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Biological performance and potential of *Fopius ceratitivorus* (Hymenoptera: Braconidae), an egg–larval parasitoid of tephritid fruit flies newly imported to Hawaii

Aimé H. Bokonon-Ganta [a,*], Mohsen M. Ramadan [b], Xin-geng Wang [a], Russell H. Messing [a]

[a] *College of Tropical Agriculture and Human Resources, Department of Plant and Environmental Protection Sciences, Honolulu, HI 96822, USA*
[b] *State of Hawaii Department of Agriculture, Division of Plant Industry, Plant Pest Control Branch, Honolulu, HI 96814, USA*

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Abstract

The host range and biological performance of *Fopius ceratitivorus* Wharton, a recently discovered African parasitoid, was studied in quarantine in Hawaii to determine its efficiency and safety for use as a biological control agent. Female *F. ceratitivorus* oviposits into eggs and only rarely in first instars of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). The three other extant fruit fly pests in Hawaii, *Bactrocera cucurbitae* (Coquillett), *Bactrocera dorsalis* (Hendel) and *Bactrocera latifrons* (Hendel) were unsuitable for *F. ceratitivorus* development. Developmental time from egg to adult and mean longevity of host-deprived females were 21.8 and 14.8 days, respectively. In both choice and no-choice tests *F. ceratitivorus* showed no positive response to the non-target tephritid *Procecidochares alani* Steyskal (eggs or larvae) on infested pamakani weed, *Ageratina riparia* (Regel), and caused neither parasitism nor mortality to this non-frugivorous fly. Studies of competition with extant parasitoids revealed that *F. ceratitivorus* and the widely established egg–larval parasitoid, *Fopius arisanus* (Sonan) have the same chance of winning in intrinsic competition with one another, depending on which one occupies the host first. Our findings suggest that release of this parasitoid as a biological control agent in Hawaii will pose minimal non-target risk and may contribute to overall fly biological control in the islands.

Keywords: Biological control; Competition; Egg–larval parasitoid; Encapsulation; *Fopius ceratitivorus*; Host range; Non-target effects; Tephritidae

1. Introduction

In Hawaii, four accidentally introduced tephritid fruit flies (Diptera: Tephritidae) are serious pests affecting fruit and vegetable production on all major islands. Besides the loss of production due to high infestation levels, infestation by these insects poses a serious risk of invasion into other states of the mainland USA. The melon fly, *Bactrocera cucurbitae* (Coquillett) and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) were introduced to Hawaii in 1895 and 1907, respectively (Back and Pemberton, 1918); the oriental fruit fly, *Bactrocera dorsalis* (Hendel) was first reported in 1945 (van Zwaluvenburg, 1947); and the solanaceous fruit fly, *Bactrocera latifrons* (Hendel) in 1983 (Vargas and Nishida, 1985). Establishment of the first three fruit flies was followed by various control attempts including bait-spray applications, cultural practices, use of sterile insect techniques, and releases of numerous hymenopteran parasitoids (Gilstrap and Hart, 1987). Releases of introduced parasitoids resulted in some of the more successful examples of classical biological control of fruit flies in

* Corresponding author. Fax: +1 808 856 2428.
E-mail address: aimehbg@hawaii.edu (A.H. Bokonon-Ganta).

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the world (Clausen et al., 1965; Wharton, 1989). These successes were achieved with a number of natural enemies including one egg–larval parasitoid, *Fopius arisanus* (Sonan), and six larval parasitoids: *F. vandenboschi* (Fullaway), *Diachasmimorpha tryoni* (Cameron), *Diachasmimorpha longicaudata* (Ashmead), *Psyttalia fletcheri* (Silvestri), *Procecidochares incisi* (Silvestri) (all Braconidae) and *Tetrastichus giffardianus* Silvestri (Eulophidae) (Bess et al., 1961; Haramoto and Bess, 1970; Wong and Ramadan, 1987; Vargas et al., 1995).

Although these parasitoids have been somewhat effective in reducing infestation levels, they do not generally maintain fly populations below economic injury levels. Introduction of new parasitoids may incrementally increase fly mortality and reducing infestation (Gilstrap and Hart, 1987; Messing, 1995; Wharton, 1989).

One potential biological control candidate, *Fopius ceratitivorus* Wharton, was recently collected in East Africa and appears to be an egg–larval parasitoid previously unknown to science (Wharton, 1999; Wharton et al., 2000). Addition of this opiine wasp to the extant parasitoid fauna in Hawaii may help contribute to a "systems approach" to achieving quarantine security for the state's tropical fruit and vegetable industries (Jang and Moffitt, 1994), as well as making more and better quality fruit available for local consumption.

The need to introduce new biological control agents should however take into account the competitive risks of any potential candidate to extant species, as well as any potential non-target impacts to endemic non-pest tephritids and other beneficial species. Among the extant fruit fly parasitoids, *F. arisanus* is the only species attacking host eggs, and is currently reported as the dominant parasitoid in Hawaii (Purcell et al., 1998; Wong and Ramadan, 1987), partly due to its intrinsic competitive superiority against all larval fruit fly parasitoids (Wang and Messing, 2002, 2003; Wang et al., 2003). In Hawaii, the use of classical biological control has been subject to increasing scrutiny and debate due to the highly sensitive island fauna and flora (Funasaki et al., 1988; Howarth, 1991). Several studies have showed that the two larval fruit fly parasitoids, *D. tryoni* and *D. longicaudata*, could attack some non-target gall-forming tephritid such as *Eutreta xanthochaeta* (Aldrich), which is itself an introduced weed biological control agent (Clancy et al., 1952; Duan et al., 1996, 1998; Purcell et al., 1997). Thus, evaluation of non-target impact of a newly introduced opiine parasitoid is appropriate in Hawaii.

This paper reports (1) the initial host range studies on the suitability of four pest tephritid fruit fly species: *C. capitata*, *B. cucurbitae*, *B. dorsalis*, and *B. latifrons* as hosts for *F. ceratitivorus*, (2) the potential non-target impact of this parasitoid on *Procecidochares alani* Steyskal, and (3) its competitive outcomes with *F. arisanus*. *P. alani* is a gall forming tephritid, introduced to Hawaii from Mexico in 1973 to control the pamakani weed *Ageratina riparia* (Regel) (Asteraceae) (Hapai, 1977), and is considered to be very effective in suppressing its target weed (Funasaki et al., 1988).

