

Effects of Extrinsic, Intraspecific Competition and Host Deprivation on the Biology of *Trichopria anastrephae* (Hymenoptera: Diapriidae) Reared on *Drosophila suzukii* (Diptera: Drosophilidae)

AP KRÜGER¹, T SCHEUNEMANN¹, JGA VIEIRA¹, MC MORAIS², D BERNARDI¹, DE NAVA^{1,3}, FRM GARCIA¹

¹Programa de pós-graduação em Fitossanidade, Univ Federal de Pelotas, Pelotas, RS, Brasil

²Faculdade de Agronomia Eliseu Maciel, Univ Federal de Pelotas, Pelotas, RS, Brasil

³EMBRAPA Clima Temperado, Pelotas, RS, Brasil

Keywords

Biological control, pupal parasitoid, spotted wing drosophila, SWD, parasitoid-host interaction, sex ratio, longevity, viability

Correspondence

A.P. Krüger, Programa de pós-graduação em Fitossanidade, Univ Federal de Pelotas, Pelotas, RS96010900, Brasil; alexandra_kruger@hotmail.com

Edited by Lessando Moreira Gontijo – UFV

Received 25 April 2019 and accepted 5 July 2019

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Abstract

The pupal parasitoid *Trichopria anastrephae* Lima (Hymenoptera: Diapriidae) shows potential to control *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), and understanding the behavior of this parasitoid in challenging environments is important to obtain a higher efficiency in mass rearing and in biological control programs. This study aimed to verify the effects of extrinsic intraspecific competition and the absence of host on the parasitism of *T. anastrephae* in *D. suzukii* pupae. Therefore, to evaluate the parasitism of *T. anastrephae* under intraspecific competition, groups of 20 pupae (24 h old) of *D. suzukii* were offered for different densities of parasitoids (1, 3, 5, or 10 couples) during a 7-day period. Whereas to evaluate the effects of host deprivation on parasitism of *T. anastrephae*, we tested different treatments: T1—no deprivation, T2—complete deprivation, T3—deprivation every other day, T4—deprivation for 3 days, and T5—deprivation for 7 days. The increase of density of parasitoids resulted in an increase of oviposition scars on pupae and a longer biological cycle, suggesting the occurrence of super-parasitism. Increased density also resulted in a higher percentage of attacked pupae, but did not affect parasitoids emergence nor sex ratio. Host deprivation affected number of parasitized pupae, number and sex ratio of offspring, and the longevity of females. Based on our findings, competition among females do not impair offspring viability, and host deprivation for a period up to 7 days do not influence parasitism capacity, indicating that it can be used as a pre-release strategy.

Introduction

The spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), is native to Asia, but it is currently distributed in Europe and North and South America (Bolda *et al* 2010; Walsh *et al* 2011; Calabria *et al* 2012; Cini *et al* 2012; Deprá *et al* 2014) and has potential to invade and establish in other continents (Dos Santos *et al*

2017). Due to its highly sclerotized ovipositor, the females are able to lay eggs in ripening and mature healthy fruits, where the larvae develop, hindering the commercialization of fresh fruits and resulting in economic losses (Schlesener *et al* 2015).

Drosophila suzukii management is based mainly on chemical products (Bruck *et al* 2011; Burrack *et al* 2015). However, the short life cycle and the limited residual control provided

by insecticides induce the frequent use of products to keep the population density low (Renkema *et al* 2016). In addition, the first case of resistance to insecticide by a strain of *D. suzukii* was recently reported (Gress & Zalom 2018), showing the urge to adopt an integrated management for this pest, encouraging the use of a variety of methods and tactics of control, such as biological control.

Studies performed in Europe and North America reported the association of *D. suzukii* with a variety of parasitoid species, although only few species showed efficiency in population growth regulation (Chabert *et al* 2012; Rossi Stacconi *et al* 2013; Gabarra *et al* 2015; Rossi Stacconi *et al* 2015; Garcia *et al* 2017). Due to the elevated immune system of *D. suzukii* larvae, pupal parasitoids such as *Trichopria drosophilae* (Perkins) (Hymenoptera: Diapriidae) and *Pachycrepoideus vindemniae* (Rondani) (Hymenoptera: Pteromalidae) seem to be more successful against this pest (Kacsoh & Schlenke 2012). The pupal endoparasitoid *Trichopria anastrephae* Lima (Hymenoptera: Diapriidae), native from South America (Garcia & Corseuil 2004; Cruz *et al* 2011), was found in fruits infested by *D. suzukii* in Brazil, and showed potential to parasitize the pest in laboratory (Wollmann *et al* 2016; Andrezza *et al* 2017). Despite *T. anastrephae* exhibit potential to be used in biological control programs to control *D. suzukii*, there is scarcity of information about this parasitoid species in the literature (Wollmann *et al* 2016; Andrezza *et al* 2017; Bernardi *et al* 2017; Schlesener *et al* 2019).

