Evaluation of the impact of *Diachasmimorpha longicaudata* on *Bactrocera invadens* and five African fruit fly species

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Bactrocera invadens, *Ceratitis*, new associations, opiine, Tephritidae

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Abstract

Diachasmimorpha longicaudata (Ashmead), a solitary koinobiont larval–prepupal endoparasitoid of fruit flies, was introduced into Kenya for testing and final release against the recently discovered invasive species, *Bactrocera invadens* Drew, Tsuruta and White in Africa. Laboratory experiments were conducted to determine host preference, host acceptability for oviposition and physiological suitability of *B. invadens* and five other indigenous tephritid fruit fly species – *Ceratitis capitata* (Wiedemann), *Ceratitis cosyra* (Walker), *Ceratitis rosa* Karsch, *Ceratitis fasciventris* (Bezzi) and *Ceratitis anonae* Graham – for the development of *D. longicaudata*. Females of *D. longicaudata* visited all host-larval patches, and were also attracted to these hosts at comparable levels. Acceptability, successful development of parasitoid progenies and their sex ratio varied widely across hosts. *C. capitata* yielded the highest parasitoid numbers whereas *B. invadens* was the only host that yielded a female-biased sex ratio. Larvae of *B. invadens*, *C. rosa*, *C. fasciventris* and *C. anonae* mounted differential immune reaction towards *D. longicaudata* eggs. Although, the parasitoid performed poorly on the target host *B. invadens*, it was able to form new association with *C. cosyra* and *C. capitata*. The prospect of using this parasitoid in biological control of African indigenous fruit flies is discussed.

Introduction

Frugivorous tephritid fruit flies are major threat to fruit and vegetable production and export wherever they occur (White and Elson-Harris 1992; Purcell 1998). However, their effect is particularly felt in Africa at all levels of the production chain, as the large majority of fruit and vegetable producers are small-scale farmers who cannot afford expensive control measures. Consequently, fruit flies can cause the loss of entire fruit and/or vegetable harvest, either directly through yield loss or through loss of export potential. This in turn negatively affects the national economy of many African countries, which rely mostly on agriculture (mainly horticulture).

In addition to the native fruit fly pest complex (mainly *Ceratitis* and *Dacus* species), which African farmers have struggled to control, four Asian species of the genus *Bactrocera* Macquart (with two species appearing within a span of 3 years) have invaded the continent, further compounding the problem. These, in the order of their invasions, are *Bactrocera cucurbitae* (Coquillett), *Bactrocera zonata* (Saunders) (CABI 1996; Hashem et al. 2001), *Bactrocera invadens* Drew, Tsuruta and White (Lux et al. 2003; Drew et al. 2005; R. Hanna, unpublished data), and more recently *Bactrocera latifrons* (Hendel) (Mwatawala et al. 2007; S. Ekesi, unpublished data). *Bactrocera cucurbitae* and *B. latifrons* are vegetable pests while the other two species are mainly fruit pests.

Bactrocera invadens, which was initially thought to be *Bactrocera dorsalis* (Hendel), was first recorded in Africa from the Kenyan coast in 2003 (Lux et al. 2003). Since then, this insect has rapidly spread across the African continent. Presently, it has been reported from 24 other countries (Drew et al. 2005; Vayssières et al. 2005; Ekesi et al. 2006). *B. invadens* infests over 39 plant species but mango, *Mangifera*

