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RESEARCH ARTICLE

Old and new host-parasitoid associations: parasitism of the invasive fruit fly *Bactrocera invadens* (Diptera: Tephritidae) and five African fruit fly species by *Fopius arisanus*, an Asian opiine parasitoid

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Fopius arisanus (Sonan), a solitary koinobiont endoparasitoid of fruit flies, was introduced for testing and final release against the recently discovered species *Bactrocera invadens* Drew, Tsuruta and White in Africa. Laboratory experiments were conducted to assess host preference, host acceptability for oviposition, and physiological suitability of *B. invadens* and five other indigenous tephritid fruit fly species, namely, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), *C. cosyra* (Walker), *C. rosa* Karsch, *C. fasciventris* (Bezzi), and *C. anonae* Graham. Females of *F. arisanus* visited all host egg patches, but showed a stronger preference to eggs of *B. invadens*, which was also most accepted for oviposition. Successful development of parasitoid progenies varied greatly across hosts, with *B. invadens* yielding the highest parasitoid progeny and *C. fasciventris* yielding no *F. arisanus* progeny. Most of the parasitoid eggs laid in *C. rosa* and *C. fasciventris* were encapsulated. Sex ratio was not influenced by host species and it was female biased in all hosts that produced parasitoid progeny. *Fopius arisanus* was able to establish a new association with *C. capitata*, *C. cosyra* and to a lesser extent *C. anonae*. The results are discussed in the light of the potential use of *F. arisanus* as a biological control agent of *B. invadens*.

Keywords: *Bactrocera invadens*; *F. arisanus*; *Ceratitis* spp.; new and old associations

Introduction

Most tephritid pest species of economic importance belong to the genera *Anastrepha* (Schiner), *Bactrocera* Macquart, *Ceratitis* MacLeay, *Dacus* Fabricius and *Rhagoletis* Loew (White and Elson-Harris 1992). Africa is the aboriginal home of the genus *Ceratitis* (De Meyer et al. 2002; De Meyer and Copeland 2005) which includes two notorious species: *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), one of the most polyphagous, widespread and damaging fruit fly pests (Barr et al. 2006 and reference therein) and *C. cosyra* (Walker), an oligophagous pest (primarily of mango) restricted to the African continent (White and Elson-Harris 1992; De Meyer 2001). *Dacus* is also mostly an Afrotropical genus, with a few species occurring on other continents (White 2006). In addition to the plethora of native fruit fly pests in Africa, several members of the genus *Bactrocera* have also invaded the continent, including *Bactrocera cucurbitae* (Coquillett), *Bactrocera zonata* (Saunders) (CABI 1996;

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Hashem, Mohamed, and El-Wakkad 2001), *Bactrocera invadens* Drew, Tsuruta and White (Lux, Copeland, White, Manrakhan, and Billah 2003; Drew, Tsuruta, and White 2005), and most recently *Bactrocera latifrons* (Hendel) (Mwatawala, De Meyer, White, Maerere, and Makundi 2007; S. Ekesi, unpublished data).

Bactrocera invadens, which was initially thought to be *Bactrocera dorsalis* (Hendel) (Lux et al. 2003), was first recorded in Africa from the Kenyan coast in 2003. Since this first report, *B. invadens* has spread rapidly across the African continent and in addition to Kenya is now known from 28 other countries including Angola, Benin, Burkina Faso, Cameroon, Comoros Island, Democratic Republic of Congo, Equatorial Guinea, Ghana, Guinea, Ivory Coast, Mali, Niger, Nigeria, Senegal, Sierra Leone, Sudan, Tanzania, Togo and Uganda (Drew et al. 2005; Vayssières, Goergen, Lokossou, Dossa, and Akponon 2005; Ekesi, Nderitu, and Rwomushana 2006; R. Hanna, unpublished data). *Bactrocera invadens* has been reported from over 30 plant species but the most preferred cultivated host plant is mango, *Mangifera indica* L. (Anacardiaceae), while Marula, *Sclerocarya birrea* (A.Rich) Hochst. (Anacardiaceae) and tropical almond, *Terminalia catappa* L. (Combretaceae) are most infested non-cultivated plants (Ekesi et al. 2006; Mwatawala, De Meyer, Makundi, and Maerere 2006; Rwomushana, Ekesi, Gordon, and Ogol 2008).

