Neotropical Entomology (2024) 53:225–235
https://doi.org/10.1007/s13744-023-01118-1

ECOLOGY AND MANAGEMENT OF D. SUZUKII

Assessing Natural Incidence of Resident Pupal Parasitoids on the *Drosophila suzukii* (Diptera: Drosophilidae) Population in Non-crop Fruits

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Received: 19 July 2023 / Accepted: 13 December 2023 / Published online: 4 January 2024

Abstract

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae), world-renowned as spotted-wing drosophila, is an invasive pest mainly affecting healthy, soft and stone fruit crops throughout Argentinian fruit-growing regions. Natural environments overgrown by exotic feral host plants apparently favour *D. suzukii* proliferation. This is common in the subtropical northwestern Argentina's berry-producing region. An assemblage of resident parasitoid species has been associated with *D. suzukii* in crop and non-crop areas of Tucumán, the Argentina's leading berries producer and exporter. Consequently, the hypothesis that the combined action of two pupal parasitoid species, *Pachycrepoideus vindemiae* Rondani (Hymenoptera: Pteromalidae) and *Trichopria anastrephae* Lima (Hymenoptera: Diapriidae), occurring in non-crop fruit areas, has a significant impact on *D. suzukii* natural regulation in such invaded habitats was tested. A survey of *D. suzukii* puparia from both feral peach [*Prunus persica* (L.) Batsch] (Rosaceae) and guava (*Psydium guajava* L.) (Myrtaceae) fallen fruits and soil surrounding them was performed in a wilderness area of Tucumán. Abundance of *D. suzukii* and associated parasitoids, and parasitism levels were assessed. Whole of 3437 *D. suzukii* puparia were recovered; 78% and 22% were surveyed from fruits and soil underneath the fruit, respectively. Tested fruits are important *D. suzukii* multiplying hosts. Both *P. vindemiae* and *T. anastrephae* accounted for 99.8% of total parasitoid individuals. Pupal parasitoids contribute to the *D. suzukii* natural mortality, as they killed a quarter of all puparia. Mostly *T. anastrephae* foraged on host puparia located in the fruit and *P. vindemiae* in both microhabitats. This information supports an augmentative biological control strategy in non-crop areas.

Keywords Spotted-wing drosophila · parasitism · biological control · wild host plants · fruit infestation level · Northwestern Argentina

Introduction

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae), world-renowned as the spotted-wing drosophila or by its acronym "SWD", is a frugivorous fly native to Eastern Asia

Edited by Eugenio E de Oliveira

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that has been accidentally introduced to the Europe and Americas in the 2000s (Asplen et al. 2015). The accelerated spread within both continents and the subsequent agricultural losses in numerous countries, particularly to commercial soft and thin-skinned fruits, highlighted *D. suzukii* as one of the most important globally invasive agricultural species (De Ros et al. 2020; Garcia 2020a). Argentina is no exception to this situation, as *D. suzukii* has quickly become one of the most important fruit pest in the country (Funes et al. 2018).

