Phenology and Egg Production of the Cactus Moth (Lepidoptera: Pyralidae): Comparison of Field Census Data and Life Stage Development in the Field[1]

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Abstract Natural phenology and development of the cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), was studied under field conditions in St. Marks National Wildlife Refuge, St. Marks, FL, from July 2006 to September 2007. Pads of cactus (*Opuntia stricta* Haw. [Cactaceae]) were visually surveyed weekly for presence of moth immature stages. Adult male *C. cactorum* populations were surveyed using a pheromone lure and wing style sticky traps. The field census data identified 3 generations per year which generally occurred in August to September, October to April, and May to July. Numbers of eggsticks peaked in midAugust, midOctober and midApril. High numbers of early larval immatures (1st to 3rd instars) were recorded in October 2006, May 2007 and September 2007. High numbers of late-stage larvae (4th to 5th instar) were recorded in September to October 2006, December to January 2006, June to July 2007. Peak numbers of *Cactoblastis* male adults occurred approximately in midOctober 2006, April to May 2007, and July to August 2007. Pupae were cryptic and difficult to sample. Development in field cages was studied by introducing cohorts of moth eggs on potted cactus plants (*Opuntia ficus-indica* (L.) Mill.) into the field at approximately the same times they were found to occur naturally. During the course of each generation, the potted plants were returned to the laboratory for determination of moth lifestage. Body weights and lengths also were recorded. In the field cages, 3 generations were observed and these coincided with the populations that were observed in the open field. However, the generations were more clearly defined because eggs were introduced as cohorts and most insects were recovered. Measurements of larval head capsules and body lengths show that development in the winter generation is slower than that of the summer and fall generations, although peak measurements are approximately identical in all 3 generations. Female pupae weighed 225.25 (± 4.8 SE) mg which was significantly heavier than males weighing 138.01 (± 5.5) mg. Pupal weights differed according to generation, but there was no effect on adult weight. Female adults weighed 130.3 (± 11.3) mg, compared with males, which weighed 60.81 (± 2.4) mg. Adult sex ratio was approximately 1:1. Male adults appeared to have emerged earlier than females in the fall generation.

Key Words life history traits, fecundity, egg production, *Opuntia stricta, Opuntia ficus-indica*

The cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), was imported from Argentina into Australia in 1926 to control invasive *Opuntia* cacti and

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became a textbook example of successful classical biological control (e.g., DeBach 1974). In 1989, the *Cactoblastis* was found in mainland North America with reports in south Florida (Mahr 2001). *Cactoblastis* likely arrived through commercial importations of *Opuntia* from the Dominican Republic into Miami (Pemberton 1995). By 1999, *Cactoblastis* had spread northwards and was found throughout the eastern Florida coastline and as far north as Tampa on the western coast (Hight et al. 2002). By 2002, the moth had expanded westward to Pensacola, FL, and northward along the eastern coast to Charleston, SC (Hight et al. 2002). In July 2004, westward migration had reached Dauphin Island, AL, and northward migration had reached Bull Island, SC (≈80 km north of Charleston) (Simonson et al. 2005). The westward migration of *Cactoblastis* in the southeastern United States is estimated at 160 km/year and soon to reach Texas (Solis et al. 2004). The moth threatens the cactus industry in the United States, where cacti are grown primarily as ornamentals in Arizona, California, Nevada, New Mexico, and Texas. Nursery production is highest in Arizona (wholesale and retail values of $4.5 million and $9.5 million, respectively), followed by southern California (Irish 2001). *Cactoblastis* was found in Isla Mujeres, Mexico, in August 2006 (Hernandez-Baeza 2006), thereby threatening the economically important cactus industry with >250,000 ha cultivated acreage producing annual economic revenue of about $50 million (1990 - 1998) (Soberón et al. 2001). The method by which *Cactoblastis* entered into Mexico is unknown, although speculation centers on winds and hurricanes, or accidental transport via tourists or commercial trade.

