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Reproductive biology of *Fopius ceratitivorus* (Hymenoptera: Braconidae), an egg–larval parasitoid of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae)

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Abstract

The reproductive biology of *Fopius ceratitivorus* Wharton, a recently discovered African parasitoid, was studied in quarantine in Hawaii to facilitate its mass production for biological control of the Mediterranean fruit fly, *Ceratitis capitata*. Mean longevity of host-deprived and ovipositing females was 17.3 ± 0.9 d and 16.2 ± 0.5 d, respectively. Ovarian maturation peaked at 61.6 mature eggs per female on the fifth day after eclosion and declined thereafter. Mean number of offspring produced per day by mated females was 5.1 ± 0.4, and realized fecundity expressed as total eggs deposited during the female's life time was 107.8 ± 12.8. Females were more attracted, to and reproduced significantly more, in fruit substrates containing odors of adult flies and eggs rather than fruit substrates artificially inoculated with fly eggs. Our findings suggest that *F. ceratitivorus* is a promising new parasitoid for biological control of *C. capitata* in Hawaii.
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Keywords: Biological control; *Fopius ceratitivorus*; *Ceratitis capitata*; Reproductive biology; Egg–larval parasitoid

1. Introduction

The egg–larval parasitoid, *Fopius ceratitivorus* Wharton (Hymenoptera: Braconidae: Opiinae), was recently discovered in east Africa and described as a new species by Wharton (1999). A rearing methodology was developed by the USDA-APHIS/MOSCAMED Quarantine Facility at San Miguel Petapa, Guatemala, using *Ceratitis capitata*-infested coffee berries (Lopez et al., 2003). The parasitoid was imported into Hawaii as part of an on-going effort to control invasive tephritid fruit flies that are serious pests affecting fruit and vegetable production, including. melon fly, *Bactrocera cucurbitae* (Coquillett), Mediterranean fruit fly, *C. capitata* (Wiedemann), introduced to Hawaii in 1895 and 1907, respectively (Back and Pemberton, 1918); oriental fruit fly, *B. dorsalis* (Hendel), first reported in 1945 (van Zwaluvenburg, 1947); and the solanaceous fruit fly, *B. latifrons* (Hendel), introduced in 1983 (Vargas and Nishida, 1985).

Attempts to manage these flies in Hawaii have included bait-spray applications, sanitation, use of sterile insect techniques, and releases of hymenopteran parasitoid species. Over 30 parasitoids have been introduced from Asia, Africa and Australia to control these pests, resulting in some of the more successful examples of classical biological control of fruit flies in the world (Bess et al., 1961; Clausen et al., 1965; Haramoto and Bess, 1970; Wong and Ramadan, 1987; Wharton, 1989; Vargas et al., 1995).

The introduction of *F. ceratitivorus* was considered because it has co-evolved with its host, *C. capitata* in its native region of sub-Saharan Africa, and also for its demonstrated ability to parasitize the egg stage of its host (Bokonon-Ganta et al., 2005; Lopez et al., 2003). It may

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contribute significantly to the biological control of *C. capitata,* because it can attack eggs located near the surface of infested fruits and vegetables, where they can be reached and parasitized more easily than larvae that burrow deep into fruit tissues as they develop.

The wasp was imported and a laboratory colony was established using *C. capitata*-infested papaya in quarantine at the Hawaii Department of Agriculture from initial stocks provided by the USDA-APHIS/MOSCAMED Quarantine Facility at San Miguel Petapa (Bokonon-Ganta et al., 2005). Host suitability and host range studies demonstrated that *F. ceratitivorus* effectively attacks eggs of *C. capitata,* but cannot successfully develop in other fruit fly pest species (Bokonon-Ganta et al., 2005; Lopez et al., 2003). Furthermore, this parasitoid appears unlikely to attack non-target tephritids in Hawaii (Wang et al., 2004; Bokonon-Ganta et al., 2005). In addition, preliminary studies on competition with the well-established egg–larval parasitoid, *Fopius arisanus* (Sonan), demonstrate that either species may win in intrinsic competition with one another, depending on which occupies the host first (Bokonon-Ganta et al., 2005).