Shortly after *B. invadens* was detected in Kenya, attempts were made to identify a native parasitoid species that would successfully develop in this host to establish what is known as a new association (Hokkanen and Pimentel 1989). Two solitary parasitoids (*Psyttalia cosyrae* (Wilkinson) and *P. phaeostigma* (Wilkinson) (Hymenoptera: Braconidae) and one gregarious parasitoid (*Tetrastichus giffardii* Silvestri (Hymenoptera: Eulophidae)) were tested. *Bactrocera invadens* was readily accepted by *T. giffardii* and to a lesser extent by the two *Psyttalia* species. However all eggs of the two *Psyttalia* species and nearly all eggs of *T. giffardii* were encapsulated in larvae of *B. invadens* (Mohamed, Wharton, von Mérey, and Schulthess 2006; S.A. Mohamed, unpublished data). None of the few individuals of *T. giffardii* progeny that escaped encapsulation were able to complete development to the adult stage. This level of parasitoid encapsulation by *B. invadens* suggests that in addition to the very destructive nature of this pest, it also has a potential for serving as a reproductive sink for some of the indigenous parasitoid fauna such as *T. giffardii*. Furthermore, 34,430 kg of various host fruits of *B. invadens* were sampled from East (Rwomushana et al. 2008) and West Africa (Hanna, unpublished data), but not a single parasitoid species was recovered. Being an alien pest and lacking resident parasitoid species in Africa, *B. invadens* represents a typical target for classical biological control, which would entail exploration for parasitoids in the pest's putative aboriginal home and importation of promising parasitoids from areas with established exotic parasitoids of closely related pest species.

Bactrocera invadens is believed to have invaded Africa from the Indian subcontinent and was discovered in Sri Lanka after it was first reported from Africa (Drew et al. 2005), where it has become a significant pest of quarantine and economic importance. At present, exploration activity is underway in Sri Lanka in search of effective parasitoids that could be utilized in the biological control of *B. invadens*. In addition to this exploration activity, the Asian parasitoids *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae), and *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) have been imported from Hawaii, where they were released following the discovery of the oriental fruit fly, *Bactrocera dorsalis*

Hendel (which is closely related to *B. invadens*) in the 1940s (van Zwaluwenberg 1947). The two parasitoid species, particularly *F. arisanus*, have been credited with outstanding successes of biological control of fruit flies (*B. dorsalis* as well as the new associated host *C. capitata*) in Hawaii (van den Bosch, Bess, and Haramato 1951; Clausen, Clancy, and Chock 1965; Vargas, Stark, Uchida, and Purcell 1993). More recently, the introduction of *F. arisanus* into the Pacific islands has resulted in up to 98% reduction in several *Bactrocera* species, including *B. dorsalis* (Vargas, Leblanc, Putoa, and Eitam 2007). Both *Diachasmimorpha longicaudata* and *F. arisanus* are koinobiont solitary parasitoids of fruit flies. The former species attacks the larva while the latter attacks the egg, and adults of the both species emerge from the puparia of their host.

The broad objective of this study was to evaluate the potential of the Hawaiian populations of *F. arisanus* as a biological control agent of *B. invadens* and its impact on the key native fruit fly species pest such as *C. capitata*, *C. cosyra*, *C. rosa* (Karsch), *C. fasciventris* (Bezzi) and *C. anonae* Graham, which share many host plants with *B. invadens*. To this end, laboratory experiments were carried out to determine the preference, acceptability for oviposition, and physiological suitability of the six fruit fly host species to this parasitoid species

Material and methods

Host insects

Ceratitis capitata, *C. cosyra*, *C. rosa*, *C. fasciventris* and *C. anonae* were reared using the procedures described by Mohamed, Overholt, Wharton, Lux, and Elameen (2003). Flies of these species had been reared in laboratory for 106 generations prior to start of the experiment. The initial cohort of *B. invadens* was obtained from samples of ripe mangoes collected from a local market in Nairobi and reared according to the methodology described in Ekesi, Nderitu, and Chang (2007). *Bactrocera invadens* was reared for 58 generations before the start of the experiments. All fruit fly cultures were rejuvenated every 6–12 months by incorporation of wild populations.