indica L. (Anacardiaceae) is the most preferred cultivated host plant (Ekesi et al. 2006). Among the non-cultivated plants, marula, *Sclerocarya birrea* (A.Rich) Hochst. (Anacardiaceae) and Indian almond, *Terminalia catappa* L. (Combretaceae) have been reported to be the most infested hosts (Ekesi et al. 2006; Mwatawala et al. 2006; Rwomushana et al. 2008). Meanwhile, the pest continues to expand its geographical and host ranges. For example, unripe banana, *Musa sapientum* L. (Musaceae) (M. Elhiwaris, unpublished data) and avocado, *Persea americana* Miller (Lauraceae) (S. Ekesi, unpublished data) were reported to be attacked by this pest. *B. invadens* not only possess some characteristics of *k-strategy*, which include being very aggressive, adapting well to new environment and being a strong competitor (I. Rwomushana, unpublished data), but also exhibit some traits of *r-strategy*, such as high fecundity (Ekesi et al. 2006). These traits have led to the displacement of the native fruit fly *Ceratitis cosyra* by *B. invadens* especially in lowland areas in Kenya and in the humid agro-ecologies of western Africa (S. Ekesi, unpublished data; R. Hanna, unpublished data).

As an immediate response to the establishment of this pest in Africa, the impact of three solitary and one gregarious native parasitoid species on *B. invadens* was evaluated. However, none was found to be effective as all or most of the eggs of these parasitoid species were encapsulated (Mohamed et al. 2006; S. Mohamed, unpublished data). Being an alien pest, with the native parasitoid species (at least for the tested species) incapable of counteracting its immune response, the ideal alternative was to identify a co-evolved parasitoid of this pest. This is an activity we are currently undertaking in Sri Lanka, the putative home of this pest (Drew et al. 2005). Another approach was to introduce parasitoid species of fruit flies that are closely related to *B. invadens* from already established parasitoid colony.

Diachasmimorpha longicaudata (Ashmead) (Hym., Braconidae), is a solitary koinobiont larval–prepupal endoparasitoid of fruit flies. This species is native to the Indo-Pacific region, where it parasitizes at least 14 tephritid species of the genus *Bactrocera* (Wharton and Gilstrap 1983). The parasitoid was originally introduced into Hawaii from the Malaysia–Philippine region between 1947 and 1952 for the biological control of *B. dorsalis* following its accidental introduction and establishment in Hawaii (Clausen et al. 1965). On Oahu, Hawaii, a 50% reduction in *B. dorsalis* was observed a year after the release of *D. longicaudata* and *Fopius vandenboschi* (Fullway) (Hym., Braconidae) (Purcell 1998). These parasitoids, together with *Fopius arisanus* (Sonan) (Hym., Braconidae), have been credited for the most successful biological control programme ever undertaken against tephritid fruit flies (van den Bosch et al. 1951; Newell and Haramoto 1968). From Hawaii, *D. longicaudata* was introduced to several other countries for control of various fruit fly species of different genera. This parasitoid species is considered successfully established in most countries, such as Colombia, Costa Rica, Guatemala, El Salvador, Mexico (López et al. 1999), Nicaragua, Trinidad, United States of America (Florida), Venezuela (Ovruski et al. 2000) and Brazil (Purcell 1998). Inspired by these encouraging results, the parasitoid was introduced from Hawaii by the International Centre of Insect Physiology and Ecology (ICIPE) to Kenya and was kept at the quarantine facility of Animal Rearing and Containment Unit for testing and final release against *B. invadens* in Africa.

The overall objective of the present study was to assess the effectiveness of *D. longicaudata* in parasitizing *B. invadens* and its potential impact on the major indigenous *Ceratitis* (Dipt., tephritidae) species (*Ceratitis cosyra* (Walker), *Ceratitis capitata* (Wiedemann), *Ceratitis rosa* Karsch, *Ceratitis fasciventris* (Bezzi) and *Ceratitis 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 species for the development of immatures of 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 et al. (2003). Flies of *C. capitata* and *C. cosyra* were reared in the laboratory for 106 generations and those of *C. rosa*, *C. fasciventris* and *C. anonae* were reared for 80–85 generations prior to the 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 by Ekesi et al. (2007). *B. 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.