These findings reveal little risk of non-target impact, or detrimental effects due to competition, and suggest that release of this parasitoid as a biological control agent in Hawaii can contribute to the overall fly biological control in the islands. However, detailed information on the reproductive attributes of *F. ceratitivorus* is lacking. Therefore, laboratory studies were undertaken on the following aspects of the bionomics of *F. ceratitivorus*: (1) survival rates of host-deprived and ovipositing females; (2) patterns of ovarian maturation; (3) realized fecundity; and (4) effect of the presence of oviposition cues on parasitoid reproduction. These data are important to an understanding of this parasitoid, regarding both the evolution of its life-history strategy (Godfray, 1994; Heimpel et al., 1998), and to facilitate its mass rearing for field colonization in biological control programs.

2. Materials and methods

2.1. Fruit flies and parasitoids

The reproductive biology of *F. ceratitivorus* was tested using its preferred host, *C. capitata*. Fly colonies were initiated at the University of Hawaii from puparia provided by the USDA/ARS Pacific Basin Agricultural Research Center in Honolulu, Hawaii. Upon eclosion, adult flies were maintained in rearing cages ($25 \times 25 \times 25$ cm) in the insectary at 28 ± 2 °C and 60–80% RH, under a 12:12 h L:D regime. The flies were provided with water in wet cotton wicks, and fed a diet made of sugar and yeast hydrolysate powder in a ratio of 3:1. Subsequent fly populations were reared on mature and half-ripe papaya fruit, *Carica payaya*. Fruits were infested with fly eggs by exposing them to 200 pairs of two week-old adult *C. capitata* in rearing cages for 24 h.

After exposure to flies, fruits were transferred to incubation units made of plastic cups (9 cm diam., 5 cm depth) with 150 g fresh wheat diet (Tanaka et al., 1969) as supplemental larval food. Each cup was placed in a 4 L plastic container (20 cm diam., 20 cm depth) with a 1-cm layer of fine vermiculite on the bottom to serve as a substrate for pupation. This vermiculite was kept moist to prevent pupal desiccation. A hole (10 cm diam.) was cut in the lid of the container and replaced with a fine mesh screen. Ten days later fruit fly puparia were sieved from the vermiculite, counted, and placed in clean rearing cages for emergence of adult flies. Flies were provided with water in wet cotton wicks, and fed a diet made of sugar and yeast hydrolysate powder in a ratio of 3:1.

A colony of *F. ceratitivorus* was initiated in similar cages at the Insect Quarantine Facility of the Hawaii Department of Agriculture at 28 ± 2 °C and 60–80% RH, under a 12:12 h L:D regime, and continued at the University of Hawaii Fruit Fly Quarantine Facility under the same conditions. Fruits were infested with tephritid eggs by exposing them to about 200 pairs of adult *C. capitata* for 24 h. Infested fruits were then exposed to parasitoids for 48 h and afterwards transferred into incubation units until parasitoid emergence. Parasitoids were provided with water and fine drops of pure honey (Sioux Honey Ass., Sioux City, IA) on the upper side of the rearing cages. For detailed rearing procedures, see Bokonon-Ganta et al. (2005). *F. ceratitivorus* is not approved for release in Hawaii yet. Therefore, all experiments were conducted in quarantine under the conditions described above.

2.2. Emergence and development of host flies and parasitoids

Patterns of parasitoid and fly emergence were based on cohorts of puparia obtained from *C. capitata* eggs exposed to female parasitoids for 24 h. Methods of exposure and subsequent handling of hosts were the same as those described for host range testing (Bokonon-Ganta et al., 2005). Puparia were collected and isolated in 0.25-L plastic containers kept in the laboratory under the same environmental conditions. Emergence and mortality were recorded once daily.

2.3. Adult parasitoid longevity

Longevity of host-deprived females was determined from five replicates of 20 female parasitoids. Each group of 20 females was held in a small Plexiglas® cage ($12 \times 12 \times 12$ cm) with a round opening (11 cm diam.) in the front side to which a sleeve was fixed to allow introduction of fruit material and insects. To allow ventilation, a round opening (4.5 cm diam.) was made in the top of the cage, to which a piece of organza material was fixed. Parasitoids were provided with water and honey. Longevity was recorded once daily. Longevity of ovipositing females was derived in a similar manner from the realized fecundity experiments (Section 2.5).

