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Influence of the original host in the preference of *Aganaspis pelleranoi* and *Doryctobracon areolatus*, parasitoids of Tephritidae larvae

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Abstract

The study aimed to evaluate the host preference and success of parasitoids from different host origins. The Tephritidae parasitoids *Aganaspis pelleranoi* (Brethes) (Hymenoptera Figitidae) (AP) and *Doryctobracon areolatus* (Szepligeti) (Hymenoptera Braconidae) (DA), native to the Neotropical region, were evaluated. Experiments were performed under laboratory conditions, in dual-choice tests, in which two oviposition units, each containing 25 larvae of either native host *Anastrepha fraterculus* (Wiedemann) (Diptera Tephritidae) (AF) or exotic host *Ceratitis capitata* (Wiedemann) (Diptera Tephritidae) (CC), were offered simultaneously to parasitoids that had emerged from pupae of both species. The average number of pupae, emerged parasitoids, parasitized pupae, and sex ratio of the offspring were evaluated. The average number of parasitoids emerged for *A. pelleranoi* that originated from *A. fraterculus* (AP-AF) was significantly higher in the host *A. fraterculus* compared with *C. capitata*. The same occurred for parasitoids originated from *C. capitata* (AP-CC), parasitizing larvae of the host specie *C. capitata*. The emergence rate of *D. areolatus* was higher in parasitoids that originated in *A. fraterculus*, in the same host species. For *A. pelleranoi* with origin in *A. fraterculus*, a higher average of parasitized pupae was observed for the host of the same species. *D. areolatus* regardless of the original host, parasitized a larger number of *A. fraterculus* pupae. *A. pelleranoi* had a male-biased sex ratio, ranging from 0.11 to 0.42 depending on the origin and the host. The sex ratio for *D. areolatus* was 50%, only in parasitoids originated from *C. capitata* (DA-CC) and having host larvae from the same species. The results for *A. pelleranoi* (AP-AF and AP-CC) and *D. areolatus* (DA-AF) indicate that original host origin of female might alter host preference. In addition, *C. capitata* was a less suitable host for rearing these species of parasitoids.

Key words: *Anastrepha fraterculus*, *Ceratitis capitata*, Neotropical parasitoids, preference for host.

Introduction

Parasitoid preference for specific hosts is related to innate search behaviour (Vet *et al*., 1995); however, successive exposure to a particular host can alter the preference, which indicates learning (Vinson, 1998). In the broad sense, learning is a change in behaviour resulting from an experience, increasing the reliability in the recognition of the location trails generated by the host in space and time, which increases the efficiency of the foraging (Vinson, 1998; Cunningham *et al*., 1999; Masry *et al.*, 2018b). For parasitoids, an individual host comprises its entire source of larval food and can greatly influence on the adult's performance. Because development depend on limited resources (host), adult preference and larval performance must be correlated to maximize fitness (Harvey *et al.*, 2012; 2015). Other host-related factors including its size can influence the fitness of the parasitoids including the number of offspring, development, longevity, and sex ratio (Messing *et al*., 1993; López *et al*., 2009; Gonçalves *et al*., 2013).