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Adult flies were kept in Perspex cages and maintained at 27–28°C, and 12 : 12 h [light : dark (L : D)] conditions. 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 1 : 3. Sexually mature flies were offered mango fruits (variety Apple) as oviposition substrate up to the fourth generation, and thereafter 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 rearing

The initial cohort of *D. longicaudata* was obtained from the University of Hawaii at Manoa in Honolulu, Hawaii (USA), where they were reared on *B. dorsalis*. The wasps were kept in quarantine at ICIPE at room temperature (25–26°C) where they were reared on larvae of *B. invadens* using a procedure similar to that described by Wong and Ramadan (1992). Early third instar larvae of *B. invadens* were placed in an oviposition unit consisting of a modified Petri dish (diameter 9 cm, depth 0.5 cm), with a tightly fitting organza lid. The oviposition units were offered to wasps kept in a rearing cage (14 × 14 × 20 cm) for 24 h. The number of wasps in the cage ranged between 30 and 50. Thereafter, host larvae were transferred to Petri dishes (8.6 cm diameter) and provided with fresh larval diet (composition described above). The Petri dishes were then placed in a plastic bowl (10.3 cm diameter, 6 cm depth) with a layer of sand at the bottom to serve as a substrate for pupation. The sand was kept moist by gently spraying water on it using a small hand sprayer (0.5 l capacity) for a few seconds to prevent pupal desiccation. When the larvae attained maturation they popped into the sand to pupate, and those which failed to jump into the sand were assisted using a pair of soft forceps. A hole of 10 cm diameter was cut in the lid of the bowl and covered with a very fine net. On the seventh day after pupation, the puparia were collected from the sand and placed in Petri dishes (8.6 cm diameter) for emergence of adult flies and parasitoids. The emerging parasitoids were added to the parasitoid colony. Parasitoids were maintained at a photoperiod of 12 : 12 h (L : D) and were provided with fine drops of pure honey and water in wet cotton wool.

Bioassay

Host preference and host acceptability

Twenty mated, naive female wasps (7–10 days old), were introduced into a cage (60 cm × 30 cm × 15 cm). Six round openings (4.5 cm diameter) in the top of the cage were covered with a piece of organza material. These openings provided ventilation for the wasps. Fifteen early third instar larvae of each host species (*B. invadens*, *C. capitata*, *C. cosyra*, *C. rosa*, *C. fasciventris*, *C. anonae*) were placed in two small Petri dishes (3.7 cm diameter 0.5 cm depth). Thereafter, the two small Petri dishes were placed in the oviposition units. This was to ensure the accessibility of ovipositing females to the larvae, by preventing them from moving away from the centre and possibly hiding under the solid edge of the oviposition unit's 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. Then, the oviposition units were re-inverted after all units had been introduced into the cage, and observations on parasitoid behaviour were initiated 5 min later. The number of searching and/or ovipositing female wasps was recorded at 15-min intervals for 3 h. After this exposure period, host larvae were removed and dissected in a saline solution (phosphate buffer saline) and inspected for the presence of parasitoid eggs. The experiment was replicated six 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 exclude the directional bias as a factor contributing to the outcome of the experiment.

Host suitability

Five mated, naive, female wasps (7–10 days old) were introduced into a small Perspex sleeve cage (12 cm × 12 cm × 12 cm). A round opening (4.5 cm diameter), for ventilation, in the top of the cage was covered with a piece of organza material. Hundred early third instar larvae of each host species (*B. invadens*, *C. capitata*, *C. cosyra*, *C. rosa*, *C. fasciventris*, *C. anonae*) were placed in two small Petri dishes (3.7 cm diameter, 0.5 cm depth), each containing 50 larvae and were placed in the oviposition unit the same way as described for the experiment above. The oviposition units were offered to the wasps in the cage

in a no-choice situation, i.e. each host was placed separately.

