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Fruit Preference, Parasitism, and Offspring Fitness of *Fopius arisanus* (Hymenoptera: Braconidae) Exposed to *Bactrocera dorsalis*' (Diptera: Tephritidae) Infested Fruit Species

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Abstract

Fopius arisanus (Sonan) (Hymenoptera: Braconidae) is a koinobiont solitary parasitoid of various fruit flies, particularly those in the genus *Bactrocera*. Researchers introduced *F. arisanus* into Africa for the biological control of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), a pest of a wide range of fruit trees and vegetables. However, the suitability of host fruit species as egg-laying substrates for parasitoid development remains poorly investigated in tropical Africa. The present study examines the preference and performance of *F. arisanus* on *B. dorsalis* reared on eleven fruit species through laboratory choice-test trials. We assessed the oviposition activity, parasitism rate, developmental time, and offspring fitness of *F. arisanus* on nine cultivated and two wild host fruits species. Oviposition attempts were higher on *Psidium guajava* (L.) (Myrtales: Myrtaceae) and *Mangifera indica* (L.) (Sapindales: Anacardiaceae) than on the other host fruits tested. The wasp parasitized host eggs in *P. guajava* in no-choice experiments. *Psidium guajava*, *Irvingia wombulu* (Vermoesen) (Malpighiales: Irvingiaceae), and *Irvingia gabonensis* (Aubry-Lecomte) Baill (Malpighiales: Irvingiaceae) were suitable for parasitism in choice tests. Of all host fruits tested, the body and hind tibia lengths of both parasitoid sexes emerging from *M. indica* were longer than on the others. The female ovipositor was long on *Annona squamosa* (L.) (Magnoliales: annonaceae) and short on *Eriobotrya japonica* ([Thunb.] Lindl.; Rosales: Rosaceae). We obtained the longest preimaginal developmental time for both sexes on *E. japonica* and the shortest for females and males on *Carica papaya* (L.) (Brassicales: Caricaceae). These results demonstrate the ability of some tested fruit species to serve for the permanent establishment of *F. arisanus* in the field.

Key words: biological control, tritrophic interaction, diversity, parasitism rate, fitness

Bactrocera dorsalis is a widely distributed fruit fly species of Asian origin (CABI 2018). Lux *et al.* (2003) first detected the insect in Africa in 2003 and initially described it as a new species, *Bactrocera invadens* (Drew, Tsuru & White) (Diptera: Tephritidae) (Drew *et al.* 2005), and was later confirmed as *B. dorsalis* (Schutze *et al.* 2015a,b, Ekesi *et al.* 2016). Since its first detection in coastal Kenya in 2003, *B. dorsalis* has been reported from 42 countries in Africa (De Meyer *et al.* 2010, Goergen *et al.* 2011, De Villiers *et al.* 2016, CABI 2018) where it is a major threat to fruit production (Ekesi *et al.* 2006; Mwatawala *et al.* 2006, 2009; De Meyer *et al.* 2010; Ndiaye *et al.* 2015). *Bactrocera dorsalis* is polyphagous, and its damage to fruits in Africa may exceed 70% on mango and guava, and 40% on citrus (De Meyer *et al.* 2008, 2010; Hanna *et al.* 2008a; Goergen *et al.* 2011).

A range of control options has been developed and tested for the integrated management of *B. dorsalis* and other fruit flies infesting fruits and vegetables. These include bait sprays, male annihilation, biological control, biopesticides, and a number of cultural methods (such as orchard sanitation, fruit bagging or wrapping, and early harvesting) (Ekesi and Billah 2006, Van Mele *et al.* 2007, Hanna *et al.* 2008b, Vayssieres *et al.* 2009, Appiah *et al.* 2014). Because of its exotic nature in Africa, researchers deemed classical biological control as a necessary option for the management of *B. dorsalis* in Africa. A collaborative effort was initiated by the International Centre of Insect Physiology and Ecology (*icipe*) and the International Institute of Tropical Agriculture (IITA) to introduce natural enemies into Africa that are effective against *B. dorsalis* elsewhere. Following this

approach, the coevolved parasitoid, *Fopius arisanus* was imported from Hawaii where it was successfully established to control *B. dorsalis* for evaluation and release in Africa (Mohamed *et al.* 2016, Gnanvossou *et al.* 2017).

Fopius arisanus is a solitary opiine endoparasitoid, native to the Indo-Pacific region and known to attack the eggs and first instars of about 40 frugivorous tephritid fruit fly species (Bautista and Harris 1996, Rousse *et al.* 2007). The parasitoid has been isolated from 85 plant species of 35 families (Chinajariyawong *et al.* 2000, Rousse 2007, Mohamed *et al.* 2016). *Fopius arisanus* is known to complete its larval and pupal development inside the host fly larvae and pupae, respectively (Calvitti *et al.* 2002, Rousse *et al.* 2005). The successful control of *B. dorsalis* populations using the parasitoid *F. arisanus* has been reported in Hawaii and French Polynesia (Manoukis *et al.* 2014; Vargas *et al.* 2007, 2012, 2013). Likewise, promising results were reported in Africa, where 74% parasitism of *B. dorsalis* by *F. arisanus* was recorded in laboratory tests (Mohamed *et al.* 2010) and up to 40% parasitism on mango, guava, custard apple, and bush mango in field experiments (Ekesi *et al.* 2010, Appiah *et al.* 2014, Ndiaye *et al.* 2015, Mohamed *et al.* 2016, Gnanvossou *et al.* 2017).

The agroecological diversity of the Central African humid tropics offers the possibility of cropping numerous fruit species, including bananas and plantains (*Musa* spp. L. [Zingiberales: Musaceae]), pineapple (*Ananas comosus* L. [Poales: Bromeliaceae]), mango (*M. indica*), guava (*P. guajava* L.), avocado (*Persea americana* Mill [Laurales: Lauraceae]), citrus (*Citrus* spp. L. [Sapindales: Rubiaceae]), papaya (*C. papaya*), among others (Temple 2001, Woin and Essang 2003, Kuate *et al.* 2006, Awodoyin *et al.* 2015). The Central African humid tropics are home to numerous indigenous fruit species, such as *I. gabonensis* and *I. wombulu* that suffer from some of the highest infestations of *B. dorsalis* (Goergen *et al.* 2011, Tchoundjeu *et al.* 2006). The variety of climates in Central Africa also allows some of the fruit species to be available throughout the year. Most of the production in much of Central Africa, however, is home gardens and mixed cropping and agroforestry systems, with scattered small orchards of improved mango and guava varieties (Woin and Essang 2003, Kuate *et al.* 2006). The availability in time and space of host plants and the quantity and quality of their fruits may affect not only the life table parameters of the pest but also its parasitoid (Eben *et al.* 2000, Awmack and Leather 2002, Ero *et al.* 2011, Ayelo *et al.* 2017). In Central Africa where researchers recently introduced *F. arisanus*, host selection behavior and offspring performance are not well documented and need to be assessed, particularly in a context where the species cannot diapause and will, therefore, need exploitable resources throughout the year to persist (Rousse 2007).

The broad objective of our study is to determine how the diversity of cultivated and indigenous fruit species in Central African humid tropics affect the performance of *F. arisanus* on *B. dorsalis*. We used a series of laboratory experiments specifically designed to shed some light on the parasitoid's choice of host fruits and the subsequent events of foraging on the fruits, successful parasitism, and the fitness of their progenies.

Materials and Methods

Experimental Conditions

Laboratory experiments were conducted in the biocontrol insectary of IITA-Cameroon in Nkolbisson, Yaounde (N 03.86403°; E 011.46277°; 769 m). Insectary room temperature and relative humidity were maintained respectively at 25 ± 1°C and 70 ± 5% with natural and fluorescent lighting used to control photoperiod

at 12L:12D. All tests were conducted in Plexiglas cages of two sizes: type I (15 × 15 × 15 cm) and type II (30 × 30 × 30 cm). Natural fruit infestations were conducted to ensure full physical and chemical features. Numbers of *B. dorsalis* and *F. arisanus* used were obtained from preliminary tests set to enable enough eggs for parasitism, where both parasitoids and fruit flies emerged in each fruit exposed. Controls were also set under same conditions in no-choice test.

