



Host Preference by *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) Reared on Larvae of *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae)

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HOST PREFERENCE BY *DIACHASMIMORPHA LONGICAUDATA* (HYMNEOPTERA: BRACONIDAE) REARED ON LARVAE OF *ANASTREPHA* *FRATERCULUS* AND *CERATITIS CAPITATA* (DIPTERA: TEPHRITIDAE)

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ABSTRACT

The preferences of *Diachasmimorpha longicaudata* (Ashmead) for larvae of *Anastrepha fraterculus* (Wiedemann) and *Ceratitis capitata* (Wiedemann) were evaluated under laboratory conditions in no-choice and dual-choice tests, based on percent parasitism, proportion of emerged parasitoids, proportion of female offspring, and number of parasitoid female visits to and ovipositor probes on the artificial oviposition device as different measures of host preference. In no-choice tests *D. longicaudata* females did not demonstrate a significant preference between *C. capitata* and *A. fraterculus* larvae. Nevertheless, *D. longicaudata* females showed a strong preference for *A. fraterculus* larvae in dual-choice test. Although female biased parasitoid progeny resulted in all assays, significantly more *D. longicaudata* female offspring emerged from *A. fraterculus* pupae than from *C. capitata* pupae. Thus, this study confirmed that both *C. capitata* and *A. fraterculus* are appropriate host for rearing *D. longicaudata*, but also provided evidence that female parasitoid progeny yield can be substantially improved by using *A. fraterculus* larvae as the host instead of *C. capitata* larvae.

Key Words: fruit flies, parasitoids, host preference, biological control, Argentina

RESUMEN

Se evaluó la preferencia de *Diachasmimorpha longicaudata* (Ashmead) por larvas de *Anastrepha fraterculus* (Wiedemann) y *Ceratitis capitata* (Wiedemann) bajo condiciones de laboratorio en situaciones de elección y no-elección. Las variables consideradas para el análisis fueron el porcentaje de parasitismo, la proporción de parasitoides emergidos, la proporción de descendientes hembras, el número de hembras que visitaron la unidad artificial de oviposición y el número de hembras que realizaron pruebas con el ovipositor en la unidad. Los resultados de los ensayos de no-elección mostraron que las hembras de *D. longicaudata* no tienen una significativa preferencia por las larvas de una u otra especie de tefrítido. No obstante, en el ensayo de elección, las hembras del parasitoide manifestaron una significativa preferencia por las larvas de *A. fraterculus*. En todos los ensayos realizados, la proporción de descendientes hembras de *D. longicaudata* obtenida fue superior a la de los machos, aunque significativamente más hembras del parasitoide se obtuvieron de puparios de *A. fraterculus*. El presente estudio confirma que tanto las larvas de *C. capitata* como las de *A. fraterculus* son adecuadas para criar *D. longicaudata* en laboratorio, aunque también señala que el empleo de larvas de *A. fraterculus* mejoran sustancialmente la producción de descendientes hembras del parasitoide.

Translation provided by the authors.

The South American fruit fly, *Anastrepha fraterculus* (Wiedemann), and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) are 2 of the major pests currently affecting fruit crops in Argentina (Guillén & Sánchez 2007). Early biological control attempts to suppress both tephritid pest species resulted in the use of exotic parasitoids (Ovruski et al. 2000). *Diachasmimorpha longicaudata* (Asmead) is 1 of 5 exotic parasitoids introduced into Argentina from Costa Rica and México (Ovruski et al. 2003). It was originally collected in the Malaysia-Philippine region and is

a solitary, koinobiont, larval-prepupal endoparasitoid of several tephritid species (Montoya et al. 2000). At present, *D. longicaudata* is considered 1 of the most significant biological control agents for augmentative releases against economically important fruit fly species in several Latin American countries (Montoya et al. 2007; Paranhos et al. 2008; López et al. 2009).

Although small scale releases of *D. longicaudata* were made in the Citrus-growing areas of northern Argentina during the 1960s (Ovruski et al. 2000), the permanent establishment of this

opiine parasitoid on *A. fraterculus* has been verified as a direct result of early classical biological control programs (Oroño & Ovruski 2007).