After an exposure period of 24 h, host larvae were transferred to small plastic containers (3.5 cm diameter 3 cm depth) with fresh larval diet. The plastic containers were then placed individually on a layer of sand in a plastic cup (5 cm diameter, 10 cm depth). When the larvae were fully grown, they popped into the sand and pupated. Those that failed to pop were assisted as described for the parasitoid rearing. The sand was kept moist until the emergence of flies and parasitoids. The total number of wasps (males and females) and uneclosed puparia was counted. When emergence of flies and parasitoids ceased, the number of unemerged puparia was recorded. Later they were dissected and the number of dead parasitoids was recorded. The number of replicates for the different host species ranged between 10 and 17 (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 of the host suitability experiment indicated that *C. rosa*, *C. fasciventris*, *C. anonae* and to a lesser extent *B. invadens*, were not suitable for development of *D. longicaudata*. To confirm these results, 100 late second instar larvae of each of these hosts were placed on oviposition units in the same way as for parasitoid rearing. Late second instar larvae were used to ensure that they do not pupate before dissection, which would have been the case if third instars were used. The oviposition units were then exposed to 10 experienced female wasps for a period of 3 h, after which the oviposition units were removed from the cages and the larvae were maintained in the same manner as in the host suitability experiment at ambient temperature (26 ± 2°C). On the second day after exposure to the wasps (i.e. parasitization), host larvae were dissected in phosphate-buffered saline solution and examined for parasitism under a binocular microscope. Dissection of each host larvae was terminated after 50 parasitized larvae were obtained, and the fate of parasitoid eggs was recorded, i.e. encapsulated, normal (including normal egg or hatched normal larvae), encapsulated + normal [when the same host larvae contained encapsulated egg(s) as well as normal egg(s)].

Statistical analysis

A univariate repeated measures analysis of variance was used to test for the effect of parasitoid choice – expressed as oviposition rate – over 13 time intervals. The number of parasitized host larva was analysed using Kruskal–Wallis test ($\alpha = 0.05$). When the Kruskal–Wallis test showed significant differences ($P = 0.05$), multiple comparison analysis was conducted using the Nemenyi test ($\alpha = 0.05$; Zar 1999). The number of superparasitized larvae and total number egg per replicate, and data on host suitability (total progeny production, per cent realized and absolute parasitism, per cent unemerged puparia, sex ratio as the proportion of females, and per cent undifferentiated mass) were analysed with one-way analysis of variance, (PROC GLM) (SAS Institute 2000).

Absolute parasitism was obtained by adding the number of uneclosed puparia containing dead parasitoids to the total number of adult parasitoids produced for each replicate and dividing by the initial number of puparia. $\text{Log}_{10}(x + 0.5)$ and arcsine square root transformation were used on counts and percentages, respectively, (Sokal and Rohlf 1981) before being subjected to ANOVA. When treatment effects were significant (i.e. $P < 0.05$), treatment mean val-

Table 1 Suitability of six fruit fly species as hosts for immature development of *Diachasmimorpha longicaudata*. Values in cells are mean ± SE

Host species	No. replicates	Total parasitoid progeny	Realized parasitism (%)	Absolute parasitism (%)	Sex ratio (proportion of female progeny)	Uneclosed puparia (%)
Bactrocera invadens	15	13.53 ± 1.62 b	13.80 ± 1.62 c	14.53 ± 1.73 c	0.59 ± 0.04 a	35.83 ± 2.28 b
Ceratitis capitata	15	52.47 ± 4.92 a	58.27 ± 3.69 a	61.20 ± 3.31 a	0.32 ± 0.02 b	37.71 ± 3.62 b
Ceratitis cosyra	14	30.57 ± 6.04 b	33.21 ± 6.05 b	34.21 ± 6.21 b	0.31 ± 0.02 b	63.40 ± 6.48 a
Ceratitis rosa	11	3.09 ± 1.06 c	3.46 ± 1.1 d	4.00 ± 1.21 d	0.33 ± 0.13 b	67.27 ± 4.69 a
Ceratitis fasciventris	11	0.18 ± 0.12 d	0.18 ± 0.12 d	0.18 ± 0.12 e	–	52.36 ± 4.06 ab
Ceratitis anonae	10	0.20 ± 0.20 d	0.30 ± 0.30 d	0.50 ± 0.50 e	–	66.80 ± 8.63 a

Mean values in the same column followed by a different letter are significantly different at $\alpha = 0.05$ (Student–Newman–Keuls, SNK test).