Insect Cultures and Host Fruits

Populations of *B. dorsalis*

The population of *B. dorsalis* used in this study was initiated from 100 pairs of individuals collected from mango in the mixed-fruit experimental orchard at IITA-Cameroon. The fruit flies were maintained in the laboratory isolated in Plexiglas cages type II for about 10 generations prior to these experiments, with conditions as described above. The laboratory colonies were replenished with about 200 wild individuals (males and females) emerging from mango fruits from the same locality at least once every 6 mo.

Parasitoid Source and Colony Maintenance

The initial cohort of *F. arisanus* was obtained from the University of Hawaii at Manoa, Honolulu, Hawaii through a joint effort between the International Institute of Tropical Agriculture (IITA) and the International Centre of Insect Ecology and Physiology (*icipe*). A cohort of 1,000 adults (approximately 70% females) was shipped to IITA-Benin station in Cotonou, Benin, for mass-production and later 4,500 parasitized pupae were shipped to IITA-Cameroon in April 2010. After releasing in the mixed-fruit experimental orchard at IITA-Cameroon, parasitoids emerging from the incubation of mango and guava fruits were used to establish a new colony in the laboratory.

The parasitoid rearing system consisted of Plexiglas cages in which papaya fruit sections were exposed to a number female *B. dorsalis* and then exposed to 10 adult pairs of *F. arisanus* (7–14 d old) isolated inside a Plexiglas cage type I for 24 h. The adult parasitoids that emerged were reared on papaya supplemented with an artificial diet for about six generations before the experiments described below were initiated. This colony was infused at least once every 3 mo with wild individuals that were collected from releases conducted in Cameroon in a mixed-fruit tree orchard.

Host Fruit Species

Eleven fruit species all known as hosts of *B. dorsalis* were used in this study, including sugar apple (*A. squamosa*), *C. papaya*, loquat [*E. japonica*], African wild mangoes (*I. gabonensis* and *I. wombulu*), *M. indica* var. camerounaise, banana (*Musa acuminata* L. [Zingiberales: Musaceae]) var. Williams, plantain (*Musa paradisiaca* L. [Zingiberales: Musaceae]) var. Essong, avocado (*P. americana*), guava (*P. guajava*), and hog plum (*Spondias cytherea* Sonner [Sapindales: Anacardiaceae]). All fruits were collected from the IITA-Cameroon orchard (N 03.86403°; E 011.46277°; 769 m), except *I. gabonensis* and *I. wombulu*, which were collected respectively from Mbalmayo (N 03.46795°; E 011.48284°; 663 m) and Nkolbisson (N 03.86325°; E 011.45712°; 642 m), and *C. papaya* which was purchased from a local market. To prevent infestations of fruits to be used in the laboratory experiments, *M. indica*, *P. guajava*, *E. japonica*, and *A. squamosa* were bagged on the trees in the mixed-fruit orchards, while *P. americana*, *S. cytherea* (which are rarely infested naturally with *B. dorsalis*) and the two *Irvingia* species, were harvested at the green maturity stage. All fruits were kept

inside paper bags in the laboratory for several days before their use in the experiments to ensure the absence of fruit flies.

Fruit Acceptability and Suitability

Choice assays

Four groups of four fruits each were tested in a series of experiments according to the seasonal availability of the fruit species targeted by this study: 1) mango, guava, *I. wombulu*, and papaya; 2) mango, avocado, *I. wombulu*, and papaya; 3) guava, *I. gabonensis*, loquat, and papaya; and 4) sugar apple, guava, hog plum, and papaya. The need to test in this way was due to differences in the timing of the availability of fruit species. Papaya was always available and therefore was represented in all four groups, followed by guava in groups I, III, and IV, *Irvingia* spp. and mango (groups I and II), while the rest of the fruit species were tested only in one of the groups. Each fruit was weighed and exposed to 15 pairs of naïve *B. dorsalis* adults isolated inside type I cages for 24 h. Due to their size, papaya and sugar apple were divided into sections, while loquat was grouped into four fruits. Immediately following this infestations, the fruits were then randomly arranged inside a type II cage for exposure to *F. arisanus*. Forty naïve *F. arisanus* females, 7–14-d old, were released in the center of each cage and allowed to oviposit for 24 h. During the first 6 h, the number of oviposition attempts was recorded hourly. Our preliminary observations indicated that the full oviposition behavior process of a female requires more than 1 h from antennation to pumping movement. Honey and water were added to each cage. At least six honey droplets (locally sourced) were distributed throughout the inside roof of each cage, and a 30 ml plastic cup fitted with a cotton roll soaked in water was placed inside each cage.

Several parasitoid behaviors were recorded during the first 6 h of parasitoid exposure to fruits, following the approach of Calvitti *et al.* (2002). The noted behaviors included: 1) antennation of fruit surface, 2) cessation of frenzied movements, 3) bending abdomen and inserting ovipositor into fruit, and 4) pumping movements. The behavioral observations were used to quantify female oviposition attempts of *F. arisanus*. Each experiment was repeated eight times with new parasitoids, while fruit position was rotated within repetitions.

At the end of each 24-h exposure period, fruits were removed from the cages and incubated individually in a plastic bucket (450-ml volume) for host suitability study. Fruits were wrapped with tissue paper to remove excess fruit juice and deposited in the incubation unit on dome-shaped wire grids placed on top of a thin layer of moist sand as a medium for pupariating larvae. Incubation units were covered with a fine-mesh cloth fixed with an elastic band to prevent larval escape and arranged on wood shelves in the laboratory. Pupae were collected after 8–12 d of fruit incubation unit and held in plastic Petri dishes (9-cm diameter) at ambient room conditions until adult emergence. Adult emergence was noted daily to check for differences in rates of emergence in relation to treatments. The following responses were used to characterize the suitability of each fruit species to *F. arisanus* oviposition and development: 1) *F. arisanus* per kilogram of fruit; 2) total number of emerged wasps and flies; 3) proportion of females (sex ratio); 4) number of nonemerged pupae, including dead wasps, and 5) percent parasitism of *B. dorsalis*. Parasitism rates of *B. dorsalis* by *F. arisanus* were quantified per fruit species as apparent (APP) and absolute (ABP) parasitism using the following calculations:

$$APP = (\text{Emerged parasitoids}) / (\text{Emerged parasitoids} + \text{Emerged flies}) * 100 \quad (1)$$

$$ABP = (\text{Emerged} + \text{Dead parasitoids}) / (\text{Total pupaeempty pupae}) * 100 \quad (2)$$

No-choice tests

In no-choice tests, the same fruit species were infested by *B. dorsalis*, exposed to *F. arisanus* and handled as in the choice experiments described above, with the following differences: 1) fruit species were individually weighed and exposed in type I cages; 2) 10 7–14-d old *F. arisanus* and 15 *B. dorsalis* were used per replication and represented one cohort; 3) 10 cohorts of fruit flies and parasitoids were used; 4) for each cohort of fruit flies and parasitoids, four fruits of same species were successively exposed for 24 h each to compare daily parasitism rates over a 4-d period. This enabled 10 replicates per day of exposure, however, since later analyses found no differences between the 4 d, the data were grouped to make 40 replicates per fruit species. Also, a similar set of fruits exposed to *B. dorsalis* but not to *F. arisanus* were used as controls to account for natural *B. dorsalis* mortality. The same parameters as in the choice experiment were used to characterize fruit suitability to *F. arisanus* and *B. dorsalis*.