The flies were kept in Perspex cages and maintained at 27–28°C, 12 h L:12 h D. They were provided with water on pumice granules and fed on a diet consisting of volumetric mixture of enzymatic yeast hydrolysate powder and sugar at 4:1. Up to the fourth generation, sexually mature flies were offered mango fruits (variety Apple), as oviposition substrate. Thereafter, they were provided oviposition substrates that consisted of a ball of artificial diet (2–3 cm diameter) wrapped in parafilm membrane (Ekesi et al. 2007), on which the hatching larvae fed. The diet contained carrot powder (24.2 g), sugar (16.2 g), brewer's yeast (8.1 g), citric acid (0.6 g), methyl p-hydroxybenzoate (0.2 g) and water (50.7 mL).

Parasitoid

The initial cohort of *F. arisanus* was obtained from the University of Hawaii at Manoa, Honolulu, Hawaii, where they have been maintained on *Bactrocera dorsalis* for over 200 generations (Bokonon-Ganta personal communication). The wasps were

kept under quarantine at the International Centre of Insect Physiology and Ecology (*ICIPE*), where they were reared on 4–18 h old *B. invadens* eggs.

Mango domes (mango fruit skin that has the seed and pulp scooped out) were offered to *B. invadens* for egg laying in the evening of the day preceding their exposure to the parasitoids. Pieces of the mango dome (5 × 4 cm) were placed on double layers of sponge pieces (Spontex make, Nairobi, Kenya) of similar dimensions to that of the mango peel pieces and 3 mm height each, placed in oviposition units (9 × 0.5 cm, diameter × depth), and covered with a tight-fitting organza lid. The oviposition units were then exposed for 8 h to *F. arisanus* wasps held in a cubical cage (35 cm^3). Thereafter, the oviposition units were removed and the mango peel pieces with the eggs placed on larval diet in a plastic bowl (10.3 × 6 cm, diameter × depth). The diet was kept moist and replenished as necessary. When the larvae attained their full size, the diet was washed out through a sieve. Mature larvae were then placed back in the plastic bowl with a layer of sand on the bottom to serve as the pupation medium. A hole of 10 cm diameter was cut in the lid of the bowl and covered with a fine net for ventilation. The sand was kept moist to prevent pupal desiccation until emergence of adult flies and parasitoids. Emerging parasitoids and flies were released in a rearing cage (35 cm^3) and the flies were later killed in 70% ethanol. Parasitoids were maintained at room temperature of 25–26°C and photoperiod of 12 h L:12 h D, and provided with fine drops of pure honey and water in wet cotton wool.

Bioassay

Host preference and host acceptability

Mango domes were exposed to ovipositing adults of each of the six fruit fly species, one dome for each species, at about 16:00 h on the day preceding the test. Thirty mated, naive, female wasps (7–10 days old), and 30 males of about the same age were introduced into a cage (60 × 30 × 15 cm). Rectangular pieces of mango dome (4 × 2 cm) with 10 fruit fly eggs were cut. Excess eggs were removed, using a fine camel hair brush when necessary to obtain the desired number of eggs. The mango pieces were then placed in the oviposition units as described in the parasitoid rearing procedure on a moistened double layer of sponge of about the same dimensions as the mango pieces, with the eggs facing the organza lid. The oviposition units were then introduced, while inverted, into the cage containing the parasitoids to avoid differential attraction by female wasps to different oviposition units based on the sequence of their introduction in the experimental cage. Thereafter, the oviposition units were re-inverted after all units had been introduced into the cage, and observations on parasitoid behavior were initiated five minutes later. The number of female wasps searching on the mango piece and/or ovipositing was recorded at 15-min intervals for 3 h. After this exposure period, host eggs were removed and dissected in a saline solution (phosphate buffer saline) and inspected for the presence of parasitoid eggs. The experiment was replicated 6 times using new parasitoid cohorts. At each repetition, the sequence of oviposition units was rotated such that each host had occupied all six positions within the cage by the time the experiment was terminated. This was necessary to rule out directional bias as a factor contributing to the outcome of the experiment.