2. Materials and methods

2.1. Fruit flies

Colonies of the four pest tephritids in Hawaii, *C. capitata*, *B. cucurbitae*, *B. dorsalis*, and *B. latifrons*, were initiated at the Fruit Fly Biological Control Laboratory of the University of Hawaii at Manoa, from 10 g cohorts of puparia of each species, provided by the USDA/ARS Pacific Basin Agricultural Research Center in Honolulu, Hawaii. Upon eclosion, adult flies were maintained in wooden cages ($25 \times 25 \times 25$ cm) with water and food (sugar and hydrolysate yeast powder in a ratio of 3:1). Subsequent fly populations were reared on half ripe papaya fruit (*Carica payaya* L.). Fruits were infested with fly eggs by exposing them to 400–600 pairs of 2-week-old adults of each of the four pest tephritids in rearing cages for 24 h.

After exposure to flies, papaya fruits were transferred to incubation units made of plastic cups 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 plastic cups with a mesh screen cover for emergence of adult flies. All rearing of flies in this study followed the same procedures.

2.2. Parasitoids

Fopius ceratitivorus was originally collected in Central Kenya in Africa from coffee berries infested by *C. capitata* (Wharton et al., 2000), and shipped to the USDA-APHIS/MOSCAMED quarantine facility at San Miguel Petapa, Guatemala, Central America. The parasitoid was propagated on *C. capitata* infested coffee berries (Lopez et al., 2003). An initial cohort of 1200 adults was shipped to the Hawaii Department of Agriculture Quarantine Facility in May 2002 for studies on its host range and biology. The parasitoid colony was maintained in the laboratory for four generations before these experiments started.

Fopius ceratitivorus rearing was achieved using papaya fruit infested by *C. capitata* eggs in papaya fruit. Despite the fact that the wasp was initially identified from coffee (Wharton et al., 2000), and cultured using coffee as host (Lopez et al., 2003), we used papaya as an

alternate host fruit because the fruit is available all the year round and easy to handle. In addition, the fruit is an important host plant for three of the four fly species studied (Liquido, 1991; Liquido et al., 1990). Infestation rates in papaya for *B. latifrons* were low in our experimental set up and justified the use of chili pepper (*Capsicum annuum* L.) as a preferred host for this fly.

Fruits were infested with tephritid eggs by exposing them to about 300 pairs of adult *C. capitata* in rearing cages for 24 h. After exposure to parasitoids, the papaya was transferred to incubation units. Emerging parasitoids were provided with water and fine drops of pure honey (Sioux Honey Ass., Sioux City, IA) on the top side of the rearing cages, and used to start new colonies.

2.3. Host preference and host suitability

Experiments were conducted in small Plexiglas cages ($12 \times 12 \times 12$ 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. Preliminary observations revealed that *F. ceratitivorus* was readily attracted to fruits infested by eggs deposited naturally by the host flies, more so than to fruits artificially infested with eggs (A.H. Bokonon-Ganta, unpublished). Consequently, experimental oviposition units were prepared at the University of Hawaii by exposing papaya fruits for 24 h to about 300 pairs of mature adults of each of the four fly species.

The fly egg-infested fruits were transported to the quarantine laboratory for tests. Each infested papaya, excluding the seeds, was cut into four equal sections. Each quarter ($8 \times 6 \times 1$ cm), representing one experimental unit, was exposed to 20 pairs of *F. ceratitivorus* in the clear Plexiglas cage for 24 h, with water and honey provided.

After exposure to parasitoids, the papaya quarters were transferred into incubation units. Newly formed host puparia were placed into plastic vials (4.9 cm diam., 8.5 cm deep) until adult flies or wasps emerged. Each of the four host fly species was tested separately. A total of 12 replicates plus three control replicates were run for *C. capitata*, eight plus two controls for *B. cucurbitae*, seven plus two controls for *B. dorsalis*, and six plus two controls for *B. latifrons* using papaya as a host fruit. Susceptibility of *B. latifrons* was further investigated using a solanaceous host, chili pepper, in six additional replicates plus two control replicates. Control replicates were infested host fruits not exposed to the parasitoids. The effect of papaya fruit itself on attractiveness to *F. ceratitivorus* was assessed in three additional replicates using non-infested papaya quarters exposed to female wasps under the same experimental conditions.

To investigate the range of host instar acceptance of *F. ceratitivorus*, first and second instar *C. capitata* were also tested. First instars were offered using 4-days-old infested papaya fruits (egg hatching of the medfly requires 48–72 h at 25 °C Back and Pemberton, 1918). Second instars *C. capitata* reared from infested papaya fruits were mixed with approximately 10 g of larval diet and tested using standard oviposition units (Wong and Ramadan, 1992) constructed of 5 diam. $\times$ 0.9 depth cm polystyrene Petri dishes with tight fitting lids covered with organdy, through which the wasps could readily oviposit.

The following variables were used to measure the response of *F. ceratitivorus* when exposed to the four different fruit fly hosts: (1) number of female parasitoids counted on the oviposition unit after 1 and 24 h, divided by the total number of female parasitoids in the cage was recorded as the percent of females attracted for oviposition; (2) number of host puparia recovered from unexposed eggs (control) and exposed eggs (parasitized); (3) number of adult parasitoids recovered from each host; plus the number of dead parasitoids in each host determined by dissecting all unemerged puparia; and (4) percent of fruit fly parasitism, indicated by the total number of parasitoids (live plus dead) divided by the total fruit fly puparia recovered.

2.4. Test for encapsulation

Results from the host suitability experiments revealed that the three *Bactrocera* species, *B. dorsalis*, *B. cucurbitae*, and *B. latifrons* were unsuitable as hosts of *F. ceratitivorus*. To provide some justification for this we conducted additional tests to determine the fate of parasitoid eggs in the three *Bactrocera* species. Infested pieces of papaya inoculated with about 160 eggs of each host were exposed to 15–20 naïve and mated female wasps 7–12 days old in a small experimental arena for 24 h. Half of the exposed eggs were set apart for dissection and the second half transferred into incubation units until flies or parasitoids emerged. From the other half kept for dissection, a sample of 15–20 eggs or larvae were dissected in saline solution and examined under a binocular microscope every day for 4 days. The number of encapsulated and/or melanized eggs were counted in each host. Test was replicated four times for each *Bactrocera* species.

2.5. Developmental time and longevity

Developmental time was measured by exposing *C. capitata* egg-infested papaya to 20 female wasps for 24 h. Methods of exposure and subsequent handlings of hosts were the same as those described above for host range testing. Puparia were collected and isolated individually in 60 ml plastic cups kept in the laboratory under the same environmental conditions. Developmental time (in days) for both sexes was recorded and

emerging wasps were set aside for subsequent observations on parasitoid longevity. Emergence and mortality were recorded once daily between 5 and 6 pm. Average quarantine laboratory conditions were 28 ± 2 °C, 60–80% RH, and a 12L:12D regime.