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ues were separated using Student–Newman–Keuls (SNK) test. Sex ratio was calculated only for the replicates that produced parasitoid progenies and per cent undifferentiated mass was calculated for replicates that had at least one uneclosed puparium. A t-test was used to compare the number of uneclosed puparia in parasitoid-exposed and control sets. For the test of encapsulation experiment the frequency of number of larvae containing parasitoid eggs of different fate (encapsulated, normal, and larvae contained encapsulated plus normal) we analysed using Fisher exact test.

Results

Host preference and host acceptability

The numbers of *D. longicaudata* females attracted to the oviposition units (Fig. 1) were comparable across host species. However, the numbers of parasitized larvae (host larva contained at least one parasitoid egg) showed significant differences among the host species ($\chi^2 = 13.27$; d.f. = 5; P = 0.0210) (Fig. 2). However, the total number of eggs oviposited per replicate (i.e. sum of egg oviposited in 15 larvae) differed among host species ($F_{5,29} = 4.38$, P = 0.0043), being highest in *C. cosyra*. This was caused by the fact that this host was also most superparasitized, with up to six eggs in one host larva. Superparasitism also varied among the tested host species ($F_{5,29} = 5.47$; P = 0.0011). The highest number of superparasitized larvae was recorded for *C. cosyra* and *C. rosa* (Fig. 3).

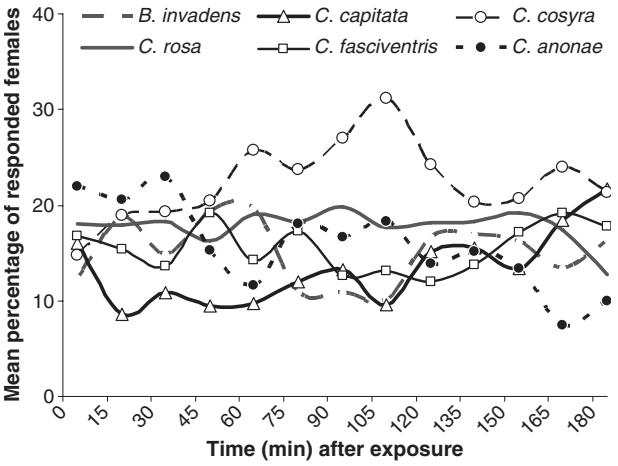

Fig. 1 Mean percentage of *Diachasmimorpha longicaudata* female respondents (searching and/or ovipositing) to six fruit fly host eggs over 3 h exposure period.

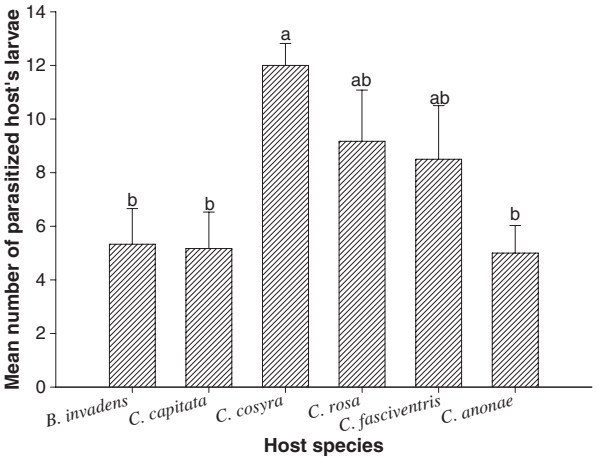

Fig. 2 Host's larvae acceptability for oviposition by *Diachasmimorpha longicaudata*. Bars with same letters are not significantly different at $\alpha = 0.05$ (Nemenyi).