2.4. Ovarian maturation

A cohort of 200 newly emerged mated female *F. ceratitivorus* was placed in a test cage at 28 ± 2 °C and 60–80% RH. Females were deprived of *C. capitata* eggs at all times. To determine the rate of ovarian development and the number of mature eggs in their ovaries, ten females were dissected in saline solution starting from ⩽12 h old and then every day until 32 day old. Reniform ovarian eggs (van den Bosch et al., 1951) in the lower portions of the ovarioles, oviducts and calyx were considered mature eggs. Eggs attached to nurse cells (immature eggs) or resorbed eggs were not added to the total number of mature eggs. Parasitoids were provided with water and fine drops of pure honey, but no hosts were provided.

2.5. Realized fecundity

To determine the reproductive activity of *F. ceratititivorus*, 20 female wasps were individually held in plastic cages (9 cm diam., 13 cm high) and provided with honey and water. Each female was confined with one 2–3 d old male, and every other day was provided a piece of papaya (2 cm long × 1 cm wide × 0.5 cm thick) infested with about 100 *C. capitata* eggs as described by Bokonon-Ganta et al. (2005). Exposed fly eggs were then reared to assess the fecundity of ovipositing females by placing the exposed papaya pieces on larval medium in 200-ml plastic cups for host development. The experiment was repeated 20 times using parasitoids of different generations. Longevity of the ovipositing females was also recorded and compared with longevity of host-deprived females (Section 2.3). The number of mature ovarian eggs remaining in the ovaries was counted at the death of each female.

2.6. Effect of host fly odor on parasitoid reproduction

This experiment was designed to investigate the effect of cues associated with the presence of fly hosts on parasitoid oviposition. Because female *F. ceratitivorus* reach their maximum mature egg load at 3–6 days post eclosion, we used 3–6 d-old female wasps. The experiment consisted of two treatments. In the first treatment, a papaya fruit was first infested with *C. capitata* eggs by exposing it to 200 pairs of two week-old adult flies for 4 h. The fruit was then cut into four pieces (4 cm long × 2 cm wide × 0.5 cm thick), each piece serving as a test unit. We estimated the mean number of *C. capitata* eggs per papaya section in this treatment by counting the number of oviposition punctures on each fruit section. Dissection of a sub sample of 20 oviposition punctures revealed that 3–5 *C. capitata* eggs were laid per puncture. The parasitism rate (total number of adult parasitoids emerged/total number of host × 100) was based on the number of pupae recovered following incubation of fruits for rearing of exposed *C. capitata* eggs.

The second treatment used un-infested pieces of papaya, cut into four small pieces of the same size as used in the first experiment. These were artificially inoculated with newly laid *C. capitata* eggs (<4-h-old). In each fruit piece, twenty holes (each 4–5 mm deep and made with a 1 mm metal needle) were arranged in four rows (i.e., 5 holes/row). Twenty eggs were inserted into each hole using a fine camel hair brush. As a control for mortality of the artificially inoculated eggs, an equal number of eggs were inoculated in another set of fruits held in separate cages as controls.

For each treatment, five pairs of wasps were released into a plastic cage and a one piece of each prepared papaya (naturally or artificially infested) was provided in each cage. The number of females observed searching or probing on either fruit surface one and 24 h after initial exposure of inoculated fruits to parasitoids was recorded. Experiments were replicated five times for each treatment each using different sets of parasitoids. At the end of a 24 h exposure period, exposed and non-exposed papaya sections were transferred into incubation units made of plastic cups to rear host eggs using the same methods described above. Newly formed host puparia were recovered and kept until adult fly or parasitoid emergence.

