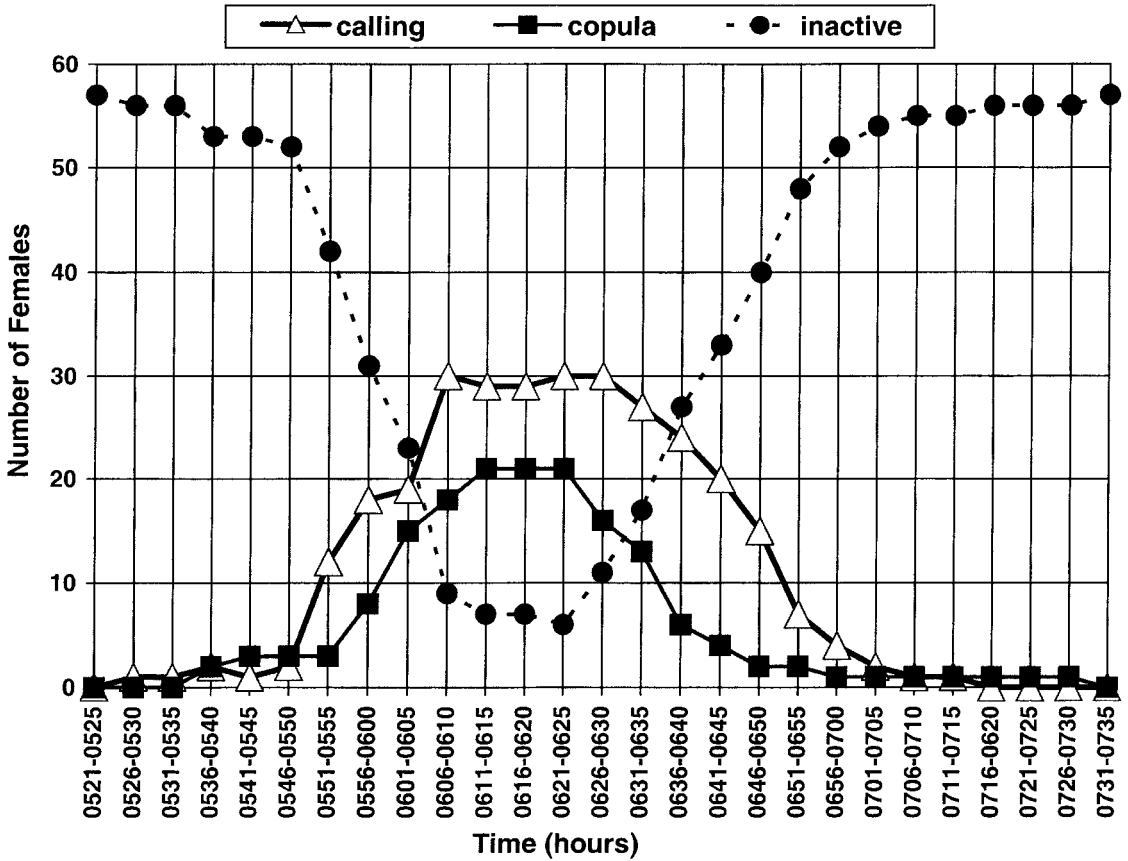


Fig. 3. Average times (in 5 min intervals) when females exhibited various courtship and mating behaviors at Alligator Point, FL during the mornings of 15-18 July 2003.

males locating pheromone-emitting females and quickly attempting copulation by lateral abdominal thrusts under the female wing without any behavioral embellishments, such as in the navel orange worm, *Amyelois transitella* (Walker) (Phelan & Baker 1990).

Our results indicate that mating behavior in *C. cactorum* closely matches the description for simple courtship behavior given by Phelan & Baker (1990). In our field studies, the initiation of calling posture by virgin female *C. cactorum* inside mating arenas was almost immediately followed by the response of males (flying around the mating tables, landing inside the mating arenas, and attempting copulation with the females) and the formation of mating pairs. The behavior sequences observed for *C. cactorum* closely match observations described for the lesser mulberry pyralid (*Glyphodes pyloalis* Walker) by Seol et al. (1986). They reported that the random flight of males continued for several tens of seconds after the females were first observed in a calling position and that males and females were observed in copula almost immediately after encountering one another.

