



Biological and Microbial Control

Demographic parameters of *Pachycrepoideus vindemiae* (Hymenoptera: Pteromalidae) reared on *Drosophila suzukii* (Diptera: Drosophilidae), *Ceratitis capitata* (Diptera: Tephritidae), and *Anastrepha fraterculus* (Diptera: Tephritidae) puparia

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Pachycrepoideus vindemiae (Rondani) is a solitary generalist pupal ectoparasitoid that parasitizes dipterans of various families and genera. This study aimed to evaluate Anastrepha fraterculus (Wiedemann), Ceratitis capitata (Wiedemann), and Drosophila suzukii (Matsumura) to determine the best host for the development and mass production of parasitoid *P. vindemiae* in the laboratory. The experiments were performed in airconditioned rooms at a temperature of 25 ± 2 °C, relative humidity of $70\% \pm 10\%$, and photophase of 12 h. Moreover, 24-h-old pupae of *A. fraterculus, C. capitata*, and *D. suzukii* were provided daily to 25 pairs of the parasitoid. The following parameters were determined: percentage of parasitism, percentage of emergence, hind tibia size, sex ratio, and longevity. A fertility life table was established using biological data. Notably, *P. vindemiae* parasitized the pupae of all 3 hosts but did not affect the sex ratio of the offspring. Parental parasitoids from the pupae of *A. fraterculus* and *C. capitata* lived longer than those from the pupae of *D. suzukii*. However, for all other parameters, parasitoids from *D. suzukii* showed better performance than those from other hosts, with shorter intervals between generations (*T*) and a higher net reproduction rate (R_o), intrinsic rate of increase (r_m), and finite rate of increase (λ).

Key words: biological control, fruit flies, drosophila, rearing, life table

Introduction

Pachycrepoideus vindemiae (Rondani) is a generalist pupal ectoparasitoid parasitizing many species of Diptera in 60 countries worldwide (Wang and Messing 2004). Its hosts include species of great economic importance, especially those in Tephritidae and Drosophilidae families (Marchiori et al. 2013, Marchiori and Borges 2017, Rasool et al. 2017, Funes et al. 2019, Zhang et al. 2021).

Among the hosts of *P. vindemiae*, fruit flies are the most affected pests impacting the global fruit market (Dias et al. 2018a). In South America, *Anastrepha fraterculus* (Wiedemann) and *Ceratitis capitata* (Wiedemann) are the most economically important pests of the tephritid group (Uchôa 2012). In addition to causing direct and indirect damage (Nava and Botton 2010), these pests necessitate the use of phytosanitary barriers, leading to fruit export restrictions (Dias and Moreira, 2023).

In addition to tephritids, *Drosophila suzukii* (Matsumura), the spotted-wing drosophila native to Southeast Asia and distributed in several countries across Europe, North America, South America, and Africa, is the most important pest of small fruits worldwide (Asplen et al. 2015, Andreazza et al. 2017a, Tait et al. 2021), especially blackberry [*Morus* sp. (Urticales: Moraceae)], cherry [*Prunus* sp. (Rosales: Rosaceae)], raspberry [*Rubus idaeus* Linnaeu (Rosales: Rosaceae)], strawberry [*Fragaria × pineapple* Duch (Rosales: Rosaceae)], and blueberry [*Vaccinium myrtillus* Linnaeu (Ericales: Ericaceae)] (Lee et al. 2011, Klick et al. 2016, Bernardi et al. 2017). *Drosophila suzukii* has received attention owing to its high harmful capacity (Cini et al. 2012, Ioriatti et al. 2015), fecundity, rapid cycle (Emiljanowicz et al. 2014), global transmission rate (Asplen et al. 2015), and host diversity (Lee et al. 2015, Poyet et al. 2015).

Despite being a facultative hyperparasitoid, *P. vindemiae* has attracted considerable interest for the biological control of fruit flies (Garcez et al. 2023). Recently, several studies have assessed the biological control potential of tephritids (Ovruski et al. 1999, Yang et al. 2020). It is also worth noting that although generalist parasitoids are often not preferable in biological control programs, their great plasticity can favor adaptation to environmental variations (Thibert-Plante and Hendry 2011, Kingsolver and Buckley 2018) and exchange of host when a preferred host is not available (Jaworski et al. 2013).