The influence of the original host on the performance of parasitoids associated with fruit flies has received little study. Ero *et al.* (2010), for example, evaluated the preference of *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera Braconidae) by four species of the genus *Bactrocera* Macquart (Diptera Tephritidae), but the parasitoid showed no preference in both the choice test and the non-choice test. Ero *et al.* (2011) studying the same parasitoid, evaluated the preference on five commercial fruit species and two species of fruit flies, *Bactrocera jarvisi* (Tryon) and *Bactrocera tryoni* (Froggatt). The parasitoid responded to all infested fruits, regardless of the species of fruit fly, although it did not show preference. Its offspring preferred guava (*Psidium guajava* L.), peach (*Prunis persica* L.), and orange (*Citrus sinensis* L.). Ovruski *et al.* (2011) evaluated the preference of the parasitoid *Diachasmimorpha longicaudata* (Ashmead), originating from the Indo-Australian region, reared on *Anastrepha fraterculus* (Wiedemann) and *Ceratitis capitata* (Wiedemann) (Diptera Tephritidae), for the host of the same origin. The authors found no difference between the two hosts in the no-choice test, but in the dual-choice test, there was higher parasitism in the *A. fraterculus* larvae. Canale and Benelli (2012) evaluated if *Psyttalia concolor* (Szepligeti) created for several generations in *C. capitata* could affect the location and parasitism when used against *Bactrocera oleae* (Rossi). The study did not show a significant difference in oviposition behaviour and host acceptance for parasitoids without previous experience, but showed that the previous experience in a given host can influence the choice of the female, prioritizing the host already known. Giunti *et al*. (2016) evaluated if the olfactory trails of the original host could affect the preference of the parasitoid *P. concolor* and if recognition of a new host could be learned during the larval stages and in the initial adult stage. The authors demonstrated that there was a preference for the original host in which the parasitoid developed but that females could learn. *D. kraussii*

also showed a significant preference for fruits infested by larvae of a host species, *B. tryoni* compared to fruits infested by non-host larvae, *Drosophila melanogaster* (Meigein) (Diptera Drosophilidae) (Masry *et al.*, 2018a). Masry *et al.* (2018b) working with the same parasitoid, parasitizing *B. tryoni* larvae in nectarine (*Prunus persica* var. *nucipersica* L.) and tomato (*Solanum lycopersicum*, var. Gourmet premium L.) fruits in an associative learning experiment, in sequential studies of olfactometer, closed field and open field. The virgin females showed preference for nectarines, not increased the choice after that had previous training. However with the same tests, the authors observed that after experience with the tomato, there was learning and the females began to recognize the fruit, increasing the choice. The knowledge of these aspects is extremely important when searching for a biological control agent to control fruit flies. For this *Aganaspis pelleranoi* (Brethes) (Hymenoptera Figitidae) (AP) and *Doryctobracon areolatus* (Szepligeti) (Hymenoptera Braconidae) (DA) have a naturally higher abundance compared with others Neotropical parasitoids species on the field. In addition, they are parasitoids on fruit fly larvae in native and exotic fruits, which increases their chances of success in parasitism (Schliserman *et al*., 2016). They are found mainly parasitizing *Anastrepha* Schiner (native to the American continent) and *Ceratitis* MacLeay (from Tropical Africa) (Uchôa, 2012). Both genera of fruit flies include species that cause high economic damage to fruit farming, such as the *A. fraterculus* (South American fruit fly) and *C. capitata* (Mediterranean fruit fly) (da Costa *et al.*, 2017; dos Santos and Guimarães, 2018). Therefore, they are considered promising species for fruit fly biological control programs (Nunes *et al*., 2011; Uchôa, 2012; Gonçalves *et al.*, 2016).

Many aspects of the life cycle of *A. pelleranoi* have already been studied, such as the description of immature stages on *A. fraterculus* and *C. capitata* (Ovruski, 1994), and their mating behaviour (Ovruski and Aluja, 2002). In this species, the females exhibit a significantly more diverse behavioural repertoire than other species of figitids (Aluja *et al.*, 2009). The effect of different temperatures on egg-adult development and biological parameters such as longevity and adult fertility were also evaluated (Gonçalves *et al.*, 2014). When reared on *A. fraterculus* the offspring and female proportion were higher, the egg-adult cycle shorter, and the survival rate higher, than when reared on *C. capitata* (exotic host) (Gonçalves *et al.*, 2013).

The parasitoids use a wide range of host-related stimuli to find hosts, usually chemical stimuli such as microhabitat, host plant, indecisive stimuli associated with host presence and host-own stimuli (Godfray, 1994). *D. areolatus* also uses these chemical cues to find its host, as described by Eitam *et al.* (2003), including markers of host fruits and fly larvae. The egg-adult development period, sex ratio, longevity of males and females, pupal survival rate, and parasitism rates against *A. fraterculus* have been also evaluated (Nunes *et al.*, 2011). The interspecific competition has been recorded between this species and the braconid *Utetes anastrephae* (Viereck), but without competitive exclusion (Aluja *et al.*, 2013). Furthermore, the natural parasitism of this species in *A. fraterculus* has been registered in different fruit trees (Costa *et al.*, 2007; Jahnke *et al.*, 2014; Júnior *et al.*, 2017).

