Preference among four *Bactrocera* species (Diptera: Tephritidae) by *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera: Braconidae)

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Abstract

Diachasmimorpha kraussii is an endoparasitoid of larval dacine fruit flies. To date the only host preference study done on *D. kraussii* has used fruit flies from outside its native range (Australia, Papua New Guinea, Solomon Islands). In contrast, this paper investigates host preference for four fly species (*Bactrocera cacuminata*, *B. cucumis*, *B. jarvisi* and *B. tryoni*) which occur sympatrically with the wasp in the Australian component of the native range. *Diachasmimorpha kraussii* oviposition preference, host suitability (parasitism rate, number of progeny, sex ratio), and offspring performance measures (body length, hind tibial length, developmental time) were investigated with respect to the four fly species in the laboratory in both no-choice and choice situations. The parasitoid accepted all four fruit fly species for oviposition in both no-choice and choice tests; however, adult wasps only emerged from *B. jarvisi* and *B. tryoni*. Through dissection, it was demonstrated that parasitoid eggs were encapsulated in both *B. cacuminata* and *B. cucumis*. Between the two suitable hosts, measurements of oviposition preference, host suitability and offspring performance measurements either did not vary significantly, or varied in an inconsistent manner. Based on our results, and a related study by other authors, we conclude that *D. krausii*, at the point of oviposition, cannot discriminate between physiologically suitable and unsuitable hosts.

Running title: Host preference by *D. krausii*

Key words: *Bactrocera cacuminata*, *Bactrocera cucumis*, *Bactrocera jarvisi*, *Bactrocera tryoni*, Opiinae, host suitability, biological control, parasitoid

INTRODUCTION

Fruit flies of the genus *Bactrocera* Macquart (Diptera: Tephritidae) are economically among the most important pests of fruits and vegetables in the Asia/Pacific region, with larval feeding within the fruit causing both quantitative and qualitative losses (Bateman, 1976; White & Elson-Harris, 1992; Waterhouse, 1993). In Australia, most *Bactrocera* species are specialists on native fruits (Drew, 1989), but a few species have become serious pests of commercial fruits and vegetables; the worst of these is the polyphagous *B. tryoni* (Froggatt) (Bateman, 1972; Fletcher, 1987; Fitt, 1986a, b, 1989, 1990).

For the last thirty years, malathion-based insecticides have been a convenient and widely accepted tool for suppressing pest fruit fly populations (Harris, 1989). However, these chemicals are under threat of withdrawal in Australia due to toxicological concerns to human health and the environment. Emphasis has rather been placed on alternatives to chemical cover-sprays for fruit fly management; a process which is already well advanced in some nations (see for example Duan *et al*., 1997; Montoya *et al*., 2000; Baeza-Larios *et al*., 2002; Rendon *et al*., 2006; Bokonon-Ganta *et al*., 2007).

Use of natural enemies such as the parasitoid wasps (e.g. *Fopius arisanus* Sonan), in combination with other compatible methods (e.g. sterile male flies), is arguably a better alternative option for sustainable pest control (Gurr & Kvedaras 2010). In Australia, classical introductions of exotic fruit fly biological control agents were carried out in the 1950s and 1960s (Snowball & Lukins, 1964; Snowball, 1966), but little active use of parasitoids for fruit fly management has been done since. Recently, however, there has been some preliminary research on the inundative release of the egg parasitoid *Fopius arisanus* and the larval parasitoid *Diachasmimorpha kraussii* (Fullaway) as part of area wide management of *B. tryoni* in Queensland, Australia (E. Hamacek unpublished data).

Diachasmimorpha kraussii is a koinobiont endoparasitoid of dacine fruit flies (Wharton & Gillstrap, 1983). Its native distribution covers an arc from north-eastern mainland Australia, through Papua New Guinea and into the Solomon Islands (Carmichael, *et al*. 2005). Over this range the parasitoid has been recorded from 17 *Bactrocera* species (Carmichael *et al*., 2005) and, like many of the fruit fly attacking opiine braconids, it is considered a polyphagous parasitoid (Wharton & Gilstrap,

1983). The wasp does, however, have limits on its host range. For example, despite *B. cucurbitae* (Coquillet) being recorded as a host by Carmichael *et al* (based on specimen label data), Messing & Ramadan (1999) demonstrated in laboratory host preference studies that this fly species encapsulated *D. kraussii* eggs and no adult wasps emerged. Such findings highlight the need for more detailed studies on the host range of this parasitoid.