With respect to timing of sexual activity, Wysoki et al. (1993) studied the reproductive behavior of the honeydew moth [*Cryptoblabes gnidiella* (Millière)]. They found that mating in this pyralid occurred 1-2 h before dawn (beginning at 0345 hours and ending around 0530 hours) and that duration of copulation averaged 100 min (range 70-145 min). Peak periods of sexual activity in the pyralids studied by Phelan & Baker (1990) varied in their distribution from 0-2 h subsequent to the initiation of scotophase to 2-0 h prior to the initiation of photophase. Vetter et al. (1997) reported that female carob moth (*Ectomyelois ceratoniae* Zeller) initiate calling in the fourth through seventh hour of scotophase and all calling terminates during the first hour of photophase. Carob moths mate during the fourth and eighth hours of scotophase and pairs remain in copula for an average of 2.35 ± 0.84 h. Flint & Merkle (1983) reported that Greater wax moth adults remain in copula for only a few minutes, yet, upon dissection, 82% of the female moths had sperm in the spermatheca.

Our observations on *C. cactorum* identified that no mating activity occurred during the scoto-

phase between 2100 hours and 0500 hours, 6-18 July 2003. During the 4 mornings of detailed observations, moth courtship/mating activities were restricted to a two-hour period (0528-0733 hours). A high percentage of insects initiated courtship/mating behaviors [female posturing (98%), male response (98%), and copulation (100%)] before civil twilight (0620 hours), the limit at which twilight illumination is sufficient for terrestrial objects to be clearly distinguished (Seidelman 1992). In fact, five females began calling (four of which began copula) just before nautical twilight (0548 hours), the time when general outlines of ground objects are distinguishable, but visual details are not clear (Seidelman 1992). This was about one hour before sunrise occurred. All but two matings were complete before sunrise. We conclude that the peak period of sexual activity for *C. cactorum* begins between nautical and civil twilight and ends before sunrise.

The underlying physiology responsible for the production of the *C. cactorum* male sex attractant is unknown; however, the female appears to be receiving stimuli that initiate the mating process before the beginning of nautical twilight. Astronomical twilight, the time at which the Sun begins to illuminate the sky (Seidelman 1992), occurred during our observations at 0513 ± 0.01 hours. Molecular scattering of ultraviolet radiation and imperceptible sky illumination in the high altitudes of the troposphere and stratosphere (Lee & Hernández-Andrés 2003) present at this time may be providing the stimuli for female *C. cactorum* to initiate their physiological and behavioral courtship/mating behaviors.

We saw no evidence of elaborate courtship behaviors after the male landed next to the female, nor prior to copulation. Mating pairs were formed soon after the male landed and only in a few instances did the female move away from the male. Mating pairs remained in copula for a short period of time (mean of 31.8 min) and almost 100% of the females were found to contain a spermatophore in the bursae copulatrix upon dissection.

The limited observations on female refractory period revealed no subsequent matings by mated females. The two mated females that exhibited calling postures failed to attract males and did not produce eggsticks after their second calling event. The average number of eggsticks produced per female was similar to reports from Australia (Dodd 1940) and South Africa (Zimmermann et al. 2000). However, additional observations over the life of mated females are planned to conclusively determine the number of matings per female and their oviposition outcomes.

Opuntia spp. occur naturally from southern Canada to South America and form a continuous distribution across the southern U.S. from Florida through the states along the Gulf of Mexico (Benson 1982). The potential spread of *C. cactorum* to

the opuntia-rich areas of the western U.S. and Mexico could have devastating effects on the landscape and biodiversity of this region. Our new discovery of *C. cactorum* on the western border of Florida intensifies the concern and shortens the time in which this insect will likely spread into the southwest. Biological control of *C. cactorum* is not a recommended pest control tactic because of the non-target concerns compiled by Pemberton & Cordo (2001). Irradiation studies have determined the dose at which *C. cactorum* males and females are 100% sterile and at which the deleterious effects of substerilizing doses inherited by the F_1 generation are minimized (Carpenter et al. 2001b). An SIT program is the most plausible approach for controlling *C. cactorum* along its leading edge to limit geographical range expansion and to eradicate isolated populations in front of the leading edge. SIT could also be used as an abatement program to protect rare and endangered *Opuntia* spp. Studies on mating behavior reported herein have advanced the development of a successful SIT program. We have demonstrated that a proportion of marked males stay near their release site and can be recovered and identified. We have determined that mating behaviors are simple and straightforward, that the majority of mating behaviors are initiated and completed before sunrise, that successful matings last, on average, 37 min (female calling plus duration of copula), and that, for the most part, females are busy ovipositing the first few nights after mating, not exhibiting additional mating behaviors. Our mating behavior study is also helpful to the ongoing *C. cactorum* research to isolate and identify the female calling pheromone. Bioassays testing the attractiveness of pheromone components and blends may need to be conducted under natural lighting with observations being made between nautical and civil twilight. Our observations will also be useful in efforts to improve traps used for monitoring, and to develop a technique to estimate adult moth population numbers.