Parasitoid and fruit fly fitness in no-choice tests

We used the following indicator traits to estimate fitness: 1) body and hind tibia lengths of both female and male parasitoids, and female ovipositor length; 2) sex ratio of emerged parasitoids (same as calculated above); and 3) developmental time of parasitoids from host egg deposition to adult emergence. A total of 50 adult female and male wasps were selected per host fruit species for body measurements. A proportion of five females and males were randomly selected per exposed fruit species according to the number of emerged adults. Body length was measured from the head to the tip of the abdomen. Similar measurements were taken for *B. dorsalis* emerging from the control fruits that were unexposed to *F. arisanus*.

Development times from egg to adult (*DT*) of *B. dorsalis* or *F. arisanus* were estimated using the formula $DT = \sum_{i=1}^n NFi * NDi / \sum_{i=1}^n NFi$ where *i* denotes an individual of a total of *n* insects; *NFi* is the daily individual insect emergence; and *NDi* is the duration in days for the development of the *i*th insect from egg to adult emergence.

Data analysis

Generalized linear models (GLMs) with a binomial error (log link) were used to analyze the female oviposition attempts, emergence, parasitism rate, sex ratio, and mortality in fruit species. A GLM with a Poisson error (log link) was also used to determine how numbers of progenies per kilogram were affected by fruit species. In the case of over-dispersion of data, a GLM with a quasi-binomial or quasi-Poisson distribution of errors was used. A GLM with a Gaussian error was used to test the number of progenies per kilogram and fitness parameters in fruit species, while the GLM with Gamma error (log link) was used for developmental time. Fruit species were treated as a fixed effect and replications were considered as a random effect. The likelihood-ratio test based on the Fischer-Snedecor test (over-dispersed data) was used to test the significance of the effects. Tukey HSD was used for pairwise comparisons of means, and Pearson correlation was used to determine the relationships between fitness parameters. All statistical analyses were performed with R version 3.5.1 (R Development CoreTeam 2018).

Results

Host Fruit Acceptability

Female *F. arisanus* showed significant oviposition behavioral differences in each of the host fruit groups in the choice tests (Fig. 1;

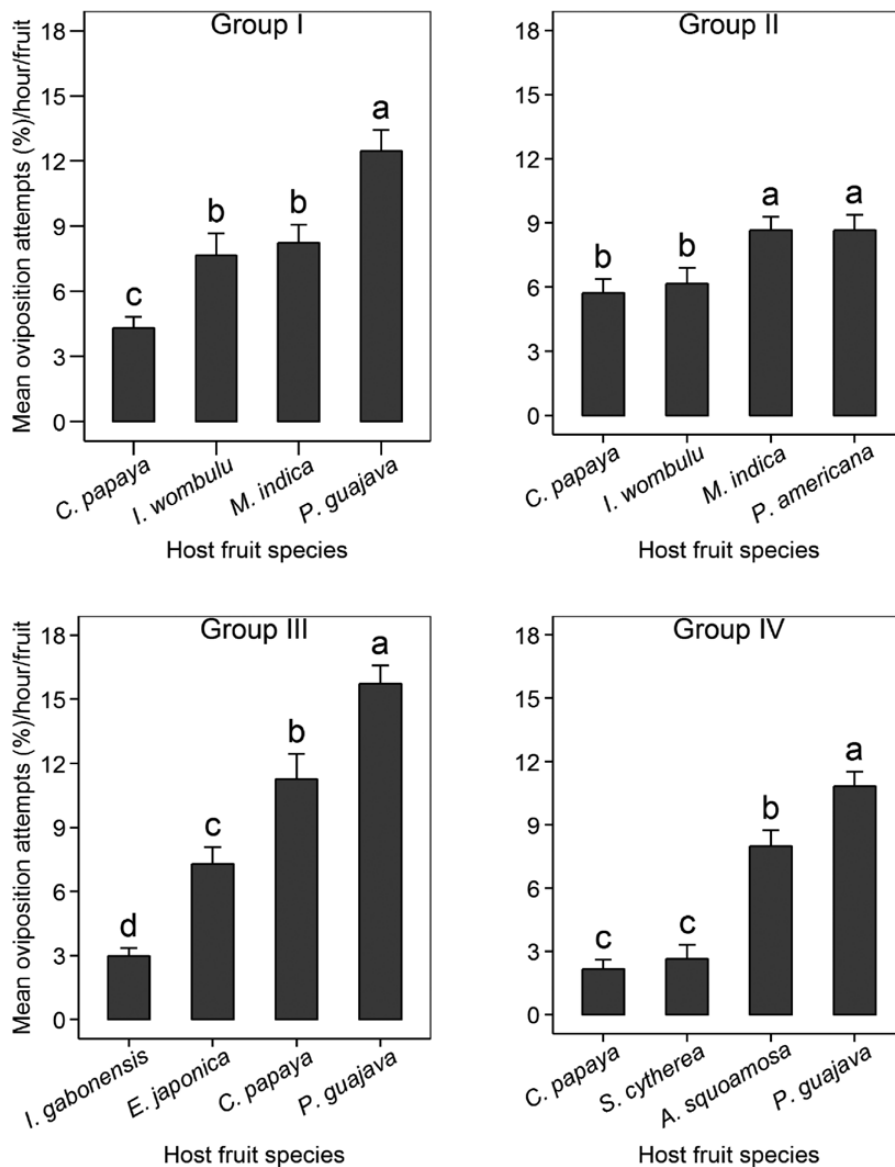


Fig. 1. Mean Percentage of *Fopius arisanus* females exhibiting oviposition behavior in four groups of host fruit species. Means followed by the same letter are not significantly different (Tukey's HSD test, $P < 0.05$).

group I: $F_{3,188} = 15.5$, $P < 0.001$; group II: $F_{3,188} = 5.10$, $P < 0.002$; group III: $F_{3,188} = 45.3$, $P < 0.001$; group IV: $F_{3,140} = 33.8$, $P < 0.001$. The percentage of oviposition attempts was greater on *P. guajava* than on all the other fruits in groups I, III, and IV, respectively, with 12.5, 15.7, and 10.8% female parasitoids displaying oviposition attempts per hour. In group III, however, *F. arisanus* females displayed a significantly higher number of oviposition attempts on *M. indica* and *P. americana* compared with the other host fruits (Fig. 1). Being present in all the four groups, the percentage of oviposition attempts recorded from *C. papaya* varied significantly with the presence of other host fruits ($F_{3,176} = 25.9$, $P < 0.001$).

Fruit suitability for *F. arisanus*

Progeny production

In choice tests, the mean number of parasitoid progeny per kilogram of fruit differed significantly among fruit types in all four groups (Table 1; group I: $F_{3,28} = 4.57$, $P < 0.009$; group II: $F_{3,28} = 7.92$, $P < 0.001$; group III: $F_{3,28} = 6.54$, $P < 0.002$; group IV:

$F_{3,12} = 9.97$, $P < 0.001$). The highest number of progenies was obtained from *I. wombulu* (group II), *I. gabonensis* (group III), and *P. guajava* (groups I and IV) (Table 2). Similarly, adult parasitoid emergence varied significantly within groups (Table 1; group I: $F_{3,28} = 6.56$, $P < 0.002$; group II: $F_{3,28} = 15.1$, $P < 0.001$; group III: $F_{3,28} = 12.2$, $P < 0.001$; group IV: $F_{3,12} = 16.1$, $P < 0.0001$). Sex ratio (proportion of females) was significantly different among fruits only in group III ($F_{3,23} = 8.27$, $P < 0.001$) and group IV ($F_{3,10} = 10.4$, $P < 0.002$) (Table 1). Adult parasitoid mortality in pupae (i.e., nonemerged adults) ranged respectively from 3.0 to 8.4% in group I, 3.5 to 8.3% in group II, 1.7 to 7.8% in group III, and 0 to 1.92% in group IV (Table 1).