In laboratory (and mass) rearing, parasitoid adults are kept in groups, in cages or vials, and hosts are offered in a periodic basis, to produce more parasitoids (Schlesener *et al* 2019). In this environment, parasitoid females are competing for hosts, and this competitive interaction can affect viability and sex ratio of offspring, and favor the occurrence of superparasitism (Hamilton 1967; Carneiro *et al* 2009; Cruz *et al* 2018). According to the Local Mating Competition theory (LMC), proposed by Hamilton (1967), when a single female oviposits in a patch, the progeny will be female-biased, whereas in competitive environments, a less female-biased offspring is expected. Consequently, the increase in male progeny can be unfavorable for mass rearing which aim to maximize female production for colony maintenance and field release (Irvin & Hoddle 2006). Moreover, if the competitive environment is extreme, it can be detrimental when it stimulates superparasitism to the point which emergence of parasitoids is influenced (Cruz *et al* 2018).

Host deprivation is another factor that can affect the success of biological control. Before releasing in the field, usually parasitoids undergo a pre-release conditioning, where they are provided with carbohydrate sources, attempting to maximize the fitness of parasitoids (Hougardy *et al* 2005; Tena *et al* 2017). During this period, host deprivation occurs, and this can affect population dynamics and production of

parasitoid offspring (Hougardy *et al* 2005). In some cases, host provision during pre-release conditioning can be positive since it can stimulate oogenesis and host searching in field (Tena *et al* 2017), while in other cases, host deprivation during this period is essential to ensure sufficient fecundity and longevity post-release (Hougardy *et al* 2005). Furthermore, after field releasing, parasitoids can undergo periods of low host availability and they may absorb oocytes or retain eggs to compensate the host absence period with an extension in reproductive life (Carneiro *et al* 2009).

Understanding the behavior of a parasitoid in intra- and interspecific interactions is important to obtain a higher efficiency in mass rearing, improvement of quality control, and help biological control programs to become more efficient (Montoya *et al* 2003). Thus, the objective of this study was to verify the effects of intraspecific competition among females and host deprivation on the parasitism of *T. anastrephae* in pupae of *D. suzukii*.

Material and Methods

Maintenance rearing of *Drosophila suzukii*

The laboratory rearing originated from flies emerged from infested blackberries (*Rubus* spp.) collected in January 2016, in Pelotas, Rio Grande do Sul, Brazil (31°38'20"S and 52°30'43"W). Since its establishment, the laboratory colony did not receive any introduction of wild flies, and the colony was maintained for over 2 years, when the experiments were conducted. The flies were reared on artificial diet in glass tubes (25 × 85 mm) capped with cotton plugs, as described by Schlesener *et al* (2017) and Schlesener *et al* (2018). The artificial diet consisted of agar (8 g), yeast (40 g), cornmeal (80 g), sugar (100 g), propionic acid (3 mL), methyl paraben (0.8 g dissolved in 8 mL of 90% ethanol), and water (1,000 mL). This diet was used as oviposition substrate by adults, as well as food for larvae and adults. All rearing and experiments were carried out in controlled conditions (temperature, 25 ± 2°C; relative humidity, 70 ± 10%; and photophase, 12 h).

Maintenance rearing of *Trichopria anastrephae*

The laboratory colony of *T. anastrephae* was established with parasitoids found in *D. suzukii* infested blackberry collected in Pelotas, Rio Grande do Sul, Brazil (31°38'24"S and 52°30'55"W) in summer 2017. Since its establishment, the laboratory rearing did not receive any introduction of wild parasitoids. After the emergence of the parasitoids that originated the laboratory colony, some specimens were collected for identification, and sent to Valmir A. Costa, who positively identify the specimens as *T. anastrephae*, according to the taxonomic

characters established by Costa Lima (1940). Adults of *T. anastrephae* were kept in plastic cages (262 × 177 × 147 mm) (length × height × width), with two side openings (80 × 100 mm), and an opening in the lid (155 × 50 mm), covered with voile cloth. The adults were fed streaks of honey the top of the cage. Daily, 24-h-old SWD pupae were placed in Petri dishes (60-mm diameter) lined with a moistened cotton layer and exposed to parasitism for 24 h. Then, the Petri dishes containing the pupae were placed in another cage, with the same dimensions as mentioned above, until the emergence of new parasitoids.