There is little information on field phenology and development of the cactus moth in field conditions. Here we studied the phenology of *Cactoblastis* in Florida using field cage experiments and sampling native cactus plants in St. Marks, FL. The study was comprised of two parts: a field assessment of native cactus plants and moth lifestage, and a manipulative cage experiment for the study of lifestage development and egg production under field-realistic conditions. The information generated in this study will aid in developing management strategies to control this invasive pest.

Materials and Methods

Experiment 1: Cactus moth field census data. Native cactus plants (*O. stricta* Haw. [Cactaceae]) were visually surveyed weekly at a dike near the picnic pond at St. Marks National Wildlife Refuge, St. Marks, FL (30.16 - 30°1' N, -84.21 - 84°1' W) from July 2006 to September 2007. Nine patches of plants (2 - 3 plants / patch and on average, 51 pads per plant and 49 cm plant height) were selected and examined for the presence of *C. cactorum* (i.e., by looking for evidence of frass on the cactus pad and feeding damage). Any eggsticks on the pad were marked, and the length (cm) was recorded. Thereafter, eggsticks were checked weekly for egg hatching. The number of eggs per eggstick was estimated based on laboratory measurements (i.e., number of eggs per eggstick, length and width of each egg) recorded from eggsticks taken from a field site near the sampling area. Larval counts were made by slicing the cactus pad sideways to avoid damaging the larvae. Old, dried pads or bark near the plants were checked for pupae. Adult male *C. cactorum* populations were surveyed using a pheromone lure and wing-style sticky traps [top trap (Scentry; Scentry Biologicals, Inc., Billings, MT) and the bottom trap (Pherocon R 1C; Trece Inc., Adair, OK)]. Three traps were placed at a distance of about 15 m apart and at a height of 1.2 m. An experimental synthetic female sex pheromone attractant lure, Centurion R (Suterra LLC, Bend, OR) was placed in each trap and replaced every 2 wks. The pheromone lure is based on a synthetic chemical formula (Heath et al. 2006). The wing style traps were replaced every week, and trap samples were transported to the laboratory to record the number of adult male *C. cactorum* collected in each trap. The stage and numbers of immature *C. cactorum* found in the pads were counted and recorded. All immature larvae were kept in the cactus pad and placed near the plant after data collection.

Experiment 2: Cactus moth development in field cage conditions. Three different trials were performed at St. Marks National Wildlife Refuge, St. Marks, FL, from October 2006 – October 2007 to correspond to the 3 generations of *C. cactorum* throughout the year. The duration of the 3 trials were as follows: Trial 1 (October 2006 – May 2007); Trial 2 (May – August 2007); and Trial 3 (August – October 2007). The start date for each trial was based on the phenology of the cactus moth from field surveys using methods above and the availability of eggsticks obtained from a laboratory colony reared at USDA, ARS, CMAVE / FAMU-CBC in Tallahassee, FL. Potted cactus plants were prepared by placing cactus plant cuttings (*Opuntia ficus-indica*) in plastic pots (28 cm diam × 29.2 cm height, Nursery Supplies, Inc., Chambersburg, PA) about 30 d before the start of each trial. Soil used was a 1:1 mixture of sand and a commercial potting medium. A slow-release fertilizer also was added. In the laboratory, a minimum of 66 cactus moth eggsticks of the same age were collected and placed in a growth chamber (Thermoforma, Marietta, OH) at 26°C with a photoperiod of 14:10 (L:D) and 50 ± 10% RH. Eggsticks were placed individually into 30-ml plastic cups (Solo, Inc., Highland Park, IL) and covered with a cardboard lid. Eggs were estimated to hatch about 21 d after eggs were deposited (Legaspi and Legaspi 2007, 2008). About 5 - 7 d before the eggs hatched, the number of eggs per eggstick was recorded. A piece of cactus (20 mm length × 20 mm width) was placed in each cup as soon as the eggs hatched. Newly-emerged first-instar larvae burrowed into the cactus piece. One to two days after the eggs hatched, the numbers of eggs that hatched were recorded and the cactus pieces containing the first-instar larvae were taken to St. Marks National Wildlife Refuge.

