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COMPARATIVE BIOLOGY OF *DIACHASMIMORPHA LONGICAUDATA* (HYMENOPTERA: BRACONIDAE) REARED ON *ANASTREPHA FRATERCULUS* AND *CERATITIS CAPITATA* (DIPTERA: TEPHRITIDAE)

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Abstract

The braconid *Diachasmimorpha longicaudata* (Ashmead) is the most widely used parasitoid in biological control programs of tephritids in the Americas. *Anastrepha fraterculus* (Wiedemann) is a major fruit fly pest of exotic and native fruits in southern Brazil. However, life history parameters such as longevity, sex ratio, preoviposition, oviposition and post-oviposition periods, fecundity and fertility of *D. longicaudata* using *A. fraterculus* as host, have not been determined. These parameters were compared to those derived from the better known host, *Ceratitis capitata* (Wiedemann), the Mediterranean fruit fly. In the laboratory, *A. fraterculus* was at least as suitable a host for *D. longicaudata* as *C. capitata.* Female parasitoids derived from *A. fraterculus* were larger and had a higher net reproductive rate (R_0). The mean numbers of superparasitism records were higher in *A. fraterculus* larvae (1.6 ± 0.22) than in *C. capitata* (0.4 ± 0.07). Other variables did not differ between hosts. Given suitable environments *D. longicaudata* may become established in *A. fraterculus* populations or successfully mass-reared on this host species and released.

Key Words: biological control; body size; fertility; life cycle; longevity

Resumo

O braconídeo *Diachasmimorpha longicaudata* (Ashmead) é o parasitóid mais utilizado em programas de controle biológico de tefritídeos nas Américas. Dentre as moscas-das-frutas de importância econômica no Sul do Brasil, *Anastrepha fraterculus* (Wiedemann) é a espécie mais importante, infestando espécies frutíferas nativas e exóticas. No entanto, os parâmetros de biologia, tais como a longevidade, razão sexual, períodos de oviposição, pré-oviposição, e pós-oviposição, fecundidade e fertilidade de *D. longicaudata* tendo *A. fraterculus* como hospedeiro não foram determinados. Tais características do parasitoide foram comparadas com insetos que se desenvolveram em larvas da mosca-do-Mediterrâneo, um hospedeiro mais conhecido, *Ceratitis capitata* (Wiedemann). No laboratório, *A. fraterculus* foi um hospedeiro igualmente adequado para *D. longicaudata* quanto *C. capitata*. Parasitoides que se desenvolveram em *A. fraterculus* tiveram maior taxa líquida de reprodução (R_0) e produziram indivíduos maiores. O registro diário de casos de superparasitismo foi maior em larvas de *A. fraterculus* (1,6 ± 0,22) do que em *C. capitata* (0,4 ± 0,07), e as demais variáveis não diferiram entre os hospedeiros. Em ambientes adequados, *D. longicaudata* pode se estabelecer em populações de *A. fraterculus*, asssim como é possível obter sucesso em uma criação massal do parasitoide neste hospedeiro.

Palavras Chave: controle biológico; tamanho corporal; fertilidade; ciclo de vida; longevidade

Opiine braconids are widely used in the control of tephritid fruit flies because their relatively high host specificity and ability to inflict substantial mortality on their hosts (Aluja et al. 1990). About 100 species of braconids have been found parasitizing tephritid larvae worldwide, and many of these belong to the genera: *Diachasmimorpha* Viereck, *Psyttalia* Walker, *Utetes* Foster and *Opius* Wesmael (Wharton 1989). The Indo-Australian *Diachasmimorpha longicaudata* (Ashmead) is a koinobiont, solitary, synovigenic, larval-prepupal endoparasitoid of several tephritid genera that has been mass-reared and used in augmentative releases against important fruit fly species in tropical and subtropical countries (Montoya et al. 2000). Biological parameters of *D. longicaudata* have been studied on *Anastrepha suspensa* (Loew) (Ashley et al. 1976; Greany et al. 1976; Lawrence

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et al. 1976), *Anastrepha ludens* Loew (Montoya et al. 2003; Montoya et al. 2011) and *Ceratitis capitata* (Wiedemann) (Ovruski et al. 2003; Viscarret et al. 2006).