2.7. Data analysis

The differences between mean developmental times and adult parasitoid longevity were compared by analysis of variance using a general linear model (PROC GLM, SAS Institute, 2000). Corresponding treatment means were separated using the Student–Newman–Keuls (SNK) test (Zar, 1999). Percent parasitism, attraction and oviposition were transformed by arcsin square root before analysis and subjected to a one-way ANOVA for comparisons among mean values (SAS Institute, 2000). Survivorship data were analyzed using a life table and a survival function test (SAS Institute, 2000), which determined the number of parasitoids living at the end of the test period and the median survival of the parasitoids.

3. Results

3.1. Emergence and developmental patterns of host flies and parasitoids

The patterns of host fly and parasitoid emergence following exposure of infested papaya were generated from a total of 6459 puparia (Fig. 1). Sixty-eight per cent of these puparia yielded flies (that emerged over a period of about 10 days). Fruit fly emergence occurred 15 days after the medfly eggs were deposited. Peak fly emergence was one day prior to the onset of parasitoid emergence. Male and female parasitoid emergences were determined from 946 and 873 eclosed adult parasitoids respectively. First emergence of male parasitoids was recorded three days after the onset of fly emergence. The first female emerged two days after the first male emergence. Male emergence increased drastically on the second day (45.7 ± 3.1%) and females peaked on the third female eclosion day

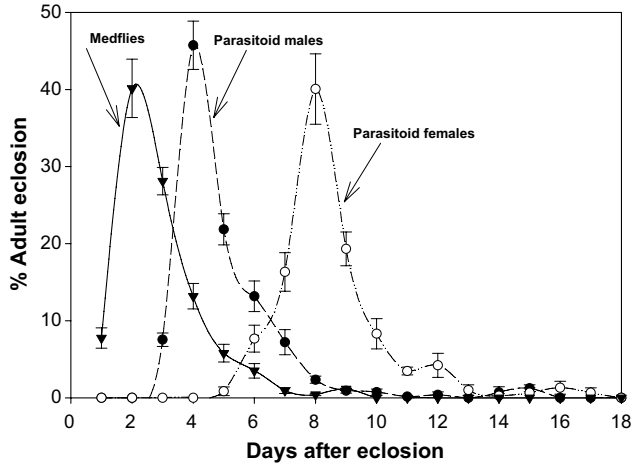

Fig. 1. Patterns of parasitoid and fly eclosions of laboratory-reared cohorts of *Fopius ceratitivorus* and its host, *Ceratitis capitata.*

(40.1 ± 4.6%). The difference between peak male and female parasitoid emergence is four days.

3.2. Adult parasitoid longevity

Mean longevity of host-deprived *F. ceratitivorus* females was 17.3 ± 0.9 d (Fig. 2). The first quartile (25% of the females) died after 13 days and the third quartile died after 21 days. The mean longevity of ovipositing females was 16.2 ± 0.5 d, which was not significantly different from the mean longevity of host-deprived females ($F_{1,19} = 0.77$, $P = 0.38$). Very few individuals in either category (⩽2%) survived beyond 30 days. The maximum longevity recorded was 35 days.

3.3. Egg maturation

Dissection of ovaries from females ⩽12 h after emergence to 32 days post-emergence yielded a potential fecundity of 30.0 ± 2.0 eggs per female per 2-day period (Mean ± SE; $n = 180$) (Range = 2–82 eggs). In these experiments, the peak in fertility occurred during the fourth day after emergence, with a mean of 61.6 ± 2.8 eggs. The number of mature eggs gradually declined thereafter, reaching a level of <20 eggs per day period by age 20 d (Fig. 3).

3.4. Realized fecundity

The realized fecundity and a summary of the reproductive attributes of *F. ceratitivorus* are presented in Fig. 4 and Table 1. The mean number of offspring produced by *F. ceratitivorus* was 5.1 ± 0.4, per day, which is 17.0% of the available mature ovarian eggs per day. Fecundity was characterized by an early peak at day 5 followed by a rapid decrease in females older than 10 d. The mean number of undeposited mature eggs at females' death was 23.7 ± 5.2.