Apart from its preliminary use for inundative releases in Australia, there is also consideration of *D. kraussii* for classical biological control releases outside its native range. In Hawaii, the species has been tested in quarantine against *B. cucurbitae*, *B. dorsalis* (Hendel), *B. latifrons* (Hendel) and *Ceratitis capitata* (Wiedemann) (Messing & Ramadan, 1999; Duan & Messing, 2000). In Guatemala it has been tested in field cage trials for its combined release with *F. arisanus* and sterile male *C. capitata* for the control of wild *C. capitata* (Rendon *et al*., 2006), while in Israel the wasp has already been released for *C. capitata* control (Argov & Gazit, 2008).

Apart from a limited amount of distributional, biological and host data (Rungrowanich & Walter, 2000a, b; Carmichael *et al*., 2005), little is known about *D. kraussii* in its native range. Information on host associations and utilisation is particularly lacking, with that available being limited largely to casual rearing records. The importance of a thorough understanding of host selection and utilisation behaviours of biological control agents prior to their field releases has been strongly advocated by many researchers (Nechols & Kikuchi, 1985; Duan *et al*., 2000; Eben *et al*., 2000; Mehrnejad & Emami, 2005). Indeed, the efficiency in finding hosts and the ability to discriminate among hosts of different quality by polyphagous parasitoids are prerequisites for their selection as biological control agents (DeBach & Rosen, 1991; Santolamazza-Carbone *et al*., 2004).

In the current study we investigate the laboratory host preference behaviour of sexually mature naïve *D. kraussii* females to four Australian *Bactrocera* species (*B. cacuminata*, *B. cucumis*, *B. jarvisi* and *B. tryoni*), all of which occur sympatrically with the wasp and are assumed to have evolved in the presence of the wasp. We offered the larvae of each fly species in both no-choice and choice situations to see if the wasp discriminated between fly species as oviposition hosts. Further, host suitability (parasitism rate, number of progeny, sex ratio) and offspring performance

(body length, hind tibial length, developmental time) were recorded to establish if these parameters varied among the different host species.

MATERIALS AND METHODS

Experimental conditions

All work was conducted in a controlled environment room with temperature and relative humidity set at 26 ± 1ºC and 70 ± 5% respectively. The room was lit through fluorescent (L10: D14) and natural lighting.

Study organisms

Fruit fly species

Four fruit fly species were used in these trials, *B. cacuminata*, *B. cucumis*, *B. jarvisi* and *B. tryoni*. *Bactrocera cucumis*, *B. jarvisi* and *B. tryoni* are all economic pests: *B. jarvisi* and *B. tryoni* have wide host ranges across many plant families, while *B. cucumis* is generally considered a cucurbit specialist, although it will infest some fruits in other plant families (Hancock *et al*. 2000). *Bactrocera jarvisi* and *B. tryoni* are recorded hosts of *D. kraussii*, while *B. cucumis* is not (Carmichael *et al*., 2005). *Bactrocera cacuminata* is a non-economic species monophagous on the woody weed *Solanum mauritianum* Scolpi and is also recorded by Carmichael *et al*. as a host of *D. kraussii*. The fly species are all natives of Australia and occur widely within the Australian component of *D. kraussii's* native range (Drew, 1989).

All flies were obtained from existing laboratory cultures. *Bactrocera tryoni* and *B. cacuminata* from colonies maintained by the [Queensland] Department of Primary Industries and Fisheries (DPI&F) (now the Department of Employment, Economic Development & Innovation), Indooroopilly; *B. jarvisi* larvae from colonies maintained by DPI&F, Cairns; and *B. cucumis* from colonies maintained at Griffith University, Nathan. For all four colonies, flies were reared using standard fruit fly rearing procedures (Heather & Corcoran, 1985) and cultures were less than two years old. All larvae used in the experiments were late second to early third instar,

consistent with other studies on this species (Messing & Ramadan, 1999; Wang & Messing, 2002).

Parasitoids

The initial stock of *D. kraussii* used in the experiment was established from fruit fly infested guavas (*Psidium guajava* L.) collected from various locations in and around Brisbane, South East Queensland, in February and March 2004 (i.e. two years prior to trials). They were reared on *B. tryoni* using opiine parasitoid rearing procedures of Carey *et al*. (1988) and Wong & Ramadan (1992). The individual parasitoids used in the experiment were sexually mature, mated naïve females (7-9 days old) taken from the main stock culture. Individuals in this age range were used because it has been demonstrated to be the most reproductively prolific (mean of 15-20 offspring per day) age range of a female's life (Rungrowanich & Walter, 2000a). Females within this age group have been used for similar studies elsewhere (Messing & Ramadan, 1999; Duan & Messing, 2000; Wang *et al*., 2003).

