Biological and Population Parameters, as well as Oviposition Preference, of Two Pupal Parasitoids of *Drosophila suzukii* (Diptera: Drosophilidae) in Mexico[1]

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Abstract   In 2013–2015, Mexico implemented a program of exploration and evaluation of native parasitoids of the spotted-wing drosophila *Drosophila suzukii* (Matsumura). Those efforts identified *Pachycrepoideus vindemmaie* Rondani and *Trichopria drosophilae* Perkins as native parasitoid species. Biological and population parameters, including oviposition preference on locally occurring species of Drosophilidae, were subsequently studied and quantified. *Trichopria drosophilae* required fewer days than *P. vindemmiae* in the larval stage, pupal stage, and development time of egg to adult, as well as exhibited a higher intrinsic rate of increase (r_m), finite rate of increase (λ), mean generation time (T), and doubling time (Dt), but its net reproduction rate (Ro) was lower. On the other hand, both parasitoids showed no differences in female longevity, sex ratio, and duration of egg stage. In the oviposition preference tests, *D. suzukii* pupae were equally preferred as those of *Zaprionus indianus* Gupta, but more than *Drosophila melanogaster* Meigen. These results indicate that local *T. drosophilae* has a higher potential to contribute to the ecological management of the invasive *D. suzukii* in Mexico than *P. vindemmiae*.

Key Words   augmentative biological control, native parasitoids, spotted-wing drosophila

The spotted-wing drosophila *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) is native to Southeast Asia (Cini et al. 2012), although, its distribution has expanded since 2008 to America, Europe, and other areas of Asia (dos Santos et al. 2017). This dipteran is a potential serious threat to the world berry industry (blackberries, blueberries, raspberries, strawberries, among others) because, due to its serrated ovipositor, this fly is able to lay eggs on fruit in the process of maturation, unlike other species of Drosophilidae that only prefer ripe fruit (Cini et al. 2012). The economic damages caused by this fly fluctuate from 20–50% in conventional crops in the United States (Bolda et al. 2010), up to total losses in organic orchards in Spain (Cuch-Arguimbau et al. 2013). Additionally, as a pest of quarantine importance (European and Mediterranean Plant Protection Organization 2019), the detection of a single infested fruit may lead to rejection of an entire shipment (Mazzi et al. 2017).

Worldwide and in Mexico, *D. suzukii* is controlled mainly through chemical products and cultural practices (Cini et al. 2012, Haye et al. 2016, Schetelig et al. 2018); however, these methods are labor-intensive (e.g., mass trapping and trees covered by insect-proof nets) (Mazzi et al. 2017) or entail risks to human and environmental health. Furthermore, they are not applied in nonagricultural areas (Haye et al. 2016), and if these sites contain 1 of the 50 wild host plants of *D. suzukii*, they could be a constant source of infestation of crops (Asplen et al. 2015, Haye et al. 2016). So, the search for more sustainable methods continues (Andreazza et al. 2017, Asplen et al. 2015, Mazzi et al. 2017).

As an alternative to current control practices, researchers in several countries have explored native parasitoids associated with this pest, and from those explorations, they collected mainly *Pachycrepoideus vindemmiae* Rondani and *Trichopria drosophilae* Perkins (Gabarra et al. 2015, Haye et al. 2016, Kacar et al. 2017). Both are cosmopolitan and pupal parasitoids. The former attacks species of two Diptera families (Guillen et al. 2002) and is reported as a facultative hyperparasitoid of six Hymenoptera families, including Braconidae and Cynipoidea (Alphen and Thunnissen 1983, Wang and Messing 2004), and the latter attacks only species of Drosophilidae (Carton et al. 1986). Subsequent evaluations of these collected species have shown biological variability at the interpopulation level; for example, *T. drosophilae* native of California presented higher values of adult survival, fecundity, and parasitism than a population of Gyeongsang, South Korea, (Wang et al. 2016), while *P. vindemmiae* from Oregon recorded higher parasitism than a population of Trento, Italy (Rossi-Stacconi et al. 2015), among other cases (Chabert et al. 2012).