In an area near the picnic pond at St. Marks, 22 screen cages (60 × 60 cm) (Bioquip, Inc.) were placed about 60 cm apart. Three potted cactus plants per cage were placed inside each screen cage. One cactus piece with first-instar larvae was pinned, using an entomological pin (#2, Bioquip, Inc. CA), onto the upper cactus pad in each pot. Each pot was considered a replicate; thus, there were 3 replicates per cage per weekly sampling. A HOBO weather recorder (Onset Computer Corp., Bourne, MA) was placed outside the cages at a height of 1.2 m to record daily maximum, minimum and average temperature (°C) readings from September 2006 to late August 2007.

After 1 - 2 wks, 1 cage with 3 potted plants was taken to the laboratory for sampling. Thereafter, 1 cage per week was returned until all cages or all adults emerged. When necessary because of increased larval development rate, cages were examined twice weekly. In the laboratory, each cactus pad was dissected to determine the number and stage of cactus moth larvae. The larval stages were determined through body length and head capsule width measurements (mm) of a minimum of 5 larvae per plant for a minimum of 15 larvae per cage. Body length was measured from dorsum of the head to the posterior end of the abdomen. Observations of visible eclosed head capsules inside the pad were also recorded. The following ranges of the head width capsule were used to differentiate the different larval stages – 1st instar (0.1 - 0.4 mm); 2nd instar (0.5 - 0.8 mm); 3rd instar (0.9 - 1.2 mm); 4th instar (1.3 - 1. 7 mm) and 5th instar (1.8 - 2.4 mm). Pupae were collected on the soil surfaces and side crevices inside and outside of the pot. Pupae were removed from its silky cocoon to determine

gender and body weight. Numbers and gender of cactus moth pupae and adults were recorded. Fresh body weight of live pupae and adults was measured (mg) using an analytical balance (Sartorius Corp., Edgewood, NY). Body weights of a minimum of 5 male and 5 female pupae or adults per pot were measured for a total of 15 male and 15 female pupae or adults per cage. All eggsticks deposited by adults were counted and recorded. The number of eggs per eggstick also was recorded. In the winter generation only, we measured the length of the eggsticks (mm), and the height (mm) and width (mm) of individual eggs from the cage sampled on 16 May 2008 ($n = 117$).

Statistical analysis. Pupal and adult weights were analyzed as a 2-Way ANOVA with sex and season as factors. Insect body weights also were analyzed separately by sex to test for differences among the generations (1-Way ANOVA). Where appropriate, means were separated by Tukey's HSD ($P = 0.05$). All statistical analyses were performed using Systat 12 (Systat Software Inc., San Jose, CA).

Results

Experiment 1. Cactus moth field census data. Temperature data during the sampling seasons at St. Marks, FL, ranged from about 0 - 37°C and are shown according to season (Fig. 1). Total number of *Cactoblastis* male moths collected in the field indicates 3 generations per year under field conditions in St. Marks, FL (Fig. 2). At each sampling occasion, total numbers of insects collected is plotted by lifestage. The generations may be broadly generalized as occurring in approximately August to September (hereafter referred to as the "fall" generation), October to April (hereafter referred to as the "winter" generation), and May to July (hereafter referred to as the