In no-choice trials, the mean number of progenies varied significantly across the 11 fruit species exposed to *F. arisanus* (Table 2; $F_{10,380} = 17.0$, $P < 0.001$). The highest number of *F. arisanus* was obtained from *I. gabonensis*, while the lowest was from *S. cytherea* (Table 2). Percent emergence also differed significantly among host fruit species ($F_{10,380} = 24.1$, $P < 0.001$), with the highest emergence obtained from *P. guajava* ($48.5 \pm 3.3\%$) (Table 2). Sex ratio did not differ significantly

Table 1. Influence of fruit species on the mean number of progenies per kilogram of fruit (\pm SE), mean percent adult emergence (\pm SE), mean apparent parasitism rate (\pm SE), mean absolute parasitism rate (\pm SE), and mean percent mortality (\pm SE) of *Fopius arisanus* in choice situation

Host fruit	Progeny kg fruit	Adult emergence (%)	Apparent parasitism (%)	Absolute parasitism (%)	Sex ratio ⁽¹⁾	Mortality (%)
Group I						
<i>I. wombulu</i>	408.4 \pm 171.9a	49.3 \pm 13.4a	67.2 \pm 14.4a	58.2 \pm 13.5a	0.49 \pm 0.09a	3.0 \pm 1.3b
<i>P. guajava</i>	227.8 \pm 50.4ab	47.6 \pm 8.4a	70.5 \pm 5.5a	62.4 \pm 7.0a	0.62 \pm 0.09a	7.5 \pm 2.0ab
<i>M. indica</i>	159.5 \pm 36.8b	29.7 \pm 5.3a	53.8 \pm 9.9a	47.9 \pm 7.3a	0.48 \pm 0.02a	8.4 \pm 1.6a
<i>C. papaya</i>	48.4 \pm 19.5b	6.30 \pm 2.9b	10.1 \pm 3.7b	15.2 \pm 5.7b	0.57 \pm 0.13a	3.5 \pm 1.4b
Group II						
<i>I. wombulu</i>	364.1 \pm 86.9a	52.1 \pm 8.8a	69.7 \pm 9.5a	60.8 \pm 9.3a	0.48 \pm 0.07a	3.5 \pm 1.0b
<i>M. indica</i>	340.7 \pm 111.5a	20.4 \pm 4.3b	49.4 \pm 10.0a	48.2 \pm 5.6a	0.37 \pm 0.06a	8.1 \pm 0.8a
<i>P. americana</i>	90.8 \pm 25.9b	11.0 \pm 2.7bc	24.6 \pm 4.2b	27.1 \pm 4.2b	0.36 \pm 0.03a	6.7 \pm 1.5ab
<i>C. papaya</i>	43.1 \pm 21.0b	5.2 \pm 2.6c	8.15 \pm 3.8b	16.5 \pm 3.4b	0.60 \pm 0.21a	8.3 \pm 2.1a
Group III						
<i>I. gabonensis</i>	618.0 \pm 149.0a	44.6 \pm 5.8a	53.2 \pm 7.3a	46.9 \pm 6.2a	0.53 \pm 0.05b	1.7 \pm 0.8b
Host fruit	Progeny kg fruit	Adult emergence (%)	Apparent parasitism (%)	Absolute parasitism (%)	Sex-ratio ⁽¹⁾	Mortality (%)
<i>C. papaya</i>	410.2 \pm 171.4a	25.7 \pm 5.4b	42.9 \pm 8.8a	33.6 \pm 5.9ab	0.41 \pm 0.05b	5.7 \pm 1.5ab
<i>P. guajava</i>	364.9 \pm 26.4a	41.7 \pm 4.6a	45.4 \pm 4.8a	44.4 \pm 4.5a	0.46 \pm 0.06b	1.8 \pm 0.4b
<i>E. japonica</i>	49.7 \pm 21.6b	8.7 \pm 2.9b	17.1 \pm 6.2b	19.1 \pm 5.9b	0.87 \pm 0.08a	7.8 \pm 3.0a
Group IV						
<i>P. guajava</i>	153.1 \pm 16.8a	36.4 \pm 4.7a	42.0 \pm 6.9a	40.8 \pm 4.5a	0.47 \pm 0.10b	1.9 \pm 1.9a
<i>A. squamosa</i>	72.1 \pm 43.4a	28.3 \pm 2.2a	39.3 \pm 4.1a	35.5 \pm 2.8a	0.38 \pm 0.09b	0.8 \pm 0.5a
<i>C. papaya</i>	16.8 \pm 5.9b	21.3 \pm 4.4b	23.2 \pm 5.2b	23.2 \pm 5.2ab	0.61 \pm 0.06b	0.0a
<i>S. cytherea</i>	6.4 \pm 0.4b	7.0 \pm 0.4c	9.2 \pm 0.7c	8.0 \pm 0.5c	1.00 \pm 0.00a	0.0a

¹Proportion of females. Mean values (\pm SE) in the same column followed by the same letter are not significantly different in each group (Tukey's HSD, $P = 0.05$).

Table 2. Influence of fruit species on the mean number of progenies per kilogram of fruit (\pm SE), mean percent adult emergence (\pm SE), mean apparent parasitism rate (\pm SE), mean absolute parasitism rate (\pm SE), and mean percent mortality (\pm SE) of *Fopius arisanus* in no-choice situation

Host fruits	Progeny per kg	Adult emergence (%)	Apparent parasitism (%)	Absolute parasitism (%)	Sex ratio ⁽¹⁾	Mortality (%)
<i>I. gabonensis</i>	565.7 \pm 98.4a	43.8 \pm 3.6ab	52.5 \pm 4.1ab	49.5 \pm 4.0ac	0.57 \pm 0.02a	1.9 \pm 0.4df
<i>A. squamosa</i>	329.0 \pm 72.9b	35.8 \pm 4.2bc	50.3 \pm 5.4abc	41.0 \pm 4.6bcd	0.48 \pm 0.03a	1.6 \pm 0.3ef
<i>M. acuminata</i>	328.3 \pm 56.0b	33.0 \pm 3.7cd	55.0 \pm 4.3ab	53.2 \pm 4.2ab	0.51 \pm 0.03a	6.6 \pm 1.3a
<i>M. paradisiaca</i>	316.8 \pm 58.5b	24.5 \pm 3.5de	32.7 \pm 4.5d	35.0 \pm 4.1d	0.56 \pm 0.04a	4.3 \pm 0.9bc
<i>P. guajava</i>	311.4 \pm 58.3b	48.5 \pm 3.3a	58.8 \pm 3.5a	56.0 \pm 3.4a	0.53 \pm 0.02a	3.0 \pm 0.5cef
<i>E. japonica</i>	233.1 \pm 35.4bc	38.9 \pm 5.3ac	64.1 \pm 6.7a	49.0 \pm 5.7ac	0.54 \pm 0.05a	2.2 \pm 0.7cef
<i>I. wombulu</i>	173.3 \pm 26.2cd	36.7 \pm 3.6bc	61.4 \pm 5.0a	55.5 \pm 4.7a	0.47 \pm 0.04a	4.0 \pm 0.7bde
<i>M. indica</i>	147.8 \pm 22.8cd	23.1 \pm 2.5e	44.3 \pm 5.2bd	38.7 \pm 3.9cd	0.45 \pm 0.02a	5.3 \pm 0.8ab
<i>P. americana</i>	99.9 \pm 26.4d	16.4 \pm 2.9e	36.1 \pm 5.2cd	30.9 \pm 4.4d	0.52 \pm 0.05a	2.0 \pm 0.6cef
<i>C. papaya</i>	27.3 \pm 5.6e	4.1 \pm 0.7f	5.6 \pm 1.0f	6.2 \pm 0.8f	0.51 \pm 0.06a	1.4 \pm 0.2f
<i>S. cytherea</i>	22.1 \pm 6.5e	7.5 \pm 1.8f	20.0 \pm 4.8e	16.7 \pm 3.7e	0.54 \pm 0.10a	4.1 \pm 1.2be

¹proportion of females. Mean values (\pm SE) in the same column followed by the same letter are not significantly different (Tukey's HSD, $P = 0.05$).

among host fruits tested ($F_{10,282} = 1.04$, $P = 0.410$) (Table 2); however, *F. arisanus* mortality inside pupae varied significantly among fruits ($F_{10,380} = 5.02$, $P < 0.001$), with the highest mortality recorded on banana (6.6 \pm 1.3%) and the lowest on *C. papaya* (1.4 \pm 0.2%).