Drosophila suzukii was first detected in the state of Michoacan, Mexico in 2011 (Centre for Agriculture and Biosciences International 2019). To contribute to the protection of the national berry industry (33,600 ha planted, 858,488 ton/year of harvested fruit and an economic value of 1,746 million USD) (Servicio de Informacion Agroalimentaria y Pesquera 2017), the Centro Nacional de Referencia de Control Biologico (CNRCB) implemented in 2013–2015 a program of exploration and evaluation of native parasitoids associated with this pest. From those explorations, mainly *P. vindemmiae* (imported from Hawaii in 1954 to control Anastrepha species [Aluja et al. 2008]) and *T. drosophilae* (Garcia-Cancino et al. 2015, Moreno et al. 2015) were collected. To find which of these two local species has a higher potential to contribute to the management of this invasive Asiatic pest, *P. vindemmiae* and *T. drosophilae* were compared in several of their biological and population parameters, as well as in their oviposition preference on Dipteran pupae found in local berries.

Materials and Methods

The study was performed at the CNRCB, a governmental institution of the Direccion General de Sanidad Vegetal of Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria and located in Tecoman Colima, Mexico (N 18°55′37.73″, W 103°53′0.41″). The specimens of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae), *D. suzukii*, *P. vindemmiae*, *T. drosophilae*, and *Zaprionus indianus* Gupta (Diptera: Drosophilidae) were obtained from CNRCB

colonies, which had been established since 2015. To maintain their genetic diversity, 300–400 wild-collected adults are introduced into each colony at the end of each year. The rearing methodology of the dipterans was described by Garcia-Cancino et al. (2015) and Moreno-Carrillo et al. (2015), and the reproduction of the parasitoids was conducted separately as follows: 160 adults of *T. drosophilae* or *P. vindemmiae* were randomly collected (≤4 days old) and placed in four transparent plastic trays (17 cm in diameter by 8 cm in height, and holes of 1.3 mm in diameter for ventilation in its upper lid) with 400 pupae of *D. suzukii* (≤2 days old) for parasitization. Subsequently, when the deposited eggs reached their adult stage, the parasitoids were collected and stored in clear plastic vials (4 cm in diameter by 3.5 cm in height) for use in the stock colony or as research subjects and so on, until the end of the study. The reproduction of both dipterans and parasitoids, as well as the execution of these experiments (described below), was conducted under laboratory conditions of 23 ± 1°C and 40 ± 5% relative humidity.

Biological parameters of parasitoids. The number of days required by *P. vindemmiae* and *T. drosophilae* to complete their various life stages, as well as their female longevity and sex ratio, was evaluated separately for each species as follows: 1,000 *D. suzukii* pupae of ≤24 h old were introduced into a cage (70 × 70 × 70 cm) for oviposition by parasitoids (2,000 randomly collected adults of ≤4 days old). Four hours later, the adults were discarded and the exposed pupae were homogeneously distributed in the bottom of 50 plastic vials (previously mentioned). Afterward, 10 randomly parasitized pupae (i.e., replicates per measurement for each treatment) were selected every 12 h by using a stereoscopic microscope from the pool of 50 vials and recorded individually for the current parasitoid life stage (egg, larva, pupa, or emergence hole), ending when only emergence holes were observed in the *D. suzukii* pupae. To avoid duplication in the data collection, all extracted pupae were discarded at the end of the observation.

From the offspring of the previous experiment, 20 adult females of ≤12 h old (replicates per treatment) were evaluated for their longevity as follows: each one was isolated in transparent plastic tubes (2.7 cm in diameter by 5.5 cm in height, with perforated lid to allow ventilation and small drops of honey as food). Mortality was determined and recorded daily. Finally, when all the parasitoids had emerged and died, the sex ratio was determined with 5 replicates per treatment based on 150 randomly collected individuals (i.e., 30 specimens per measurement). This evaluation process and all of its replications per treatment were performed three times.