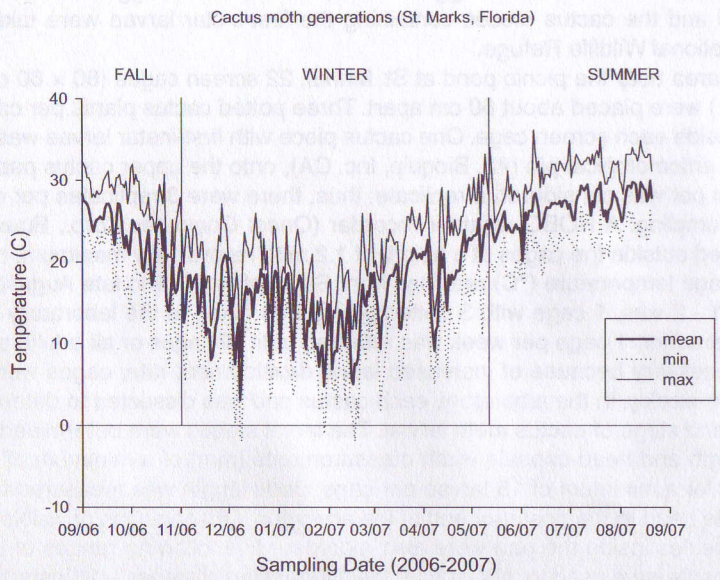

Fig. 1. Daily mean, minimum and maximum temperatures at the field site (St. Marks, FL), during the 2006 - 2007 field season.

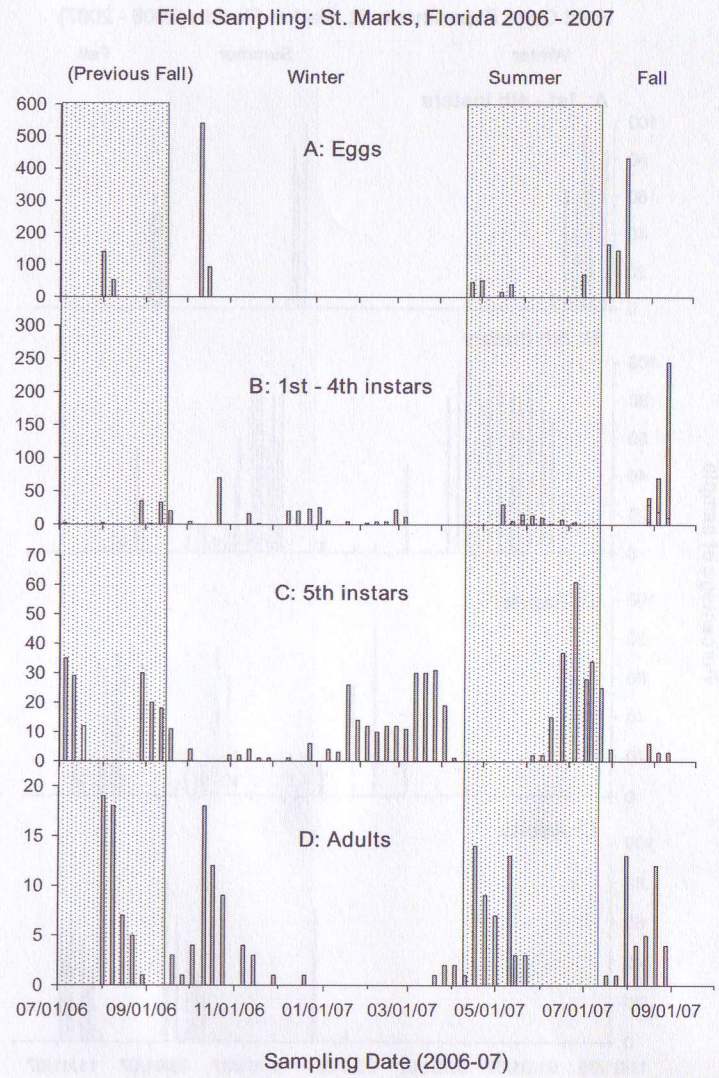

Fig. 2. Cactus moth phenology in St. Marks, FL. Field counts over time are shown by insect lifestage (eggs, 1st – 4th instars, 5th instars, and adults).