Percentage parasitism

In the choice experiments, apparent parasitism rates were significantly different within all tested fruit groups (Table 1; group I: $F_{3,28} = 8.42$, $P < 0.0003$; group II: $F_{3,28} = 12.1$, $P < 0.001$; group III: $F_{3,28} = 4.97$, $P < 0.007$; group IV: $F_{3,12} = 11.9$, $P < 0.001$), with highest apparent parasitism rates recorded on *P. guajava* (group I and group IV), *I. wombulu* (group II), and *I. gabonensis* (group III) (Table 1). Absolute parasitism rates also differed significantly among fruits in groups (Table 1; group I: $F_{3,28} = 5.63$, $P < 0.004$; group II: $F_{3,28} = 10.7$, $P < 0.001$; group III: $F_{3,28} = 4.79$, $P < 0.008$; group IV: $F_{3,12} = 11.6$, $P < 0.001$). Between group comparisons did not reveal any significant difference (but with numerical difference)

in either apparent parasitism ($F_{3,108} = 2.32$, $P = 0.079$) or absolute parasitism ($F_{3,108} = 2.48$, $P = 0.065$). Since papaya occurred in all the four groups, the statistical analysis indicated that apparent parasitism rate in this fruit species varied significantly with the presence of other host fruit species ($F_{3,24} = 7.60$, $P < 0.001$), but absolute parasitism rate in papaya was unaffected by the presence of other fruit species ($F_{3,24} = 0.63$, $P = 0.073$).

In the no-choice tests, apparent parasitism rates ranged from 5.63 \pm 0.99% to 64.1 \pm 6.67% (Table 2), with significant differences among exposed host fruits ($F_{10,380} = 17.8$, $P < 0.001$) (Table 2). Differences in absolute parasitism rates among fruits (Table 3; $F_{10,380} = 19.2$, $P < 0.001$) allowed the classification of fruit species into three groups of fruit preferences by *F. arisanus*: 1) fruits with highest parasitism rates ($\geq 50\%$)—*P. guajava*, 56.0%; *I. wombulu*, 55.5%; banana 53.1%; 2) fruit with parasitism rates ranging from 20 to 50%—*I. gabonensis* (49.5%), *E. japonica* (49.0%), *A. squamosa* (41.0%), *M. indica* (38.7%),

Table 3. Development time (days; mean \pm SE) of *Fopius arisanus* and its host fly *Bactrocera dorsalis* reared on eleven fruit species

Fruit species	<i>F. arisanus</i> developmental time (days)		<i>B. dorsalis</i> developmental time (days)	
	Female	Male	Female	Male
<i>E. japonica</i>	27.4 \pm 0.6a	26.4 \pm 0.5a	26.2 \pm 0.6a	25.9 \pm 0.6a
<i>S. cytherea</i>	26.3 \pm 0.8b	25.1 \pm 0.6b	23.9 \pm 0.5c	23.8 \pm 0.5c
<i>P. guajava</i>	26.2 \pm 0.4c	24.7 \pm 0.4c	23.9 \pm 0.3c	23.8 \pm 0.3c
<i>I. wombulu</i>	25.5 \pm 0.3d	23.8 \pm 0.3e	25.2 \pm 0.6b	25.5 \pm 0.7b
<i>M. indica</i>	25.4 \pm 0.5d	24.6 \pm 0.5d	22.4 \pm 0.4e	22.5 \pm 0.5e
<i>I. gabonensis</i>	24.7 \pm 0.4e	23.0 \pm 0.4f	22.8 \pm 0.4d	23.0 \pm 0.4d
<i>M. acuminata</i>	24.0 \pm 0.3f	22.0 \pm 0.2h	20.5 \pm 0.2g	20.5 \pm 0.2g
<i>M. paradisiaca</i>	23.5 \pm 0.3g	22.0 \pm 0.3i	19.9 \pm 0.3h	20.1 \pm 0.3h
<i>P. americana</i>	23.3 \pm 0.3h	22.4 \pm 0.4g	21.8 \pm 0.4f	22.1 \pm 0.5f
<i>A. squamosa</i>	21.8 \pm 0.4i	20.1 \pm 0.4j	19.5 \pm 0.3i	19.4 \pm 0.3i
<i>C. papaya</i>	21.4 \pm 0.4j	20.0 \pm 0.2k	18.6 \pm 0.2j	18.7 \pm 0.2j

Mean values (\pm SE) in the same column followed by the same letter are not significantly different (Tukey's HSD, $P = 0.05$).

plantain (35.0%), and *P. americana* (30.9%); and 3) fruit species with lowest parasitism rates ($< 20\%$)—*S. cytherea* (16.7%) and *C. papaya* (6.2%).

In the no-choice experiment, we were able to evaluate changes in absolute parasitism per fruit type over four consecutive days of exposure times (i.e., same parasitoids were exposed to a new batch of fruit type over 4 d). Absolute parasitism for all fruit types did not change over the 4-d duration of the trial ($F_{3,387} = 0.93$, $P = 0.428$).

Fopius arisanus and *B. dorsalis* body size

The influence of host fruit on three physical body parameters—the hind tibia, ovipositor length, and body length—of *F. arisanus* was determined in the no-choice laboratory experiment described above and in the control fruit experiments for *B. dorsalis* that were not exposed to *F. arisanus*. For *F. arisanus*, body and tibia lengths of both females and males, and ovipositor length of females were highly affected by fruit species ($F_{10,687} = 46.3, 31.8, \text{ and } 18.2, P < 0.001$ for females; and $F_{10,687} = 49.5 \text{ and } 40.7, P < 0.001$ for males; Figs 2–4). Overall, body and hind tibia lengths were correlated (Females: $r = 0.806, P < 0.001$; males: $r = 0.788, P < 0.001$) and female body length was correlated with ovipositor length ($r = 0.659, P < 0.001$). Body and hind tibia lengths of *F. arisanus* females and males that emerged from *M. indica* were significantly larger than those emerging from other host fruits. Interestingly, ovipositor lengths of females that emerged from *A. squamosa* were significantly longer than those from other fruits, with ovipositor lengths being the shortest for females emerging from *P. americana* and *E. japonica* (Fig. 4).

For *B. dorsalis*, female and male body and hind tibia lengths were also affected by fruit type (Figs 5 and 6; female body length: $F_{10,747} = 149.1, P < 0.001$; female hind tibia length: $F_{10,747} = 307.0, P < 0.001$; male body length: $F_{10,747} = 294.7, P < 0.001$; male hind tibia, $F_{10,747} = 281.8, P < 0.001$), with those emerging from *M. indica* exhibiting the longest female body length and males emerging from *C. papaya* had the longest body length. Males that emerged from *A. squamosa* and females obtained from *M. indica* had significantly longer hind tibia length than all males that emerged from all other fruits (Fig. 5). As for *F. arisanus*, female and male body lengths of *B. dorsalis* were highly correlated with hind tibia lengths (Females: $r = 0.671, P < 0.001$; males: $r = 0.566, P < 0.001$). Interestingly, however, *B. dorsalis* body lengths formed two distinct clusters, with a body length of individuals that emerged from *P. americana* and *I. wombulu* being of the shortest body length (2.19–2.28 mm) while those that emerged from the other fruit types were spread within the second cluster (6.49–7.18 mm).