Population parameters of parasitoids. The net reproduction rate (Ro), intrinsic rate of increase (r_m), finite rate of increase (λ), mean generation time (T), and doubling time (Dt) were evaluated separately for *P. vindemmiae* and *T. drosophilae* as follows: 10 virgin pairs of adults ≤24 h old (replicates per treatment) were placed in 10 clear plastic vials (4 cm in diameter by 3.5 cm in height and lid of organza fabric) with small drops of honey as food, wet cotton as a source of water, and 30 pupae of *D. suzukii* (≤24 h old) for oviposition. Every 24 h, the pairs were transferred to new vials until the natural death of females, and the used vials were left aside for incubation; in the situations that the male died before the female, it was replaced by another of the same age. Finally, when all parasitoids had emerged and died, the number of parasitized pupae (indirect measurement of parasitoid

oviposition) per treatment was counted under a stereoscopic microscope. This entire evaluation process was conducted three times.

Oviposition preference of parasitoids. The oviposition preference on pupae of three species of Drosophilidae, commonly found in the berry zones of Colima and Jalisco (Garcia-Cancino et al. 2015), was evaluated separately for *P. vindemmiae* and *T. drosophilae* as follows: 10 pairs of adults $\geq$24 to $\leq$72 h old (replicates per treatment) were introduced in the center of 10 containers (8.7 cm in diameter by 11.3 cm in height and lid of organza fabric) with three groups of pupae ($\leq$24 h old) distributed in the vertices of an imaginary triangle, namely, 10 of *D. melanogaster*, 10 of *D. suzukii*, and 10 of *Z. indianus*. Twenty-four hours later, the adults were removed and discarded, and the containers were left aside for incubation. Afterward, when all parasitoids had emerged and died, the number of parasitized pupae (indirect measurement of preference) was counted under a stereoscopic microscope. This entire evaluation process was replicated seven times.

Statistical analysis. The statistical differences between treatments (parasitoids) in the biological parameters (except sex ratio) were based on the Wilcoxon test from the PROC LIFETEST with Bonferroni adjustment, and the population parameters were calculated by Student's *t* test using the lifetable.sas program (Embrapa Environment 2019, Maia et al. 2000). Differences between treatments in sex ratio (females/progeny) and oviposition preference were calculated through analysis of variance of one factor, with Tukey's multiple comparison tests. All data were analyzed using the statistical package SAS version 9.2 (SAS Institute, Cary, NC) and $P \leq 0.05$.

Results and Discussion

Comparing the biological parameters of *P. vindemmiae* and *T. drosophilae*, there were no significant statistical differences between both parasitoids in duration of egg stage, longevity of the females ($\chi^2 \geq 0.1208$; df $= 1$; $P \geq 0.6742$), and sexual proportion of the progeny ($F = 1.12$; df $= 1$; $P = 0.3463$) (Table 1), but *T. drosophilae* required fewer days than *P. vindemmiae* in the larval stage, pupal stage, and development time of egg to adult ($\chi^2 \leq 14.16$; df $= 1$; $P \leq 0.0004$), that is its adults emerged 2 days earlier. This result indicates that *T. drosophilae* could control more efficiently the populations of *D. suzukii* because its biological cycle is shorter. When two populations of insects are compared, under the premise that the other biological parameters have similar numerical values, short biological cycles result in larger rates of population growth (Russell et al. 2008).

Regarding the population parameters of both parasitoids, *P. vindemmiae* showed a higher net reproduction rate than *T. drosophilae* (Student's t test: *t* value not reported by lifetable.sas program; df $= 1$; $P = 0.0004$) (Table 2), which by itself appears to favor *P. vindemmiae*; however, it recorded statistically and biologically worse in the intrinsic rate of increase, finite rate of increase, mean generation time, and doubling time (Student's *t* test: *t* value not reported by lifetable.sas program; df $= 1$; $P \leq 0.0051$), which gives an overall advantage to *T. drosophilae*. In biological control, the intrinsic rate of increase is used to compare different species or populations of parasitoids, and an organism is considered to be more effective

Table 1. Biological parameters of the parasitoids *Pachycrepoideus vindemmiae* and *Trichopria drosophilae* developed in *Drosophila suzukii* pupae.