Although introduced to Brazil in 1990 (Carvalho & Nascimento 2002), *D. longicaudata* has been used sporadically and plans for further introductions and/or augmentation releases are still in early stages. In Brazil, *D. longicaudata* has been reared on the Mediterranean fruit fly, *C. capitata*, but less is known about its performance on the South American fruit fly, *Anastrepha fraterculus* (Wiedemann) (Kovaleski et al. 2000). This work aimed to evaluate biological parameters of *D. longicaudata* on *A. fraterculus* and provide data for mass-rearing this parasitoid.

Materials and Methods

Puparia of *C. capitata* parasitized by *D. longicaudata* were provided by "Embrapa Mandioca e Fruticultura Tropical", Cruz das Almas, state of Bahia, Brazil (Dr. Antônio Nascimento) and maintained according to the methods described by Carvalho et al. (1998). Host larvae were obtained from a laboratory culture established in 2007 from wild fruit flies. We used 16th to 28th generation fruit flies and 7th to 35th generation parasitoids.

Diachasmimorpha longicaudata Colony Rearing

Approximately 50 couples of *D. longicaudata* were maintained in cages (20 × 15 × 15 cm), covered by organdy screen and kept at 25 ± 2 °C; 65 ± 10% RH and 14:10 h L:D. Water and food were provided *ad libitum*. Diet consisted of water (120 ml), honey (120 ml), agar (0.8 g), ascorbic acid (0.05 g), and nipagin (0.005 g). Approximately 40 to 50 third instar larvae of *C. capitata* were introduced to the cages and exposed to parasitoids for 1 h in parasitism units made of organdy screen (225 cm^2). Host larvae were placed in the center of the screen and the edges wrapped with a rubber band forming a spherical unit that was hung from the upper part of cage. Up to 3 units were hung in each cage per day. After exposure, larvae were transferred individually to 100 ml plastic vials with sterilized sand until emergence.

Anastrepha fraterculus and *Ceratitis capitata* Colony Rearing

The flies were reared using the methods described by Salles (1992) and Terán (1976), and maintained at 25 ± 2 °C; 65 ± 10% RH and 14:10 h L:D.

Life History Traits of *D. longicaudata* Reared on *A. fraterculus* and *C. capitata*

Egg-Adult Phase

Five groups with 40-50 third-instar larvae of *A. fraterculus* (about 10-day-old) were exposed for 1 h to fifty 3-10-day-old experienced couples of *D. longicaudata*, previously reared on *A. fraterculus* larvae. The putatively parasitized larvae were placed individually in vials (25 ml) with sterilized sand and wet paper, and covered with plastic film. Larvae were maintained at 25 ± 2 °C; 65 ± 10% RH and 14:10 h L:D and observed every day for emergence. The same procedure was applied to third-instar larvae of *C. capitata,* which were exposed for 1 h to fifty 3-10-day-old experienced couples of *D. longicaudata*, previously reared on *C. capitata* larvae. The total developmental period (egg-adult) and immature viability of 215 and 225 parasitized larvae of *A. fraterculus* and *C. capitata* were recorded, respectively.

Longevity, Sex Ratio, Fecundity and Fertility

Two groups of *D. longicaudata* adults, one composed of 52 females and 56 males that had emerged from *A. fraterculus*, and another of 55 females and 54 males that emerged from *C. capitata*, were individually kept in plastic vials (140 mL) provided with food and water to determine the longevity of virgin adults. Females of these 2 groups did not receive larvae for oviposition during the experiment. We observed 10 parasitoid couples that had emerged from *A. fraterculus,* and were maintained with food and water *ad libitum,* and offered *A. fraterculus* larvae (10 per female) for 1 h oviposition periods in a daily basis. When a parasitoid female died, we reduced the number of larvae in order to keep the larva/female ratio, until all females had died. Each dead male was replaced to avoid competition for sexual partners and to guarantee the maximum reproductive potential by females. After exposure, the larvae were removed and kept at 25 ± 1 °C, 60 ± 10% RH and complete darkness. After 72 h the pupae were opened to count the number of parasitoid eggs and/or larvae, and the number of viable fruit fly larvae. We considered fertility as the number of parasitoid larvae and fecundity the number of larvae plus the number of eggs; superparasitism was evaluated by counting eggs and larvae inside the pupae. Longevity of mated *D. longicaudata* was also recorded. Fecundity, fertility and superparasitism of *D. longicaudata* reared on *C. capitata* or *A. fraterculus* were recorded for 25 couples on each host.