Oviposition preference test

No-choice experiment

We used oviposition events (number of times that the female wasp fully inserted its ovipositor into the carrot medium and performed egg depository movements) as the index for measuring host acceptance by naïve *D. kraussii* females. To determine this, we first conducted a no-choice experiment with individual host species in an enclosed Petri dish (diam. 85mm, ht 14mm). Approximately 10 grams of carrot medium (= artificial diet, Heather & Corcoran, 1985) was placed in the centre of the Petri dish, ensuring that sufficient space was allowed between the medium and the Petri dish lid for the wasp to walk about and oviposit. Ten larvae of the fly species to be tested were then placed in the carrot medium and left for five minutes, during which they burrowed into the diet medium.

After larvae had settled, an individual female *D. kraussii* was released into the centre of the Petri dish and left for three minutes (which allowed time for the wasp to recover self-orientation after handling, but not enough time that it had begun host

searching). After this time, we counted the number of oviposition events into the carrot medium containing the larvae for 20 minutes. Preliminary trials showed that most oviposition occurred within 20 minutes of wasp introduction to the experimental arena and this is why we chose this period for experiments. Oviposition was regarded as the number of times that the female wasp fully inserted its ovipositor into the carrot medium and performed egg depository movements. Egg depository movements were identified by us during preliminary studies as the wasp momentarily lowering and raising of the abdomen (and consequently the ovipositor) into the medium while the thorax and head remained steady. Dissection of fruit fly larvae indicated that eggs were only oviposited when this sequence of movements were made. Insertion of the ovipositor into the medium without egg depository movements was regarded as probing and was not counted.

After 20 minutes of observation, the wasp was removed and the Petri dish base containing the larvae was filled with additional diet and the larvae reared through to adult emergence. For *B. cucumis* larvae, the tests were conducted in carrot medium (to avoid diet medium difference effect on wasp preference behaviour) before transferring the larvae to pumpkin medium for rearing (required for this cucurbit breeding species). Experiments were replicated 20 times for each fly species; a new female was used for each replicate.

Choice experiment

Following the no-choice experiment, we conducted a choice experiment to see if the wasps showed discriminatory behaviour when larvae of multiple species were concurrently available. The experimental procedures were similar to those in the no-choice experiment except that we conducted paired choice tests where larvae of two fly species, placed in separate portions of carrot medium within the same Petri dish, were offered simultaneously to individual wasps. The portions of carrot medium were separate from each within the Petri dish. We offered cohorts of ten larvae of each species at a time. The positions of the two species were rotated for each replicate to avoid bias. For all tests, we offered *B. tryoni* as a reference species (i.e. control), while the second test fly species varied (i.e. either *B. cacuminata*, *B. cucumis*, *B. jarvisi* or *B. tryoni*). For the test between *B. tryoni* cohorts we randomly assigned one cohort as the ‘reference cohort’ and the other as the ‘test cohort’. Preliminary

analysis showed no difference in oviposition preference between 'reference' and 'test' cohorts of *B. tryoni* (t-test: t_{38} = -0.25, P = 0.80), implying that the design produced unbiased results.

For analysis we used, as our data, proportional differences in oviposition for the test cohort against the reference cohort, i.e. if oviposition occurred four times in the test cohort and five times in the control, then the number used for analysis was 4/5, i.e 0.8 (as proportional datum, this number was then arc sine transformed before analysis). The need to test in this way arose from not having access to all fruit fly species at the same time, thus there was a need to refer all experiments back to a standard reference. Identical data to that in the no-choice trials were recorded in each of the 20 replicate control-test species pairings.

Measures of host suitability and wasp performance

Following both the no-choice and choice experiments, all larvae and subsequently the pupae were maintained under the same environmental conditions (Temp: 26 ± 1ºC, RH: 70 ± 5%, photoperiod: L10: D14) until adult wasp emergence when we recorded the following for each replicate: number and sex of offspring, mean development time (days), and mean body and hind tibial lengths (mm). Mean body length was measured from the head to the tip of the abdomen, with the animal straightened to avoid error caused by curvature of the abdomen. Percent parasitism, number of progeny and sex ratio were used as indices of host suitability for the parental wasp, while body length, hind tibial length and developmental time were used as measures of wasp offspring performance. Sex ratio is presented as proportion of females in offspring (Godfray, 1994).

Mixed choice experiment (*B. jarvisi* and *B. tryoni*)

From the experiments above, we found *B. jarvisi* and *B. tryoni* to be suitable hosts of *D. kraussii* and that the wasps showed a slight but not significant preference for the former over the latter species in the choice experiment (see Results). To further investigate the oviposition preference between these two hosts, we placed six larvae of each of the two species in the same portion of diet medium and exposed them to a female wasp for 20 minutes. Following exposure, we reared the larvae through and

used the subsequent emergence of adult flies as a measure of host preference (the assumption being that if one fly species was more preferred than the other, fewer adults of that species would emerge as more maggots would have been parasitised). At emergence we counted both the emergent flies and wasps: any difference between the sum of flies and wasps and the initial larval cohort size was assumed to be due to non-parasitoid induced larval mortality. The experiment was replicated 20 times.