The female of *D. suzukii* tends to lay eggs mainly on healthy, ripe fruits as it has a highly sclerosed serrated ovipositor, which makes it different from other sympatric drosophilid species into invaded areas (Atallah et al. 2014). In addition, *D. suzukii* has a broad host range, which includes numerous crops, non-crop and ornamental plants, although soft fruit are the primary hosts of this novel pest (Wollmann et al. 2020). Kirschbaum et al. (2020) summarise both naturally infested fruit species in the field and those artificially infested in laboratories on a worldwide basis. Several non-crop fruit species growing in wild vegetation areas may provide suitable hosts in order to maintain and multiply *D. suzukii* populations within invaded areas (Lee et al. 2015; Kenis et al. 2016). In this regard, evidence on wild host status on which invasive *D. suzukii* may increase in numbers is critical to support management strategies of this novel pest, particularly in habitats surrounding commercial berry crops (Lee et al. 2015, Wang et al. 2016). In addition, in e wild host fruits, there may also be a natural biological regulation of *D. suzukii* populations by resident natural enemies, including some parasitoid species (Arno´ et al. 2015; Gabarra et al. 2015; Daane et al. 2016; Garcia et al. 2022; Abram et al. 2022). In this framework, parasitoid surveys revealed a large assemblage of resident species associated with *D. suzukii* in both crop and non-crop areas throughout Argentina. Particularly larval parasitoid species belonging to Figitidae were recorded, such as *Leptopilina clavipes* Hartig, *Ganaspis hookeri* Crawford (Lue et al. 2017), *Leptopilina boulardi* Barbotin, Carton and Kelner-Pillault (Garrido et al. 2018), *Dieucoila octofagella Reche* (Reche et al. 2021), *Euxestophaga argentinensis* Gallardo, *Hexacola bonaerensis* Reche (Gallardo et al. 2022a), *Ganaspis brasiliensis* (Gallardo et al. 2022b, Funes et al. 2023), *Leptopilina heterotoma* Thomson and *Hexacola hexatoma* Harting (Fischbein et al. 2023). Both *D. octofagella* and *G. brasiliensis* were the only figitid species recovered from *D. suzukii* puparia, while the remaining species were only recorded from liquid traps together with *D. suzukii* adults. However, *D. octofagella* and *G. brasiliensis* were not abundant nor did they exerted control over *D. suzukii*. However, resident pupal parasitoid species has lately been associated with *D. suzukii* through tested trophic relationships in non-crop areas of northwestern (NW) Argentina (Buonocore Biancheri et al. 2022, 2023), as well as in southern Brazil (Wollmann et al. 2016, da Costa Oliveira et al. 2021). Particularly, three resident idiobiont pupal parasitoids, *Pachycrepoideus vindemiae* Rondani, *Spalangia* cf. *endius* Walker (Hymenoptera: Pteromalidae) and *Trichopria anastrephae* Lima (Hymenoptera: Diapriidae) were mainly found in close trophic association with *D. suzukii* on feral peaches [*Prunus persica* (L.) Batsch] (Rosaceae) occurring in wild vegetated environments of NW Argentina (Buonocore Biancheri et al. 2022). Both *P. vindemiae* and *T. anastrephae* were the most abundant and significant parasitoid species associated with *D. suzukii* (Buonocore Biancheri et al. 2022). The pteromalid *P. vindemiae* is a worldwide cyclorrhaphous dipteran parasitoid that was introduced in several American countries as a biocontrol agent against tephritid pests (Garcia et al. 2020), although it was first record in Argentina dates back to the 1940s, but misidentified as *Pachycrepoideus dubius* Ashmead (Ovruski et al. 2000). *Pachycrepoideus vindemiae* is a pupal ectoparasitoid, because the female lays the egg inside the space between the puparium shell and host pupal body (Wang and Messing 2004). In contrast, the diapriid *T. anastrephae* is native to the South American Neotropical region (Garcia et al. 2020), and it is an endoparasitoid because the female lays the egg into the hemocoel of the host pupa (da Costa Oliveira et al. 2021). The cosmopolitan *S. endius* is also a polyphagous dipteran ectoparasitoid, but mainly associated with tephritid and synanthropic flies (Morgan et al. 1975). The three pupal parasitoid species can be successfully lab reared (Wang et al. 2016; Krüger et al. 2019; Zheng et al. 2021), but both *P. vindemiae* and *T. anastrephae* have shown potential as *D. suzukii* biological control agents in the Americas (Garcia 2020b).