2.6. Competition with extant parasitoids

Competition between *F. ceratitivorus* and *F. arisanus* within *C. capitata* was studied following the procedures described by Wang and Messing (2002). Eggs of *C. capitata* were sequentially exposed to the two parasitoids in four different treatments: (1) *F. arisanus* alone; (2) *F. ceratitivorus* alone; (3) *F. arisanus* first, followed after 24 h by *F. ceratitivorus*; and (4) *F. ceratitivorus* first, followed after 24 h by *F. arisanus*. To determine the mechanisms employed by each parasitoid to compete with other individuals or species when superparasitism or multiparasitism occurred, up to 200 fly eggs from each treatment were randomly selected and dissected under a stereomicroscope, after exposure at each of three intervals (24, 48, and 72 h). The number and condition of both parasitoids' eggs were recorded. In addition, samples of 200 host larvae for each treatment were reared to adult emergence to determine the survival and successful development of both the medfly and its parasitoids. All fly larvae were reared using fresh artificial diet and all tests were replicated five times using new parasitoids.

2.7. Impact on non-target tephritid species

Tests were conducted using the non-target pamakani gall fly, *P. alani*. A laboratory colony of the fly was initiated from galls collected at the Pali area on Oahu Island. Newly emerged *P. alani* (12 pairs/plant) were confined in a cage with a potted pamakani plant, *A. riparia* in a large wooden cage (65 × 45 × 45 cm) for 4 days before the introducing the parasitoids. Usually females *P. alani* mate and deposit eggs 2–4 days following emergence and continue to lay eggs for up to 2 weeks when fed honey and water. Egg incubation period of *P. alani* is 3–5 days (Nakao and Hin Au, 1974; Hawaii Department of Agriculture, unpublished report). To insure the presence of eggs and larval stages for parasitoid exposure, *F. ceratitivorus* were released in the cage when small swellings (2–3 mm diam.) appear on terminal shoots. Cohorts of *F. ceratitivorus* per cage were made to match anticipated number of galls (= egg patches) by counting the visible terminal and lateral shoots on the stems at the beginning of the test. Before parasitoid introduction, lateral shoots were sampled to insure the presence of eggs and a main stem was isolated as a control. We could not count the total number of eggs without breaking off the tender shoots. Provided with honey and water, flies and parasitoids were confined in the cage all the time and tests were terminated when all the parasitoids perished in the cage.

In no-choice tests, a cohort of 61 female *F. ceratitivorus* were released onto one potted plant of *A. riparia* which contained 19 main stems and several lateral shoots infested with *P. alani*. On this potted plant, one main stem was considered as control, and excluded using a fine mesh sleeve from all parasitoid contact.

In choice tests 29 female parasitoids were offered the choice between eggs or larvae of *P. alani* and *C. capitata* eggs (⩽48 h old) exposed in an infested 120 g papaya half. This infested papaya half was held 10 cm apart from the pamakani plant and kept in the cage for 48 h. Following the 48 h exposure period, the papaya unit was replaced with a new similar unit and the previously exposed unit transferred into incubation units. Three infested papaya units were tested one after the other against eggs and larvae of *P. alani*. In this choice test, the infested *A. riparia* plant had 12 main stems and about 40 branching shoots. The control in this experiment was one main stem with eight terminal shoots excluded from all parasitoid contact using a fine mesh sleeve.

In both choice and no-choice tests, female parasitoids were mated and 7–10 days old. Upon release of parasitoids onto potted plants, responses of the parasitoids to eggs and larvae of *P. alani* and *C. capitata* eggs were observed continuously for 20 min and then for 5 min every 2 h three times a day. The number of times parasitoids were observed landing or probing on terminal shoots, or stems searching for *P. alani* eggs or galls was recorded.

In addition to behavioral observations, parasitoids were left continuously in their cages for 3 weeks after which all parasitoids died. Plants were kept in cages until most flies eclosed, then all galls were dissected to determine the presence of unmerged flies, or parasitoids. All uneclosed puparia within the galls were dissected under no-choice and choice conditions, respectively.

2.8. Data analysis

Analysis of variance using a general linear model was performed for count data for gall length, width, number of emergence holes, number of pupae, number of emerged flies, and adult parasitoids (PROC GLM, SAS Institute, 2000). Corresponding treatment means were separated using the Student–Newman–Keuls (SNK) test (Zar, 1999). Percent parasitism, multiparasitism, and mortality were calculated, transformed by arcsin square root before analysis and subjected to a one-way ANOVA for comparisons among mean values (SAS Institute, 2000).

Specimens of *F. ceratitivorus* were confirmed by Robert Wharton of Texas A&M University. Voucher specimens are deposited in the insect collection of the State of Hawaii Department of Agriculture, Division of Plant Industry, Plant Pest Control Branch, and Department of Plant and Environmental Protection Sciences, University of Hawaii at Manoa, both in Honolulu, Hawaii.

3. Results

3.1. Ovipositional preference and host suitability

During both 1 and 24 h after exposures, medfly egg-infested papaya fruits were significantly more attractive to *F. ceratitivorus* than papaya infested by any of the other three fly species ($F_{5,36} = 34.2$, $P < 0.01$; $F_{5,36} = 81.3$, $P < 0.01$) (Fig. 1). There was very little attraction to the three *Bactrocera* species but significantly higher than the control. *Bactrocera latifrons* egg-infested papaya was significantly more attractive to *F. ceratitivorus* than the other two *Bactrocera* species (Fig. 1). *B. cucurbitae* and *B. dorsalis* were the least attractive to this parasitoid. *B. latifrons* egg-infested pepper was significantly more attractive to *F. ceratitivorus* than the other *Bactrocera* species.

Fopius ceratitivorus successfully reproduced almost exclusively on the egg stage of *C. capitata* and very limited development was observed in treatments with first instar medfly (six parasitoids out of 1020 exposed hosts) (Table 1). The parasitoid had no interest in larvae older than first instars.