Parasitoids exhibit great potential to control *D. suzukii* (Bezerra da Silva et al. 2019, Bonneau et al. 2019), but their use remains controversial. Augmentative release of *P. vindemiae* to control *D. suzukii* in caneberry hoop house crops in Minnesota, Oregon, and California in the USA resulted in a high parasitism rate only in Oregon (Hogg et al. 2022). The authors revealed that the release of a high quantity of *P. vindemiae* increases the parasitism of *D. suzukii* in areas with large populations of *D. suzukii* with conditions unsuitable for dispersal.

Improving *P. vindemiae* rearing techniques is essential to enhancing its production in the laboratory. The host for multiplication should be selected considering the production cost and ability to host parasitoids with high reproductive capacity and long life, similar to wild insects (Parra et al. 2021). Several hosts, such as *Drosophila melanogaster* (Meigen) (Diptera: Drosophilidae) (Hogg et al. 2022), *D. suzukii* (Mariano-Macedo et al. 2020, Missere et al. 2023), and *Musca domestica* Linnaeus (Diptera: Muscidae) (Peterssen et al. 1992), have been used for parasitoid rearing. In Brazil, *A. fraterculus*, *C. capitata*, and *D. suzukii* are produced in several laboratories for the research and development of control methods. This study aimed to determine the best host among *A. fraterculus*, *C. capitata*, and *D. suzukii* for the development of *P. vindemiae* parasitoid and its mass production in the laboratory.

Materials and Methods

Insect Rearing

The insects used in this study were obtained from the maintenance rearings of the Entomology Laboratory of Embrapa Clima Temperado, Pelotas, Rio Grande do Sul, Brazil. Colonies of *A. fraterculus* and *C. capitata* were reared during the larval stage on an artificial diet based on wheat germ following the methodology adapted from Nunes et al. (2013) and Gonçalves et al. (2013), respectively. *Drosophila suzukii* colony was maintained in test tubes (2.5 cm × 8.5 cm) on an artificial diet based on corn flour according to the methodology proposed by Andreazza et al. (2017b).

Parasitoid *P. vindemiae* was obtained from fruit collections infested with fruit flies from peach orchards in the Municipality of Pelotas, RS, Brazil. In the laboratory, after emergence, the parasitoids were kept in plastic cages (26.2 cm × 17.7 cm × 14.7 cm) and fed pure honey solution (Bezerra da Silva et al. 2019). For the experiments, parasitoids reared for 15 generations in the 3 hosts (*D. suzukii, A. fraterculus*, and *C. capitata*) were used. All populations were kept in an air-conditioned room at a temperature of 25 ± 2 °C, relative humidity of 60% \pm 10%, and photophase of 12 h.

Biology of P. vindemiae

To study the biology of *P. vindemiae*, 25 pairs of 5-day-old parasitoids were obtained from each host (*A. fraterculus*, *C. capitata*, and *D. suzukii*). The pairs were individualized and kept in cages consisting of plastic cups (200 ml) inverted in the respective lids and closed

at the top with *voile* fabric. Pure honey, as a source of food, and water soaked in cotton were provided separately on plastic plates (2.2 cm diameter \times 0.7 cm height). The food was replaced every 48 h to avoid fermentation and contamination by microorganisms, and water was replenished daily.

From the day of the formation of pairs of each population until the death of the females, 10-24-h old puparia from each host (*A. fraterculus, C. capitata*, and *D. suzukii*) were offered to each female parasitoid species. The puparia were placed on cotton moistened with distilled water on plastic plates (2.2 cm diameter × 0.7 cm height). After 24 h of exposure, the puparia were removed and placed in acrylic tubes (2.5 cm diameter × 4.5 cm height) closed at the top with cotton wool to prevent the adults from escaping during emergencies. In the case of no emergence, pupal dissection was performed to verify the presence of parasitoids/flies.

Based on the emergence data, parasitism of *P. vindemiae* was determined in each host as well as the sex ratio of the offspring population and number of parasitized pupae. To determine the longevity of the parents, the insects were fed honey and evaluated daily until death. After determining the biological parameters, a fertility life table was constructed, estimating the interval between generations (*T*), net reproduction rate (R_o), intrinsic rate of increase (r_m), and finite rate of increase (λ), as described by Southwood (1995). The algorithms used to estimate these parameters are described below.