Understanding parasitism preference is important to select a biological control agent. However, the influence of their original host on the performance and preference of parasitoids associated to the fruit fly has been insufficiently studied. Thus, the aim of this study is to evaluate the host preference and success of the parasitoids *A. pelleranoi* and *D. areolatus* in larvae of *A. fraterculus* and *C. capitata* as affected by their original host.

Materials and methods

Study site

The study was conducted in the Laboratory of Biology, Ecology, and Biologic Control of Insects (Bioecolab), at the Federal University of Rio Grande do Sul, under controlled conditions (26 ± 1 °C, 60 ± 10% RH), and a photoperiod of 14:10 (L:D).

Host rearing

Rearing of *A. fraterculus* (AF) and *C. capitata* (CC) was based on the methodology described by Terán (1977), with adaptations. The adults of fruit flies were kept in wooden cages (45 × 30 × 30 cm), covered on the sides with voile tissue and front opening for manipulation (sleeve), receiving distilled water and a solid diet *ad libitum*, which consisted of crystal sugar, hydrolyzed protein, soybean extract (3:1:1:1), and vitamin complex, in proportion to two tablets macerated for each 250 g of diet (adapted from Jaldo *et al*., 2001). The egg-laying substrate used for *C. capitata* was a yellow plastic tube (250 ml), with orifices (FAO/IAEA/USDA, 2003), and for *A. fraterculus* the substrate was a bag as described by Meirelles *et al.* (2016). The eggs were collected daily and transferred to a polystyrol tray (23.5 × 18 × 1 cm) containing artificial diet (carrot, beer yeast, corn flour, sugar and distilled water) (modified from Terán, 1997). After seven days, these were placed inside larger plastic trays (51 × 30 × 9.5 cm), with sterilized sand and covered by voile, where they remained for approximately seven days for pupation. After this, the sand was sifted and the collected pupae placed in plastic pots (6.6 × 6.6 × 6 cm) until emergence, under controlled conditions (26 ± 1 °C, 60 ± 10% RH), and a photoperiod of 14:10 (L:D).

Parasitoids rearing

To rear *A. pelleranoi*, araçá fruit, *Psidium cattleianum* Sabine (Myrtaceae), infested with *A. fraterculus* was collected from native fruit orchards at Fundação Estadual de Pesquisa Agropecuária, in Taquari, RS, Brazil (29°48'00"S 51°51'35"O). In the laboratory, the fruit were placed in plastic trays (51 × 30 × 9.5 cm) on a layer of sterilized sand and covered by voile. The sand was sifted after 15 days and the collected pupae kept until the emergence of fruit flies or parasitoids at plastic pots (6.6 × 6.6 × 6 cm). Adult parasitoids were placed in wood cages (19.5 × 16.5 × 25.5 cm) and received water

by capillary and honey diluted in water (7:3), offered in Petri dishes with cotton wicks. The third-instar larvae of the hosts *C. capitata* or *A. fraterculus* (approximately 6 and 9 days old, respectively) were offered daily to the parasitoids (5-15 days of life) (van Nieuwenhove and Ovruski, 2011; Gonçalves *et al.*, 2014; Oliveira *et al.*, 2014). The larvae were placed in oviposition units made of a plastic plate (4 cm of diameter), with a border of 0.3 cm, wrapped in white voile. After six hours of exposure, the larvae were placed on artificial diet in a polystyrol tray (15.5 × 15.5 × 1 cm) placed on a plastic tray (41 × 28 × 7 cm) with sterilized sand covered by voile, where they remained for approximately seven days for pupation. After this, the sand was sifted and the collected pupae placed in plastic pots (6.6 × 6.6 × 6 cm) until emergence, under controlled conditions (26 ± 1 °C, 60 ± 10% RH), and a photoperiod of 14:10 (L:D).