Morphometry of *D. longicaudata* Reared in *A. fraterculus* and *C. capitata*

We measured the length of the right hind tibia and the area of the right forewing of 100 *D. longicaudata* adult females and 100 adult males

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that emerged from *A. fraterculus* and *C. capitata*. These body parts were removed and photographed under an optical microscope and measured with a micrometer. The photos were analyzed and compared with the software Image Tool 3.00®. Mean larval weights of *A. fraterculus* and *C. capitata* were estimated by weighing 10 groups each of 10 larvae.

Data Analysis

Data were tested for normality by D'Agostino test and compared with a t-student or Mann-Whitney test. The sex ratio (sr) and fertility were calculated as described by Silveira Neto et al. (1976). The mean weight of larvae, tibia length and forewing area were compared between hosts by Kruskal-Wallis test. We estimated and compared the life table parameters, (net reproductive rate (R_0), finite rate of increase (λ), rate of population increase (r_m) and doubling time (TD)) of parasitoids reared on 2 hosts were estimated using the "Jackknife" technique (Meyer et al. 1986) following the procedures described in Maia et al. (2000) and Maia & Luiz (2006). The significance level used in all the tests was $\alpha = 0.05$.

Results

Life History Traits of *D. longicaudata* Reared on *A. fraterculus* and *C. capitata*

Egg-Adult Phase

The mean egg-adult development periods of *D. longicaudata* females and males were similar on both hosts. However, females had a longer lifespan than the males ($H = 91.9402$; df = 3; $P < 0.05$) (Table 1).

Longevity, Sex Ratio, Fecundity and Fertility

Virgin females that emerged from *A. fraterculus* lived longer than those emerged from *C. capitata* ($t = -2.7008$; df = 105; $P = 0.008$). By contrast, the longevities of mated females did not differ between hosts ($t = -0.0776$; df = 38; $P = 0.9386$). The longevities of virgin and mated males from both hosts was similar ($t' = 1.0727$; df = 91.07; $P = 0.2862$ and $U = 160$; $P = 0.4424$, respectively) (Table 2).

Virgin individuals of *D. longicaudata*, regardless the host, lived longer (31 ± 1.19 days) than mated ones (17.7 ± 1.21 days) ($t' = 7.8427$; df = 229.11; $P < 0.0001$) (Table 2).Virgin females reared on *A. fraterculus* lived longer than virgin males from the same host ($t' = 5.2652$; df = 89.50; $P < 0.0001$), but there was no difference between the longevities of the sexes when mated ($U = 90.50$; $P = 0.3615$). Conversely, for insects reared from *C. capitata*, the mean longevity of virgin females did not differ from that of males ($t = -0.07832$; df = 107; $P = 0.4352$), while mated females lived longer than males ($U = 201$; $P = 0.0305$) (Table 2).

On the first day of parasitoid emergence, only males emerged from both hosts. On the second day of emergence, males predominated. From the third day onwards the female ratio increased. The sex ratio of *D. longicaudata* on *A. fraterculus* (0.59) was similar to that on *C. capitata* (0.55) ($\chi^2 = 1.978$; df = 1; $P = 0.1776$) (Fig. 1).