Intraspecific competition

We tested four different densities (treatments): 1, 3, 5, and 10 couples of *T. anastrephae* (1 day old). The couples were kept at plastic cups (500 mL) containing a hole in the top (40-mm diameter) covered with voile fabric to allow ventilation, and a side opening (40-mm diameter) also made with voile fabric, to allow the change of the parasitism units. Each parasitism unit was composed of 20 *D. suzukii* pupae (< 24 h old) distributed on a plastic plate (25-mm diameter) lined with a moistened cotton layer. The insects were offered a plastic plate (25-mm diameter) containing a cotton ball soaked in honey, which was replaced every other day. The parasitism units were changed every 24 h, for 7 consecutive days. The experimental design was completely randomized with 12 replicates per treatment.

After each exposition of the pupae to the parasitoids, we observed the number of oviposition scars on the surface of each pupae produced by the insertion of parasitoid ovipositor in ovipositions or oviposition attempts. Then, the pupae were individualized, according to treatment, replicate and number of scars, in microtubes (2.0 mL). Daily, the pupae were observed to verify the duration of the biological cycle (egg-adult period) of offspring. After the emergence, the parasitoids were separated by sex to determine sex ratio ($sr = \text{number of females} / \text{number of females} + \text{males}$). The percentage of attack was calculated based on the total number of pupae with oviposition scars divided by the total number of offered pupae, and the viability was calculated from the number of emerged parasitoids divided by the number of pupae containing scars.

Host deprivation

Couples of *T. anastrephae* (1 day old) were placed in plastic cups (200 mL), with a hole (15-mm diameter) on top, covered with voile fabric. Honey was provided to the parasitoids as food source, as described previously. The following treatments were tested: (T1) hosts provided daily, until the death of the female, (T2) complete host deprivation during the entire life of the female, (T3) provision of hosts in alternated

days, (T4) host deprivation during the first 3 days, and (T5) host deprivation during the first 7 days. In treatments T4 and T5, after the host deprivation period, host was provided daily during the entire life of the female. As host, 20 pupae of *D. suzukii* were exposed to each couple in parasitism units as described before, for a period of 24 h. After exposure period, pupae were removed and placed in acrylic tubes (25 × 45 mm).

Daily the tubes containing the exposed pupae were observed to verify the emergence of parasitoids and, thus, determine the biological cycle of offspring. After emergence, parasitoids were sexed and counted. In addition, the flies that emerged from the pupae exposed to each treatment were counted, and the pupae that remained intact were dissected, and the presence of flies or parasitoids was recorded to determine the actual parasitism rates. Longevity of males and females, number of parasitized pupae (number of emerged + non-emerged parasitoids) per female, number of offspring generated per female, and their sex ratio were evaluated. The experimental design was completely randomized with 15 replicates per treatment.

Statistical analysis

All data were verified for normality and the homoscedasticity of the residues through the Shapiro Wilk and Bartlett tests, respectively. Data from the intraspecific competition bioassay were evaluated using regression models ($p \leq 0.05$). Total number of parasitized pupae and sex ratio data from the host deprivation bioassay were submitted to analysis of variance ($p \leq 0.05$), and when confirmed statistical significance data was compared using Duncan test ($p \leq 0.05$). Total number of offspring and duration of biological cycle data from the host deprivation bioassay did not meet the normality and homoscedasticity assumptions, and were therefore submitted to the Kruskal-Wallis test ($p \leq 0.05$), and when confirmed statistical significance, data was compared by the Dunn's test ($p \leq 0.05$). The longevity of parasitoids was evaluated using the survival curves in the Kaplan-Meier estimator, and subsequently compared to each other using the log-rank test. All statistical analyses were performed in R software (R Development Core Team 2011).