Host suitability

Five mated, naive female wasps and five males of the same age as described above were introduced into a small Perspex cage ($12 \times 12 \times 12$ cm). A sleeve made of fine net was fixed to one side of the cage. A round opening (4.5 cm diameter) was made at the top of the cage to which a piece of organza material was fixed.

Rectangular pieces of mango dome (4×2 cm) with 100 fruit fly eggs (4–18 h old) were cut. Excess eggs were removed, using a fine camel hair brush when necessary to obtain the desired number of eggs. Then the mango pieces were placed on the oviposition unit in the same way as described in the previous experiment. The oviposition units were then introduced into the cages containing the parasitoids for 24 h. The oviposition units were then removed and the mango pieces with the eggs were placed on the larval diet in plastic containers ($4.3 \times 3.3 \times 2.8$ cm, top diameter $\times$ bottom diameter $\times$ height) covered with a fine net held with a rubber band. Fresh diet was added as necessary. When the larvae attained their full size, the containers were opened and placed in a larger plastic cup ($8 \times 5 \times 9.5$ cm, top diameter $\times$ bottom diameter $\times$ height) with a layer of sand for pupation. The sand was kept moist until fly and parasitoid emergence.

The total number of wasps (males and females), and uneclosed puparia were counted. When emergence of flies and parasitoids ceased, the number of unmerged puparia was recorded. Later they were dissected and their contents (numbers of dead parasitoids or undifferenenitaed biomass) were recorded. This experiment was conducted with each of the six host species, in a no-choice manner, and number of replicates for the different host species ranged between 12 and 18 (Table 1). Another set of each host was treated in the same manner but without exposure to the parasitoids to serve as controls to assess the hosts' natural mortality.

Test for encapsulation

Results from the host suitability experiment indicated that *C. rosa*, *C. fasciventris*, and to a lesser extent *C. anonae*, were not suitable for development of *F. arisanus*. To verify and confirm these results, 500 eggs of each of the host species tested were placed on oviposition units in the same way as described above. The oviposition units were then exposed to 30 experienced female wasps (female with prior oviposition experience), in a rearing cage to maximize the rate of parasitism. After the exposure period of 6 h the oviposition units were removed from the cages and the eggs were maintained in the same manner described for the host suitability experiment. On the 7th day of incubation, host larvae were dissected in a phosphate buffer saline and examined for parasitism under a binocular microscope. Dissection of host larvae was terminated after 50 parasitized larvae of each host species were obtained, and the fate of parasitoid eggs was recorded.

Statistical analysis

A univariate repeated measure analysis of variance was used to analyze the variation in parasitoid choice – expressed as oviposition rate – over 13 time intervals. Pairwise *t*-test option PDIFF (*t*-test, with $P = 0.05$) was used to separate the means when treatment effects were significant ($P = 0.05$).

Data for host acceptability (number of parasitized host egg) and host suitability (total progeny production, percent realized (number of emerged viable parasitoid wasps/total number of retrieved puparia $\times 100$) and absolute parasitism, percent unmerged puparia, sex ratio as the proportion of females, and percent undifferentiated biomass) were analyzed with one-way ANOVA (PROC GLM, SAS Institute 2000).

Absolute percent parasitism was obtained by adding the number of unenclosed puparia containing dead parasitoids to the total number of adult parasitoids produced for each replicate, dividing by the starting number of puparia and multiplying by a 100. $\text{Log}_{10}+0.5$ and arcsine square root transformation were used, respectively, on counts and percentages before statistical analyses (Sokal and Rohlf 1981). When treatment effects were significant (i.e., $P<0.05$), treatment means were separated using Student–Newman–Keuls (SNK) test. Sex ratio was calculated only for the replicates that produced parasitoid progeny and percent undifferentiated biomass was calculated for replicates that had at least one uneclosed puparium. A *t*-test was used to compare number of uneclosed puparia in parasitoid-exposed and controls sets.