Net reproduction rate (R_o) , indicating the sum for the entire oviposition period, was determined by multiplying the average number of eggs produced per female per day by the corresponding accumulated survival at each date:

$$Ro = \sum Lx \cdot Mx$$

Approximate estimate of the interval between generations (*T*) corresponds to the average of the oviposition age (*x*) weighted by the net number of descendants (L_{\downarrow} , M_{\downarrow}) produced at that date:

$$T = \sum \frac{Mx \cdot Lx \cdot X}{Lx \cdot Mx}$$

Intrinsic growth rate (r_m) was determined as described by Silveira Neto et al. (1976) using the net reproduction rate (R_o) as follows:

$$rm = \frac{\log \text{Ro}}{\text{T x } 0,4343}$$

Finite growth rate (λ) was calculated using the following equation:

$$\lambda = e^{rr}$$

After the emergence of the first offspring of each host, 50 individuals of each sex were sacrificed to measure the size of hind tibia, which were subsequently arranged on slides. A stereoscopic microscope (Zeiss, Jena, Germany) was used at 4 × magnification, and the tibiae were captured using a camera (Leica Biosystems). Offspring longevity was verified by sampling 15 pairs from each host, which were kept under similar conditions as their parents but without pupae.

Statistical Analyses

The experiments were conducted using an entirely randomized design with 3 treatments (parasitoids from *A. fraterculus*, *C. capitata*, and *D. suzukii*) and 25 replicates (pairs of parasitoids). All data were checked for normality and homoscedasticity of residuals using the Shapiro–Wilk and Bartlett tests, respectively. Data on the percentage of parasitism, number of parasitized pupae, percentage of emergence, tibia length, and sex ratio did not meet the assumptions of normality and homoscedasticity; therefore, they were analyzed via the Kruskal–Wallis test ($P \le 0.05$). When statistical significance was confirmed, the data were compared using Dunn's test ($P \le 0.05$). Longevity data of males and females and their offspring in different treatments were analyzed via survival curves using the Kaplan–Meier estimator and compared using the log-rank test ($P \le 0.05$). Statistical analyses were conducted using the R software version 4.0.3 (R Core Team 2020). Parameters of the fertility life table were determined using the jackknife technique applying the "lifetable.sas" procedure developed by Maia et al. (2000) with SAS 9.1 (SAS Institute 2011).

Results

Effects of Host Species on P. vindemiae

Parasitism (H = 16.20; df = 2; P = 0.0003), number of parasitized pupae (H = 16.20; df = 2; P = 0.0003), emergence (H = 5.99; df = 2; P = 0.0500), and tibia lengths in males (H = 67.11; df = 2; P < 0.0001) and females (H = 101.87; df = 2; P < 0.0001) were significantly affected by the host species. Females of P. vindemiae on D. suzukii parasitized an average of 47.91% of the pupae, which was much higher than the average pupae parasitized in A. fraterculus (24.78%) and C. capitata (11.76%). The number of pupae parasitized per day was 2.39 ± 0.35 in *D. suzukii*, 1.24 ± 0.19 in A. fraterculus, and 0.59 ± 0.13 in C. capitata. Similarly, higher emergence was observed in D. suzukii (96.43%) and A. fraterculus (81.22%) than in C. capitata (62.82%). Males and females of A. fraterculus exhibited the longest tibia length (416.25 \pm 2.51 and $428.39 \pm 1.33 \mu m$, respectively) compared to those of C. capitata (397.94 ± 4.23 and 421.86 ± 1.56 µm, respectively) and D. suzukii $(386.40 \pm 1.64 \text{ and } 385.55 \pm 1.33 \mu \text{m}, \text{ respectively})$. Notably, sex ratio was not significantly affected by the host species (H = 4.49; *df* = 2; *P* = 0.1061; Table 1).

Longevity of parental females (χ^2 : 27.6; P < 0.001) and males (χ^2 : 15.6; P < 0.001) was significantly affected by the host species, with *A. fraterculus* and *C. capitata* exhibiting the longest-living insects superior to those of *D. suzukii* (Fig. 1). However, in the descendants (F1), the log-rank test showed that the longevity of males (χ^2 : 5.6; P = 0.06) and females (χ^2 : 0.3; P = 0.90) was not significantly affected by the host species (Fig. 2).