"summer" generation). Eggsticks peaked in midAugust, midOctober and midApril. High numbers of early larval immatures (1st to 3rd instars) were recorded in October 2006, May 2007 and Sept. 2007. High numbers of late larval immatures (4th to 5th instar) were recorded in September to October 2006, December to January 2006, June to July 2007. Peak numbers of *Cactoblastis* male adults occurred approximately in midOctober 2006, April to May 2007, and July to August 2007. Pupae are not shown because they are cryptic and difficult to sample. Only 5 pupae were found; 3 were

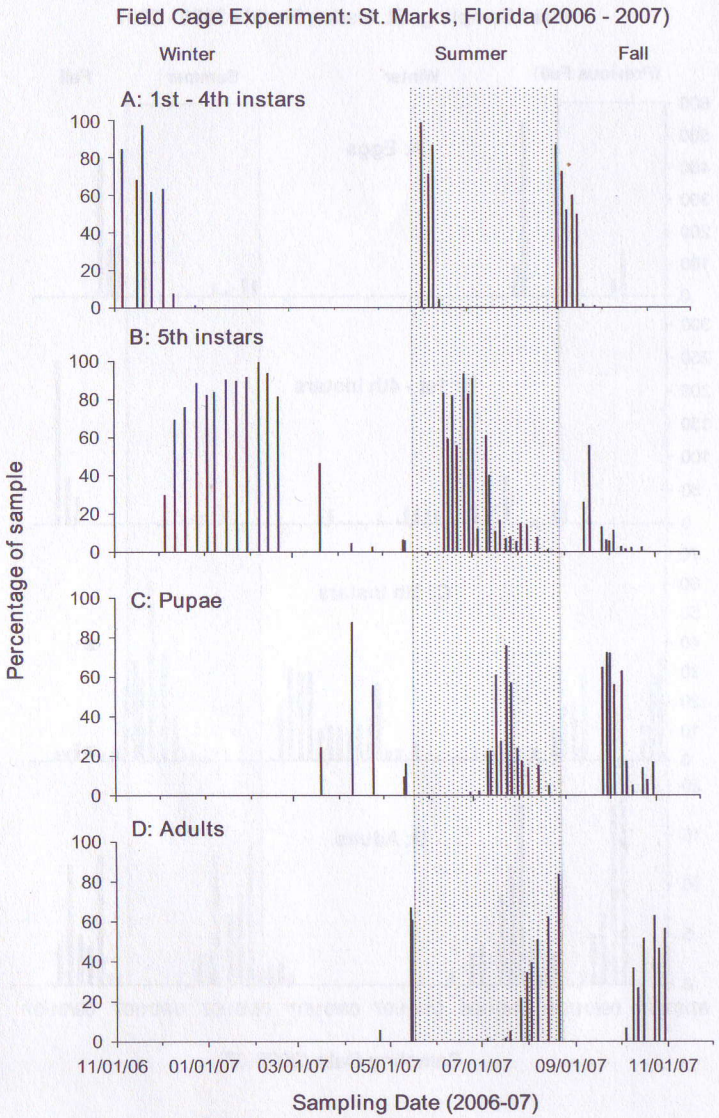

Fig. 3. Proportions of samples from field cages. Cactus moth lifestages (1st – 4th instars, 5th instars, pupae and adults) are shown as proportions of samples returned through time.

collected on 18 July 2006 and 2 were collected on 3 October 2006. Field phenology is complicated by some overlap in the different stages because oviposition occurred over several days and insect development is not a discrete process (Legaspi et al. 1997).