Results

Host preference

Mean percentage of gravid *F. arisanus* females that landed and searched on all host species tested ranged between 16.92 ± 2.40 and 25.90 ± 2.11 over all 13 observation time intervals (based on a cohort of 30 females/cage). Female wasps searched on all host species, but showed strongest preference for *B. invadens* ($F=11.94$; df $=5,30$; $P<.0001$), as they spent most of their foraging time on *B. invadens* egg patches. Other host species were comparably attractive to female parasitoids (Figure 1).

Host acceptability

The longer searching time on egg patches of *B. invadens* resulted in significantly higher oviposition into the eggs of this host species ($F=12.93$; df $=5,30$, $P<0.0001$), while all *Ceratitis* species were parasitized equally and received comparable numbers of parasitoid eggs (Figure 2). Superparasitism was found only in *B. invadens*, but was low; out of 33 parasitized eggs of this host, only 9.4% contained a maximum of two parasitoid eggs.

Host suitability

Fopius arisanus was able to complete development in all host species but *C. fasciventris*. The total number of parasitoid offspring varied considerably across host species, with *B. invadens* yielding the highest number of wasps followed, in sequence, by *C. capitata*, *C. cosyra*, and *C. anonae* (Table 1). *Ceratitis rosa* produced the lowest number of wasps which was not significantly different from *C. fasciventris* that yielded no parasitoid progeny (Table 1). There was also significant inter-specific variability with regard to percent realized parasitism which followed the same trend as that of the total number of parasitoid offsprings (Table 1). However, the percent

Table 1. Host suitability (Mean ± SE) of six fruit fly species for immature development of *Fopius arisanus*.

Host species	No. of reps	Total number of parasitoid progeny	Realized parasitism (%)	Absolute parasitism (%)	Sex ratio (proportion of females)	Uneclosed puparia (%)	Undifferentiated biomass (%)
B. invadens	16	51.94 ± 3.25a (29–73)	73.63 ± 3.18a (50–88)	74.31 ± 3.15a (50–88)	0.59 ± 0. 03a (0.34–0.77)	6.63 ± 1.46b (0–20)	3.61 ± 0.94b (0–12.07)
C. capitata	17	25.71 ± 3.51b (6–70)	36.41 ± 4.08b (8–83)	36.82 ± 4.13b (8–83)	0.61 ± 0.06a (0–0.95)	7.00 ± 1.19b (0–17)	3.25 ± 0.97b (0–9.57)
C. cosyra	18	11.78 ± 2.40c (0–34)	27.28 ± 5.97c (0–77)	27.61 ± 5.92b (0–77)	0.54 ± 0.08a (0–1.00)	9.06 ± 2.72b (0–46)	4.64 ± 1.50b (0–19.78)
C. anonae	13	3.92 ± 0.92d (0–10)	8.23 ± 2.36d (0–30)	9.85 ± 2.75c (0–35)	0.53 ± 0.11a (0–1.00)	41.77 ± 7.40a (0–77)	16.72 ± 2.92a (3.13–35.48)
C. rosa	12	0.42 ± 0.23e (0–2)	1.58 ± 0.93e (0–10)	1.58 ± 0.93d (0–10)	0.67 ± 0.17a (0.50–1.00)	18.08 ± 5.24b (0–60)	5.11 ± 1.30b (0–13.04)
C. fasciventris	10	0 ± 0e	0 ± 0e	0 ± 0d	–	7.50 ± 1.96b (2–23)	2.52 ± 0.75b (0–7.81)
F		62.67	51.69	51.58	0.48	9.71	7.54
df		5,80	5,80	5,80	4,57	5,80	5,70
P		<0.0001	<0.0001	<0.0001	=0.748	<0.0001	<0.0001

Means followed by the same letter in the same column are not significantly different ($P = 0.05$), Student–Newman–Keuls (SNK) test.
Figures in parenthesis are the ranges.