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REFERENCES CITED

- BENSON, L. 1989. The Cacti of the United States and Canada. Stanford University Press, Stanford, CA.
CARPENTER, J. E., K. A. BLOEM, AND S. BLOEM. 2001a. Applications of F_1 sterility for research and manage-

- ment of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). Florida Entomol. 84: 531-536.
- CARPENTER, J. E., S. BLOEM, AND K. A. BLOEM. 2001b. Inherited sterility in *Cactoblastis cactorum* (Lepidoptera: Pyralidae). Florida Entomol. 84: 537-542.
- DODD, A. P. 1940. The Biological Campaign Against Prickly Pear. Commonwealth Prickly Pear Board, Brisbane, Australia.
- FERRO, D. N., AND R. D. AKRE. 1975. Reproductive morphology and mechanics of mating of the codling moth, *Laspeyresia pomonella*. Ann. Entomol. Soc. America 68: 417-424.
- FLINT, H. M., AND J. R. MERKLE. 1983. Mating behavior, sex pheromone responses, and radiation sterilization of the Greater Wax Moth (Lepidoptera: Pyralidae). J. Econ. Entomol. 76: 467-472.
- HABECK, D. H., AND F. D. BENNETT. 1990. *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae), a Phycitine new to Florida. Florida Dept. of Agric. and Cons. Serv. Division of Plant Industry. Entomology Circular 333.
- HELLER AND ACHMANN. 1995. Ultrasound communication in the pyralid moth species *Symmoracma minoralis* (Lepidoptera: Pyralidae: Nymphulinae). Entomol. Gen. 20: 1-9.
- HIGHT, S. D., J. E. CARPENTER, K. A. BLOEM, S. BLOEM, R. W. PEMBERTON, AND P. STILING. 2002. Expanding geographical range of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America. Florida Entomol. 85: 527-529.
- JOHNSON, D. M., AND P. D. STILING. 1996. Host specificity of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an exotic *Opuntia*-feeding moth, in Florida. Environ. Entomol. 25: 743-748.
- JULIEN, M. H., AND M. W. GRIFFITHS. 1998. Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds. 4th Edition. CABI Publishing, UK.
- LEE, R. L., JR., AND J. HERNÁNDEZ-ANDRÉS. 2003. Measuring and modeling twilight's purple light. Appl. Optics 42: 445-457.
- MCBRIEN, H. L., AND G. J. R. JUDD. 1996. A Teflon®-walled mating table for assessing pheromone-based mating disruption. J. Entomol. Soc. British Columbia 93: 121-125.
- MORAN, V. C., AND H. G. ZIMMERMANN. 1984. The biological control of cactus weeds: achievements and prospects. Biocontrol News Inf. 5: 297-320.
- PEMBERTON, R. W., AND H. A. CORDO. 2001. Potential and risks of biological control of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America. Florida Entomol. 84: 513-526.
- PETTEY, F. W. 1948. The biological control of prickly pear in South Africa. Sci. Bull., Dept. of Agric. Union of South Africa 271: 1-163.
- PHELAN, P. L., AND T. C. BAKER. 1990. Comparative study of courtship in twelve Phycitine moths (Lepidoptera: Pyralidae). J. Ins. Beh. 3: 303-326.
- SEIDELMAN, P. K. (ed.). 1992. Explanatory Supplement to the Astronomical Almanac. Univ. Science Books, NY.
- SEOL, K. Y., H. HONDA, AND Y. MATSUMOTO. 1986. Mating behavior and sex pheromone of the lesser mulberry Pyralid, *Glyphodes pyloalis* Walker (Lepidoptera: Pyralidae). Appl. Entomol. Zool. 21: 228-235.
- SOBERÓN, J., J. GOLUBOV, AND J. SARUKHAN. 2001. The importance of *Opuntia* in Mexico and routes of invasion and impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). Florida Entomol. 84: 486-492.
- STILING, P. 2002. Potential non-target effects of a biological control agent, prickly pear moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), in North America, and possible management actions. Biol. Invasions 4: 273-281.
- SWEETMAN, H. L. 1936. The Biological Control of Insects with a Chapter on Weed Control. Comstock, Ithaca, NY. 461 pp.
- VETTER, R. S., S. TATEVOSSIAN, AND T. C. BAKER. 1997. Reproductive behavior of the female carob moth, (Lepidoptera: Pyralidae). Pan-Pacific Entomol. 73: 28-35.
- WYSOKI, M., S. B. YEHUDA, AND D. ROSEN. 1993. Reproductive behavior of the honeydew moth, *Cryptoblades gnidiella*. Invert. Reprod. Developm. 24: 217-223.
- ZIMMERMANN, H. G., V. C. MORAN, AND J. H. HOFFMANN. 2000. The renowned cactus moth, *Cactoblastis cactorum*: its natural history and threat to native *Opuntia* in Mexico and the United States of America. Div. Distrib. 6: 259-269.