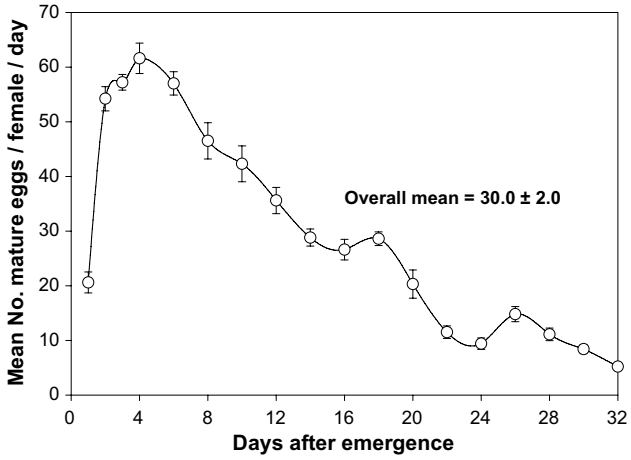

Fig. 3. Pattern of *F. ceratitivorus* ovarian maturation. Females were reared in the laboratory on *C. capitata*. Each data point is a mean of 10 replicates. Lines at data points indicate S.E.M.

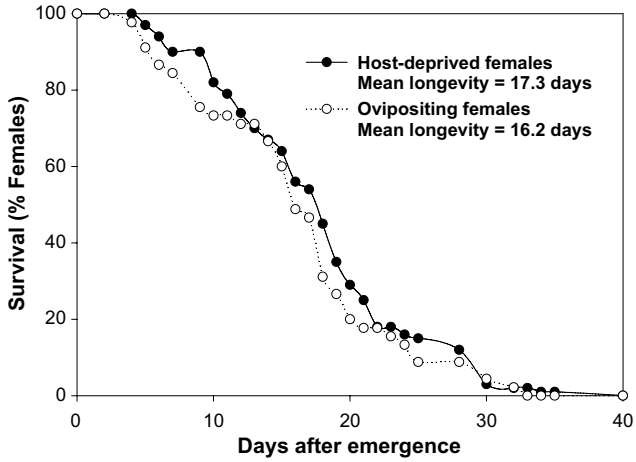

Fig. 2. Survivorship patterns of host-deprived (five replicates of 20 females each) and ovipositing females ($n = 20$) of laboratory reared *F. ceratitivorus*.

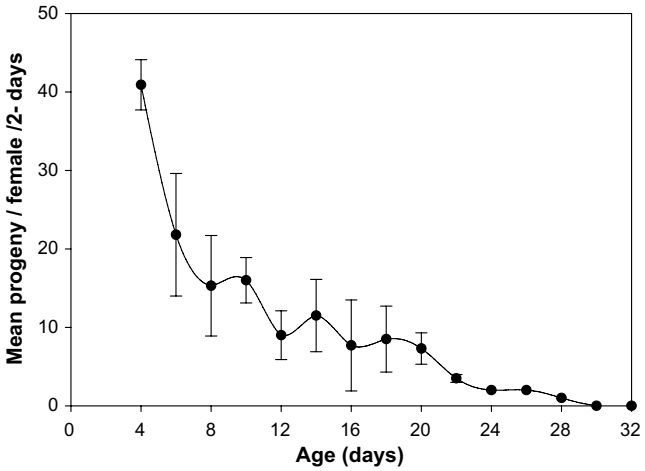

Fig. 4. Realized fecundity of mated female *F. ceratitivorus* in *C. capitata* eggs. Data points represent progeny per 2-day oviposition periods.

Table 1
Reproductive attributes of individually reared mated female *F. ceratitivorus* ($n = 20$) exposed daily to oviposition units infested with *C. capitata* eggs

Parameters	Mean ± S.E.	Units
Longevity	16.2 ± 0.5	Days
Age at first oviposition	1.6 ± 0.3	Days
Egg deposition period	11.6 ± 2.1	Days
Post oviposition period	3.3 ± 0.6	Days
Age at peak oviposition	5.4 ± 0.7	Days
Peak oviposition	40.9 ± 3.2	Highest number of eggs per day
Realized fecundity (RFEC)	107.8 ± 12.8	Total eggs deposited
Ovarian eggs at death (OVEGGS)	23.7 ± 5.2	Number mature ovarian eggs
Potential fecundity	131.8 ± 8.9	RFEC + OVEGGS
Oviposition per day	5.1 ± 0.4	Number eggs deposited per day