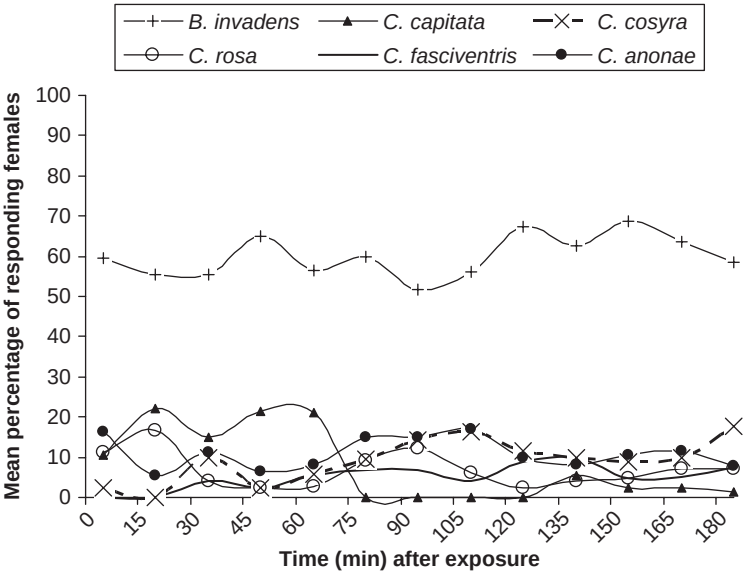

Figure 1. Mean percentage of *F. arisanus* female respondents (searching and/or ovipositing) to different fruit fly host eggs over three hours exposure period.

absolute parasitism was comparable for *C. capitata* and *C. cosyra*; otherwise the trend was also consistent with that of the previous two parameters (Table 1). Parasitoid progeny sex ratio was female biased and similar for all five host species that produced progeny (Table 1).

Percent uneclosed puparia varied significantly among host species tested and it was highest in *C. anonae* (Table 1). Upon dissection of the uneclosed puparia, those of *C. anonae* were found to have the highest number of undifferentiated remains (Table 1). When percent uneclosed puparia of the parasitized sets were compared with those of their respective controls; only *C. anonae* was significantly lower from its control (Table 2).

Test for encapsulation

Nearly all parasitoid eggs laid in *C. fasciventris* and *C. rosa* (96 and 90%, respectively) died as eggs or larvae. All un-hatched eggs in these host species (74% in the former and 78% in the latter) were encapsulated, while the dead parasitoid larvae showed no sign of encapsulation in either host (except one which was partially encapsulated in *C. rosa*). On the other hand, only 10% of eggs oviposited in *C. anonae* were encapsulated, while none were encapsulated in *C. capitata*, *C. cosyra*, and *B. invadens.*

Discussion

The results of this study demonstrate the ability of *F. arisanus* to differentiate among different host species upon the first contact with the hosts' micro-environment. The type of host-associated oviposition marking cues, which could have been exploited

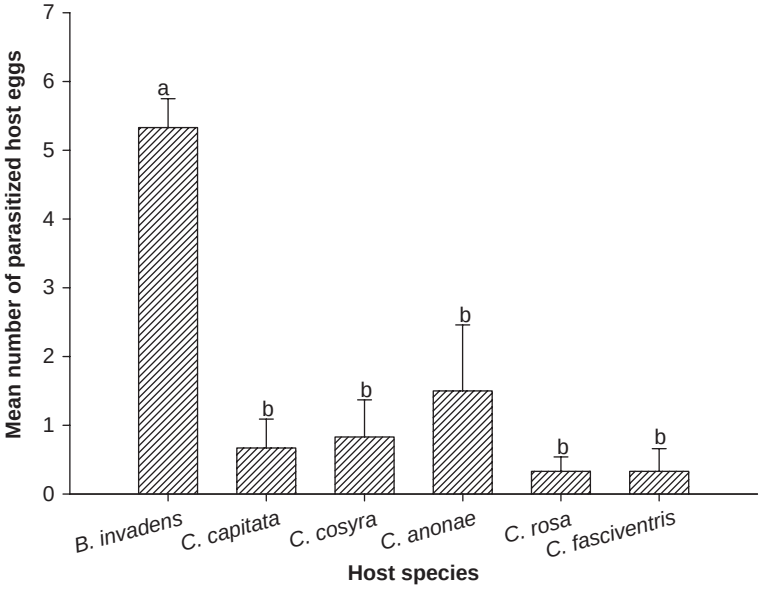

Figure 2. Acceptability of six fruit fly host eggs for oviposition by *F. arisanus* Bars with the same letter are not significantly different at $P = 0.05$ (Student–Newman–Keuls, SNK test).