The mean daily fecundity ($U = 4.50$; $P = 0.0947$), total ($t = 1.3987$; df = 8, $P = 0.1994$) and mean fertility ($\chi^2 = 1.141$; df = 1; $P = 0.3599$) were similar in *D. longicaudata* emerged from *A. fraterculus* and *C. capitata*. The preoviposition ($t = 1.0$; df = 4; $P = 0.3739$), oviposition ($U = 10$; $P = 0.6015$) and post-oviposition ($t' = -0.7977$; df = 4.38; $P = 0.4697$) periods did not differ for females reared on the 2 hosts (Table 3). Superparasitism was recorded during all the oviposition period in the wasps reared from both hosts. The mean number of superparasitism records per day and per female were higher on *A. fraterculus* (1.6 ± 0.22) than on *C. capitata* (0.4 ± 0.07) ($U = 164$; $P = 0.0002$). Up to 3 parasitoid eggs were recorded in a single *C. capitata* larva, while in *A. fraterculus* we recorded up to 6 eggs (Fig. 2).

Based on generation time (T), net reproductive rate (R_0), finite rate of increase (λ), infinitesimal rate of increase (r_m) and doubling time (DT), the

Table 1. Duration (days) (Mean ± SE) of the egg to adult development of *Diachasmimorpha longicaudata* females and males reared on *Anastrepha fraterculus* and *Ceratitis capitata* [25 ± 2 °C; 65 ± 10% RH; 14:10 h L:D].

	Females		Males	
Host	Duration	Range	Duration	Range
A. fraterculus	18.8 ± 0.17 Aa (53)	17-23	17.2 ± 0.13 Ab (61)	15-22
C. capitata	19.2 ± 0.23 Aa (55)	17-26	18.5 ± 0.13 Ab (54)	17-21

Means followed by different letters (capitals within columns and lowercase letters within rows), were significantly different according to a Kruskal-Wallis test ($\alpha = 0.05$).Values between parentheses show the number of observations.

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TABLE 2. MEAN LONGEVITY (DAYS) (± SE) OF VIRGIN AND MATED *DIACHASMIMORPHA LONGICAUDATA* FEMALES AND MALES REARED ON *ANASTREPHA FRATERCULUS* AND *CERATITIS CAPITATA* [25 ± 2 °C; 65 ± 10% RH; 14:10 H L:D].

		Females		Males	
Host	Status	Longevity	Range	Longevity	Range
A. fraterculus	Virgins	40.4 ± 2.43 Aa (52)	6-76	25.04 ± 1.61 Ab (56)	3-45
	Mated	20.4 ± 3.39 Ba (15)	4-49	15.6 ± 2.09 Ba (15)	6-32
C. capitata	Virgins	30.9 ± 2.49 Aa (55)	1-77	28.2 ± 2.49 Aa (54)	1-67
	Mated	20.7 ± 2.11 Ba (25)	1-38	14.2 ± 20.3 Bb (25)	2-41

Means followed by different letters were significantly different (t-test) (uppercase letters represent comparisons between mated and virgin individuals on a same host and same sex) and by Mann-Whitney test (lowercase letters represent comparisons between sexes for a same host and same mating status) ($\alpha = 0.05$).Values between parenthesis show number of observations.

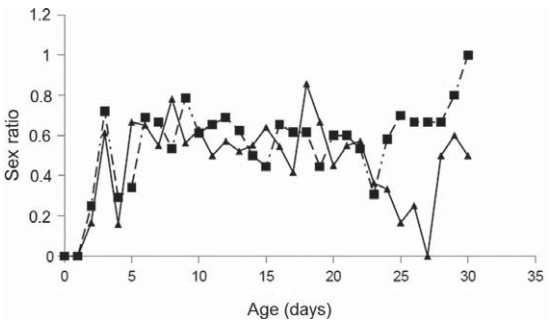


Fig. 1. Daily sex ratio of *Diachasmimorpha longicaudata* reared on *Anastrepha fraterculus* (■) and on *Ceratitis capitata* (▲) [25 ± 2 °C; 65 ± 10% RH; 14:10 H L:D]. A sex ratio value that is greater than 0.5 represents a population with more females than males. A sex ratio of less then 0.5 represents a population with more males than females.

fitness of *D. longicaudata* reared on *A. fraterculus* was higher than when reared on *C. capitata* (Table 4).