Results

Intraspecific competition

The number of oviposition scars found on pupae of *D. suzukii* increased exponentially as the density of couples of parasitoids also increased ($F = 1171.71$, $df = 3$, $p = 0.0009$, Fig 1a). The duration of the biological life cycle of the progeny did not adjust to any regression model

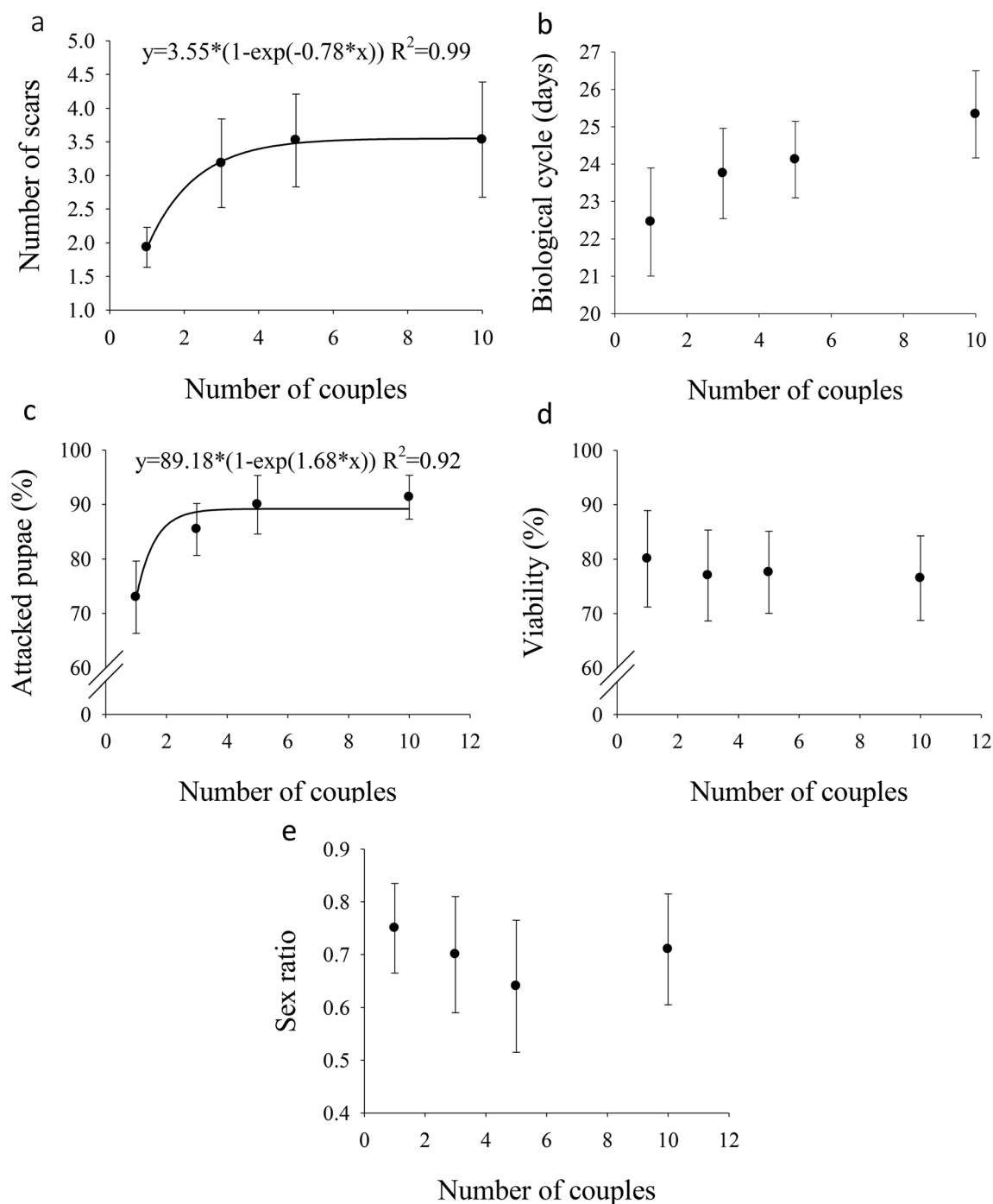


Fig 1 Average number of ovipositor scars (a), duration of egg-adult period (days) (b), attacked pupae (%) (c), viability of parasitized pupae (%) (d), and sex ratio (e) of different densities of *Trichopria anastrephae* reared on *Drosophila suzukii* pupae. Vertical bars represent SD.