Currently, the suitability for successfully rearing *D. longicaudata* on larvae of either *C. capitata* or *A. fraterculus* is being studied in the PROIMI insectary in San Miguel de Tucumán—Argentina, as part of an augmentative release program against both tephritid fruit fly species. Therefore, the study here presented was conducted to evaluate the effects of both *C. capitata* and *A. fraterculus* on parasitism, parasitoid emergence, and sexual ratio of offspring in *D. longicaudata* under laboratory conditions. Furthermore, both the number of visiting and oviposition events was documented to assess the parasitoid female preference for 1 or the other host tephritid species.

MATERIALS AND METHODS

The study was performed at the Biological Control Division of Planta Piloto de Procesos Industriales Microbiológicos y Biotecnología (PROIMI) located in San Miguel de Tucumán, Argentina. The colony of *D. longicaudata* was originally established in 1999 with individuals imported from México (Ovruski et al. 2003), where this colony had been reared in the laboratory on *Anastrepha ludens* (Loew) larvae (Montoya et al. 2000). First, *D. longicaudata* was successfully reared at the PROIMI laboratory on late-third instars of *C. capitata*. Then, in 2005 a second colony of *D. longicaudata* was established on late-third instars of *A. fraterculus*. Parasitoid colonies were held in cubical Plexiglas cages (30 cm) covered by organdy screen on both lateral sides, at a capacity of 300 pairs per cage at $25 \pm 1^\circ\text{C}$; $75 \pm 5\%$ RH, and 12:12 (L:D) h photoperiod. The parasitoid rearing cage was provided with water and honey every other day. The general *C. capitata* and *A. fraterculus* rearing procedures were carried out as described by Ovruski et al. (2003) and by Vera et al. (2007), respectively. Both *A. fraterculus* and *C. capitata* puparia were selected from different samples and weighed for host quality evaluation.

Each species of fruit fly was exposed to 10 mated *D. longicaudata* females in cubical Plexiglas cages (30 cm) under both dual-choice and no-choice assays. In the choice assay, an oviposition unit (an organdy screen-covered petri dish, 8 cm diameter, 0.8 cm deep) containing 300 laboratory-reared third-instars of *A. fraterculus* (11 d old) was placed on the floor of the test cage along with another oviposition unit containing 300 laboratory-reared third-instars of *C. capitata* (6 d old). Larvae of both fruit fly species were placed in the units with artificial diet (brewer yeast + wheat germ + sugar + water). Oviposition units were positioned in the central part of the test cage; each unit was placed 1 cm from the side wall and separated by 10 cm from the other unit. In the no-

choice assays, an identical oviposition unit containing 300 third-instars of *A. fraterculus* (or 300 third-instars of *C. capitata*) was placed on the floor of the central part of the test cage away from the walls. All female parasitoids used in experiments were 7-8 d old and deprived of any host larvae before testing. The females used in no-choice tests came either from parasitized puparia of *A. fraterculus* or from parasitized puparia of *C. capitata*. In the choice assay, 5 females stemming from parasitized puparia of *A. fraterculus* and 5 females stemming from parasitized puparia of *C. capitata* were used jointly. This combination of parasitoids from different origins was used so as to ameliorate a possible conditioned response by the previous experience with the host on which it was reared (Godfray 1994). Two control tests (no parasitoids) were made to determine both natural *A. fraterculus* and *C. capitata* mortality and emergence rates. Each test, including control treatments, was replicated 22 times. Each replicate lasted 24 h. All assays were conducted in the laboratory under the environmental conditions described previously.

Behavioral observations can be used to provide evidence of host preference for solitary parasitoids (Mansfield & Mills 2004). For this reason, upon release of parasitoids into each test cage, the number of female visits to and ovipositor probes in the oviposition units was recorded. Odor concentrations of host fruit (Messing & Jang 1992) or oviposition-detering pheromone of tephritid fly (Prokopy & Webster 1978) were not considered in the assays because oviposition units with artificial diet were used. The female parasitoids were observed once every 15 min during the first 3 h and each observation lasted 30 s (Duan & Messing 2000a). A visit was recorded each time a female arrived on the oviposition unit after release. An ovipositor probe was confirmed each time a female parasitoid inserted its ovipositor through the top organdy screen of the oviposition dish. After the 3-h observations, all oviposition units remained exposed to female parasitoids for 21 h to finish a 24-h period (Duan & Messing 2000a). Then, all oviposition dishes were removed from the cages, and fly larvae were directly transferred into plastic cups (7 cm diameter, 6.7 cm deep) containing a 2 cm-vermiculite layer on the bottom as pupation medium. Later, each cup was tightly covered with a piece of organdy cloth on the top. Thus, fly pupae were held within plastic cups with moist, sterilized vermiculite until eclosion. After that, the number and sex of the emerged parasitoids, the number of emerged flies, and the number of unclosed puparia were checked. Unclosed puparia were dissected 2 weeks after emergence of the last adult parasitoid in each cup to check for the presence or absence of recognizable immature parasitoid stages (larvae, prepupae, or pupae) and/or fully developed pharate-adult parasitoids.