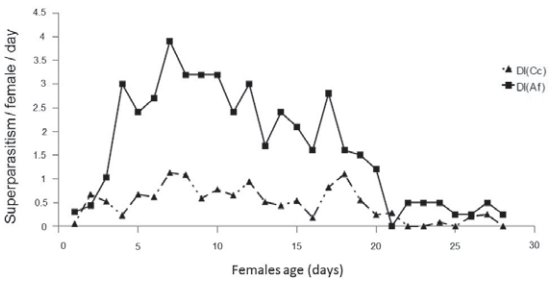


Fig. 2. Daily number of superparasitisms observed per *Diachasmimorpha longicaudata* female on *Ceratitis capitata* (Dl(Cc)) and *Anastrepha fraterculus* (Dl(Af)).

Morphometry of D. longicaudata Reared in A. fraterculus and C. capitata

Third-instar larvae of *A. fraterculus* were heavier (0.0203 ± 0.00027 g) than those of *C. capitata* (0.0121 ± 0.00025 g) (t = - 22.4084; df = 18, $P < 0.0001$). Females that emerged from *A. fraterculus* had a larger wing area (F = 1.7393; df = 211; $P < 0.0001$) and longer tibia length (F = 3.5723; df = 220; $P < 0.0001$) than those derived from *C. capitata*. Males reared from *A. fraterculus* also had larger wings (F = 2.3671; df = 201; $P < 0.0001$) and longer tibiae (F = 2.0931; df = 204; $P < 0.0001$). Females were always larger than males regardless the host species (Table 5).

DISCUSSION

The longer lifetime observed for *D. longicaudata* females compared to males can be related to additional time required for maturation of reproductive organs (Ramadan et al. 1992). This seems be a pattern in braconids, as recorded in *Diachasmimorpha tryoni* (Cameron) (Hurtrel et al. 2001), *Biosteres persulcatus* Silvestri (Ibrahim et al. 1993) and *Biosteres arisanus* (Sonan) (Bautista et al. 1998). Moreover, male parasitoids usually emerge sooner, which expedites locating emerging females and ensures mating. The male-dominated sex ratio on the first and second day of emergence may be a strategy increases the likelihood of males copulating newly emerged females (Godfray 1994). The shorter longevity of mated females compared to virgin females may be related to the energy used for copulation and oviposition (Greany et al. 1976).

Host size may affect sex ratio, particularly of idiobionts, because more females are produced from larger hosts (Ueno 1999; Ode & Heinz 2002). As expected of a koinobiont parasitoid, we

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TABLE 3. PREOVIPOSITION, OVIPOSITION AND POST-OVIPOSITION PERIODS (DAYS) (MEAN ± SE), DAILY FECUNDITY AND TOTAL FECUNDITY (MEAN ± SE), FERTILITY (%) (MEAN ± SE)) OF *DIACHASMIMORPHA LONGICAUDATA* REARED ON *ANASTREPHA FRATERCULUS* (DL (AF)) (N = 11) AND ON *CERATITIS CAPITATA* (DL (CC)) (N = 25) [25 ± 2 °C; 65 ± 10% RH; 14:10 H L:D].

	Dl (Af)		Dl (Cc)	
Biological Variables	$\bar{x}$ ± SE	Range	$\bar{x}$ ± SE	Range
Period (days)				
Preoviposition^{ns}	1 ± 0	1-1	1.1 ± 0.2	1-2
Oviposition^{ns}	29.6 ± 2.98	20-38	27.4 ± 3.17	18-35
Post-oviposition^{ns}	3.2 ± 1.71	1-10	1.8 ± 0.37	1-3
Fecundity (eggs/female)				
Daily^{ns}	6.2 ± 0.57	5.2-8.3	4.9 ± 0.34	4.1-5.6
Total^{ns}	193.5 ± 27.79	110.5-274	145.9 ± 19.45	110.7-206.2
Fertility (%)^{ns}	64.5 ± 1.11	61.2-67.3	71.7 ± 4.12	62.8-85.6

ns = non significant (t- test - preoviposition, post-oviposition and total fecundity; Mann-Whitney test - oviposition and daily fecundity; qui-square test - fertility) (α = 0.05).