The rearing of *D. areolatus* was established with *A. fraterculus* parasitized pupae provided by Embrapa Clima Temperado, Pelotas, RS, Brazil (31°46'19"S 52°20'34"O). The colony was maintained under the same conditions cited for *A. pelleranoi*, in the *A. fraterculus* and *C. capitata* hosts. Except the instar of the larvae offered in the parasitism units for the maintenance of the breeding, following Eitam *et al.* (2003), were second instar (3 days of life for *C. capitata* and 4 days of life for *A. fraterculus*), and the parasitism units were exposed for eight hours (van Nieuwenhove and Ovruski, 2011; Gonçalves *et al.*, 2013).

Experimental design

The experiment was conducted in wooden cages (15 × 15.5 × 20 cm) covered by voile. Each cage contained five couples of *A. pelleranoi* (AP) or *D. areolatus* (DA), eight days old. The parasitoids received water and food as described previously. Within each cage, oviposition units were arranged with 25 larvae of *A. fraterculus* and 25 larvae of *C. capitata* (from third instar larvae to *A. pelleranoi* and second instar larvae to *D. areolatus*). To assess if there were preference, the following treatments were adopted with the hosts AF and CC: parasitoid *A. pelleranoi* with origin from *A. fraterculus* (AP-AF); *A. pelleranoi* with origin from *C. capitata* (AP-CC); parasitoid *D. areolatus* with origin from *A. fraterculus* (DA-AF); and, *D. areolatus* with origin from *C. capitata* (DA-CC). The experiment was conducted with 40 replicates for AP-AF and AP-CC; and for DA-AF. For DA-CC 35 replicates were made (the smallest number of insect replications used here is due to the small laboratory emergency of the parental generation). The larvae were offered in separate oviposition units, made of a plastic plate (2.7 cm in diameter), with a border of 0.2 cm, wrapped in white voile. To dispose the parasitism units inside the cages, small glass jars (2.3 × 2.3 × 3.8 cm) were used as carriers. The units were exposed for six hours for *A. pelleranoi* and eight for *D. areolatus*, then returned to diet in a polystyrol tray (15.5 × 15.5 × 1 cm) placed on a plastic tray (35 × 17.5 × 10 cm) with sterilized sand covered by voile, where they remained for approximately five days (second instar larvae) and seven days (third instar larvae) for pupation. Next, the sand was sifted and the pupae placed in plastic pots (6.6 × 6.6 × 6 cm) until the emergence of fruit flies or parasitoids, under the same conditions as described previously.

In the control treatment, second and third-instar larvae were placed in oviposition units, and positioned in the cages for the same period of time described previously, but without parasitoids. Concomitant with the treatments, this procedure was replicated during five consecutive days to verify larvae mortality, without the parasitoid action.

We recorded the number of pupae formed, emerged parasitoids, parasitized pupae (emerged parasitoids from the puparia + dissected puparia with parasitoids presence) and the sex ratio of the parasitoids.

Data analysis

The mean values of pupae, emerged parasitoids, and parasitized pupae were tested for normality by Shapiro-Wilk test. Subjected to analysis of variance, the means being compared by Kruskal-Wallis, followed by a Dunn HSD post-hoc at the 5% significance level, by the software BioEstat 5.0 (Ayres *et al.*, 2007). The sex ratio was determined by the following equation: sr = number of females/ number of females + number of males. The χ^2 test of heterogeneity was applied to compare the sex ratio between the species. The apparent parasitism was calculated by the equation: ap = number of emerged parasitoids / total number of emerged insects × 100; and the real parasitism by: rp = total number of parasitoids emerged and dissected / total number of insects × 100.