Confirmation of egg-encapsulation

In order to determine the fate of wasp eggs in fly larvae from which wasps did not subsequently emerge, we exposed larvae of all four fly species to parasitoids for 48 hours. Larvae were then placed into 70% alcohol and dissected within 48 hrs to check for egg-encapsulation, which was scored visually.

Data Analysis

Data for oviposition counts, percentage fruit fly emergence and percentage larval mortality from both the no-choice and choice experiments were analysed using one-way ANOVA, following tests for normality of variance. The oviposition data from the two-way choice experiments were proportional data (i.e. the response as a proportion of *B. tryoni* control) and were therefore arcsine transformed before the analysis. For the host suitability and wasp performance data of the emergent wasps, as well as the mixed choice experiment data, independent samples t-tests were used to test for differences among each trait between the two fly hosts which yielded wasps. The data were analysed using SPSS Vs 16.0.

Results

Oviposition response

There was no significant difference in the mean number of observed wasp oviposition events between fly species in both no-choice ($F_{3, 76} = 0.10$, $P = 0.96$) (Fig. 1) and choice ($F_{3, 76} = 2.38$, $P = 0.08$) (Fig. 2) tests.

Host suitability (percentage parasitism, number of progeny and sex ratio)

Despite being oviposited into, no wasps emerged from either *B. cacuminata* or *B. cucumis* in both the no-choice and choice trials.

In the no-choice experiment, percentage larval mortality ($F_{3,76}$ = 1.95, P = 0.13) did not differ between the four fly species. *Bactrocera cacuminata* and *B. cucumis* had significantly higher adult fly emergence than *B. jarvisi* and *B. tryoni* ($F_{3,76}$ = 33.47, P < 0.001). Percentage parasitism (t_{38} = -0.11, P = 0.92), total progeny per mother (t_{38} = 1.64, P = 0.11) and the offspring sex ratio (t_{38} = 0.69, P = 0.49) did not differ significantly between *B. jarvisi* and *B. tryoni*, but the number of female progeny per mother was higher for *B. jarvisi* (t_{38} = 2.43, P = 0.02) (Table 1).

In choice trials, the percentage larval mortality caused by other factors did not differ significantly between the four fruit fly species ($F_{3,76}$ = 2.45, P = 0.07). The percentage successful adult fruit fly emergence differed significantly between the four fly species ($F_{3,76}$ = 59.94, P < 0.001), with the number of emergent adult flies from *B. cacuminata* and *B. cucumis* significantly higher than those of *B. jarvisi* and *B. tryoni*. None of the host suitability parameters relating to emergent parasitoids differed significantly between *B. tryoni* and *B. jarvisi* (percentage parasitism: t_{38} = -0.43, P = 0.67; total progeny per mother: t_{38} = 0.11, P = 0.92; number of females per mother: t_{38} = 0.31, P = 0.76; sex ratio: t_{38} = -0.47, P = 0.64) (Table 1).

Wasp performance (developmental time, body size and hind tibial length)

Diachasmimorpha kraussii developed successfully in *B. jarvisi* and *B. tryoni*, but not in *B. cacuminata* and *B. cucumis*. Juvenile wasp developmental time differed between the fruit fly hosts in both the no-choice and choice trials, but in an inconsistent fashion between the sexes. In no-choice trials, developmental time differed significantly for males (t_{23} = -7.65, P < 0.001) but not for females (t_{42} = -0.66, P = 0.51). Conversely, in the choice test, developmental time differed significantly for females (t_{57} = 3.97, P < 0.001) but not for males (t_{36} = 1.90, P = 0.07). Body length also differed in an inconsistent fashion. Male and female parasitoids from *B. jarvisi* were significantly larger than those from *B. tryoni* in the no-choice trial (Males: t_{23} = 12.23, P < 0.001; Females: t_{42} = 4.25, P < 0.001), whilst male wasps from *B. tryoni*

were significantly larger than those from *B. jarvisi* in the choice trial (t_{36} = -8.06, P < 0.001). Body length of female parasitoids in the choice trial did not differ significantly (t_{57} = -0.19, P = 0.85) between the host species. Hind tibial length for both males and females in the choice trial did not differ significantly (Males: t_{36} = -1.56, P = 0.13, Females: t_{57} = -0.19, P = 0.85), but in the no-choice trial hind tibial length differed significantly for males (t_{23} = 2.45, P = 0.02) and not for the females (t_{42} = 1.80, P = 0.08) (Table 2).