Both the parasitism percentage and the number and sex ratio of emerged parasitoid progeny were used as 3 suitable variables to measure host preference, in addition to the behavioral observations (Mansfield & Mills 2004). Parasitism percentage was calculated by dividing the total number of emerged and unemerged parasitoids into the total number of larvae exposed in the oviposition unit. The proportion of emerged parasitoids was calculated as the total number of emerged offspring divided by the total number of recovered pupae. The proportion of emerged flies was computed as the total number of retrieved adult flies divided by the total number of recovered pupae. The proportion of dead pupae was determined as the total number of pupae that did not yield flies or parasitoids divided into the sum of eclosed and uneclosed puparia.

Data on parasitism, parasitoid and fly emergences, sexual ratio of parasitoid offspring (as proportion of females), pupal mortality, and the number of female visits to and ovipositor probes on the artificial oviposition device were analyzed by a 2-sample unpaired *t*-test ($P = 0.05$) in no-choice assays, and by a paired *t*-test ($P = 0.05$) in the choice assay. Moreover, the numbers of emerged adults and dead pupae recorded from each fruit fly species per assay were statistically compared with control treatments by means of one-way analyses of variance ($P < 0.05$). Means were separated with a Tukey honest significant difference test (HSD) ($P = 0.05$). The proportion data were transformed to arcsine square root before analysis. All untransformed means (\pm SEM) were presented in the text. Pupal weight difference between *A. fraterculus* and *C. capitata* was analyzed by a Mann-Whitney Rank Sum test ($P = 0.05$).

RESULTS

From the dual-choice test, significantly higher parasitism and emerged adult parasitoid percentages were recorded from *A. fraterculus* than from *C. capitata* (Table 1). When these 2 fruit fly species were analyzed in the no-choice tests, there was no significant difference for either of these 2 measures of host preference (Table 1). Sex ratios were female biased when *D. longicaudata* was reared from either host fruit fly species. However, the proportion of female offspring was always significantly higher when the parasitoid was reared on *A. fraterculus* than on *C. capitata* (Table 1).

The proportion of emerged *A. fraterculus* and *C. capitata* adults was significantly different between dual-choice, no-choice, and no-exposure control tests ($F_{(2,63)} = 260.0, P < 0.0001$ for *A. fraterculus*; $F_{(2,63)} = 311.8, P < 0.0001$ for *C. capitata*, Table 2). A significantly higher proportion of *A. fraterculus* adults were recovered from the no-choice test than from dual-choice test (Table 2). In contrast, significantly

TABLE 1. MEAN (\pm SEM) PERCENTAGE PARASITISM BY *DIACHASMIMORPHA LONGICAUDATA*, AND PROPORTION OF ADULT PARASITOID AND FEMALE PROGENY EMERGED FROM *CERATITIS CAPITATA* AND *ANASTREPHA FRATERCULUS* FOR BOTH DUAL-CHOICE AND NO-CHOICE TESTS.

Fly species	Dual-choice test			No-choice test		
	% Parasitism	% emerged adult parasitoids	% parasitoid female progeny	% Parasitism	% emerged adult parasitoids	% parasitoid female progeny
<i>C. capitata</i>	17.4 \pm 1.5 a	13.3 \pm 1.1 a	50.7 \pm 2.8 a	37.6 \pm 2.0 a	32.1 \pm 1.5 a	55.0 \pm 1.1 a
<i>A. fraterculus</i>	35.5 \pm 2.1 b	25.3 \pm 2.3 b	82.4 \pm 1.5 b	43.2 \pm 2.2 a	36.3 \pm 1.8 a	79.5 \pm 1.6 b
	paired- <i>t</i> = 7.60 <i>df</i> = 21.0 $P < 0.0001$	paired- <i>t</i> = 5.86 <i>df</i> = 21.0 $P < 0.0001$	paired- <i>t</i> = 5.86 <i>df</i> = 21.0 $P < 0.0001$	unpaired- <i>t</i> = 1.90 <i>df</i> = 42.0 $P = 0.0643$	unpaired- <i>t</i> = 1.95 <i>df</i> = 42.0 $P = 0.0585$	unpaired- <i>t</i> = 12.5 <i>df</i> = 42.0 $P < 0.0001$

Values in the same column with the same letter are not significantly different (paired and unpaired *t*-test, $P = 0.05$).