Fertility LifeTable

Fertility life table parameters of *P. vindemiae* were significantly affected by the host species. The shortest interval between generations (*T*) was observed for *P. vindemiae* on *D. suzukii* (*T* = 29.65 days) compared to that for *P. vindemiae* on *A. fraterculus* (*T* = 35.03 days) and *C. capitata* (*T* = 36.16 days). The net reproduction rate (R_o), intrinsic rate of increase (r_m), and finite rate of increase (λ) were high for *P. vindemiae* on *D. suzukii* ($R_o = 31.85$; $r_m = 0.12$; $\lambda = 1.12$; Table 2).

Discussion

In this study, *P. vindemiae* development was observed in all 3 host species, but to varying degrees, with *D. suzukii* providing the best conditions for its multiplication. This growth capacity of parasitoids can be attributed to their highly adaptive evolution (Jones et al. 2015, Woltering et al. 2019). Generalist species, such as *P. vindemiae*, exhibit phenotypic plasticity, allowing individuals to adapt to different hosts (Zepeda-Paulo et al. 2013, Wang et al. 2021). Therefore, development of *P. vindemiae* can change over several generations in the host (Jones et al. 2015).

In addition to a higher percentage of parasitism, higher number of parasitized pupae was obtained with *D. suzukii* than with *A. fraterculus* and *C. capitata* for *P. vindemiae*, with approximately 2- and 4-times more parasitized pupae, respectively. However, adult females from *D. suzukii* were smaller ($385.55 \pm 1.33 \mu m$) than those from *C. capitata* ($421.86 \pm 1.56 \mu m$) and *A. fraterculus* ($428.39 \pm 1.33 \mu m$). The size of the parasitoid is possibly related to the size of the host puparia, which is large in tephritids. According to Jervis (2005), large parasitoids exhibit high fertility and fecundity; however, further studies should assess the associations between the size and reproductive parameters of parasitoids. Development of *D. suzukii* in the laboratory is easier than that of tephridids, especially *A. fraterculus*, which require high labor costs to obtain the ingredients for the larval diet.

Here, longevity of parasitoids from *D. suzukii* was short. Lampson et al. (1996) suggested that large parasitoids exhibit a long lifespan and high competitiveness. Mariano-Macedo et al. (2020) reported longer mean longevity in female parasitoids (32.2 ± 1.83 days) than in male parasitoids (28.2 ± 1.06 days), in contrast to our study, where females exhibited shorter longevity (TMS = 14.1 days) than the males (18.6 days). However, analysis of F1 generation with no parasitism yielded results similar to those of Mariano-Macedo et al. (2020), with the average survival time being 37.1 days for females and 34.1 days for males. The short longevity of parasitoids from *D. suzukii* is possibly due to the energy spent by females under parasitism.

High number of females increases the population growth and parasitism rates, as observed in this study, where the sex ratio was high. Percentages of *P. vindemiae* females for the hosts evaluated in this study did not differ from those previously reported for other host species (Cancino et al. 2004, Wang and Messing 2004, Zhao et al. 2013). However, further studies are needed to determine the proportions of males and females suitable for mass rearing and assess the reproductive characteristics, such as age and size, affecting the sex ratio. Sun et al. (2013) indicated that mating with virgin males results in the low emergence of male offspring; however,

Table 1. Percentage of parasitism, number of pupae parasitized per day, percentage of emergence, tibia length (males and females), and sex ratio (average \pm standard error) of *P. vindemiae* reared on pupae from three hosts. Temperature 25 \pm 2 °C, relative humidity 60% \pm 10% and photophase 12 h

Hosts	Parasitism (%) ^α	Parasitized pupae ^α	Emergence (%) ^α	Hind tíbia length (µm)		
				Male ^α	Female ^a	Sex ratio ^β
A. fraterculus	24.78 ± 3.86b	1.24 ± 0.19b	81.22 ± 6.99ab	416.25 ± 2.51a	428.39 ± 1.33a	0.78 ± 0.08
C. capitata	11.76 ± 2.65c	0.59 ± 0.13c	62.82 ± 11.93b	397.94 ± 4.23b	421.86 ± 1.56b	0.98 ± 0.01
D. suzukii	47.91 ± 7.09a	2.39 ± 0.35a	96.43 ± 3.45a	$386.40 \pm 1.64c$	385.55 ± 1.33c	0.94 ± 0.04

^aMeans followed by same letter within the column do not differ according to Dunn test ($P \le 0.05$). ^βns, not significant.