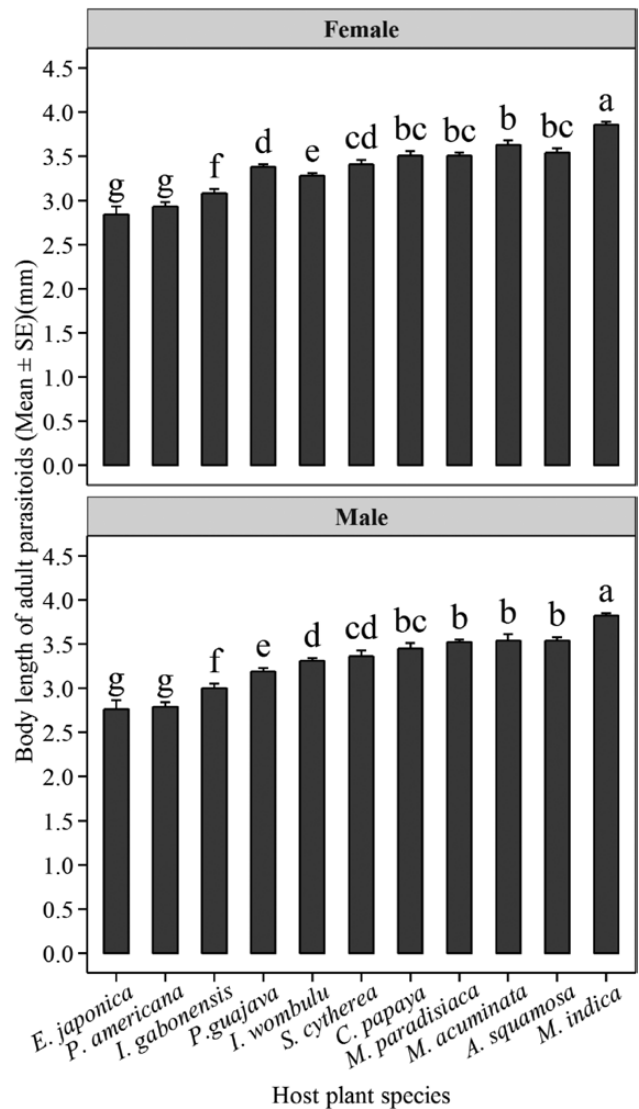


Fig. 2. Female and male body lengths (mm; mean \pm SE) of *Fopius arisanus* reared on *Bactrocera dorsalis* on different host fruit species. Means followed by the same letter are not significantly different (Tukey's HSD test, $P < 0.05$).

Fopius arisanus completed development in all the host fruit species tested (Table 3). However, its developmental time varied

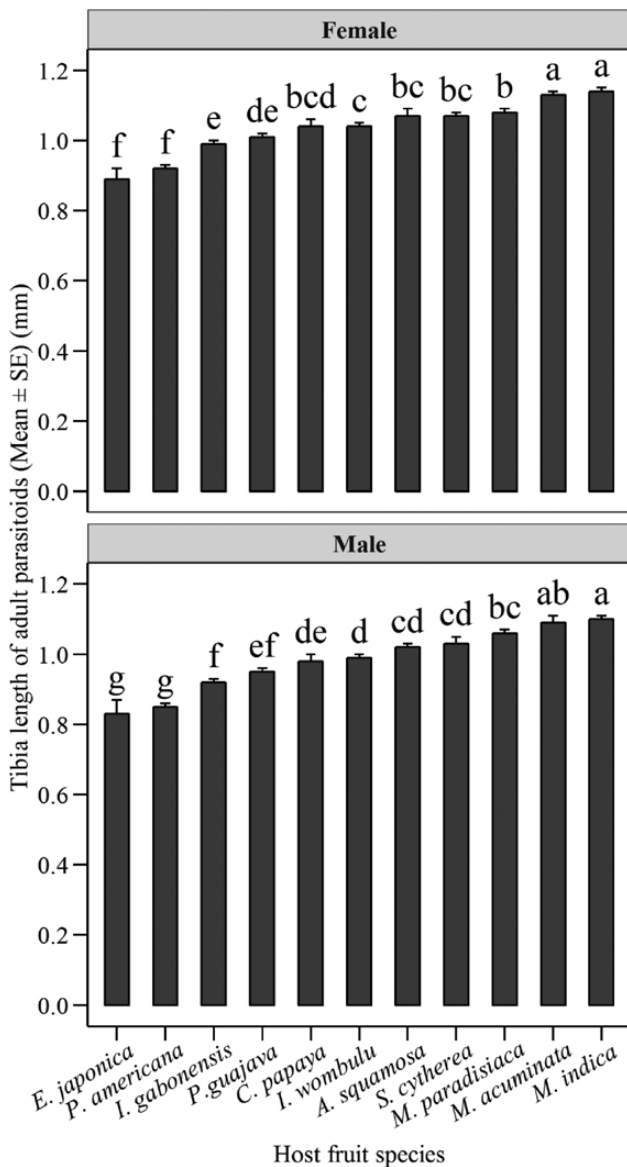


Fig. 3. Female and male hind tibia lengths (mm; mean ± SE) of *Fopius arisanus* reared on *Bactrocera dorsalis* on different host fruit species. Means followed by the same letter are not significantly different (Tukey's HSD test, $P < 0.05$).

significantly among fruit species (females: $F_{10,261} = 19.0$, $P < 0.001$; males: $F_{10,290} = 27.0$, $P < 0.001$). Both female and male wasps developed faster on *C. papaya* and *A. squamosa*, while in *E. japonica* development was slow (Table 3).

Development time of the host fly *B. dorsalis* ranged from 18.6 ± 0.61 d to 26.2 ± 0.63 d and from 18.7 ± 0.20 d to 25.9 ± 0.59 d for females and males, respectively (Table 3) and varied significantly among host fruits (Females: $F_{10,307} = 39.7$, $P < 0.001$; males: $F_{10,305} = 39.0$, $P < 0.001$). Development time was significantly longer for flies emerging from *E. japonica* than those emerging from the other host fruits (Table 3).

Discussion

In this study, we demonstrated how naive adult *F. arisanus* females discriminated between *B. dorsalis* eggs-infested host fruit species in

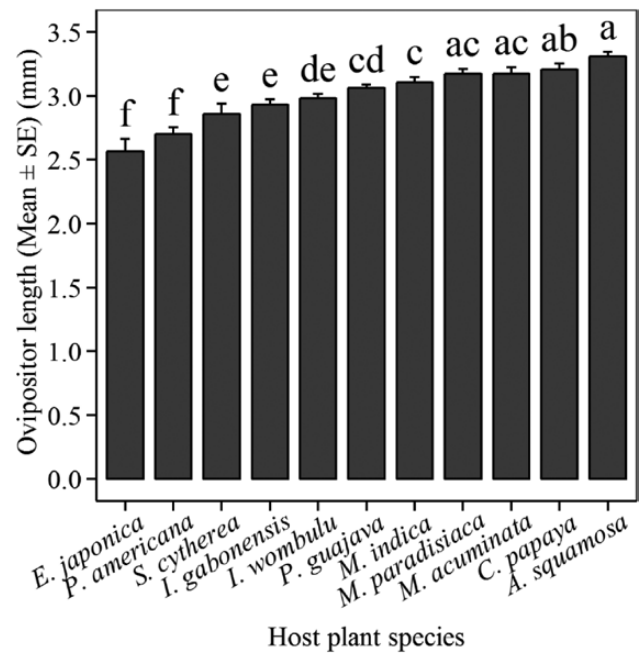


Fig. 4. Ovipositor length (mm; mean ± SE) of female *Fopius arisanus* reared on *Bactrocera dorsalis*. Means followed by the same letter are not significantly different (Tukey's HSD test, $P < 0.05$).