Results

Aganaspis pelleranoi (AP) (table 1)

Original host influenced the number of emerged parasitoids, parasitized pupae, and the sex ratio at the AP-AF treatment. This effect was also observed in the number of emerged parasitoids in AP-CC. The apparent parasitism was 62.9% in AF hosts and 43% in CC hosts offered to parasitoids originating from AF. In parasitoids originated from CC, the apparent parasitism was 6.7% and 9.3 % in hosts from AF and CC, respectively. The real parasitism was 64.2% in AF hosts and 43.9% in CC hosts, both offered to parasitoids originated from AF. For AF hosts offered to parasitoids originated from CC, the index was 15.6% and the CC host, 13.5%.

Comparing parasitoids with the same origin (AP-AF) in relation to the two hosts (CC and AF), the mean of emerged parasitoids was higher in the AF host ($H = 4.9150$; $df = 1$; $P = 0.0203$). If exposed to the AP-CC treatment, the mean emergence was higher in the same original host (CC) ($H = 3.2170$; $df = 1$; $P = 0.0397$). Considering the same host in relation to the different origins of the parasitoids, the mean number of emerged parasitoids from AF host pupa was higher in the ones exposed to the AP-AF treatment ($H = 47.4457$; $df = 1$; $P < 0.0001$). Parasitism was higher in CC host offered to the parasitoids of AF-AP treatment ($H = 20.2714$; $df = 1$; $P < 0.0001$). The mean number of parasitized pupae, considering the emerged parasitoids plus the ones inside the dissected puparia, was higher in

Table 1. Average number (± SE) of pupae, emerged parasitoids, parasitized pupae (*), and sex ratio of *A. pelleranoi* originating from *A. fraterculus* (AP-AF) and *C. capitata* (AP-CC), in *A. fraterculus* and *C. capitata*. (N = number of larvae per replicate).

Host	Origin: *A. fraterculus*		Origin: *C. capitata*	
	A. fraterculus N = 25	*C. capitata* N = 25	*A. fraterculus* N = 25	*C. capitata* N = 25
Pupae	23.9 ± 0.21 Aa	23.9 ± 0.45 Aa	23.5 ± 0.28 Aa	24.1 ± 0.26 Aa
Emerged parasitoids	9.8 ± 0.90 Aa	7.5 ± 0.94 Ba	0.9 ± 0.19 Bb	1.8 ± 0.44 Ab
Parasitized pupae (*)	12.2 ± 1.07 Aa	8.1 ± 0.96 Ba	2.8 ± 0.48 Ab	3.0 ± 0.60 Ab
Sex ratio	0.42 Aa	0.21 Ba	0.37 Ab	0.11 Bb

Upper case letters compare parasitoids from the same origin in the different hosts. Lowercase letters compare parasitoids from different origins to the same host. Using the Kruskal-Wallis test, followed by Dunn ($P < 0.05$). Sex ratio, tested by χ^2 for heterogeneity. (*) parasitoids emerged from the puparia + puparia dissected with parasitoids presence.

Table 2. Average number (± SE) of pupae, emerged parasitoids, parasitized pupae (*), and sex ratio of *D. areolatus* originating from *A. fraterculus* (DA-AF) and *C. capitata* (DA-CC), in *A. fraterculus* and *C. capitata*. (N = number of larvae per replicate).

Host	Origin: *A. fraterculus*		Origin: *C. capitata*	
	A. fraterculus N = 25	*C. capitata* N = 25	*A. fraterculus* N = 25	*C. capitata* N = 25
Pupae	18.7 ± 0.70 Aa	18.0 ± 0.97 Aa	18.7 ± 0.76 Aa	12.9 ± 1.18 Bb
Emerged parasitoids	4.2 ± 0.89 Aa	2.4 ± 0.73 Ba	0.4 ± 0.16 Ab	0.2 ± 0.09 Ab
Parasitized pupae (*)	4.8 ± 0.96 Aa	2.9 ± 0.79 Ba	1.2 ± 0.32 Ab	0.4 ± 0.14 Bb
Sex ratio	0.30 Ab	0.34 Ab	0.38 Ba	0.50 Aa