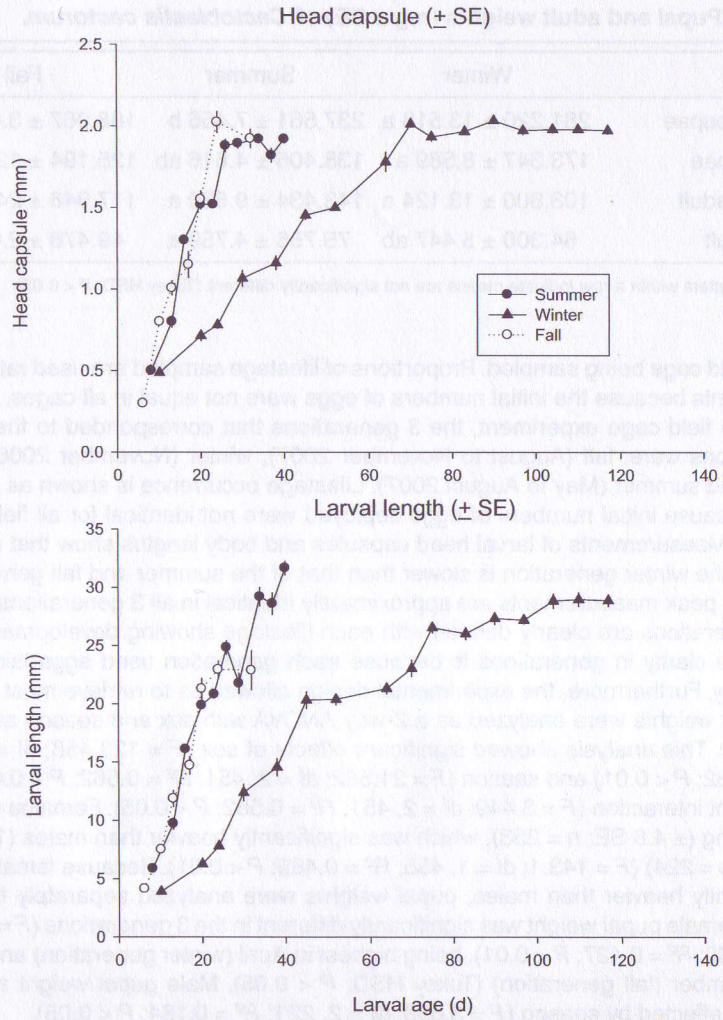

Fig. 4. Body measurements (head capsule width and body length, mm) of larval stages with time. The May and August generations show similar development rates. The November generation developed more slowly, but reached the same level as the other generations.

Experiment 2. Cactus moth development in field cage conditions. Eggs were placed in the field at about the same times they would occur naturally as described in Experiment 1. However, phenology did not match those of the natural population exactly because egg deployment was contingent on the availability of eggs from the laboratory colony, thus introducing a time lag of about 4 wks. At each sampling occasion, lifestage sampled is shown as a percentage of the number of eggs initially placed

Table 1. Pupal and adult weights (mg ± SE) of *Cactoblastis cactorum*.

	Winter	Summer	Fall
Female pupae	281.220 ± 13.518 a	237.561 ± 7.456 b	188.967 ± 3.606 c
Male pupae	173.347 ± 8.589 a	138.406 ± 4.616 ab	125.194 ± 12.638 b
Female adult	103.800 ± 13.124 a	143.434 ± 9.690 a	117.946 ± 24.259 a
Male adult	64.300 ± 5.447 ab	75.756 ± 4.759 a	49.478 ± 2.082 b

Common letters within a row indicate means are not significantly different (Tukey HSD, $P < 0.05$)

in the field cage being sampled. Proportions of lifestage sampled are used rather than total counts because the initial numbers of eggs were not equal in all cages.

In the field cage experiment, the 3 generations that corresponded to the natural generations were: fall (August to November 2007), winter (November 2006 to May 2007) and summer (May to August 2007). Lifestage occurrence is shown as percentages because initial numbers of eggs deployed were not identical for all field cages (Fig. 3). Measurements of larval head capsules and body lengths show that development in the winter generation is slower than that of the summer and fall generations, although peak measurements are approximately identical in all 3 generations (Fig. 4). The generations are clearly defined with each lifestage showing development to the next. The clarity in generations is because each generation used eggs laid on the same day. Furthermore, the experimental design allowed us to retrieve most insects.