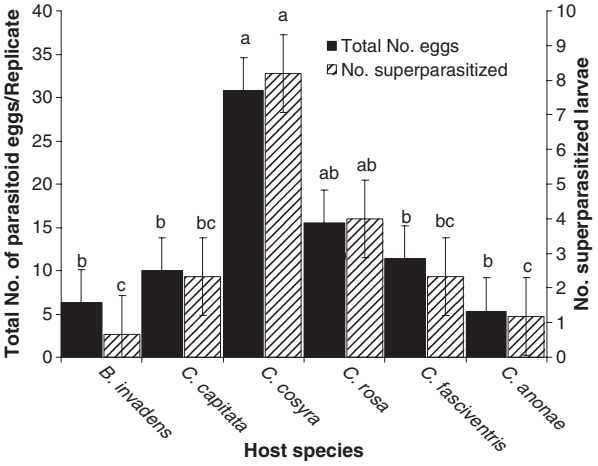

Fig. 3 Mean number of total *Diachasmimorpga longicaudata*'s egg/replicate and number of superparasitized larvae of six fruit species. Bars with same letters for the same category are not significantly different at $\alpha = 0.05$ (Student–Newman–Keuls, SNK test).

Host suitability

Diachasmimorpha longicaudata was able to complete development in all host species, though at varying degrees (Table 1). The total number of parasitoid progeny, realized parasitism (number of emerged viable parasitoid wasps/total number of retrieved puparia) as well as absolute parasitism (number of emerged viable parasitoid wasps + number of dead parasitoid within the host puparia/total number of retrieved puparia) varied among the host species, with *C. capitata* being the most parasitized ($F_{5,70} =$

Table 2 Mean percent (± SE) uneclosed puparia in parasitoid *Diachasmimorpha longicaudata* exposed and control eggs of six fruit fly host species

Host species	Mean percent uneclosed puparia		t-test value	Probability
	Treated	Control		
Bactrocera invadens	35.83 ± 2.28	3.93 ± 1.44	−11.14	<0.0001
Ceratitis capitata	37.71 ± 3.62	11.77 ± 4.61	−4.48	0.0002
Ceratitis cosyra	63.40 ± 6.48	77.33 ± 3.68	1.87	0.076
Ceratitis rosa	67.27 ± 4.69	9.11 ± 1.55	−11.79	<0.0001
Ceratitis fasciventris	52.36 ± 4.06	6.20 ± 1.91	−10.29	<0.0001
Ceratitis anonae	66.80 ± 8.63	53.69 ± 8.47	−1.08	0.29

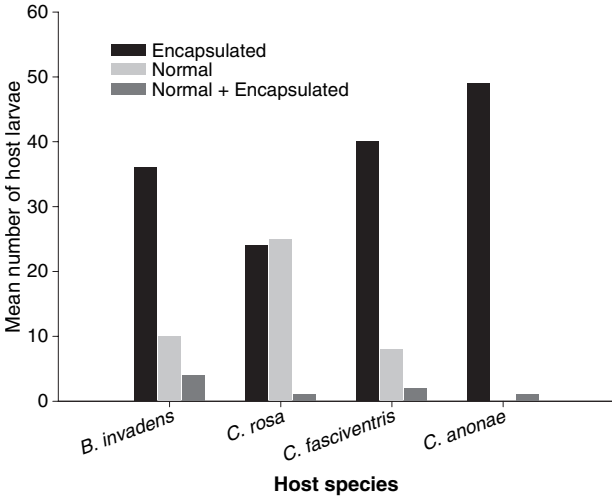

Fig. 4 Number of host larvae containing *Diachasmimorpha longicaudata* of different fate (n = 50 host larvae).

69.21; $P < 0.0001$ and $F_{5,70} = 71.67$; $P < 0.0001$ for realized parasitism as well as absolute parasitism, respectively). Similarly, the total number of parasitoid progeny was strongly influenced by host species ($F_{5,70} = 69.07$; $P < 0.0001$), with *C. capitata* yielding the highest number of parasitoid progeny, followed by *C. cosyra*/*B. invadens*, and *C. rosa*, while *C. fasciventris* and *C. anonae* produced the least parasitoid progeny.