(polynomial or exponential); however, it was possible to observe a higher duration when pupae were exposed to more couples of parasitoids (Fig 1b). Not surprisingly, the numbers of attacked pupae increased when they were exposed to a higher number of parasitoids ($F = 24.99$, $df = 3$, $p = 0.0378$, Fig 1c); however, viability was not affected (Fig 1d). Sex ratio of offspring data also did not adjust to any regression model and was not affected by

parasitoid density (Fig 1e); however, in all treatments, tested the progeny was female-biased.

Host deprivation

Host deprivation did not affect the duration of biological cycle ($H = 2.29$, $df = 3$, $p = 0.5145$, Table 1). When hosts were offered in alternated days (T3), females parasitized a lower

Table 1 Average (\pm SD) duration of biological cycle (days), total number of parasitized pupae per female, total number of offspring generated per female and sex ratio of *Trichopria anastrephae* obtained from *Drosophila suzukii* pupae, when parasitoids were host-deprived for different periods.

Treatment*	Egg-adult period (days) ^{ns}	Number of parasitized pupae ^β	Number of offspring ^α	Sex ratio ^β
T1	18.77 \pm 0.36	205.40 \pm 32.66 a	146.40 \pm 25.55 a	0.34 \pm 0.20 b
T3	19.33 \pm 2.03	119.73 \pm 47.70 b	99.07 \pm 38.47 c	0.54 \pm 0.25 a
T4	18.96 \pm 0.29	187.87 \pm 51.58 a	123.13 \pm 27.17 bc	0.54 \pm 0.19 a
T5	18.94 \pm 0.26	195.07 \pm 31.63 a	131.47 \pm 15.02 ab	0.49 \pm 0.21 ab

*T1—hosts provided daily; T3—provision of hosts in alternated days; T4—host deprivation for three days; and T5—host deprivation for seven days. T2 (complete host deprivation) is not shown in the table, since parasitoids had no chance to parasitize.

^α Means followed by the same letter in the column did not differ by the Dunn test ($p \leq 0.05$).

^β Means followed by the same letter in the column did not differ by the Duncan test ($p \leq 0.05$).

^{ns} Not significant according to the Kruskal-Wallis test ($p \leq 0.05$).

number of pupae when compared to other treatments; meanwhile, host-deprived females for 3 (T4) or 7 days (T5) were able to parasitize an amount of pupae comparable to those who were host-provided (T1) ($F = 24.57$, $df = 3$, $p < 0.0001$, Table 1). And as soon as hosts became available, deprived females were able to immediately use their eggs (Fig 2). The different periods of absence of host also affected the total number of offspring generated per female ($H = 17.10$, $df = 3$, $p = 0.0007$, Table 1), and the highest number of offspring was obtained when females were not submitted to any host deprivation (T1) and when they were submitted to 7 days of host deprivation (T5) (146.40 \pm 25.55 and 131.47 \pm 15.02 parasitoids, respectively). In addition, sex ratio of offspring was also affected by the treatments ($F = 4.49$, $df = 3$, $p = 0.0386$, Table 1). Ultimately, longevity of males was not affected by host deprivation ($H = 1.90$, $df = 4$, $p = 0.7540$, Fig 3a), whereas longevity of females was affected ($H = 48.50$, $df = 4$, $p < 0.0001$, Fig 3b), and females that never received hosts lived longer (73.33 days).

Discussion

In our study, we verified an increase of oviposition scars when pupae were exposed to a higher density of females. Besides oviposition, these scars may be the result of a behavior of host feeding or host evaluation. In the case of parasitoids from the Genus *Trichopria*, adults do not show host-feeding behavior (Carton *et al* 1986), so the scars left on the host may be the result of the insertion of ovipositor for internal evaluation followed by the decision to lay an egg or not. Once female parasitoids find a host, they may insert their ovipositor into their host to evaluate quality of the host or to destroy competing eggs or larvae from other parasitoids before laying their own eggs (Abram *et al* 2019). Most species of parasitoids are able to recognize and reject hosts that were previously parasitized by conspecifics or by themselves (Montoya *et al* 2012). Although parasitized hosts are considered of lower quality, females can lay their eggs on parasitized hosts and this is called superparasitism (Van