3.5. Effect of host odors on parasitoid reproduction

After one hour and 24 h exposures to the substrates, *F. ceratitivorus* was more attracted to naturally infested than artificially infested papaya (Fig. 5). ($F_{1,8} = 21.93$, $P = 0.0016$; $F_{1,8} = 23.45$, $P = 0.0013$). Similarly, after one and 24 h exposures to infested fruit, a significant difference was found between *F. ceratitivorus* ovipositing in naturally infested hosts and artificially infested hosts ($F_{1,8} = 14.23$, $P = 0.0054$; $F_{1,8} = 5.47$, $P = 0.0475$).

Fopius ceratitivorus successfully reproduced in medfly eggs in both artificially infested and naturally infested fruit. However, the mean percentage parasitism in naturally infested hosts was threefold higher than in artificially infested hosts ($F_{3,46} = 91.55$, $P < 0.0001$).

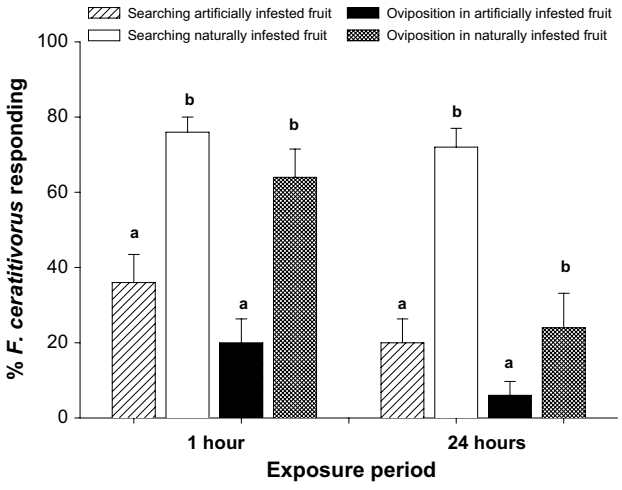

Fig. 5. Percentage *F. ceratitivorus* (Mean ± S.E.) searching or ovipositing into artificially or naturally infested fruit units after 1 h and 24 h exposure periods. Means with same letter within each exposure period and behavioral aspect are not significantly different from each other ($P > 0.05$).

4. Discussion

We report here an overlap in the emergence of *F. ceratitivorus* and its host medflies that has not been documented in other opiine parasitoids of tephritid fruit flies including *Diachasmimorpha longicaudata* (Ashmead), *Fopius vandenboshi* (Fullaway), *Psyttalia incisi* (Silvestri), *P. fletcheri* (Silvestri) (Ramadan et al., 1991) and *Fopius arisanus* (Sonan) (Bautista et al., 1998). *F. ceratitivorus* males emerge earlier than females. This early emergence of male parasitoids has been linked by several authors to an improvement of males' reproductive success (Legner, 1969; Nadel and Luck, 1985).

Because of the lack of difference in longevities of host-deprived and ovipositing females of *F. ceratitivorus*, it seems likely that this parasitoid depends mainly on external food sources for continued survival. Some opiine parasitoids may resorb mature ovarian eggs when deprived of hosts, and longevity may thus be increased at the expense of reproductive materials; e.g., in *Diachasmimorpha tryoni* (Ramadan et al., 1989). Other species like *Fopius arisanus* may resorb eggs but still depend mainly on external nutrition for enhanced longevity (Bautista et al., 1998; Ramadan et al., 1992; Wang and Messing, 2003).