Mixed choice experiment (*B. jarvisi *and* B. tryoni*)

Significantly more *B. tryoni* adults (3.72 ± 0.36) emerged than *B. jarvisi* (1.68 ± 0.29) (t_{48} = 4.44, P < 0.001) when both species were simultaneously exposed to *D. kraussii* in mixed larval cohorts.

Egg-encapsulation

Dissection of maggots exposed to *D. kraussii* confirmed egg deposition in larvae of all four fly species. However, the eggs in *B. cacuminata* and *B. cucumis* larvae were encapsulated in all cases. Encapsulated eggs (thick walled and dark) were easily distinguishable from non-encapsulated eggs (fine walled and clear) recovered from *B. tryoni* and *B. jarvisi* larvae (Fig. 3).

DISCUSSION

The results from this study contradict the results from studies on some other braconids, which have indicated that the level of female host acceptance varies according to the host's suitability for offspring development (i.e. where wasps only oviposit in suitable hosts and reject unsuitable hosts) (van Alphen & Janssen, 1982; van Alphen & Vet, 1986; Mohamed *et al*., 2003), but is consistent with another study on *D. kraussii* where oviposition occurred in both suitable and unsuitable hosts (Messing & Ramadan, 1999). In the current study, despite being readily used as oviposition hosts, eggs laid into both *B. cacuminata* and *B. cucumis* were encapsulated, a process whereby hemocytes form a multi-layered envelope around the

invading organism (Salt, 1970; Strand & Pech, 1995). While we kept no formal measurements of adult flies emerging from parasitism trials, we observed no obvious negative impact of the attempted parasitism on *B. cacuminata* and *B. cucumis* adults.

Egg encapsulation is a typical immune response by host insects in response to attack by parasitoids and has been reported as occurring against a number of opiine wasps (Ramadan *et al*., 1994a,b; Mohamed *at al*., 2003; Bokonon-Ganta *et al*., 2005; Rousse *et al*., 2006). Messing & Ramadan (1999), in a study similar to ours, noted that *D. kraussii* oviposited readily into *B. cucurbitae, B. dorsalis, B. latifrons* and *C. capitata*, but adult wasps only emerged from the latter two species; in *B. cucurbitae* and *B. dorsalis* wasps failed to develop due to egg encapsulation. The difference, however, between our study and Messing and Ramadan's, is that in their study each of the hosts was evolutionarily novel to the wasp and there is thus potential difficulty in interpreting their findings. This is because oviposition into non-suitable hosts may have been an abnormal behaviour, an artefact of the host flies used, or conversely it may be normal behaviour for the wasp. In contrast, all the flies used in our study co-occur with the wasp in its native range, yet the same pattern of oviposition into non-suitable hosts occurred. Hence, we might conclude that this wasp is an indiscriminate ovipositor between suitable and non-suitable hosts, the behaviour having been found in two independent studies using novel and native hosts. We note, however, that our results (and those of Messing and Ramadan's) are based on laboratory studies. In the field, other host location mechanisms may mean the wasp is never in a position where it can attempt oviposition into a physiologically unsuitable host.

Despite the wasp's inability to discriminate between suitable and non-suitable host flies in our trials, the wasp appeared to oviposit more frequently into *B. jarvisi* than *B. tryoni* when preference tested between these two hosts in a mixed choice test. Also, comparison of the mean figures of overall preference ranking (Figs. 1 & 2), as well as the suitability and performance parameter measurements between the two species (Tables 1 & 2), shows that for 15 of 22 measurements wasps preferred, or performed better, in *B. jarvisi* than *B. tryoni*, although these differences were rarely statistically significant. Whether this suggests a real biological difference between hosts is unclear and would need to be explored further.

The failure of *D. kraussii* to successfully develop from *B. cacuminata* casts doubt on previous records that the fly is a host for this wasp (Snowball *et al*., 1962;

Snowball & Lukins, 1964; Snowball, 1966; Wharton & Gilstrap, 1983; Waterhouse, 1993; Carmichael *et al*., 2005). Subsequent to the results from this study, we suggest two possible scenarios to explain past records. Firstly, the identification of the parasitoid species may have been erroneous, as the species is usually difficult to tell apart from close relatives (e.g. *Diachasmimorpha longicaudata*) (Waterhouse 1993; A. Carmichael, QUT, pers. comm.). Secondly, with field records, there is a possibility that another parasitoid which does successfully attack *B. cacuminata* (e.g. *Fopius arisanus*) may have previously parasitised and broken down the host's immune system, thus enabling the successful development of *D. kraussii* larvae in the weakened host. This phenomenon has been noted in *B. cucurbitae* (Pemberton & Willard, 1918; Messing & Ramadan, 1999) and *C. capitata* (Ramadan *et al*., 1994). It should also be noted that the references cited above after Snowball (1966) (i.e. Wharton & Gilstrap (1983), Waterhouse (1993), Rungrowanich & Walter (2000a) and Carmichael *et al.,* 2005) are simply repeating the same earlier record and are not new records of their own.