The proportion of female parasitoid progenies was also affected by host species ($F_{3,47} = 9.52$; $P < 0.001$). Parasitoid sex ratio was male-biased in all host species, except in *B. invadens* for which it was female-biased.

The percentage of uneclosed puparia (puparia which produced neither flies nor parasitoids) varied across the host species and was highest when the parasitoid was reared on *C. rosa* and lowest when the parasitoid was reared on *B. invadens* ($F_{5,70} = 7.92$; $P < 0.0001$) (Table 2).

Parasitoid encapsulation

Among the four host species, *B. invadens*, *C. rosa*, *C. fasciventris* and *C. anonae*, the number of host larvae with encapsulated parasitoid egg(s) also varied greatly ($P < 0.0001$) (Fig. 4). *C. anonae* exhibit the strongest immune response followed by *C. fasciventris*, with the least encapsulation occurring in *C. rosa*. Comparing the two closely related species, *C. rosa* and *C. fasciventris*, it was observed that the number of larvae that contained encapsulated egg was significantly lower ($P = 0.0006$) in *C. rosa* (48%) than in *C. fasciventris* (80%).

Discussion

There is a common conception that host acceptability by parasitoids mirrors host suitability (van Alphen and Janssen 1982; van Alphen and Vet 1986). Our results of host preference/acceptability do not support the argument that the parasitoid females accept hosts according to their profitability for their offspring development, as the tested host species were equally accepted regardless of the fate of the parasitoid progeny in these hosts. However, the failure of *D. longicaudata* to discriminate among various host species could have been caused by low host–parasitoid ratio. Female parasitoids were therefore forced to lay eggs in poor-quality (e.g. *C. fasciventris* and *C. anonae*) and previously parasitized hosts (*C. cosyra* and *C. capitata*). This was evident by the high number of total eggs laid per replicate as well as the average number of eggs laid per larva such as in *C. cosyra*.

Physiological suitability of the target host is the most crucial criterion for the success of biological control (Salt 1938; Hailemichael et al. 1997). Host species is known to have a strong influence on the suitability for development of parasitoid immatures. In this study, there were substantial differences in host suitability for *D. longicaudata* – in terms of number of total parasitoid progeny, realized per cent parasitism and absolute per cent parasitism – among the six host species tested. These findings agree with those reported for *Anastrepha oblique* (Macquart)

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(Dipt., Tephritidae) and *Anastrepha ludens* (Loew) which varied in their suitability for immature development of *D. longicaudata* (Eben et al. 2000). Differential host suitability is also well documented for other related Opiine parasitoids of fruit flies (e.g. Quimio and Walter 2001; Zenil et al. 2004; Bokonon-Ganta et al. 2005; Rousse et al. 2006; Mohamed et al. 2007).

The variation in physiological suitability of the tested hosts could be explained largely by the differential cellular immune response – primarily through encapsulation – mounted by the host species against eggs of *D. longicaudata*. Although, *B. invadens* was not a physiologically suitable host, it had the highest female proportion of parasitoids. This could have been due to its relatively large size as compared with the others. This agrees with the findings of Eben et al. (2000) and Mohamed et al. (2003) for other opiine–tephritid associations.

The low parasitism of *C. cosyra* reported in this study, despite being a relatively preferred host for oviposition, might have been caused by the relatively high rate of superparasitism in this host which could have increased mortality of both parasitoid and host. In addition, *C. cosyra* larvae do not perform well on carrot-based diets (S. Ekesi, unpublished data). In this study, it is interesting to note that *C. rosa* and *C. fasciventris*, which are nearly identical, and until recently were known under one taxon (De Meyer 2001), varied significantly with regard to their immune response to *D. longicaudata*.