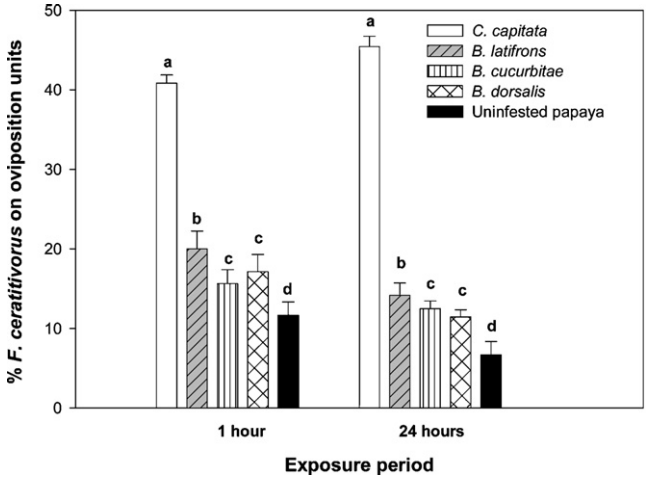

Fig. 1. Percent *F. ceratitivorus* (mean ± SE) attracted to oviposition units (papaya fruits infested with tephritid eggs) after 1 and 24 h exposure period. Means with same letter within each exposure period are not significantly different from each other ($P > 0.05$).

Table 1
Mean ± SE number of hosts per replicate and percent parasitism by *Fopius ceratitivorus* exposed to four fruit fly species

Fly species	No. of hosts	Parasitism (%)[a]		
		Egg	First instar	Second instar
B. cucurbitae	125.8 ± 9.5 a	0 (8)	—	—
B. dorsalis	128.3 ± 9.8 a	0 (7)	—	—
B. latifrons	123.7 ± 7.6 a	0 (6)	—	—
C. capitata	128.3 ± 13.1 a	10.0 ± 0.9 (12)	0.6 ± 0.5 (6)	0 (5)

[a] Numbers in parentheses refer to the number of replicates. Means followed by the same letters are not significantly different ($p > 0.05$).

The dissection of a sub-sample of 285 *C. capitata* eggs exposed to *F. ceratitivorus*, resulted in 177 with no parasitoid eggs, 105 with one parasitoid egg each, and only three containing two parasitoid eggs (⩽2.7% superparasitism). Not a single parasitoid progeny emerged from *B. cucurbitae*, *B. dorsalis* or *B. latifrons* (Table 1).

3.2. Encapsulation of F. ceratitivorus by Bactrocera species

Dissection of 68 eggs and 248 larvae *B. dorsalis*, 48 h after exposure revealed that eggs of *F. ceratitivorus* were encapsulated (7) or melanized (70) either partially or completely as a result of encapsulation (Fig. 2). The encapsulated egg is close to the size of a 2–8 h. egg in a normal *C. Capitata* host (mean maximum width = 72.5 μm, $n = 5$). It is slightly wider than a mature ovarian egg (mean maximum width = 56 μm, $n = 5$) indicating a slight increase in size before a complete encapsulation took place. A 48 h. *F. ceratitivorus* egg, ready to hatch in a normal *C. capitata* host is 1.4 times wider (mean maximum width = 104 μm, $n = 10$) than the encapsulated egg. There was no change in

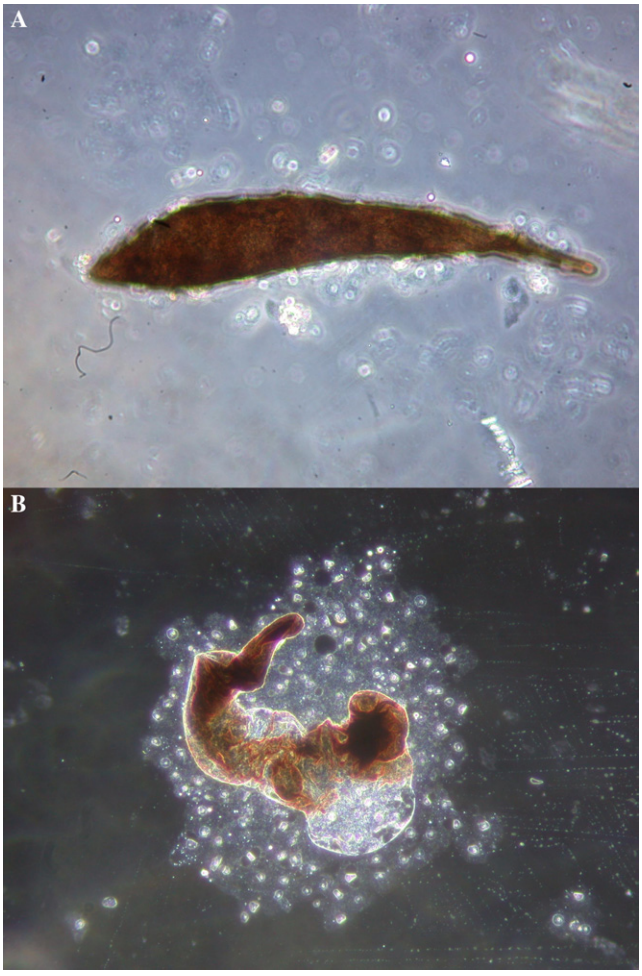

Fig. 2. Encapsulated and melanized eggs of *F. ceratitivorus*, 48 h after deposition in *B. dorsalis*.

length of the three egg categories (mean length = 490.8 μm, $n = 24$).

A similar result was obtained with *B. latifrons* and *B. cucurbitae*, the latter being much less accepted for egg deposition than the other two *Bactrocera* species.

For the three *Bactrocera* species, parasitoid eggs were encapsulated in the host's egg stage and melanized later during larval stage. No parasitoids emerged from subsamples of parasitized eggs of each species, exposed to *F. ceratitivorus* and subsequently reared for flies or parasitoids emergence. Detailed study of the encapsulation process of *F. ceratitivorus* by the three *Bactrocera* species will be presented elsewhere.

3.3. Developmental time and longevity

Mean ± SE developmental period from deposition of the egg until adult emergence was 21.8 ± 1.1 days for females ($n = 92$), and 20.0 ± 0.4 days for males ($n = 76$) at 28 ± 2 °C, 60–80% RH, and a 12:12 h LD regime. Mean longevity of host-deprived females was 14.8 ± 0.8 days ($n = 91$). Mean longevity of mated males was 5.2 ± 0.4 days ($n = 43$).

3.4. Competition with extant egg–larval parasitoid

Parasitism by *F. ceratitivorus* (13.1% ± 10.1, $n = 5$) was considerably lower than parasitism by *F. arisanus* (67.6% ± 13.6, $n = 5$) when each had access to medfly eggs for the same duration (Table 2). Superparasitism of medfly eggs by both *F. ceratitivorus* and *F. arisanus* was very low (⩽2%).