Understanding behavioural aspects, such as host preference and utilisation behaviour, of biological control agents before their field release is becoming an increasingly integral part of biological control programs (Nechols & Kikuchi, 1985; Mehrnejad & Emami, 2005). Results presented here suggest that *B. jarvisi* and *B. tryoni* are both equally suitable hosts for *D. kraussii*, although the former may be slightly preferred over the latter, while *B. cacuminata* and *B. cucumis* are not suitable hosts. Hence, this study provides the preliminary information that the parasitoid is a suitable candidate for argumentative releases for the biological control of *B. tryoni* and *B. jarvisi* in Australia, but should not be considered for the control of the specialist cucurbit attacking fly, *B. cucumis*.

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Table 1. Emergence results (mean ± SE) for flies and parasitoids following the exposure of larvae of four *Bactrocera* species to the parasitoid *Diachasmimorpha kraussii* in no-choice and choice experiments. The numbers in parentheses are the results of the choice trial. Each trial, for each fly species, consists of 20 replicates, each replicate consisting of 10 maggots exposed to an individual naïve female wasp for 20 minutes. Sex ratio is presented as the proportion of females in the total number of offspring. Means in each row that are followed by the same letter are not significantly different ($P > 0.05$).

Parameters	***B. jarvisi***	***B. tryoni***	***B. cacuminata***	***B. cucumis***
% successful fly emergence	71.00 ± 2.61a [69.50 ± 2.46a]	72.00 ± 3.67a [71.50 ± 3.50a]	98.50 ± 0.82b [100.00 ± 0.00b]	94.00 ± 1.79b [99.00± 0.69b]
% Parasitism	25.00 ± 3.44a [28.00 ± 2.77a]	24.50 ± 4.00a [26.00 ± 3.80a]	0.0 [0.0]	0.0 [0.0]
% other larval mortality	4.00 ± 1.12a [2.50 ± 0.99a]	3.50 ± 1.09a [2.50 ± 0.99a]	1.50 ± 0.82a [0.00 ± 0.00a]	6.00 ± 1.97a [1.00 ± 0.69a]
Total wasp progeny per mother	2.50 ± 0.26a [2.50 ± 0.26a]	1.70 ± 0.32a [2.45 ± 0.40a]	0.0 [0.0]	0.0 [0.0]
Female wasp progeny per mother	1.85 ± 0.22a [1.45 ± 0.30a]	1.10 ± 0.22b [1.60 ± 0.39a]	0.0 [0.0]	0.0 [0.0]
Sex ratio of wasp progeny	0.72 ± 0.01a [0.76 ± 0.01a]	0.63 ± 0.01a [0.68 ± 0.01a]	NA [NA]	NA [NA]

Table 2. Mean (± SE) developmental time, body length and hind tibial length of emergent *Diachasmimorpha kraussii* from *Bactrocera jarvisi* and *B. tryoni* in no-choice and choice experiments. The numbers in parentheses are the results of the choice trials. Across a row, means with different letters between the species for each sex are significantly different ($P < 0.05$).

	Male		**Female**	
	B. jarvisi	***B. tryoni***	***B. jarvisi***	***B. tryoni***
Sample size	**No-choice n = 13 Choice, n = 21**	**No-choice n = 12 Choice, n = 17**	**No-choice n = 37 Choice, n = 29**	**No-choice n = 23 Choice, n = 37**
Developmental time (days)	16.00 ± 0.00a [16.14 ± 0.10a]	17.42 ± 0.19b [15.88 ± 0.81a]	18.75 ± 0.41a [21.03 ± 0.57a]	19.05 ± 0.09a [18.63 ± 0.23b]
Body length (mm)	5.00 ± 0.00a [4.14 ± 0.32a]	4.17 ± 0.07b [4.88 ± 0.05b]	5.69 ± 0.09a [5.64 ± 0.09a]	5.03 ± 0.13b [5.83 ± 0.06a]
Hind tibial length (mm)	2.00 ± 0.00a [1.83 ± 0.05a]	1.83 ± 0.07b [1.94 ± 0.04a]	1.94 ± 0.04a [1.89 ± 0.04a]	1.83 ± 0.06a [1.90 ± 0.04a]