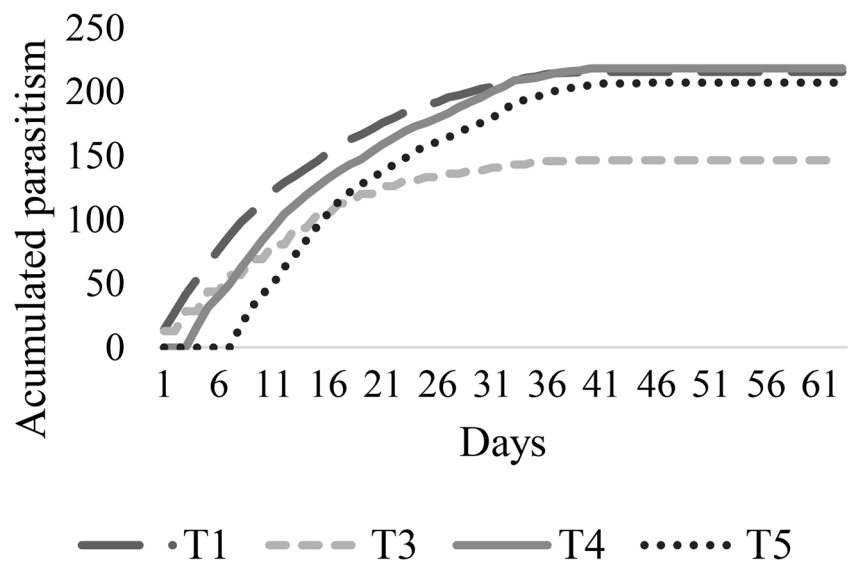


Fig 2 Cumulative number of parasitized pupae of *Drosophila suzukii* by *Trichopria anastrephae* exposed to different periods of host deprivation (T1—hosts provided daily; T2—complete host deprivation; T3—provision of hosts in alternated days; T4—host deprivation for 3 days; and T5—host deprivation for 7 days).