Exposure of hosts first to *F. arisanus* and then to *F. ceratitivorus* resulted in a mean of 16.5% multiparasitism, compared to 9.6% multiparasitism when eggs previously parasitized by *F. ceratitivorus* were then exposed to *F. arisanus*. There was no significant difference in the percent multiparasitism between those two exposures ($F_{1,7} = 0.57$, $P = 0.47$) (Table 2).

The percent mortality of *F. arisanus* from treatment in which hosts were first exposed to *F. arisanus* and then to *F. ceratitivorus* was significantly different from treatment in which hosts were first exposed to *F. ceratitivorus* followed by *F. arisanus* ($F_{1,7} = 15.1$, $P < 0.05$) (Table 2). The percent mortality of *F. ceratitivorus* from treatment in which hosts were first exposed to *F. arisanus* and then to *F. ceratitivorus* was also significantly different from treatment in which hosts were first exposed to *F. ceratitivorus* followed by *F. arisanus* ($F_{1,7} = 8.6$, $P < 0.05$) (Table 2).

The percent adult emergence of *F. ceratitivorus* from the treatment in which host eggs were exposed to *F. ceratitivorus* alone was not significantly different from that in which the hosts were exposed in succession to *F. ceratitivorus* and *F. arisanus* ($F_{1,7} = 2.1$, $P > 0.18$) (Table 3).

3.5. Impact on non-target fly species

In both choice and no-choice experiments, none of the *F. ceratitivorus* female parasitoids tested was observed searching terminal shoots or probing on stems and growing points of the pamakani weed and, no parasitoids accepted gall fly eggs or larvae for oviposition (Table 4).

In choice experiments female *F. ceratitivorus* were observed searching and ovipositing only into *C. capitata* eggs offered in infested papaya fruits. A total of 46 parasitoids were reared out of 1048 medfly exposed as eggs in three replicates. Furthermore, no significant difference was found in either uneclosed puparia or partially emerged flies between *P. alani*-infested plants exposed to *F. ceratitivorus* and the control *P. alani*-infested stems with *F. ceratitivorus* excluded ($F_{1,65} = 0.30$, $P = 0.59$;

Table 3
Outcome of interspecific competition between *Fopius arisanus* and *Fopius ceratitivorus* within *Ceratitis capitata* eggs

Exposure of hosts to	No. of eggs dissected	Mean ± SE parasitism (%)	
		F. arisanus	*F. ceratitivorus*
F. arisanus (*Fa*) alone	548 (4)	57.3 ± 4.2 a	—
Fa followed by *Fc*	499 (5)	38.7 ± 9.5 a	—
F. ceratitivorus (*Fc*) alone	613 (5)	—	8.4 ± 1.8 a
Fc followed by *Fa*	695 (5)	—	4.7 ± 1.3 a

Numbers in parentheses refer to the number of replicates. Mean values in the same column followed by different letters are significantly different. (All proportional data were transformed by arcsin square root before analysis of variance, one-way ANOVA, $p < 0.05$).

Table 2
Mean ± SE percent parasitism or multi-parasitism of *Ceratitis capitata* eggs exposed to *Fopius arisanus* (*Fa*) or *Fopius ceratitivorus* (*Fc*) alone, or to both species in succession, and mean (±SE) percent mortality of one species individuals killed in presence of the other species in multi-parasitized hosts at dissection

Treatment	Eggs dissected	% Parasitism		% Multi-parasitism	% Mortality	
		Fa	*Fc*		*Fa*	*Fc*
F. arisanus	324 (5)	67.6 ± 13.6				
F. ceratitivorus	532 (5)		13.1 ± 10.1			
Fa followed by *Fc*	362 (5)	65.3 ± 5.6	29.4 ± 5.4	16.5 ± 5.9 a	1.7 ± 1.2 a	53.8 ± 19.3 a
Fc followed by *Fa*	310 (4)	54.6 ± 12.8	18.3 ± 5.5	9.6 ± 6.3 a	34.9 ± 10.3 b	12.9 ± 12.9 b

Numbers in parentheses refer to the number of replicates. Mean values in the same column followed by different letters are significantly different (All proportional data were transformed by arcsin square root before analysis, one-way ANOVA, $p < 0.05$).

Table 4
Response of *Fopius ceratitivorus* to *Procecidochares alani* infesting potted plants of the pamakani weed, *Ageratina riparia* in the presence (choice test) or absence (no-choice test) of its natural host, *Ceratitis capitata*

Parameters (per gall)	*P. alani* exposed to *F. ceratitivorus*[c]		*P. alani* with *F. ceratitivorus* excluded[c]	
	No. of galls	Mean ± SE	No. of galls	Mean ± SE
No-choice test				
Gall length (cm)	92	1.5 ± 0.0	8	1.1 ± 0.1
Gall width (cm)	92	0.4 ± 0.0	8	0.4 ± 0.0
Emergence holes	92	2.5 ± 0.2	8	2.9 ± 0.6
Flies emerged	92	2.6 ± 0.2	8	3.0 ± 0.7
Uneclosed puparia	92	0.7 ± 0.1	8	0.4 ± 0.2
Partially emerged flies	92	0.2 ± 0.1	8	0.4 ± 0.3
Puparia with scars or parasitoid cadavers	92	0	8	0
Parasitoids landed on terminal shoots or galls[a]	92	0	—	—
Choice test				
Gall length (cm)	58	1.5 ± 0.1	9	1.5 ± 0.2
Gall width (cm)	58	0.4 ± 0.0	9	0.5 ± 0.1
Emergence holes	58	2.2 ± 0.2	9	1.9 ± 0.5
Flies emerged	58	2.6 ± 0.3	9	2.1 ± 0.8
Uneclosed puparia	58	0.3 ± 0.1	9	0.4 ± 0.2
Partially emerged flies	58	0.2 ± 0.1	9	0.4 ± 0.2
Puparia with scars or parasitoid cadavers	58	0	9	0
Parasitoids landed on terminal shoots or galls[a]	58	0	—	—
Parasitoids emerged from papaya unit[b]	—	15.3 ± 3.3	—	—

[a] Parasitoids response to hosts was recorded continuously for 20 min and then every two hours following their release in cages. Subsequent observations were made three times every day until parasitoids death.
[b] Mean number of parasitoids emerged from 3 U of medfly-infested papaya exposed to parasitoids in three consecutives days.
[c] There were no significant differences between the two treatments among all the measured parameters (PROC GLM, $P > 0.05$).

$F_{1,65} = 1.51$, $P = 0.22$; respectively). The same conclusion was reached in experiments under no-choice conditions ($F_{1,98} = 0.59$, $P = 0.45$; $F_{1,98} = 0.38$, $P = 0.54$; respectively).