by *F. arisanus* as a kairomone, might have varied with host species tested as the majority of the females were attracted to *B. invadens* eggs within a few minutes after starting the test. Moreover, the persistent search on the egg patch of this host suggest that the *B. invadens* associated cue also served as an arrestant for the females, resulting in longer residence time on egg patch of this host. The nature and the chemical identity of compound(s) that elicited such behavior in *F. arisanus* warrants further study bearing in mind the crucial role of semiochemicals as a tool for manipulating parasitoid searching behavior and enhancing efficacy of biological control programs (Vet and Dicke 1992).

Contrary to our finding of differential host species preference, Harris and Bauista (1996) reported that *F. arisanus* females were equally attracted to egg patches of the different host species such as *B. dorsalis*, *C. capitata*, *B. latifrons*, and

Table 2. Mean percent ($\pm$SE) of uneclosed puparia in parasitoid exposed vs. control sets of different host species.

	Mean percent uneclosed pupuaria			
Host species	Parasitoid-exposed	Non-exposed (control)	*t*-value	*P*
B. invadens	6.67 $\pm$ 1.50a	3.46 $\pm$ 0.64a	1.97	0.0634
C. capitata	6.99 $\pm$ 1.18a	5.63 $\pm$ 0.81a	0.96	0.3769
C. cosyra	9.09 $\pm$ 2.73a	5.40 $\pm$ 1.66a	1.16	0.2581
C. rosa	18.02 $\pm$ 5.23a	12.89 $\pm$ 1.80a	0.93	0.3708
C. fasciventris	7.61 $\pm$ 1.99a	5.99 $\pm$ 1.30a	0.70	0.4910
C. anonae	41.85 $\pm$ 7.41a	7.64 $\pm$ 1.43b	4.54	0.0006

Means within the same row followed by the same letter are not significantly different (*t*-test, $P = 0.05$).

B. cucurbitae that they tested. This discrepancy between our finding and that of Harris and Bauista (1996) could be explained by the difference in the experimental set-ups. While the latter investigators conducted the host preference test in a no-choice situation, in this study the wasps were provided with a choice of host species.

The longer foraging by *F. arisanus* females on *B. invadens* observed in this study resulted in significantly higher acceptance (number of host eggs containing parasitoid eggs) of this host species. Similar results of varying degrees of acceptability for egg oviposition by *F. arisanus* in various parasitoid-host associations have been reported (Harris and Bautista 1996; Quimio and Walter 2001). However, Ramadan, Wong, and Bearddsley (1992) recorded no ovipositional favoritism between *C. capitata* and *B. dorsalis* by the same parasitoid species.

The strong oviposition bias by *F. arisanus* in *B. invadens* suggests that the female wasps could have perceived that this host was of superior quality to the other host species. Alternatively, this strong bias might have been caused by the fact that the parasitoids were reared on *B. invadens* for at least five generations prior to the test, and on *B. dorsalis* for over 200 generations before its importation from Hawaii (Bokonon-Ganta personal communication). A report by Lawrence, Harris, and Bautista (2000) which supports the first of these assumptions, suggesting that the tip of the ovipositor of *F. arisanus* females is equipped with sensilla basiconica-type chemoreceptors, which helps the wasp to detect the host biochemical suitability for oviposition and subsequent development of its progeny. This was further substantiated by the outcome of the host suitability experiment, which mirrored the host acceptability, with the most accepted host, *B. invadens* being the most suitable in terms of progeny production and percent parasitism.