Parasitoid	Duration (d)*				Longevity (♀)	Sex Ratio (♀/Progeny)
	Egg	Larva	Pupa	Egg to Adult		
P. vindemmiae	4.57 ± 0.16a	6.74 ± 0.13b	8.17 ± 0.26b	19.38 ± 0.26b	31.38 ± 1.33a	0.65 ± 0.03a
T. drosophilae	4.34 ± 0.26a	5.76 ± 0.21a	7.36 ± 0.21a	17.38 ± 0.21a	36.32 ± 3.22a	0.62 ± 0.03a

* Means ± SE (same column) followed by the same letter are not statistically different ($P \leq 0.05$).

Table 2. Population parameters of the parasitoids *Pachycrepoideus vindemmiae* and *Trichopria drosophilae* in *Drosophila suzukii* pupae.*

Parasitoid	Net Reproduction Rate (Ro)	Intrinsic Rate of Increase (r_m)	Finite Rate of Increase (λ)	Mean Generation Time (T)	Doubling Time (Dt)
P. vindemmiae	96.37 ± 17.61a	0.65 ± 0.07b	1.91 ± 0.15b	6.98 ± 0.88b	1.05 ± 0.11b
T. drosophilae	55.68 ± 6.87b	0.98 ± 0.09a	2.68 ± 0.24a	4.05 ± 0.45a	0.7 ± 0.06a

* Means ± SE (same column) followed by the same letter are not statistically different ($P \leq 0.05$).
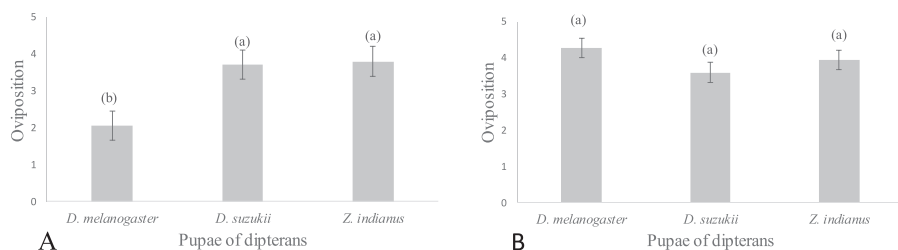
Fig. 1. Oviposition of *Pachycrepoideus vindemmiae* (A) and *Trichopria drosophilae* (B) in pupae of *Drosophila melanogaster*, *D. suzukii*, and *Zaprionus indianus*. Means ± SE followed by the same letter are not statistically different (*P* ≤ 0.05).

when it has a higher rate than its counterpart (Huffaker et al. 1976). Consequently, these results indicate that *T. drosophilae* could contribute more in the reduction of populations of *D. suzukii* than *P. vindemmiae*.

In the oviposition preference tests, *P. vindemmiae* parasitized equally the pupae of *D. suzukii* and *Z. indianus*, but laid a small number of eggs in *D. melanogaster* ($F = 5.95$; df = 2; $P = 0.0031$) (Fig. 1); for its part, *T. drosophilae* oviposited a statistically equal amount in the pupae of the three evaluated dipterans ($F = 1.59$; df = 2; $P = 0.2057$). The results that the pupae of *D. suzukii* were equally preferred to those of *Zaprionus indianus* Gupta but more than *D. melanogaster* indicate that both parasitoids could have the same degree of efficiency combating this invasive pest. These oviposition tests had to be performed because these three dipterans have been reported coexisting in berry crops of Colima and Jalisco, Mexico (Garcia-Cancino et al. 2015), and to date, the behavior or preference of either *P. vindemmiae* or *T. drosophilae* has not been studied in relation to the simultaneous presence of these three hosts, except for the reports of Mazzetto et al. (2016) and Wang et al. (2016), who found that *T. drosophilae* oviposits indistinctly in pupae of *D. melanogaster* or *D. suzukii*.