Female *F. ceratitivorus* emerge with a small load of eggs and mature eggs over time, reaching a peak at 4–6 days after emergence. This parasitoid expresses a synovigenic reproductive biology similar to the closely related opiine egg–larval parasitoid, *F. arisanus* (Ramadan et al., 1992). Female *F. ceratitivorus* deposit a limited number of eggs per day, similar to *F. vandenboschi* (Ramadan et al., 1995), but lower than the egg–larval parasitoid *F. arisanus* and the larval parasitoids *D. longicaudata* and *P. incisi* (Ramadan et al., 1992). The limited number of eggs deposited per day by *F. ceratitivorus* is probably a consequence of the relatively long host selection and oviposition time by the females (Bokonon-Ganta, unpublished), which may enable females to distribute their progeny slowly, and in different host patches, and therefore reduce the occurrence of intraspecific competition and the risk of host elimination. This behavior has previously been documented in *F. vandenboschi* (Ramadan et al., 1992), which was found to have established and persisted in the field in Hawaii when many others opiines (15 species) were never recovered (van den Bosch et al., 1951; Newell and Haramoto, 1968). These conclusions can be applied equally well to *F. ceratitivorus,* and may predispose the wasp to become an efficient biological control agent of medfly in Hawaii. The fact that about 50% of mature eggs may be found in the ovaries of dead females suggests that longevity in *F. ceratitivorus* is independent of recycling reproductive materials.

The determination of the age at which *F. ceratitivorus* females achieve their highest reproductive potential is important in mass rearing and field releases in classical biological control programs. Our finding that female *F. ceratitivorus* became less productive three weeks after emergence concurs with that reported for *F. arisanus* by

Bautista et al. (1998) and Ramadan et al. (1992, 1994), and should justify discarding females older than 20 d in mass rearing. Although one female parasitoid lived for 30 days after emergence, most eggs are deposited early in the adult's life time. Insectary colonies should therefore be supplied with *C. capitata* eggs during the first three weeks for better results.

The potential fecundity of ovipositing *F. ceratitivorus* is higher than for non-ovipositing females, as in *F. arisanus* (Haramoto, 1953; Ramadan et al., 1992; Lawrence et al., 2000; Wang and Messing, 2003).

The realized fecundity of *F. ceratitivorus* represents 3–4 times the number of mature eggs in the ovaries at eclosion, and 1–2 times the maximum egg load. The total progeny produced by *F. ceratitivorus* was much lower than *F. arisanus,* which was reported to deposit as many as 102 eggs per day and an average of 741 eggs during the life span (Haramoto, 1953). This big discrepancy between the numbers of eggs deposited by the two parasitoids should be analyzed with caution. *F. arisanus* was studied in the oriental fruit fly, in papaya, while *F. ceratitivorus* in our experiments was studied on medfly in papaya (which is an alternate plant host used instead of coffee, the preferred host for medfly). Despite the fact that the wasp was initially collected from coffee (Wharton et al., 2000), and cultured using coffee as a host (Lopez et al., 2003), we used papaya as an alternate host fruit because it is available all year round and is easy to handle.

Our finding that *F. ceratitivorus* distinguished between naturally infested papaya fruits and mechanically infested fruits suggests that this species' host selection and oviposition decision is influenced by host fly odors. Similar results were reported with several other opiine parasitoids that attack tephritid fruit flies (Carrasco et al., 2005; Eben et al., 2000; Wang and Messing, 2003; Cornelius et al., 2000; Jang et al., 2000; Greany et al., 1977; Messing and Jang, 1992; Messing et al., 1996). For example, *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) females significantly preferred to visit infested mangoes over healthy or mechanically damaged mangoes (Carrasco et al., 2005); Eben et al. (2000) found that *D. longicaudata* females visited more fruits infested with *Anastrepha ludens* Loew larvae than healthy ones. In *F. arisanus*, searching time increased in the presence of host-associated cues (Wang and Messing, 2003).

In conclusion, this study provides information that may be of use for mass rearing and release of *F. ceratitivorus* in classical biological control programs. The observation that attraction and oviposition is enhanced by the presence of fruit fly hosts suggests that further experimental studies should document the mechanisms involved in host selection and sex allocation by this parasitoid. Taken together with recent studies documenting the reproductive behavior of *F. ceratitivorus*, its potential coexistence with *F. arisanus*, and the demonstrated absence of harmful impacts on non-target (non-frugivorous) fly species, the present data throw more light on the positive attributes of this parasitoid as a tephritid biological control agent and warrant its introduction for Mediterranean fruit fly control in Hawaii and other regional *C. capitata* integrated pest management programs.

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