laboratory choice tests. We found that *P. guajava* in group I and IV, *I. wombulu* in group II and *I. gabonensis* in group III were more preferred for oviposition than all other fruits included in the experiments. This oviposition preference was correlated with the parasitism level. We hypothesize that odors emitted from wild mangoes (*I. wombulu* and *I. gabonensis*) and *P. guajava* (as well as their size and color) when infested by host fly, associated with host fly cues may have increased attractiveness to *F. arisanus*. While using same parasitoid species and same host insect species, fruit fly attacks on different host fruits are expected to lead to production of different herbivore-induced plant volatiles (HIPVs) that are expected to elicit different levels of responses in the higher trophic level (Gebreziher 2018, Turlings and Erb 2018). Physical features and volatile chemicals from host plants are known to be important cues for orientation by parasitoids during foraging for oviposition opportunities, and for adult food and mating sites (Greany et al. 1977, Messing and Jang 1992, Caron et al. 2008, Stuhl et al. 2011, Pérez et al. 2012, Segura et al. 2012, Mohamed et al. 2016). Further studies are, therefore, warranted to identify the key compounds in *I. wombulu*, *I. gabonensis* and *P. guajava* and exploit possibilities to use them to recruit the parasitoid for timely control of fruit flies. In contrast, the parasitism of *B. dorsalis* by *F. arisanus* in *P. americana* did not correspond with the percentage of oviposition attempts observed, meaning that the high attractiveness of the parasitoid to a fruit alone is not enough to guarantee successful parasitization of the host (Bautista and Harris 1996).

Despite differences of fruit size and quality, *F. arisanus* successfully emerged from all infested host fruit species exposed in both choice and no-choice tests. Under artificial conditions, adult female *F. arisanus* lay their eggs in almost all the fruits exposed to them and, in most cases, the larvae become viable adults (Rousse 2007). *Fopius arisanus* has been classified as a generalist parasitoid that can develop on approximately 78 host fruits belonging to 36 families, including all the fruit species and families tested in this study (Rousse 2007, Gnanvossou et al. 2016). These data are unfortunately qualitative and give us no

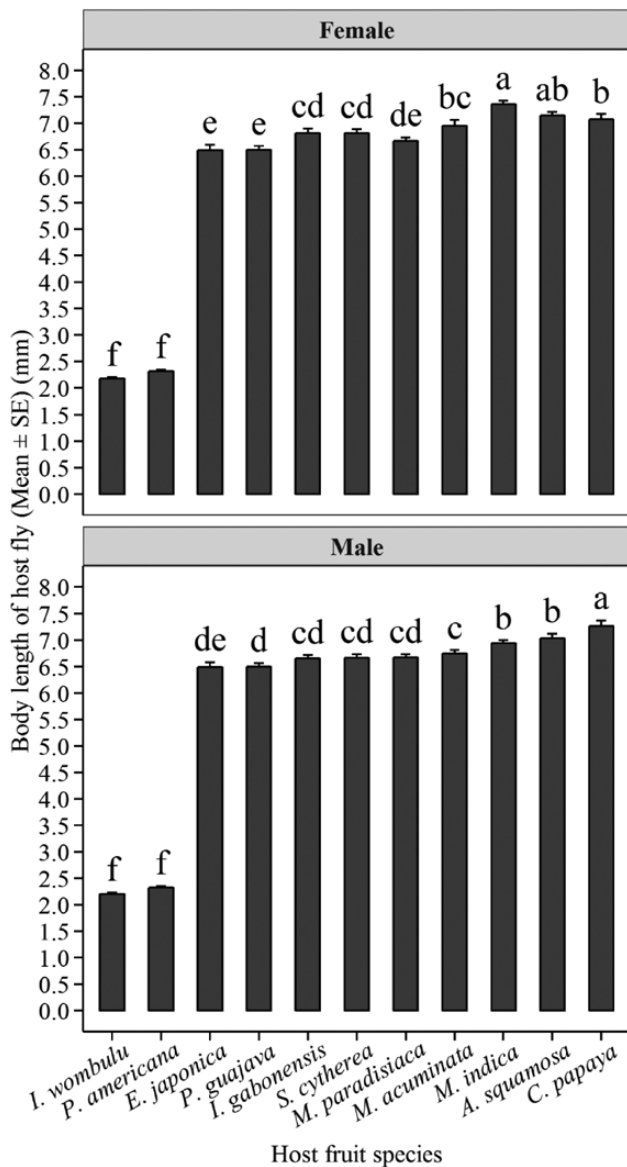


Fig. 5. Female and male body lengths (mm; mean \pm SE) of *Bactrocera dorsalis* reared on various host fruits. Means followed by the same letter are not significantly different (Tukey's HSD test, $P < 0.05$).

idea on the actual parasitoid's performance and distribution on these host fruit species in nature. The microenvironment location behavior of *F. arisanus* appears to be plastic, and its capacity to develop on a given host fruit can be modified (Dukas and Duan 2000, Rouse 2007). Further field studies are warranted to elucidate this.

Results from choice tests indicated that *I. wombulu* in group I and group II, *I. gabonensis* in group III and *P. guajava* in group IV produced more progeny per kilogram of fruit, while in no-choice tests, the rank order of progeny production was *I. gabonensis* > *A. squamosa* > *M. acuminata* > *M. paradisiaca* > *P. guajava*. The results also show that *B. dorsalis* infesting wild mangoes (*I. gabonensis* and *I. wombulu*) and *P. guajava* was more parasitized than in other host fruit species in both tests. The higher oviposition attempts reported in our choice tests on these host fruits, together with their nutritional status and flesh texture are factors that may determine their suitability for larval development, resulting in high parasitism rates. In laboratory conditions, Mohamed *et al.* (2010) and Bautista and Harris (1996) reported a parasitism rate of 74.3% in mango

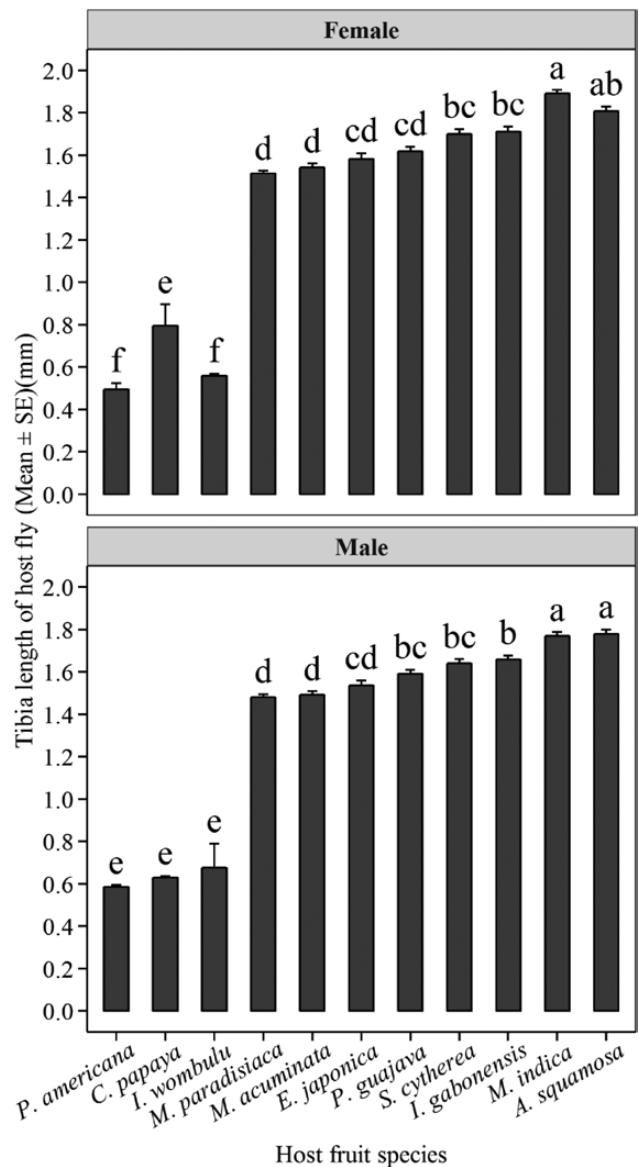


Fig. 6. Female and male hind tibia lengths (mm; mean \pm SE) of *B. dorsalis* reared on various host fruits. Means followed by the same letter are not significantly different (Tukey's HSD test, $P < 0.05$).

and 72.0% in *P. guajava* infested by *B. dorsalis* in no choice experiments. These results differed from those recorded on the same fruits in our study, probably due to differences in the experimental set-ups. By contrast, in field studies in Hawaii and Benin, *F. arisanus* parasitism of *B. dorsalis* is respectively 54.7% in *P. guajava* and 46.5% in *I. gabonensis* (Eitam and Vargas 2007, Gnanvossou *et al.* 2016), which are close to the parasitism rate obtained in our study.