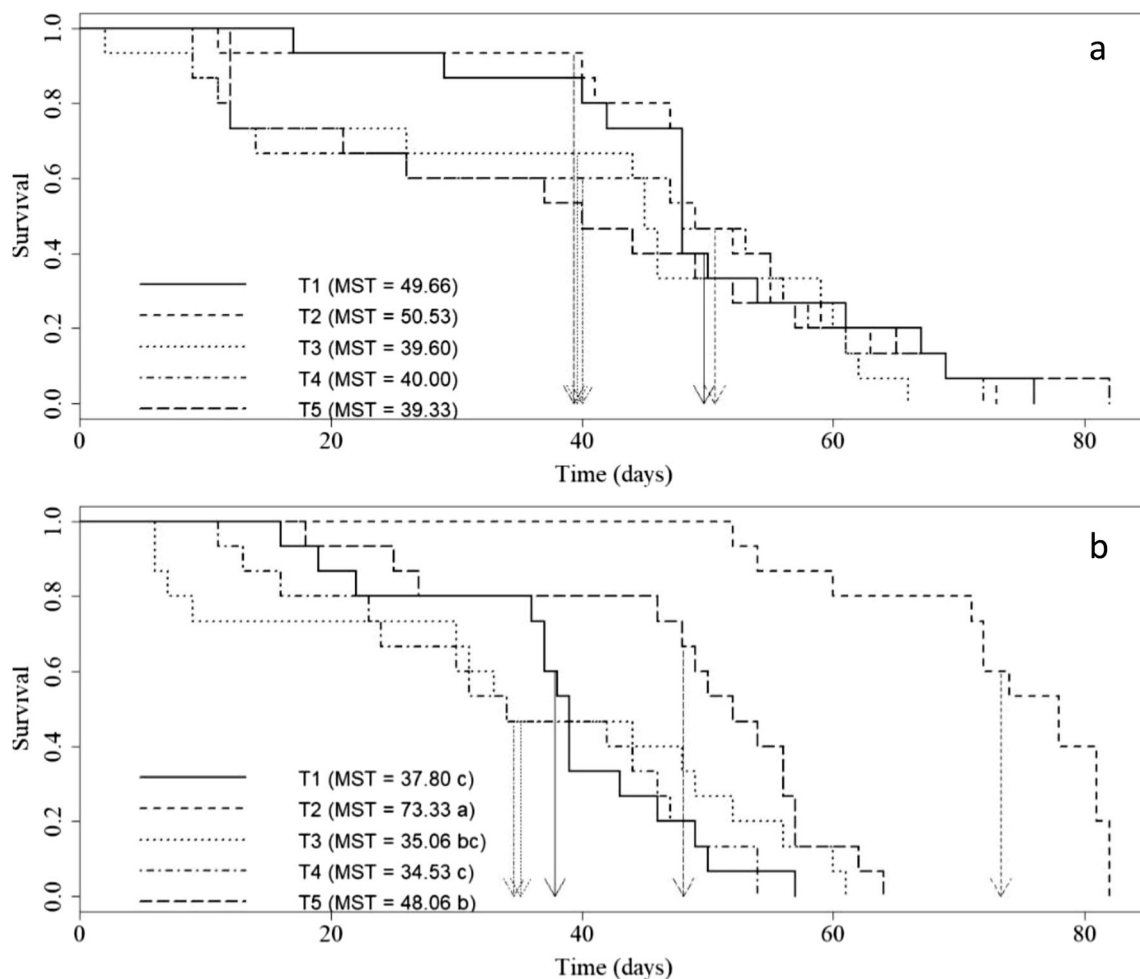


Fig 3 Longevity (days) of males (a) and females (b) of *Trichopria anastrephae* exposed to different periods of host deprivation (T1—hosts provided daily; T2—complete host deprivation; T3—provision of hosts in alternated days; T4—host deprivation for 3 days; and T5—host deprivation for 7 days). The arrows indicate the mean survival time (MST).

Alphen & Visser 1990). Some of the conditions that lead to the occurrence of superparasitism are the low cost in laying extra eggs, high quality of the host, an increase in the probability of offspring survival due to suppression of the host's immune system, and intraspecific competition (Van Alphen & Visser 1990; Montoya *et al* 2012). Although we did not dissect pupae to confirm the presence of supernumerary eggs, superparasitism in the Genus *Trichopria* was confirmed by Boulétreau (unpublished data) (see Carton *et al* 1986) and also by O'Neill (1973). Thus, the increase of oviposition scars found on pupae exposed to a higher density of females could be due the occurrence of superparasitism in this species, despite only one adult emerge per parasitized pupae.

The egg-to-adult period was higher in treatments of higher density, probably due to occurrence of superparasitism in the host. The extension of development period of parasitoids in conditions of superparasitism was previously reported for other species of parasitoids, probably due

competition for resources (Parra *et al* 1988; Tunca & Kilincer 2009). Host deprivation of parasitoids could lead to self-superparasitism once host became available, resulting in an extension of the development period, as observed when host was exposed to high densities of foundress. However, host deprivation did not result in any change in the duration of the biological cycle, and although self-superparasitism cannot be completely discarded, it seems not so likely to have occurred.

In different competitive environment, the highest percentage of attacked pupae was achieved when pupae were offered to the highest number of foundress females. Although this result was expected, it is interesting that not all the pupae were attacked even in the higher density tested. Patch underexploitation was already observed in other parasitoids (DaSilva *et al* 2016; Tena *et al* 2017). Pierre *et al* (2003) suggested that the decision of leaving unparasitized host in a patch could be due a sampling performed by female

parasitoids, and the decision of giving up a patch is taken after a female parasitoid encounters too many parasitized hosts during the exploitation.

Furthermore, the viability of parasitized pupae (i.e., number of emerged parasitoids divided by the number of pupae containing scars) was not affected by density, contrasting with others studies, where competition for host resulted in a higher mortality of parasitoids during their development (Gonzalez *et al* 2007; Cruz *et al* 2018).

The reproductive success of a parasitoid also depends on the ability of females in adjusting their egg production according to host availability (Hougardy *et al* 2005; Carneiro *et al* 2009). When females are host-deprived, some species can resorb their oocytes, as a nutritional source, resulting in a decrease in parasitism (Hougardy *et al* 2005), while others can retain their eggs and keep their parasitism rate (Carneiro *et al* 2009). We observed that even after a period of 7 days of host deprivation, parasitism was comparable to females which received a daily supply of hosts; thus, oocytes resorption did not seem to occur. However, provision of hosts in alternated days decreased the total number of parasitized pupae per female. Although parasitoids were provided honey during their entire lifetime in all treatments, it is possible that sugar availability did not prevent oocyte resorption. In fact, storage capacity can be insufficient and, when hosts are scarce, ovisorption occurs so the ultimate output of ripe eggs is not affected (Flanders 1950).