4. Discussion

Host range tests are conducted to support decisions as to whether an exotic insect can be released safely within a new ecosystem. We studied the host preference and host suitability of *F. ceratitivorus* on the four pest fruit fly species: *C. capitata*, *B. cucurbitae*, *B. dorsalis*, and *B. latifrons*. Most opiine parasitoids of tephritids are larval endoparasitoids (Wharton, 1989). The few exceptions are *F. arisanus* and *F. caudatus*, both of which deposit eggs into the eggs of their hosts (Wharton, 1999; Wharton et al., 2000). Our data confirm that *F. ceratitivorus* can successfully oviposit into *C. capitata* eggs (Lopez et al., 2003). Oviposition in first instar larvae yielded very few progeny, and the parasitoid showed no interest in older larvae (Lopez et al., 2003). Oviposition in the egg stage and occasionally in the first larval stage is similar to *F. arisanus* (Bautista et al., 1998; Bess et al., 1961; Haramoto, 1953; Quimio and Walter, 2001; Zenil et al., 2004). None of the three *Bactrocera* species was suitable host for the development of *F. ceratitivorus*.

Fopius ceratitivorus appears to have a very narrow host range. All parasitoids eggs laid in *B. cucurbitae*, *B. latifrons*, and *B. dorsalis* died, killed by the host's immune system. Endoparasitoid eggs or larvae may be killed by a host's immune system (Jervis and Copland, 1996), mainly through encapsulation (Salt, 1970). Similar observations have been reported with other opiine parasitoids of *C. capitata* encapsulated in *Bactrocera* species (Mohamed et al., 2003; Pemberton and Willard, 1918; Ramadan et al., 1994a,b). Failure of the parasitoid to develop in *B. cucurbitae*, *B. latifrons* and *B. dorsalis* is probably due to lack of physiological compatibility with these hosts. This argument can be made because *F. ceratitivorus*, which is of African origin, has no evolutionary history with the three *Bactrocera* species of Asian origin.

Fopius arisanus, which is of Asian origin, attacks at least seven tephritid pest species (Wharton and Gilstrap, 1983). It was originally introduced to Hawaii in 1948 for the control of *B. dorsalis* (Bess et al., 1961). But soon *F. arisanus* also became established on *C. capitata* populations and outnumbered other parasitoids of *C. capitata* in Hawaii, including *D. tryoni*, *F. vandenboschi*, *D. longicaudata*, and *P. incisi*, as well as the gregarious eulophid *T. giffardianus* (Bess et al., 1961; Haramoto and Bess, 1970).

The relative success of *F. arisanus* has stimulated exploration for other egg-attacking *Fopius* parasitoids. The demonstrated ability of *F. ceratitivorus* to parasitize eggs in this study suggests significant potential for this parasitoid to contribute to the biological control of *C. capitata*. It can attack eggs located near the surface of infested fruits and vegetables, which are particularly vulnerable. In addition, the early presence of the parasitoid inside the hosts gives it a competitive edge over other

parasitoids (i.e., larval attacking species) arriving later into the system.

In general, parasitoids attacking hosts early are better competitors than those attacking the hosts at a later developmental stage (Bokonon-Ganta et al., 1996; Wang and Messing, 2002; Wang et al., 2003). Several cases of competitive displacements among introduced parasitoid species under field conditions have been documented (Back and Pemberton, 1918; Bennett et al., 1976; Bess et al., 1961). Among the best illustrations are the displacements of the several early or concurrently introduced larval parasitoids by *F. arisanus* (Bess et al., 1961). *F. arisanus* physiologically suppresses egg development of larval parasitoids when competition occurs (van den Bosch and Haramoto, 1953; Wang and Messing, 2002; Wang et al., 2003).

However, those replacements were accompanied by a higher total parasitism and a greater overall reduction in the pest infestation than the first introduced species had achieved (Bennett et al., 1976). The attack of host eggs by *F. ceratitivorus*, like *F. arisanus* would probably give the parasitoid an advantage to win the competition against larval fruit fly parasitoids. It could therefore play an important role in population management of *C. capitata* in Hawaii and other tropical and subtropical countries around the world where the pest has spread.

Even though *F. ceratitivorus* and *F. arisanus* are both egg–larval parasitoids, the first prefers older eggs (Bokonon-Ganta, unpublished; Lopez et al., 2003) while the latter more readily attacks young eggs (Harris and Bautista, 1996; Ramadan et al., 1992). This might explain a competitive superiority of *F. arisanus* over *F. ceratitivorus* when both species are in the same host. In our study, with an artificial arrangement of the order of oviposition, dissections of multiparasitized host eggs and adult emergence data revealed that both species have an equal chance to win the competition against the other species, depending on which one occupied the host first. This might not be true in nature where *F. arisanus* will usually find the host first.

In the present study, the total rate of parasitism when the two parasitoids attacked together was no better than when they acted alone. Improvement might be achieved in the field in areas of high infestation, as in other systems where the establishment and coexistence of a second parasitoid resulted in a better control level in various ecological zones (Bokonon-Ganta et al., 1996; Neuenschwander et al., 1994).

Several authors have raised concerns about potential environmental impacts of new parasitoid species introduced against tephritid pests in Hawaii (Duan et al., 1996, 1998; Howarth, 1991). Gall-forming tephritids such as *P. alani*, *Procecidochares utilis* stone, and *E. xanthochaeta* are already attacked by the extant opiine parasitoids *D. longicaudata* and *D. tryoni* in the field (Clancy et al., 1952). All of these are larval parasitoids. To our knowledge, not a single case of an egg–larval parasitoid attacking non-target tephritid flies has been reported to date, despite several intensive field surveys (Duan et al., 1996; Wong et al., 1984). Adult gall-forming tephritids lay eggs on the tips of growing shoots of their host plants and hatching larvae bore into stem tissues and eventually induce spheroid galls on the apical region of plant stems (Hapai, 1977). *Fopius ceratitivorus* deposits its eggs inside host eggs inserted in fruit, and does not recognize or attack fly eggs inserted between folded leaves at the tips. Results from our laboratory experiments demonstrate that *F. ceratitivorus*, exposed to infested potted plant with a range of fly stages including eggs, early and late larval stages, completely lacks oviposition responses to the non-target fly, *P. alani*. Therefore, utilization of *F. ceratitivorus* in biological control programs targeted against the frugivorus pest, *C. capitata*, would likely have no harmful impact on gall-forming tephritids.