On the other hand, progeny per kilogram of fruit, adult emergence and parasitism rates recorded on *C. papaya* and *S. cytherea* were lower in both experiments. These results were lower than the 53% parasitism reported by Bautista and Harris (1996) and closer to 22.4% parasitism reported by Eitam and Vargas (2007) when *B. dorsalis* eggs were in *C. papaya*. This low performance on papaya was despite the fact that it was used as rearing host for colonies of fruit fly and parasitoid used in this experiment. The parasitoid did not therefore exhibit any learning behavior on this host. Low infestation rates by the host fly *B. dorsalis* reported on papaya throughout tropical Africa (Goergen *et al.* 2011, Cugala *et al.* 2017) could have

affected the parasitism rates by *F. arisanus*. It is possible that parasitized host fly larvae need nutrients that are not optimally available in *C. papaya* when used alone, because during our mass rearing the laboratory, papaya was supplemented with an artificial diet (Ekesi and Mohamed 2011).

Fruit fly diet is known to affect the longevity, daily survival, size, and progeny of their parasitoids, due to their continuous feeding after parasitization (Eben *et al.* 2000; Ero *et al.* 2010, 2011; Ayelo *et al.* 2017). We found that *M. indica* and *A. squamosa* exposed to the host fly *B. dorsalis* produced adult flies with larger body size. The nutritional status of these host fruits associated with their flesh texture may explain the success of larval development. *Mangifera indica* and *A. squamosa* have been reported to be most utilized by *B. dorsalis* across Africa (Rwomushana *et al.* 2008, N'Dépo *et al.* 2009, Goergen *et al.* 2011). Consequently, *F. arisanus* took advantage by producing better quality parasitoid favored by more resources contained in parasitized host fly larvae. The parasitoid quality was represented by body, hind tibia, and ovipositor lengths, which appear to play an important role in the ability of the adult parasitoids to move actively and to reproduce and respond to chemical complexity in an environment (Visser 1994, Sarfraz *et al.* 2009, Wäschke *et al.* 2013). Studies on other parasitoids indicated that larger females showing higher walking speeds parasitized more eggs, although this hypothesis is yet to be tested on *F. arisanus* (Pitcairn and Gutierrez 1992, Jervis and Copland 1996, Bennett and Hoffmann 1998, Oslow and Andow 1998, Sagarra *et al.* 2001). In our study, the fitness characteristics of parasitoid offspring did not match the parasitism level recorded on different host fruit species. *Psidium guajava* and *Irvingia* spp., which had the highest parasitism rates, produced adults with intermediate fitness parameters. This inconsistency in parasitism rate and offspring fitness could be because *P. guajava* and *Irvingia* spp. were smaller in size and/or have higher progeny number compared with *M. indica* and *A. squamosa*. However, further studies are warranted to elucidate this as well as document effect of fruit species on daily survival and longevity.

The parasitoid sex ratio was balanced among host fruit species tested in no-choice tests. Previous studies in the same conditions reported that the proportion of female parasitoids reared on *B. dorsalis* was 0.59 on *M. indica* and 0.63 on *C. papaya*. These results differ from 0.45 and 0.51 recorded on *M. indica* and *C. papaya* in our conditions may be because of differences between methodologies. In choice trials, however, the sex ratio was female-biased on *E. japonica* in group III and *S. cytherea* in group IV. Probably, the presence of a lower proportion of host eggs to be parasitized in fruit tested could skew the sex ratio, as indicated with the low number of pupae per kilogram. While these are mixed results, a balanced or female-biased sex ratio in parasitoids shows demography stability and higher efficiency of host fly population control compared to male-biased one, as only females contribute directly to pest mortality (Ode and Heinz 2002, Chow and Heinz 2005).

Parasitoid developmental time was shown to vary with host fruit species on which *B. dorsalis* fed. Similar results have been reported repeatedly for the majority of solitary parasitoids (Werren *et al.* 1992, Leather *et al.* 2005, Sétamou *et al.* 2005, Caron *et al.* 2008). For example, female and male parasitoids completed development time in 22.9 and 21.1 d, respectively, when *B. dorsalis* eggs were found in *C. papaya* (Bautista *et al.* 1998), values closer to those reported in our study. The preimaginal developmental time was longer for both sexes of *F. arisanus* and its host fly on *E. japonica*. Our results were corroborated by Harvey and Strand (2002), who showed that parasitoid offspring always displayed a lag phase in development when reared in a smaller host as observed on *E. japonica*.

In contrast, *F. arisanus* showed the opposite strategy of minimizing the development time in *C. papaya* and *A. squamosa*, where the parasitoid body length was longer. Intermediate between these extremes was fruit species where parasitoid development was optimum. These results suggest that parasitoid body size and development time vary with host fly feeding ecology and may have an impact on the population dynamics of the parasitoid. Above all, our study indicates that the successful development of *F. arisanus* in fruit species tested under laboratory conditions is promising for its release in Central African humid tropics.

In this study, we showed that *F. arisanus* could parasitize *B. dorsalis* in a wide range of host fruits that are widely distributed in the Central African humid tropics. On this basis, the parasitoid is expected to establish permanently due to the presence of numerous different suitable fruit species having different phenologies. The African wild mango fruits, which induced the highest attractive response and intermediate fitness characteristics in our study, are widely spread and could constitute an important reservoir of parasitoid populations, primarily since wild mangoes have been domesticated and distributed widely (Tchoundjeu *et al.* 2006). Wild mangoes offer another advantage in that, only the seeds are harvested, while the pulp is left under the trees, allowing the continuation of the development of both host fruit fly and parasitoids. Guava, mango, banana, and plantain are cropped for commercial purposes and constitute a refuge for *F. arisanus* populations. However, the disadvantage of these fruit species lies in the fact that their harvest is intended to direct consumption, which reduces both parasitoid and host fly populations significantly. For the mass-rearing purposes of the parasitoid in the laboratory, banana, which showed the third best rate of absolute parasitism in no-choice tests, could serve as a suitable substrate for larval development. Additionally, the fruit is available throughout the year. On the contrary, *B. dorsalis* was poorly parasitized when it laid eggs in *C. papaya*, *S. cytherea*, *P. americana*, and we could consider these host fruit as imperfect host fruits for the establishment and persistence of the wasp in nature. Based on the seasonality of the different fruit species used in this study and the polyphagy and multivoltinism status of *B. dorsalis*, *F. arisanus*, with its high dispersal ability, may persist and spread in habitats where these fruit species are widely distributed. In mixed fruit orchards that include a combination of fruit species that are attractive to *F. arisanus*, females could be used to facilitate the establishment and persistence of the parasitoid. Further studies are also warranted to identify the chemical compound(s) emitted by infested fruits that can induce high parasitism of the female parasitoids.

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