TABLE 2. MEAN (\pm SEM) PROPORTION OF EMERGED ADULTS AND DEAD PUPAE FROM *CERATITIS CAPITATA* AND *ANASTREPHA FRATERCULUS* RECORDED IN CHOICE, NO-CHOICE, AND CONTROL TESTS.

Tests	% emerged	% emerged	% dead	% dead
	<i>A. fraterculus</i> adults	<i>C. capitata</i> adults	<i>A. fraterculus</i> pupae	<i>C. capitata</i> pupae
Dual-choice	17.3 \pm 1.8 a	63.2 \pm 1.7 a	34.2 \pm 1.4 a	25.5 \pm 1.1 a
No-choice	24.6 \pm 2.6 b	25.1 \pm 1.9 b	32.3 \pm 2.0 a	37.4 \pm 2.5 b
Control	82.4 \pm 1.3 c	85.3 \pm 1.6 c	17.6 \pm 1.3 b	14.7 \pm 1.6 c

Values in the same column with the same letter are not significantly different (Tukey's test, $P < 0.05$).

2.5-times greater proportion of *C. capitata* adults emerged from the dual-choice test than from no-choice test (Table 2). The significantly lowest proportion of dead fly pupae was recorded from no-exposure control tests ($F_{(2,63)} = 28.6$, $P < 0.0001$ for *A. fraterculus*; $F_{(2,63)} = 38.9$, $P < 0.0001$ for *C. capitata*, Table 2). Significantly greater proportion of dead *C. capitata* pupae was recorded from no-choice tests than from dual-choice tests (Table 2).

Under both dual- and no-choice conditions, the mean numbers of *D. longicaudata* female visits to the oviposition units containing *A. fraterculus* larvae were significantly similar to those of parasitoid visits to the oviposition units containing *C. capitata* larvae (paired- $t = 1.89$, $df = 21.0$, $P = 0.0732$ for dual-choice test; unpaired- $t = 0.47$, $df = 42.0$, $P = 0.6435$ for no-choice test; Fig. 1 A). Similarly, in the no-choice assays, there were no significant differences in the mean numbers of parasitoid females probing the oviposition artificial devices (unpaired- $t = 0.58$, $df = 42.0$, $P = 0.5631$; Fig. 1 B). In contrast, in the dual-choice test, a significantly greater number of *D. longicaudata* females were observed probing the oviposition unit containing *A. fraterculus* larvae than the device containing *C. capitata* larvae (paired- $t = 5.54$, $df = 21.0$, $P < 0.0001$; Fig. 1 B).

DISCUSSION

While *D. longicaudata* attacked both *C. capitata* and *A. fraterculus* larvae at similar rates when only 1 of the species was present, they preferred *A. fraterculus* when provided a choice. This divergence may be suggestive of the relative host size differences. For example, *A. fraterculus* larvae used as host in this study were twice as large as *C. capitata* larvae ($T = 60100.0$, $P < 0.0001$, $n = 200$). Previous studies conducted by Messing et al. (1993), Cancino et al. (2002) and López et al. (2009), found that *D. longicaudata* females prefer large hosts. Eben et al. (2000) also pointed to the progeny sex ratio as a measure of host larva preference in *D. longicaudata*. These authors found that *D. longicaudata* reared from a larger species, *A. ludens* (Loew), in mango (*Mangifera indica* L.) had a much higher proportion of female progeny than those parasitoids that had developed in a smaller species, *A. obliqua* (Macquart), infesting the same fruit.