Pupal weights were analyzed as a 2-way ANOVA with sex and season as factors (Table 1). This analysis showed significant effects of sex ($F = 123.458$; df = 1, 451; $R^2 = 0.562$; $P < 0.01$) and season ($F = 21.562$; df = 2, 451; $R^2 = 0.562$; $P < 0.01$), with significant interaction ($F = 3.449$; df = 2, 451; $R^2 = 0.562$; $P < 0.05$). Females weighed 225.25 mg (± 4.8 SE; $n = 233$), which was significantly heavier than males (138.01 ± 5.5 SE; $n = 224$) ($F = 143.1$; df = 1, 455; $R^2 = 0.489$; $P < 0.01$). Because females were significantly heavier than males, pupal weights were analyzed separately for the 2 sexes. Female pupal weight was significantly different in the 3 generations ($F = 25.644$; df = 2, 230; $R^2 = 0.427$; $P < 0.01$), being highest in April (winter generation) and lowest in September (fall generation) (Tukey HSD, $P < 0.05$). Male pupal weight also was similarly affected by season ($F = 3.858$, df = 2, 221; $R^2 = 0.184$; $P < 0.05$).

A 2-way ANOVA on adult weights showed significant effects of sex ($F = 12.43$; df = 1, 267; $R^2 = 0.382$; $P < 0.01$), but season ($F = 2.684$; df = 2, 267; $R^2 = 0.382$; $P = 0.07$) and the sex X season interaction were insignificant ($F = 0.196$; df = 2, 267; $R^2 = 0.382$; $P = 0.822$). As in pupae, female adults were heavier (1-way ANOVA; $F = 39.448$; df = 1, 271; $R^2 = 0.356$; $P < 0.01$). Females weighed 130.3 mg (± 11.4 SE; $n = 129$), compared with male adults which weighed 60.81 mg (± 2.45 SE; $n = 144$). Adult weights were also analyzed separately according to sex. Female adult weight was not significantly different among the 3 generations ($F = 0.759$; df = 2, 126; $R^2 = 0.109$; $P = 0.47$). However, male adults were heavier in the July generation ($F = 16.042$, df = 2, 141; $R^2 = 0.431$; $P < 0.01$). The summer generation (in July) produced the heaviest males (Tukey HSD, $P < 0.05$). Recorded adult sex ratio was approximately 1:1 (47.3% female; 129 ♀♀ and 144 ♂♂).

Examination of adult emergence by sex did not reveal any consistent trends. For the winter generation, only one date of emergence (in April) with 8 ♀♀ and 9 ♂♂ were

Table 2. Egg production of cactus moth in 1 cage over 3 generations. St. Marks, FL, 2007.

Generation	Weeks after start of experiment during egg production	Sampling duration during egg production (2007)	Weeks after start of experiment (Sample date, 2007)	Number egg sticks	♀ emerged	Eggs / eggstick (± SE)	Eggs laid per cage (total)	Eggs laid / Eggsticks / ♀♀ (mean) ♀♀ (mean)
Winter (Apr.) *	25 –29	Apr. 24 – May 16	29 (May 16)	117	27	58.1 (± 2.49)	6,799	251.8 4.3
Summer (July)	9 –13	July 27 – Aug. 21	10 (July 31)	224	51	47.9 (± 1.32)	10,697	209.7 4.3
Fall (Oct.)	7 - 11	Oct. 12 – Oct. 30	10 (Oct.26)	132	26	48.5 (± 1.46)	6,406	246.3 5.0

* Additional measurements recorded in winter generation only (sampled May 16, 2007) – mean length of eggstick = 24.3 mm (± 1.02 SE); mean height of one egg = 0.3 mm (± 0.0 SE); mean width of one egg = 1.0 mm (± 0.0 SE) ($n = 117$).

recorded. Within the first 10 d of adult emergence in the summer generation (July), 122 ♀♀ and 15 ♂♂ adults emerged. For the fall generation (October), 8 ♀♀ and 40 ♂♂ emerged within the first 10 d, suggesting that males may emerge earlier than females in this generation. Egg production over the 3 generations is shown in Table 2. Eggs were produced earlier in the fall generation compared with the summer and winter generations. Although the eggs were produced much later in the winter (29 wks after the start of the experiment) compared with the summer and fall generations (10 wks after the start of the experiment), egg fecundity generally remained consistent among the 3 generations. The mean number of eggs per eggstick ranged from 48.5 - 58.1 per female. The total eggs laid per female ranged from 210 - 252, and we observed a mean number of 4 - 5 eggsticks laid per female (Table 2).