In conclusion, our findings demonstrate that *F. ceratitivorus* is an egg–larval parasitoid that successfully parasitizes *C. capitata*. This fly is already attacked by a handful of imported parasitoid species, including another egg–larval parasitoid, *F. arisanus*, and less frequently, by *D. tryoni*, *P. incisi* (all solitary larval parasitoids) and *T. giffardianus*. Results of competiton studies have shown that *F. arisanus* and *F. ceratitivorus* in an artificial condition have an equal chance to win the competition against each other. *F. arisanus* was shown to win the competition over all other opiines in Hawaii, which are larval parasitoids (Wang and Messing, 2002, 2003; Wang et al., 2003). Nevertheless, these larval parasitoids co-exist with *F. arisanus* in many habitats (Wong and Ramadan, 1987), perhaps due to the diversity host microhabitats in Hawaiian ecosystems. Therefore, we predict that *F. ceratitivorus* can coexist with *F. arisanus* in some habitats, and could even dominate in Hawaii in some high elevation sites where *F. arisanus* is not abundant and conditions favor the preferred host, *C. capitata*.

Overall, 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 are positive attributes for an efficient 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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References

Back, E.A., Pemberton, C.E., 1918. The Mediterranean fruit fly in Hawaii. US. Dept. Agric. Bull. 536, Washington D.C.

Bautista, R.C., Harris, E.J., Lawrence, P.O., 1998. Biology and rearing of the fruit fly parasitoid *Fopius arisanus*: clues to insect propagation. Entomol. Exp. Appl. 89, 79–85.

Bennett, F.D., Rosen, D., Cochereau, P., Wood, B.J., 1976. Biological control of pests of tropical fruits and nuts. In: Huffaker, C.B., Messenger, P.S. (Eds.), Theory and Practice of Biological Control. Academic Press, NY, pp. 359–395.

Bess, H.A., van den Bosch, R., Haramoto, F.H., 1961. Fruit fly parasites and their activities in Hawaii. Proc. Hawaii. Entomol. Soc. 17, 367–578.

Bokonon-Ganta, A.H., van Alphen, J.J.M., Neuenschwander, P., 1996. Competition between *Gyranusoidea tebygi* and *Anagyrus mangicola*, parasitoids of the mango mealybug, *Rastrococcus invadens*: interspecific host discrimination and larval competition. Entomol. Exp. Appl. 79, 179–185.

Clancy, D.W., Marucci, P.E., Dresner, E., 1952. Importation of natural enemies to control the oriental fruit fly in Hawaii. J. Econ. Entomol. 45, 85–90.

Clausen, C.P., Clancy, D.W., Chock, Q.C., 1965. Biological control of the oriental fruit fly (*Dacus dorsalis* Hendel) and other fruit flies in Hawaii. USDA Technol. Bull. 1322, 1–102 Washington, DC.

Duan, J.J., Purcell, M.E., Messing, R.H., 1996. Parasitoids of non-target tephritid flies in Hawaii: implications for biological control of fruit fly pests. Entomophaga 41, 245–256.

Duan, J.J., Messing, R.H., Purcell, M.F., 1998. Association of the opiine parasitoid *Diachasmimorpha tryoni* (Hymenoptera: Braconidae) with the lantana gall fly (Diptera: Tephritidae). Environ. Entomol. 27, 419–426.

Funasaki, G.Y., Lai, P.Y., Nakahara, L.M., Beardsley, J.W., Ota, A.K., 1988. A review of biological control introductions in Hawaii: 1890 to 1985. Proc. Hawaii Entomol. Soc. 28, 105–160.

Gilstrap, F.E., Hart, W.G., 1987. Biological control of Mediterranean fruit fly in the United States and Central America. US Dept. Agric. ARS 56, 1–64.

Hapai, M.M., 1977. The Biology and Ecology of the Hamakua Pamakani Gall Fly. Master's Thesis, University of Hawaii at Manoa, Honolulu, 77p.

Haramoto, F.H., 1953. Observations on the biology of *Opius oophilus* Fullaway (Hymenoptera: Braconidae). In: Valenzuela, P., Bernardo, G.A. (Eds), Proceedings of the 8th Pacific Science. Congress 3, Manila, pp. 1275–1289.

Haramoto, F.H., Bess, H.A., 1970. Recent studies on the abundance of the oriental and Mediterranean fruit flies and the status of their parasites. Proc. Hawaii. Entomol. Soc. 20, 551–566.

Harris, E.J., Bautista, R.C., 1996. Effects of fruit fly host, fruit species, and host egg to female parasitoid ratio on the laboratory rearing of *Fopius arisanus*. Entomol. Exp. Appl. 79, 187–194.

Howarth, F.G., 1991. Environmental impact of classical biological control. Annu. Rev. Entomol. 36, 485–509.

Jang, E.B., Moffitt, H.R., 1994. Systems approaches to achieving quarantine security. In: Sharp, J.L., Hallman, G.L. (Eds.), Quarantine Treatments for Pests of Food Plants. Westview Press, Boulder, Colorado, pp. 225–239.

Jervis, M.A., Copland, M.J.W., 1996. The life cycle. In: Jervis, M., Kidd, N. (Eds.), Insect Natural Enemies, Practical Approaches to Their Study and Evaluation. Chapman and Hall, London, pp. 63–160.

Liquido, N.J., 1991. Effect of ripeness and location of papaya fruits on the parasitization rates of oriental fruit fly and melon fly (Diptera: Tephritidae) by braconid (Hymenoptera) parasitoids. Environ. Entomol. 20, 1732–1736.

Liquido, N.J., Cunningham, R.T., Nakagawa, S., 1990. Host plants of the Mediterranean fruit fly (Diptera: Tephritidae) on the island of Hawaii (1949–1985 survey). J. Econ. Entomol. 83, 1863–1878.

Lopez, M., Sivinski, J., Rendon, P., Holler, T., Bloem, K., Copeland, R., Trostle, M., Aluja, M., 2003. Colonization of *Fopius ceratitivorus*, a newly discovered African egg-pupal parasitoid (Hymenoptera: Braconidae) of *Ceratitis capitata* (Diptera: Tephritidae). Fla. Entomol. 86, 53–60.

Messing, R.H., 1995. Status and needs of biological control research for tephritid flies. In: McPheron, B.A., Steck, G. (Eds.), Economic Fruit Flies: A World Assessment of Their Biology and Management. St. Lucie Press, FL, pp. 365–367.

Mohamed, S.A., Overholt, W.A., Wharton, R.A., Lux, S.A., Eltoum, E.M., 2003. Host specificity of *Psyttalia cosyrae* (Hymenoptera: Braconidae) and the effect of different host species on parasitoid fitness. Biol. Control 28, 155–163.