Upper case letters compare parasitoids from the same origin in the different hosts. Lowercase letters compare parasitoids from different origins to the same host. Using the Kruskal-Wallis test, followed by Dunn ($P < 0.05$). Sex ratio, tested by χ^2 for heterogeneity. (*) parasitoids emerged from the puparia + puparia dissected with parasitoids presence.

the host AF ($H = 7.4370$; $df = 1$; $P = 0.0064$) when both hosts were offered to the treatment from AP-AF. There was no difference between the different hosts (AF and CC) offered for the parasitoids from AP-CC treatment ($P > 0.05$). *A. fraterculus* host larvae, when exposed to parasitoids from the same origin, resulted in a higher average number of parasitized pupae than those offered to parasitoids with origin in CC ($H = 35.3600$; $df = 1$; $P < 0.0001$). For CC host when offered to parasitoids of different origins, the highest mean percentage of parasitism for the AP species originated from AF host ($H = 14.3709$; $df = 1$; $P = 0.0002$).

The sex ratio of the offspring obtained in both specie of host larvae, promoted by parasitoids originated from both treatments (AP-AF and AP-CC), was male biased (more than 50% were males). Parasitoids from AP-AF treatment that parasitized AF host larvae, generated a higher number of females ($\chi^2 = 58.3$; $df = 2$; $\alpha = 0.05$) compared to the parasitoids from the same origin, parasitizing CC host larvae. The sex ratio of the generated offspring of parasitoids from AP-CC, was superior in AF ($\chi^2 = 47.2$; $df = 2$; $\alpha = 0.05$). The sex ratio of the offspring were superior in both hosts when the parasitoids from the AP-AF treatment, compared to the same host species parasitized by *A. pelleranoi* with CC origin.

There was no significant difference in the mean number of pupae formed for both hosts (AF and CC), when offered to parasitoids from the same or distinct origin. The number of formed pupae also did not differ from the control on the different treatments ($P > 0.05$).

Doryctobracon areolatus (DA) (table 2)

When the larvae of AF hosts larvae were offered to DA-AF treatment, the average number of emerged parasitoids and parasitized pupae was higher than CC host. Origin affected sex ratio as well: when the hosts were CC, parasitized by females from DA-CC the sex ratio was higher. The average number of parasitized pupae reflects the real parasitism, which was 27.8% in the AF hosts and 18.6% in the CC hosts, both offered to the parasitoids with origin in AF. For the hosts offered to the parasitoids originated from CC, the ratio was 8.1% in the AF and 4.6% in the CC. The apparent parasitism (only emerged parasitoids) was 26.4% in the AF hosts and 16.5% in the CC, offered to parasitoids originated from AF. Those originated from CC achieved 4.0% of parasitism, in the AF host and 2.5% in the CC host.

For parasitoids from DA-AF treatment in relation to the different hosts, the mean number of emerged parasitoids was higher in the host AF than in CC ($H = 6.1401$; $df = 1$; $P = 0.0144$). There was no difference between the average numbers from the hosts AF and CC ($H = 0.3079$; $df = 1$; $P = 0.5790$) offered to DA-CC treatment. Considering the AF host in relation to the different origins of parasitoids (DA-AF and DA-CC), the emergence was higher when the parasitoids had the same origin of the host ($H = 9.8123$; $df = 1$; $P = 0.0017$). A higher emergence was verified when the CC hosts were exposed to DA-AF ($H = 5.9704$; $df = 1$; $P = 0.0473$), compared to DA-CC. The mean number of parasitized pupae was higher in the host *A. fraterculus*

compared to *C. capitata,* regardless of the parasitoids' origins (H = 4.1706; df = 1; P = 0.0421, AF-DA, and H = 3.2170; df = 1; P = 0.0341, CC-DA). There was a higher number of parasitized pupae in the host AF when exposed to the treatment DA-AF (H = 5.2238; df = 1; P = 0.0223), compared to DA-CC treatment. The CC host also had a higher number of parasitized, when exposed to the treatment DA-AF (H = 3.2284; df = 1; P = 0.0314), than those originated from DA-CC.