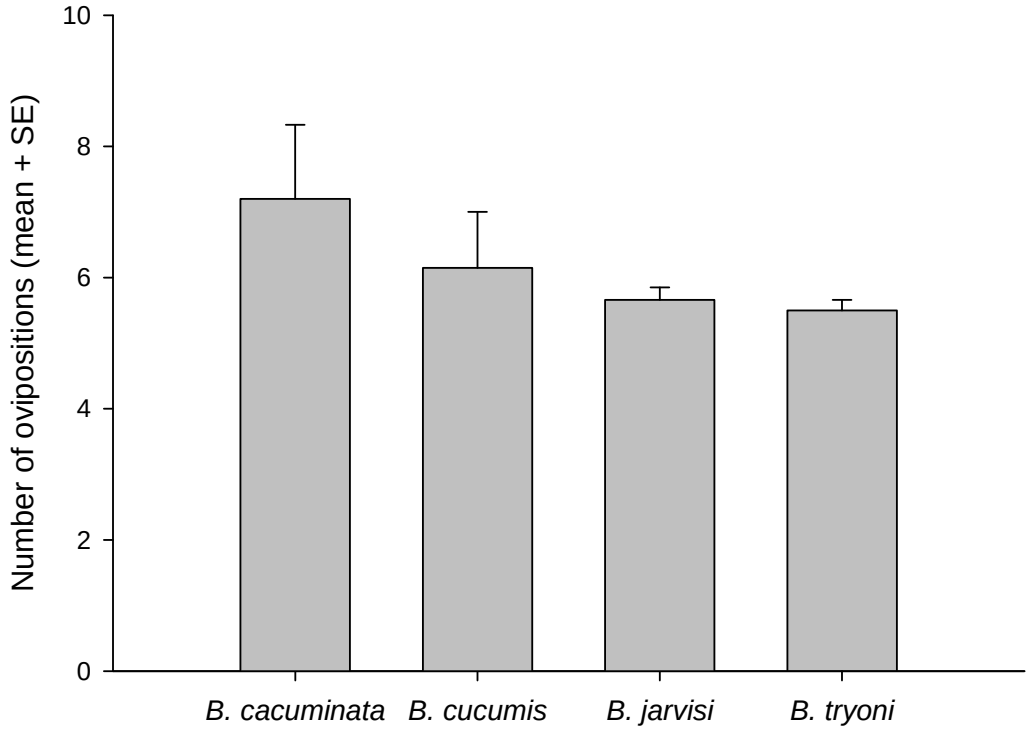

Figure 1. Mean (+ SE) oviposition in a 20 minute period by *Diachasmimorpha kraussii* females against larval cohorts of four *Bactrocera* species offered under no-choice conditions (n = 20 cohort replicates, 10 larvae per cohort for each fly species).