did not observe such effect in our study. Host size may have a direct influence on parasitoid size (Godfray 1994), as demonstrated in this study. Larger parasitoids may have higher levels of fertility and fecundity (Jervis 2005). However, the heavier females reared from *A. fraterculus* larvae did not have higher fertility or fecundity. Differences in host size or quality may not necessarily influence reproductive parameters. Some parasitoids may allocate resources to host searching, having a somehow fixed reproductive budget (Cicero et al. 2011). In fact, parasitoids are able to compensate for differences in host quality by modifying their resource allocation strategy (Cicero et al. 2012). The higher incidence of superparasitism in *A. fraterculus* may be related to the size of the larvae and the parasitism unit. *Anastrepha fraterculus* is larger than *C. capitata,* while the parasitism units were the same size for both hosts. Thus, parasitoid females contacted fewer larvae of *A. fraterculus* than of *C. capitata*. Superparasitism by *D. longicaudata* appears to be common. Superparasitized hosts were recorded even in the presence of unparasitized larvae with no apparent detrimental effects on the offspring's demographic parameters (Montoya et al. 2012).

Differences in the size of parasitoids produced by different hosts should be taken into account in biological control projects. The parasitoid size may influence their host searching efficiency (Lawrence et al. 1976).

In summary, in the laboratory *A. fraterculus* was at least as suitable as a host as *C. capitata* for *D. longicaudata.* Female parasitoids derived from *A. fraterculus* had a higher net reproductive rate (R_0) and produced larger individuals. The number of superparasitism records was higher in *A. fraterculus* than in *C. capitata*;other variables, such as longevity, sex ratio, preoviposition, oviposition and post-oviposition periods, fecundity and fertility did not differ between the host species. Given suitable environments, *D. longicaudata* may become established in Brazilian *A. fraterculus* populations or successfully mass-reared and released for augmentative biocontrol.

TABLE 4. NET REPRODUCTIVE RATE (R_0), INFINITESIMAL RATE OF INCREASE (R_m), FINITE RATE OF INCREASE (λ), MEAN (T) (DAYS), AND DOUBLING TIME (DT) (DAYS) (VALUES ± SE) OF *DIACHASMIMORPHA LONGICAUDATA* REARED ON *ANASTREPHA FRATERCULUS* AND ON *CERATITIS CAPITATA* [25 ± 2 °C; 65 ± 10% RH; 14:10 H L:D].

Host	R_0	R_m	λ	T	DT
A. fraterculus	53.82 ± 10.001 a	0.17 ± 0.031 a	1.19 ± 0.051 a	22.57 ± 0.594 a	3.92 ± 0.082 b
C. capitata	45.56 ± 5.685 a	0.14 ± 0.019 b	1.15 ± 0.028 b	26.03 ± 0.451 a	4.73 ± 0.074 a

Means followed by different letters within columns were significantly different (t-test, α = 0.05).

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TABLE 5. RIGHT FOREWING AREA (MM²) (MEANS ± SE) AND HIND TIBIA LENGTH (MM) OF FEMALES AND MALES OF *DIACHASMIMORPHA LONGICAUDATA* REARED FROM *ANASTREPHA FRATERCULUS* (DL (AF)) AND FROM *CERATITIS CAPITATA* (DL (CC)) [25 ± 2 °C; 65 ± 10% RH; 14:10 H L:D].

	Dl (Af)		Dl (Cc)	
	Females	Males	Females	Males
Wings (mm²)	4.6 ± 0.05 Aa (100)	4.2 ± 0.06 Ba (100)	2.9 ± 0.04 Ab (103)	2.4 ± 0.04 Bb (113)
Legs (mm)	1.79 ± 0.016 Aa (111)	1.64 ± 0.014 Ba (102)	1.24 ± 0.012 Ab (104)	0.93 ± 0.016 Bb (111)

Means followed by different letters in the same line differed significantly by t-test ($\alpha = 0.05$) between sexes for a same host (uppercase) and between different hosts for a same sex (lowercase). Values between parentheses represent the number of observations.

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