Comparative Biology of Diachasmimorpha longicaudata (Hymenoptera: Braconidae) Reared on Anastrepha fraterculus and Ceratitis capitata (Diptera: Tephritidae)

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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). 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 parasitóide foram comparadas com insetos que se desenvolverem 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. Parasitóides que se desenvolverem em A. fraterculus tiveram maior taxa líquida de reprodução (R) 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, assim como é possível obter sucesso em uma criação massal do parasitóide 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
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...
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 (R₀), finite rate of increase (λ), rate of population increase (r_m) and doubling time (DT)) 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 α = 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*).

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) (*χ² = 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 (*χ² = 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 (R₀), 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 *Diachasmimora longicaudata* Females and Males Reared on *Anastrepha fraterculus* and *Ceratitis capitata* [25 ± 2 °C; 65 ± 10% RH; 14:10 h L:D].

<table>
<thead>
<tr>
<th>Host</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Duration</td>
<td>Range</td>
</tr>
<tr>
<td><em>A. fraterculus</em></td>
<td>18.8 ± 0.17 Aa (55)</td>
<td>17-23</td>
</tr>
<tr>
<td><em>C. capitata</em></td>
<td>19.2 ± 0.23 Aa (55)</td>
<td>17-26</td>
</tr>
</tbody>
</table>

Means followed by different letters (capitals within columns and lowercase letters within rows), were significantly different according to a Kruskal-Wallis test (α = 0.05). Values between parentheses show the number of observations.
fitness of *D. longicaudata* reared on *A. fraterculus* was higher than when reared on *C. capitata* (Table 4).

**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 than 0.5 represents a population with more males than females.

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

**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]).

| Host         | Status  | Females | |          | Males | |
|--------------|---------|---------||          |       |          |
|              |         | Longevity | Range |          | Longevity | Range |
| *A. fraterculus* | Virgins | 40.4 ± 2.43 Aa | 6-76 |          | 25.04 ± 1.61 Ab | 3-45 |
|              | Mated   | 20.4 ± 3.39 Ba | 4-49 |          | 15.6 ± 2.09 Ba | 6-32 |
| *C. capitata* | Virgins | 30.9 ± 2.49 Aa | 1-77 |          | 28.2 ± 2.49 Aa | 1-67 |
|              | Mated   | 20.7 ± 2.11 Ba | 1-38 |          | 14.2 ± 2.03 Bb | 2-41 |

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

**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 = 3.0931; df = 204; P < 0.0001). Females were always larger than males regardless of 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 to 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 to increase 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 idiobions, because more females are produced from larger hosts (Ueno 1999; Ode & Heinz 2002). As expected of a koinobiont parasitoid, we
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 (*R₀*) 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 3. Preoviposition, Oviposition and Post-oviposition Periods (days) (Mean ± SE), Daily Fecundity and Total Fecundity (Mean ± SE) of *Diachasmimorpha longicaudata* Reared on *Anastrepha fraterculus* (Di (Af)) (N = 11) and on *Ceratitis capitata* (Di (Cc)) (N = 25) [25 ± 2 °C; 65 ± 10% RH; 14:10 h L:D].

<table>
<thead>
<tr>
<th>Biological Variables</th>
<th>Di (Af)</th>
<th>Range</th>
<th>Di (Cc)</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preoviposition</td>
<td>1 ± 0</td>
<td>1-1</td>
<td>1.1 ± 0.2</td>
<td>1-2</td>
</tr>
<tr>
<td>Oviposition</td>
<td>29.6 ± 2.98</td>
<td>20-38</td>
<td>27.4 ± 3.17</td>
<td>18-35</td>
</tr>
<tr>
<td>Post-oviposition</td>
<td>3.2 ± 1.71</td>
<td>1-10</td>
<td>1.8 ± 0.37</td>
<td>1-3</td>
</tr>
</tbody>
</table>

### Table 4. Net Reproductive Rate (*R₀*), Infinitesimal Rate of Increase (*Rₚ*), 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].

<table>
<thead>
<tr>
<th>Host</th>
<th><em>R₀</em></th>
<th><em>Rₚ</em></th>
<th><em>λ</em></th>
<th>T</th>
<th>DT</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. fraterculus</em></td>
<td>53.82 ± 10.001</td>
<td>0.17 ± 0.031</td>
<td>1.19 ± 0.051</td>
<td>22.57 ± 0.594</td>
<td>3.92 ± 0.082</td>
</tr>
<tr>
<td><em>C. capitata</em></td>
<td>45.56 ± 5.685</td>
<td>0.14 ± 0.019</td>
<td>1.15 ± 0.028</td>
<td>26.03 ± 0.451</td>
<td>4.73 ± 0.074</td>
</tr>
</tbody>
</table>

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

We thank Dra. Aline Barcellos for the critical revision and valuable comments and to CNPq for fellowships awarded to the authors and the financial support (grant 475287/2010-0).

REFERENCES CITED


Table 5. Right forewing area (mm²) (Means ± SE) and hind tibia length (mm) of females and males of Diachasmimorpha longicaudata reared from Anastrepha fraterculus (Di (AF)) and from Ceratitis capitata (Di (Cc)).

<table>
<thead>
<tr>
<th></th>
<th>Di (AF)</th>
<th></th>
<th>Di (Cc)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Females</td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>Wings (mm²)</td>
<td>4.6 ± 0.05 Aa</td>
<td>4.2 ± 0.06 Ba</td>
<td>2.9 ± 0.04 Ab</td>
</tr>
<tr>
<td>(100)</td>
<td>(100)</td>
<td>(103)</td>
<td>(113)</td>
</tr>
<tr>
<td>Legs (mm)</td>
<td>1.79 ± 0.016 Aa</td>
<td>1.64 ± 0.014 Ba</td>
<td>1.24 ± 0.012 Ab</td>
</tr>
<tr>
<td>(111)</td>
<td>(102)</td>
<td>(104)</td>
<td>(111)</td>
</tr>
</tbody>
</table>

Means followed by different letters in the same line differed significantly by t-test (α = 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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