The results obtained in the evaluations of biological and population parameters indicate that *T. drosophilae* has a higher growth rate than *P. vindemmiae*; so, it is concluded that *T. drosophilae* has a greater potential to contribute in the control of *D. suzukii* in Mexico. Studies indicate that the natural parasitism of *T. drosophilae* fluctuates between 2% (Miller et al. 2015) and 10% (Gabarra et al. 2015), but in laboratory conditions, it increases up to 85% (Chabert et al. 2012), indicating that field parasitism could be augmented by inundative releases (Miller et al. 2015, Wang et al. 2016). Mathematical models based on experimental data show that the percentages of parasitism are inversely correlated with *D. suzukii* density (Miller et al. 2015, Wiman et al. 2016), thus, higher field parasitism rates should correlate with lower pest densities.

The result that *T. drosophilae* showed better biological characteristics than *P. vindemmiae* coincides with those obtained by Kacar et al. (2017), Rossi-Stacconi et al. (2017), and Wang et al. (2016), who compared several biological aspects of both parasitoids in laboratory conditions and concluded that *T. drosophilae* has a greater potential to be used as a biological control agent of *D.*

suzukii. However, this result differs with those obtained by Knoll et al. (2017) who found that two populations of *T. drosophilae* collected in two regions of Switzerland (Ticino and Vaud) had a higher and a lower parasitism rate than *P. vindemmiae*, respectively.

Since *D. suzukii* was detected in Mexico in 2011, the government has implemented three criteria to combat this invasive pest. The first criteria is to search and evaluate local parasitoids associated with this pest instead of importing exotic ones, for four reasons: (a) the uncertainty of whether imported parasitoids will adapt to the geographical conditions of Mexico; (b) the danger that exotic agents could disturb trophic systems adjacent to the release areas, a situation that does not occur with local species (Louda et al. 2003); (c) the loss of genetic vigor (e.g., inbreeding depression) that the exotic organisms might suffer during its importation process (Hoddle 2004); and (d) local species represents an option that can be implemented immediately, unlike exotic ones, whose complicated importation process can be delayed for many years (Hoddle 2004). The second criteria is to evaluate only the more abundant parasitoids because when several species of natural enemies attack the same prey or host, their relative abundance during field sampling is indirect evidence of their extrinsic (e.g., search ability) and intrinsic (e.g., prey specificity) properties as a biological control agent (Huffaker et al. 1976). Consequently, although four species were collected in the explorations conducted in Colima, namely, *P. vindemmiae*, *T. drosophilae*, *Spalangia simplex* Perkins (Hymenoptera: Pteromalidae), and *Leptopilina boulardi* Barbotin, Carton & Kelner-Pillault (Hymenoptera: Figitidae) (Garcia-Cancino et al. 2015), only two were evaluated. And, because of reported biological variability at the interpopulation level (examples indicated in the introduction), the third criteria consisted of the following: to determine if either local *P. vindemmiae* or *T. drosophilae* has a higher potential to be used as biological control agent, instead of making a decision based on published results.

By July 2018, *D. suzukii* has expanded its distribution to six states of Mexico (Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria 2018), but mathematical models based on physiological and demographic information of this fly, as well as climatological data, indicate that its potential distribution is the whole country, predicting an abundance of 750, 2,800, and 2500 pupae/km^2 for the north, center, and south regions, respectively (Gutierrez et al. 2016). Given this likely scenario of wide distribution and its consequent economic losses, the use of local parasitoids represents a good option that can be performed immediately. In this sense, *T. drosophilae* has a higher potential than *P. vindemmiae* to contribute to the management of this invasive Asiatic pest. Trials are underway to assess its effectiveness in the Mexican fields before undertaking a program involving innundative releases.

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