The offspring's sex ratio was male biased, except in parasitoids emerged from CC larvae offered to the same origin that generated 50% of females. Parasitoids originated from DA-AF treatment, did not show sex ratio difference, between the distinct hosts (AF and CC). The DA-CC treatment generated more females when parasitizing CC (χ^2 = 47.6; df = 2; α = 0.05). When compared to the same hosts offered to the parasitoids with different origins, the ones exposed to DA-CC treatment had a higher sex ratio.

No difference was observed in the average number of formed pupae in both hosts (AF and CC), when offered to DA-AF (P > 0.05). A difference in the average number of pupae was recorded at the CC host expose to the DA-CC treatment (H = 12.1290; df = 1; P = 0.0005). The average values of formed pupae obtained in the treatments did not differ from the control in both host species AF and CC (P > 0.05).

Discussion

The similarity in the number of formed pupae in the treatments in relation to the control was expected, considering that both species are koinobionts (Ovruski, 1994), that is, do not immediately kill or cause injury in the larval development, allowing pupation before causing death. It is known that fruit fly parasitoids from the families Braconidae and Figitidae only emerge in the host's pupal stage (Guimarães and Zucchi, 2004; Aluja *et al.*, 2013). The number of emerged parasitoids, related to the apparent parasitism or the female success (Ovruski *et al.*, 2011), of *A. pelleranoi* originating from CC was higher in the hosts from the same species, though overall AF was a far superior host regardless of parasitoid origin. However, for *D. areolatus*, only females with origin in AF had more success in hosts from the same species. Considering the real parasitism, the performance of the parasitoids originated from AF was superior than the CC, regardless of the host larvae.

The better performance of *A. pelleranoi* and *D. areolatus* in *A. fraterculus* larvae, when compared to other Tephritidae hosts, was previously mentioned by Gonçalves *et al*. (2013; 2016), in which the authors report that the number of offspring was affected by the host species, *A. fraterculus* being the superior host. The authors discuss that this occurred due to the bigger larval size of *A. fraterculus* compared to *C. capitata*. According to Ovruski *et al.* (2004), the parasitoids of the Neotropical region may not be able to parasitize the larvae of the host *C. capitata*, and when it does it harms the development of their offspring. Harvey (2005) and Harvey *et al*. (2012) pointed out that the diet used for the host can affect their development and survival too. However, in our study, both host species were already reared for a long time with the same diet and adapted very well; therefore, we believe that this would not affect our results.

The data on *A. pelleranoi* indicate that this species may be influenced by the original host, because the female displayed an oviposition preference for the Tephritidae larvae (AF or CC) in which it had developed. The choice of the female for different larvae can be related to variables such as perception of the fruit volatiles (host habitat) and the hosts (Eben *et al.*, 2000; Silva *et al.*, 2007; Segura *et al.*, 2016). Thus, the use of chemical cues can be the result of memory or learning (Segura *et al.*, 2007; Tognon *et al.*, 2013). The learning can occur through the chemical legacy, whereby the parasitoid that emerged from a specific host is able to distinguish the odour of its original host (Tognon *et al.*, 2014). Thus, the learning process occurs in a different way in each species. However, the data from this study was for only one generation, and it is likely that behavioural changes could occur over the next generations.

A. fraterculus is the ancestral host of both species and probably there was a coevolution between them, since the host *C. capitata* was recently introduced on the American continent (Ovruski *et al*., 2004; Gonçalves *et al.*, 2013), therefore preference was expected by the AF host. Nevertheless, for *A. pelleranoi*, after just one generation in CC, an alteration in the preference was recorded, suggesting that this species may have learning by chemical legacy (Tognon *et al*., 2014). Canale and Benelli (2012) and Giunti *et al.* (2016) working with *P. concolor*, observed that the parasitoids preferred to lay their eggs and were more successful parasitizing the host where they were reared. This may be due to learning the chemical signals recognition from original host larvae, because according to Hopkins' host-selection principle the larval instar of the parasitoids can learn from their environment and that memory is transported from pre-imaginary stages to the adult (Barron, 2001; Giunti *et al.*, 2016). Masry *et al.* (2018a) working with *D. kraussii* observed the preference of the parasitoid by the host in which it is naturally found. The parasitoids used had experience of oviposition, suggesting that these wasps learn odours specific to host-infested fruit. The authors define learning as a change in behaviour after an experiment, since the experiment was not designed to characterize the type of learning.