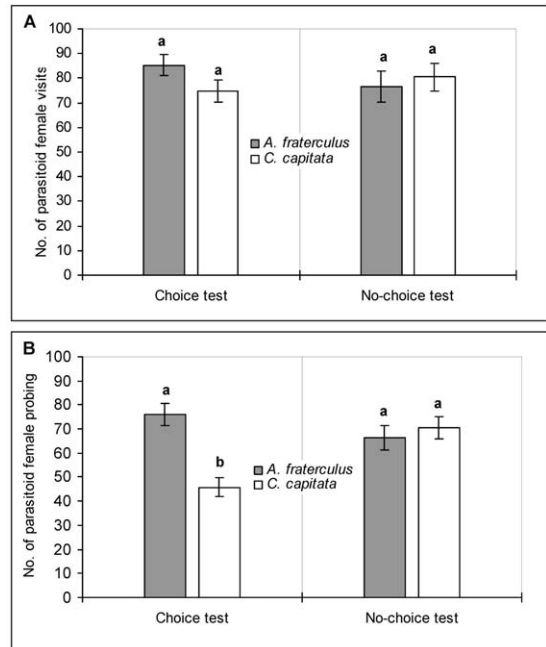


Fig. 1 (A and B). Mean (\pm SEM) (A) number of *D. longicaudata* female visits to, (B) and ovipositor probes on the oviposition units containing artificial diet plus third-instars of *A. fraterculus* or *C. capitata* recorded in no-choice and dual-choice tests. Bars in each graph followed by the same letter indicate no significant differences [unpaired t -test ($P = 0.05$) in the no-choice tests, and paired t -test ($P = 0.05$) in the dual-choice test]

Behavioral observations provided further evidence for a preference for *A. fraterculus* over *C. capitata* larvae. In dual-choice tests *D. longicaudata* females are more likely to exhibit oviposition behaviors on devices containing *A. fraterculus*. However, Silva et al. (2007) found that *D. longicaudata* females did not discriminate between the volatiles produced by *C. capitata* or *A. fraterculus* larvae. In contrast to the present study, the larvae exposed by Silva et al. (2007) were feeding inside infested guava fruits (*Psidium guajava* L.). It has been repeatedly demonstrated that *D. longicaudata* females respond to fruit volatiles, especially from rotting fruits (Greany et al. 1977; Leyva et

al. 1991; Messing & Jang 1992; Purcell et al. 1994; Eben et al. 2000; Carrasco et al. 2005). Chemical cues derived from fermentation of the artificial rearing medium can be exploited for host searching by *D. longicaudata* (Duan & Messing 2000b). However, it is possible that differences in host larval substrates might have influenced *D. longicaudata*'s host detection ability.

Duan & Messing (2000b) found that *C. capitata* larvae outside of the substrate on which they fed generated vibration and chemical cues that stimulated oviposition in *Diachasmimorpha tryoni* Cameron, another generalist opiine fruit fly larval parasitoid (Wharton 1989). In the case of *D. longicaudata*, chemical cues produced by *C. capitata* larvae had little influence on probing behavior (Duan & Messing 2000b). However, it is possible that *D. longicaudata* females may respond more positively to chemical cues of *A. fraterculus* larvae than to those from *C. capitata* larvae. In addition to larval frass, other parts of the host larva such as hemolymph, alimentary canal, fat bodies, labial glands, and mandibular glands may be the source of 1 or more kairomones that stimulate oviposition movements in larval parasitoid species (Arthur 1981). Therefore, additional research should be performed to further define specificity of *D. longicaudata* female responses to chemical cues from both *A. fraterculus* and *C. capitata* larvae. Based on this requirement, we plan to conduct a second series of future experiments with *D. longicaudata* and 2 neotropical opiine fruit fly larval parasitoids.

Although dual-choice test results obtained in the present study provide reliable information on host rank order preferences for *D. longicaudata*, the ecological considerations on preference cannot be conjectured from this data. Therefore, we are currently verifying the host preference by *D. longicaudata* in field-cage tests using different host fruit species which are commonly infested by *C. capitata* and/or *A. fraterculus* larvae in the field.

Finally, this study confirmed previous data indicating that both *C. capitata* (Ovruski et al. 2003; Viscarret et al. 2006) and *A. fraterculus* (Ovruski et al. 2007) are suitable hosts for laboratory rearing of *D. longicaudata* in Argentina. It also provided evidence that female parasitoid progeny yield can be highly improved by using *A. fraterculus* larvae as host instead of *C. capitata* larvae.

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