Discussion

Early descriptions of the biology of the cactus moth can be found in Dodd (1940), Pettey (1948), and Mann (1969). More contemporary studies are those of Sarvary et al. (2008), Legaspi and Legaspi (2007, 2008), Legaspi et al. (2009) and McLean et al. (2006). The moth is known to have 3 nonoverlapping generations in the southern U.S. (Hight and Carpenter, 2009, Zimmermann et al. 2004), as was observed in this study. In some other parts of the world, the cactus moth was reported to undergo 2 - 3 generations, depending on climate and season. In South Africa, summer and winter generation times are 113 - 132 and 234 - 256 d, respectively. In Australia, summer and winter generation times are 100 - 120 and 235 - 265 d, respectively (Zimmermann et al. 2004). Robertson (1989) reported summer generations time of 161 - 188 d in South Africa and 75 - 120 d in Australia.

Adult lifespan is short (≈9 d) and duration of lifestages is generally: egg stage (50 d); larval (130 - 180 d); pupal (40 - 70 d) (Zimmermann et al. 2004). In laboratory conditions, adult lifespan typically ranges from ≈5 d at 34°C to ≈12 d at 18°C in females (Legaspi and Legaspi 2007, 2008, Legaspi et al., in press). Under constant temperature conditions, calculated generation times are as follows: 185.54 d (18°C); 129.58 d (22°C); 75.07 d (26°C); 67.14 d (30°C); and 68.95 d (34°C) (Legaspi and Legaspi 2007). Development and reproduction were both close to optimal at about 30°C. Clear correlations between temperature and development or reproduction are obviously much more difficult to measure in the field. Time duration from first emergence of eggs to last observation of adults was: 189 d (winter), 80 d (summer) and 62 d (fall).

Head capsule and body length measurements of the immature stages show little difference in development rates between the summer and fall generations. However, the winter generation develops more slowly, although all 3 generations attain approximately similar body sizes. Larval measurements were recorded over 32 d in the fall generation, 40 d in the summer and 140 d in the winter, giving some indication of immature durations in the 3 generations. Larval lengths reached a plateau of about 30 mm in all 3 generations. In the laboratory, extreme constant temperatures have resulted in declining development rates, as well as differences in maximal body lengths attained (Legaspi and Legaspi 2007).

As in recent studies (e.g., Legaspi and Legaspi 2007, 2008, Sarvary et al. 2008), we found female cactus moths weighed more than males. Differences in pupal weights among the generations was largely absent in adults. Therefore, conclusions regarding weight differences among cactus moth generations are preliminary and must be subject to verification. This study also supports previous work showing that cactus moth adult sex ratio is typically 1:1 (e.g., Robertson and Hoffmann 1989). Male moths have been shown to mate successfully throughout their lifetimes when provided with females (McLean et al. 2007).

Field results were in broad agreement with previous laboratory research on *Cactoblastis* immature development (Legaspi and Legaspi 2007, Legaspi et al. 2009). The summer and fall generations showed faster development than the winter generation. In the laboratory, development was longest at 18°C, declining significantly at 22°C, and shortest at 26, 30 and 34°C. Based on the field weather data collected, estimated mean temperatures by season were: winter (October 2006 – April 2007) 15.93°C; summer (May – July 2007), 26.4°C; fall (August – September 2006) 25.98°C. Fecundity was somewhat higher than that found in our previous laboratory study (Legaspi and Legaspi 2007), but comparable to findings by other workers (e.g., Zimmermann et al. 2004). Data provided here on field phenology, seasonal development and egg production may be useful in developing management strategies against the cactus moth.

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