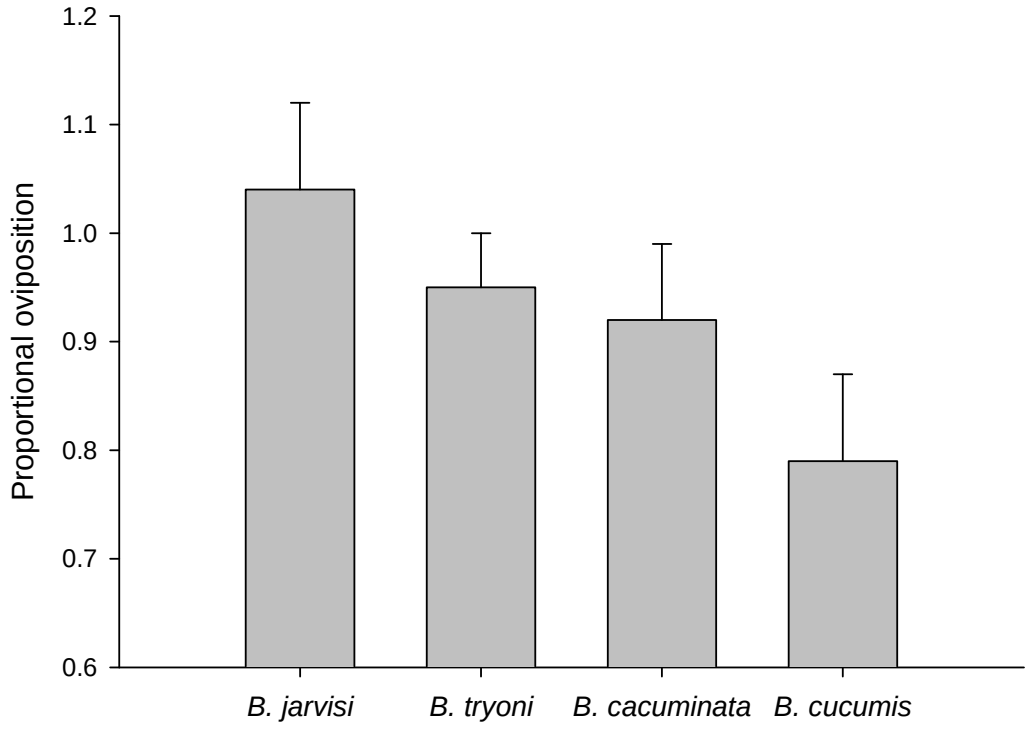

Figure 2. Mean (+ SE) proportional oviposition by *Diachasmimorpha kraussii* females into larvae of four *Bactrocera* species offered under two-way choice conditions. Results are proportionate to oviposition into *B. tryoni* larvae which was offered as a comparative control in all treatments. Larvae were offered in replicated cohorts of 10 larvae per fly species (n = 20 cohort replicates, 10 larvae per cohort for each fly species).

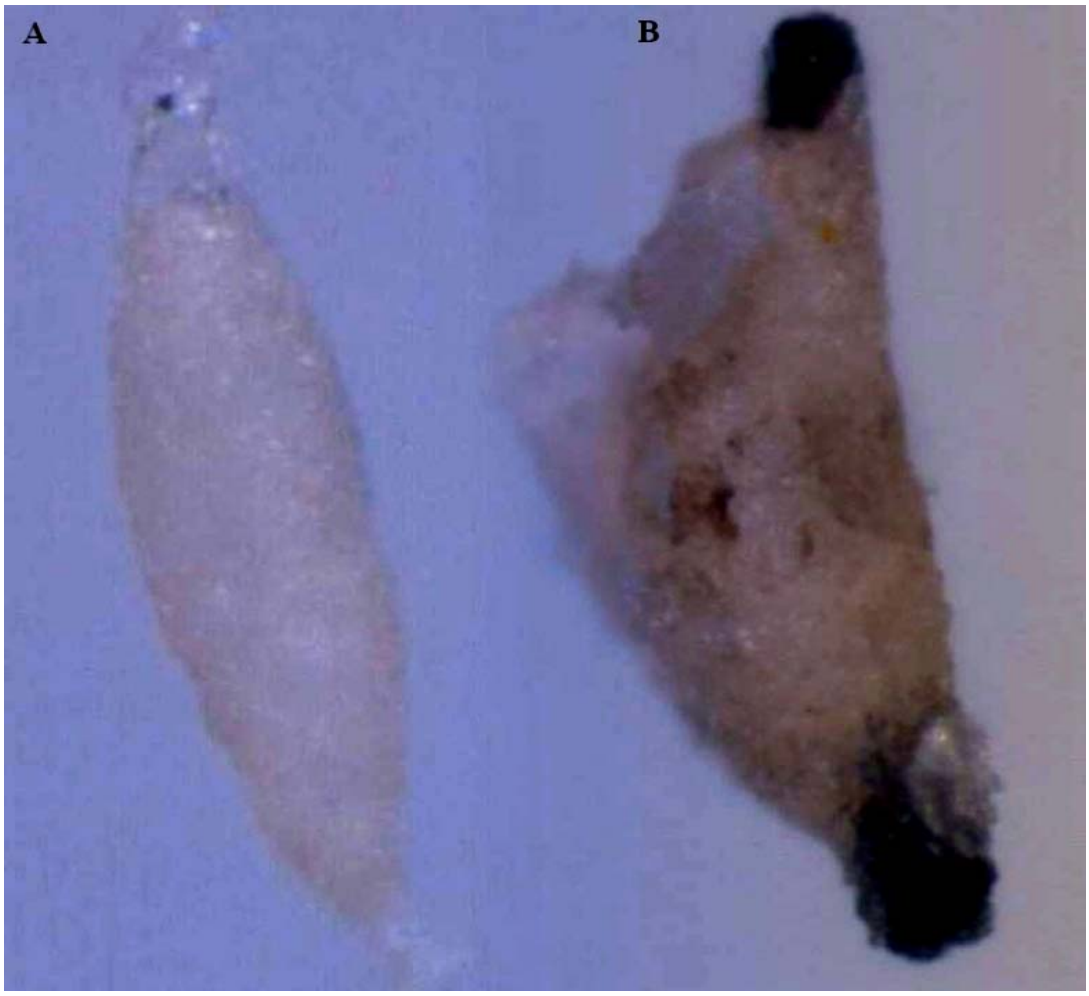

Figure 3. A normal egg (A) and an encapsulated egg (B) of *Diachasmimorpha kraussii* dissected from *Bactrocera tryoni* and *B. cacuminata* respectively (115x). The larvae were dissected 48-50 hours after oviposition.