Although host availability can be easily manipulated in laboratory conditions to increase reproductive potential of parasitoids that will be released in the field (Hougardy *et al* 2005), the response to host deprivation is species specific. While in some species, provision of hosts to freshly emerged females can stimulate oogenesis, for others it can decrease the remaining reproductive capacity (Fleury & Bouletreau 1993; Hougardy *et al* 2005; Carneiro *et al* 2009). Our results show that host deprivation for a period up to 7 days post-emergence do not impair the parasitism capacity of females. Thus, it can be used as a pre-release strategy in cases where release at that particular moment is not possible.

Regarding sex ratio, it is expected that insect population has equal investments in both sexes, resulting in a sex ratio close to 0.5 (Fisher 1930). However, deviation in this proportion are not rare and can be attributed to ecological, physiological, and behavioral factors (Flanders 1939; Peruquetti & Lama 2003). In a study with *T. drosophilae*, a sex ratio close to 0.5 was verified when a higher number of foundress were competing for *D. melanogaster* pupae (Li *et al* 2018), while in our study, the proportion of females in offspring was always higher than 0.5, regardless the density. In fact, despite the variation, sex ratio of offspring produced by females in different competition environments were female-biased. Female-biased offspring is an asset, since females are responsible for both population growth and pest mortality

(Montoya *et al* 2012). Nevertheless, when evaluating mean sex ratio of total offspring produced by females during their lifetime (i.e., in the host deprivation bioassay), we found an overall lower percentage of females produced. In most Hymenoptera species, parasitoid sex ratio decrease with maternal age, since after the oviposition of fertilized eggs (which generate females), parasitoids can continue to lay unfertilized eggs (males). This switch occurs probably due to sperm depletion or depletion of spermathecal gland secretions (Kopelman & Chabora 1986; Rossi Stacconi *et al* 2017). It is true that in our study, females were coupled with males during their lifetime; thus, they had plenty opportunity for mating; however, there is no information in literature if *T. anastrephae* performs multiple mating, or if they are able to mate when they are older, and then, replenish their sperm storage. Moreover, the higher percentage of males in progeny was obtained when we offered hosts daily to *T. anastrephae*. Curiously, in *Nasonia vitripennis* Walker (Hymenoptera: Pteromalidae), host deprivation increased the proportion of males in progeny (King 1962). However, Flanders (1939) suggested that as eggs remain longer in the ovariole of host-deprived females, they have a better chance of being fertilized and thus produce females.

A trade-off between reproduction and survival is common in insects (Ellers *et al* 2000; Hougardy *et al* 2005). The lack of host deprivation effects on male longevity was expected, since males do not interact with hosts as much as females. Meanwhile, longevity of females varied greatly according to host availability. Completely host-deprived females lived longer than the females submitted to any other treatment. A similar trend was observed in *T. drosophilae*, where host-provided females lived shorter than host-deprived ones (Rossi Stacconi *et al* 2017). It has been suggested that the longer life of host-deprived parasitoids is related to egg-resorption, since ovariole has a limited storage capability the non-use of eggs due to host deprivation leads to the resorption of mature eggs and recycling of nutrients (Jervis *et al* 2001). However, the longer longevity can also be related to resource reallocation, since host-deprived parasitoids will invest less into egg production and oviposition, and they will invest more into lifespan, in order to enable them to reach more resourceful places (i.e., with plenty of hosts) (Wajnberg *et al* 2012; Bezerra Da Silva *et al* 2019).

Here, we show that the extrinsic intraspecific competition among females of *T. anastrephae* result in a higher number of oviposition scars on host and an extension of egg-to-adult period, suggesting the occurrence of superparasitism. However, this competitive environment has no detrimental effect on the emergence of the offspring. Meanwhile, females can be host-deprived for a period up to 7 days without a negative effect on their capacity to parasitize pupae; however, provision of hosts in alternated days decreased the total number of parasitized pupae per female. Determining

the parasitism behavior of a parasitoid in an environment of competition or host deprivation facilitates the understanding of the interaction between parasitoid and host. This knowledge can be applied through the manipulation of this interaction to optimize mass rearing and to provide basic information to improve biological control programs.

Author Contribution Statement APK, TS, JGAV, DB, DEN, and FRMG planned and designed the research. APK, TS, JGAV, and MCM conducted experiments. APK and TS conducted statistical analysis. APK wrote the manuscript. DB, DEN, and FRMG contributed material. DEN and FRMG secured funding. All authors read and approved the manuscript.

Funding Information This study received financial support provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) – Finance Code 001 and was partially supported by FAO/IAEA grant 22214.

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