In this study and others, the larvae were offered in oviposition units, without the presence of fruit or other substrates (Carvalho *et al*., 1998). Nevertheless, the parasitism occurred, indicating that the females are able to recognize the hosts outside natural conditions. This was already observed in the behaviour of *Diachasmimorpha tryoni* (Cameron) and *D. longicaudata* with washed or individualized larvae (Duan and Messing, 2000). The latter authors also demonstrated that the species examined their hosts using the ovipositor independent of the substrate type, as well as used larval vibration as a guide. In the natural environment, however, the larvae are located in fruit, which certainly influences the search and choice of the parasitoids. Possibly the parasi-

toids use chemical clues as a guide, especially those in the fruit peel (Eitam *et al*., 2003). According to Eitam *et al.* (2003), when the peels were removed and the pulps exposed, there was a drop in the ovipositions by *D. areolatus*. Thus, the host plants appear to be an important source of information for parasitoids during their search for the host, and the parasitoids attracted by plants that provide nutritionally better hosts are favoured by natural selection (Canale, 2003; Segura *et al*., 2016). This must be considered when lab rearings are kept using hosts from artificial diets for later release in the field.

The sex ratio of the offspring, in which the majority of the cases was male biased, could be an indication that the female considered that host or the environment conditions were not ideal for the parasitism (Godfray and Shimada, 1999). Despite this fact, *A. pelleranoi* produced a higher number of females in the treatments whose host larvae were AF compared to CC. The sex ratios obtained in this study are similar to those obtained by Gonçalves *et al.* (2013), which were 0.42 in the AF host and 0.19 in the CC host. Although that study did not evaluate the original host, they discuss that the higher number of females in the AF host could be related to the size or chemical differences in the hosts.

D. longicaudata showed higher proportions of females in larvae from the host AF than in CC, in which size may have favored choice for egg deposition (Ovruski *et al*., 2011). It is known that parasitoids lay eggs that result in males in smaller hosts and eggs that generate females in the larger ones, selecting the better host for its descendants (Godfray and Shimada, 1999). Another study found interesting results for *D. longicaudata*, females that emerged from medium and large-size hosts had benefits such as longer life expectancy, higher fertility and faster foraging (López *et al.*, 2009). For *D. areolatus*, although only in parasitoids originated from CC and having as hosts larvae from the same species, the sex ratio was 50%, opposing the host size idea related to the sex ratio. However, the parasitism and emergence rates were significantly lower in this treatment. Therefore, the smaller sample number of the offspring may be responsible for this percentage.

A. pelleranoi and *D. areolatus* are native and widely distributed in the Neotropical region and are common parasitoids of *A. fraterculus* in Brazil (Canal and Zucchi, 2000; Schliserman *et al*., 2016). Therefore, it is presumed coevolution between the species occurred, which could explain the more effective response to this host compared to the exotic *C. capitata*. Another factor that could influence the parasitoids during the choice experiment is the larval size. Because many studies have demonstrated that the host size can ensure benefits to the offspring (López *et al.*, 2009; Gonçalves *et al.*, 2013; 2016), and as demonstrated in our study, *C. capitata* is not a good host for the rearing of these parasitoids, because it generates fewer offspring and a sexual ratio almost always with fewer females. This offspring originating from larger hosts may be predisposed to have greater reproductive success, as was observed in parasitoids originated from *A. fraterculus*, which demonstrated more success in the parasitism for both hosts (AF and CC).

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