The inability of *D. longicaudata* to develop in three *Ceratitis* species (*C. rosa*, *C. fasciventis* and *C. anonae*) is not surprising as these hosts, being of African origin, share no evolutionary history with this parasitoid species. However, the same argument cannot be used to explain the failure of *D. longicaudata* to counteract the immune response of *B. invadens*, both being of the same origin (Asia). In an analogous parasitoid-host association studied earlier, eggs of African parasitoids, two opiine species [*Psyttalia concolor* (Szepligeti) (Hym., Braconidae) and *Psyttalia cosyrae* (Wilkinson) (Hym., Braconidae)] and one eulophid [*Tetrastichus giffardii* Silvestri (Hym., Eulophidae)] were encapsulated by the melon fly *B. cucurbitae*, which is of Asian origin (Mohamed et al. 2003, 2007). Ramadan et al. (1994) reported that eggs of a congeneric of *D. longicaudata*, *Diachasmimorpha kraussii* (Fullaway) (Hym., Braconidae) were encapsulated in the larvae of the oriental fruit fly, *B. dorsalis*.

The difference in encapsulation of *D. longicaudata* eggs by various host fruit fly species is somewhat intriguing, given the fact that this parasitoid has a symbiotic association with an entomopoxvirus that suppresses the immune system of its host. *D. longicaudata* is known to introduce an entomopoxvirus in its host during oviposition (DlEPV) (Lawrence and Akin 1990; Lawrence 2002, 2005). The virus replicates in the haemocytes of the host and disrupts the encapsulation process by making the haemocytes lose their adhesive property (Lawrence 2005). Nevertheless, in our study, *D. longicaudata* failed to suppress the immune response of *C. rosa*, *C. fasciventris*, *C. anonae* and *B. invadens*. A similar phenomenon of interspecific variation in encapsulation ability was recorded for *Drosophila* species/strain against it parasitoid *Leptopilina boulardi* Carton and Kelner-Pillaut. (Hym., Eucoilidae) (Dupas and Boscaro 1999; Dubuffet et al. 2007). This parasitoid also injects virus into its host (Rizki and Rizki 1990). However, the results presented herein are the first record that a frugivorous tephritid parasitoid which harbours symbiont virus known to inhibit encapsulation, can do so in some host species but not in the others. Additional studies are needed to elucidate why the same mechanism of encapsulation disruption does not apply when *D. longicaudata* eggs are oviposited in *C. anonae*, *C. fasciventris*, *B. invadens* and *C. rosa*, and also whether this virus plays any role in immunosuppression of these host species.

Contrary to our prediction, *D. longicaudata* performed poorly on *B. invadens.* Nevertheless, this parasitoid was able to successfully establish a new association with *C. cosyra* and *C. capitata* (new on the evolutionary time scale). Consequently, we anticipate that this parasitoid is likely to contribute substantially to the overall parasitism of *C. cosyra* and *C. capitata*, for which percentage parasitism by native parasitoid species is generally low (Copeland et al. 2006), especially in large-sized fruits such as mango (Lux et al. 2003). It is anticipated that *D. longicaudata*, with its relatively longer ovipositor (as the name implies) than most native fruit fly parasitoid species, would gain greater access to host larvae that are beyond the reach of the native parasitoid species, which have shorter ovipositors. It has been suggested that if the length of the ovipositor of an introduced parasitoid is substantially different from that of species already present, the introduced parasitoid would be more likely to find an empty niche in its new environment, become established, and add to the control of its host (Sivinski and Aluja 2001). Furthermore, *D. longicaudata* tend to forage more frequently on the over-ripe and rotten fruits (Purcell et al. 1998), a behaviour that may enhance overall parasitism through attacks on late instar larvae

which may have escaped parasitization by egg and early larval instar parasitoid guilds. The poor performance of *D. longicaudata* on the target host *B. invadens* calls for continuing the search for other promising candidate larval parasitoids to complement parasitism by the egg parasitoid *F. arisanus* (also an introduced species) which was shown to be an efficient parasitoid of *B. invadens* (S. Mohamed, unpublished data). Plans are underway for field releases of *F. arisanus* in eastern and western Africa.

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