The low superparasitism rate recorded in the study is a typical biological behavior for this parasitoid (e.g., Harris and Bautista 1996; Quimio and Walter 2001; Moretti and Calvitti 2003; Rousse, Gourdon, and Quilici 2006; Wang and Messing 2008). Also the phenomenon of differential host suitability is well documented for *F. arisanus.* For example, among three Australian *Bactrocera* species, *B. tryoni* (Froggart) was the most suitable for development of *F. arisanus* while *B. cucumis* (French) was not suitable at all (Quimio and Walter 2001). Similarly, Zenil et al. (2004) reported that *C. capitata* was more suitable for *F. arisanus* than *Anastrepha serpentia* (Wiedemann) (Diptera: Tephritidae), which in turn is more suitable than *A. ludens* (Loew), whereas *A. obliqua* (Macquart) was unsuitable. Rousse et al. (2006) grouped the host species they tested into three categories (i.e., non-host, poor host and good host), in terms of their suitability for *F. arisanus* development. However, there are some discrepancies between our findings and that reported by Rousse et al. (2006) in the Reunion islands. First, the authors rated *C. capitata* as an equally poor host as *C. rosa* for development of *F. arisanus*, while according to our finding, *C. capitata* ranked second to *B. invadens* with regard to total offspring production and percent parasitism, ranging between 6–70 wasps and 8–83%, respectively. Secondly, contrary to our finding that eggs oviposited in *C. rosa* were encapsulated, Rousse et al. (2006) showed that encapsulation of *F. arisanus* eggs in this host was avoided. These discrepancies might have been due to geographical differences in the island and mainland populations of the two host species. However, in this study the mortality of the parasitoid larvae in *C. fasciventris* and almost all of the larvae in *C. rosa* cannot be explained by the same immune response responsible for egg mortality as no capsule formations were observed around these larvae.

Though *F. arisanus* was able to establish a new association with *C. cosyra* and to a lesser degree with *C. anonae*, it failed to establish any new associations with *C. fasciventris*. Evidently, the parasitoid has a strong affinity for the genus *Bactrocera* and *B. invadens* in particular. In fact the performance of *F. arisanus* on *B. invadens* in terms of percent parasitism and total parasitoid progeny produced was higher than what was reported for *Bactrocera dorsalis*, the host known prior to the results of this test, as the most suitable host (Harris and Okamoto 1991; Harris, Okamoto, Lee, and Nishida 1991; Ramadan et al. 1992; Harris and Bautista 1996). For example Bautista, Harris, and Lawrence (1998), working with the same host-parasitoid ratio and the same duration of host exposure to parasitoids used in this study, reported 52.3% parasitism of *B. dorsalis* by *F. arisanus* compared with 73.6% parasitism of *B. invadens* in our study. This has led us to hypothesize that *B. invadens* might have been a natural host for this parasitoid and by introducing this parasitoid species into Africa, *F. arisanus* and this host will ultimately be reunited, with the plausible expectation that it will be an efficient biological control agent.

In another scenario, contrary to the one presented in this study, an African con-generic, *F. ceratitivorus* was tested for its preference and ability to develop in *C. capitata* and three Asian *Bactrocera* species. The parasitoid was reported to prefer and only successfully develop in its old associated host *C. capitata*, while the three *Bactrocera* species were physiologically unsuitable for the development of the parasitoid immature stages, as all parasitoid eggs were encapsulated in these hosts (Bokonon-Ganta, Ramadan, Wang, and Messing 2005). A shared evolutionary history between the parasitoid and the host is known to enable the parasitoids to evolve mechanisms to counteract the host immune response of its host.

When considering a polyphagous parasitoid such as *F. arisanus* for biological control, it is crucial to establish whether the target host species is frequently parasitized, and whether it will serve as a suitable host for the development of the candidate parasitoid (Quimio and Walter 2001). Our results show that *B. invadens*, was the most preferred, the most accepted and the most suitable host species. These, coupled with effective searching behavior and high foraging efficiency (Wang and Messing 2003, are clear indications that *F. arisanus* can be considered as an efficient bio-control agent for *B. invadens*. However, for eggs that might escape parasitization by *F. arisanus*, an efficient larval parasitoid is needed to complement bio-control of *B. invadens*. *Diachasmimorpha longicaudata*, a larval-pupal parasitoid also imported from Hawaii, is not sufficiently capable of counteracting the immune response of *B. invadens* (Mohamed, Ekesi, and Hanna 2008). Efforts are presently under way to explore for parasitoid guilds of *B. invadens* in its putative aboriginal home of Sri Lanka.

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