Neuenschwander, P., Boavida, C., Bokonon-Ganta, A.H., Gado, A., Herren, H.-R., 1994. Establishment and spread of *Gyranusoidea tebygi* Noyes and *Anagyrus mangicola* Noyes, two biological control agents released against the mango mealybug, *Rastrococcus invadens* Williams (Homoptera: Pseudococcidae) in Africa. Biocontrol Sci. Technnol. 4, 61–69.

Pemberton, C.E., Willard, H.F., 1918. Interrelations of fruit fly parasites in Hawaii. J. Agric. Res. 12, 285–303.

Purcell, M.F., Duan, J.J., Messing, R.H., 1997. Response of three hymenopteran parasitoids introduced for fruit fly control to a gall-forming tephritid, *Procecidochares alani*. Biol. Control 9, 193–200.

Purcell, M.F., Herr, J.C., Messing, R.H., Wong, T.T.Y., 1998. Interactions between augmentatively released *Diachasmimorpha longicaudata* and a complex of opiine parasitoids in a commercial guava orchard. Biocontrol. Sci. Technol. 8, 139–151.

Quimio, G.M., Walter, G.H., 2001. Host preference and host suitability in an egg-pupal fruit fly parasitoid, *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae). J. Appl. Entmol. 125, 135–140.

Ramadan, M.M., Wong, T.T.Y., Herr, J.C., 1994a. Is the oriental fruit fly (Diptera: Tephritidae) a natural host for the opiine parasitoids *Diachasmimorpha tryoni* (Hymenoptera: Braconidae)?. Environ. Entomol 23, 761–769.

Ramadan, M.M., Wong, T.T.Y., McInnis, D.O., 1994b. Reproductive biology of *Biosteres arisanus* (Sonan), an egg–larval parasitoid of the oriental fruit fly. Biol. Control 4, 93–100.

Ramadan, M.M., Wong, T.T.Y., Beardsley, J.W., 1992. Reproductive behavior of *Biosteres arisanus* (Sonan) (Hymenoptera: Braconidae), an egg–larval parasitoid of the oriental fruit fly. Biol. Control 2, 28–34.

Salt, G., 1970. The Cellular Defense Reactions of Insects. Cambridge University Press, Cambridge, UK.

SAS Institute, 2000. SAS User's Guide. Release 8.1, Cary, SAS Institute, USA.

Tanaka, N., Steiner, L.F., Ohinata, K., Okamoto, R., 1969. Low-cost larval rearing medium for mass production of Oriental and Mediterranean fruit fly. J. Econ. Entomol. 62, 967–968.

Vargas, R.I., Nishida, T., 1985. Survey for *Dacus latifrons* (Diptera: Tephritidae). J. Econ. Entomol. 78, 1311–1314.

Vargas, R.I., Walsh, W.A., Nishida, T., 1995. Colonization of newly planted coffee fields: dominance of Mediterranean fruit fly over

oriental fruit fly (Diptera: Tephritidae). J. Econ. Entomol. 88, 620–627.
van den Bosch, R., Haramoto, F.H., 1953. Competition among parasitoids of the oriental fruit fly. Proc. Hawaii. Entomol. Soc. 15, 201–206.
van Zwaluvenburg, R.H., 1947. Notes and exhibitions. Proc. Hawaii. Entomol. Soc. 13, 8.
Wang, X.G., Messing, R.H., 2002. Newly imported larval parasitoids pose minor competitive risk to the extant egg–larval parasitoid of fruit flies in Hawaii. Bull. Entomol. Res. 92, 423–429.
Wang, X.G., Messing, R.H., 2003. Intra- and interspecific competition by *Fopius arisanus* and *Diachasmimorpha tryoni* (Hymenoptera: Braconidae), parasitoids of Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae). Biol. Control 27, 251–259.
Wang, X.G., Messing, R.H., Bautista, R.C., 2003. Competitive superiority of early acting species: a case study of opiine fruit fly parasitoids. Biocontrol Sci. Technol. 16, 391–402.
Wharton, R.A., 1989. Classical biological control of fruit infesting Tephritidae. In: Robinson, A., Harper, G. (Eds.), World Crop Pests. Fruit Flies: Their Biology, Natural Enemies, and Control, vol. 3b. Elsevier, Amsterdam, pp. 303–313.
Wharton, R.A., 1999. A review of the old world genus *Fopius*, with description of two new species reared from fruit-infesting Tephritidae. J. Hymen. Res. 8, 48–64.
Wharton, R.A., Gilstrap, F.E., 1983. Key and status of opiine braconid (Hymenoptera) parasitoids used in biological control of *Ceratitis capitata* and *Dacus*, s.l. (Diptera: Tephritidae). Ann. Entomol. Soc. Am. 76, 721–742.
Wharton, R.A., Trostle, M.K., Messing, R.H., Copeland, R.S, Kimani-Njogu, S.W., Lux, S., Overholt, W.A, Mohamed, S., Sivinski, J., 2000. Parasitoids of medfly, *Ceratitis capitata*, and related tephritids in Kenyan coffee: a predominantly koinobiont assemblage. Bull. Entomol. Res. 90, 517–526.
Wong, T.T.Y., Ramadan, M.M., 1987. Parasization of the Mediterranean and oriental fruit flies (Diptera:Tephritidae) in the Kula area of Maui, Hawaii. J. Econ. Entomol. 80, 77–80.
Wong, T.T.Y., Ramadan, M.M., 1992. Mass rearing biology of larval parasitoids of Tephritid flies in Hawaii. In: Anderson, T.E., Leppla, N.C. (Eds.), Advances in Insect Rearing for Research and Pest Management. Westview Press, Boulder Colorado, pp. 405–426 (Chapter 23).
Wong, T.T.Y., Mochizuki, N., Nishimoto, J.I., 1984. Seasonal abundance of parasitoids of the Mediterranean and oriental fruit flies (Diptera: Tephritidae) in the Kula area of Maui, Hawaii. J. Econ. Entomol. 13, 140–145.
Zar, J.H., 1999. In: Biostatistical Analysis. Prentice Hall, Upper Saddle River, New Jersey 663 pp.
Zenil, M., Liedo, P., Williams, T., Valle, J., Cancino, J., Montoya, P., 2004. Reproductive biology of *Fopius arisanus* (Hymenoptera: Braconidae) on *Ceratitis capitata* and *Anastrepha* spp. (Diptera: Tephritidae). Biol. Control 29, 169–178.