Fig. 1. Longevity (days) of the parental females A) and males B) de *P* vindemiae reared on different hosts. TMS represents the mean time of survival. Lowercase letters represent the significant difference according to log-rank test ($P \le 0.05$).

increase in the mating time and duration of oviposition of females decreases the sex ratio.

Of the hosts evaluated in this study, *D. suzukii* exhibits the shortest life cycle, remaining in the pupal stage for approximately 6 days (Emiljanowicz et al. 2014), whereas the tephritids exhibit longer life cycles, with approximately 11 days for *A. fraterculus* (Nunes et al. 2013, Dias et al. 2018b) and 10 days for *C. capitata* (Nestel and Nemny-Lavy 2008, Ricalde et al. 2012). Evolutionary studies have indicated that parasitoid populations are highly adaptive to their hosts (Stireman et al. 2006, Henry et al. 2008, Forbes et al. 2009). Studies on larval parasitoids have indicated that they can slow down

their maturation rate (Beckage 1993), remaining in a specific instar stage until the host reaches a stage meeting their nutritional needs using hormonal stimuli (Pennacchio et al. 1993, Kadono-Okuda et al. 1995, Hu et al. 2002). Therefore, short interval between generations (*T*) of *P. vindemiae* in this study is possibly related to the synchronization of the parasitoid life cycle with that of its host. Wang and Messing (2004) also demonstrated that *P. vindemiae* shows rapid development in *D. melanogaster* but slow development in *C. capitata*.

Net reproduction rate (R_o) of *P. vindemiae* parasitoid in *D. suzukii* host was high with 31.85 females generated per female per



Fig. 2. Longevity (days) of the descendant females A) and males B) of P. vindemiae reared on different hosts. TMS represents the mean time of survival.

Table 2. Parameters of fertility life table of *P. vindemiae* reared on pupae from 3 hosts. Temperature 25 ± 2 °C, relative humidity 60% ± 10%, and photophase 12 h

Hosts	T (days)	Ro(Q/Q)	<i>rm</i> (♀/♀*day)	λ
A. fraterculus	35.03 ± 0.46b	13.90 ± 0.68b	0.07 ± 0.001b	1.08 ± 0.002b
C. capitata	$36.16 \pm 0.35b$	9.53 ± 1.28b	$0.06 \pm 0.004c$	$1.06 \pm 0.004c$
D. suzukii	$29.65 \pm 0.45a$	31.85 ± 3.99a	$0.12 \pm 0.003a$	$1.12 \pm 0.004a$

T = interval between generations; R_o = net reproductive rate, r_m = intrinsec growth rate, and λ = finite rate of increase. Values represent means ± SE obtained using Jackknife method in SAS program. For each evaluated parameter, values followed by the same letter are not statistically different (P > 0.05).

generation, which is more than double that of *A. fraterculus* (13.90) and triple that of *C. capitata* (9.53). Similarly, the innate capacity for population growth (r_m) , which determines whether the species can thrive in a given environment (Dias et al. 2010), and finite rate of increase (λ), which represents the number of females added to the population per female, were high in insects on *D. suzukii* ($r_m = 0.12$; $\lambda = 1.12$) and low in insects on *C. capitata* ($r_m = 0.06$; $\lambda = 1.06$).

Overall, this study showed that *P. vindemiae* on *D. suzukii* exhibited performance superior to that of *A. fraterculus* and *C. capitata.* Therefore, among those evaluated, *D. suzukii* was the most suitable for parasitoid rearing in biological control programs. However, further studies should investigate the implications of using *P. vindemiae* for biological control. Furthermore, development of *D. suzukii* in the laboratory is easier than that of tephritids, requiring simpler ingredients for the artificial diet, which is economical and easily accessible in the market. However, owing to the constant improvement in rearing techniques, future studies should optimize the different phases of development for both *P. vindemiae* and its host.

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Author contributions

Dori Nava (Conceptualization [equal], Data curation [equal], Funding acquisition [equal], Project administration [equal], Supervision [equal], Writing—original draft [equal], Writing—review & editing [equal]), Amanda Garcez (Conceptualization [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Writing—original draft [equal]), and Alexandra Kruger (Conceptualization [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Writing—original draft [equal], Writing—review & editing [equal])

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