In view of the above, the hypothesis of the current study argues that the combined action of both pupal parasitoid species, occurring most frequently in non-crop fruit areas, has a significant impact as a natural regulation factor on *D. suzukii* populations. Therefore, in order to test this hypothesis, three aims were set as follows: (1) to assess the abundance of *D. suzukii* and associated parasitoids in non-crop hosts such as feral peach and guava (*Psydium guajava* L.) (Myrtaceae); (2) to analyse the influence of the host puparium origin, i.e. recovered from fruit or the soil adjacent to the fruit, associated with the sampled fruit species on the *D. suzukii* parasitism and (3) to determine the relevance of parasitism individually inflicted by *P. vindemiae* and by *T. anastrephae* on *D. suzukii* puparia recovered from both fruit and soil. The findings of this research are discussed with regard to the potential use of both *P. vindemiae* and *T. anastrephae* against *D. suzukii* within an area-wide integrated pest management approach (Haye et al. 2016; Garcia 2020b) in the fruit-growing NW region of Argentina, in which the pest populations apparently thrive on alternative, non-crop host plants (Buonocore Biancheri et al. 2022). This subtropical fruit-producing region, where the rainforest is an important part of the landscape, is a major soft fruit producer and exporter from Argentina (Funes et al. 2017, 2018). However, results of the study may be used for developing biological control strategies against *D. suzukii* in the remaining fruit-growing regions of Argentina and in other places in America and the world.

Material and methods

Sampling area

The study was carried out in a 14,174-ha area of protected wildlife known as "Sierra de San Javier" Park. It belongs to the Universidad Nacional de Tucumán and it is located in Horco Molle, Yerba Buena district, Tucumán province, in NW Argentina. This wilderness area belongs to the southernmost extension of the South American subtropical montane rainforest, locally known as "Selva de Yungas". In this region, the climate is humid warm-temperate with a rainy-warm season between October and April, and a dry-cold season between May and September; mean annual rainfall and temperature are about 1500 mm and 21.5 °C, respectively (Schliserman et al. 2016). Sampling sites were located on the eastern slope of the San Javier Mountain at 26°43′00″S latitude, 65°22′00″W longitude, and 600–800 m altitude. Sites consisted of tropical rainforest environments of low and medium disturbed secondary structure, with combined fruit species such as exotic guava, peach, and *Citrus aurantium* L. (sour orange) (Rutaceae) and natives to the Neotropic such as *Juglans australis* Grisebach (wild walnut) (Juglandaceae) and *Myrcianthes pungens* (O. Berg) D. Legrand (mato) (Myrtaceae).

Drosophila suzukii puparia sampling and processing

Puparia of *D. suzukii* were collected from both fallen fruit and soil in feral peach and guava tree-dominated environments. Samplings were performed throughout two peach and guava fruiting seasons, i.e. December 2016- January 2017 and December 2017-January 2018, and March 2017-April 2017 and March 2018-April 2018, respectively. Feral peach and guava were chosen because both host species are abundant in disturbed wild vegetation areas adjacent to berry crops, and fruiting periods cover from late spring to early autumn in northern Argentina (Schliserman et al. 2014, 2016). Mean (± SE) air temperature and relative humidity (RH) recorded during both peach and guava fruiting periods were 26.9 ± 0.6°C–82.9 ± 1.1% and 21.8 ± 0.9°C–68.4 ± 3.1% for the first collecting period, respectively, and 26.3 ± 0.8°C–82.5 ± 2.1% and 21.3 ± 0.4°C– 72.4 ± 1.7% for the second collecting period, respectively. The meteorological data were recorded by a weather station located at 700 m in the Sierra de San Javier Park. Forty peach and guava trees were selected for *D. suzukii* puparia sampling. On each sampling date, four peach or guava trees were randomly selected, and then, five fallen ripe fruit per each fruit tree were sampled. In addition, all *D. suzukii* puparia located on the soil underneath each fruit or close to it were also collected. Each sampled fruit was placed individually into a cloth bag, and its top was closed with a rubber band. Likewise, the soil underneath each fruit and the soil close to the fruit were dug with a hand shovel up to ~ 2 cm deep to find buried puparia. Then, the extracted soil from the sector relating to each fruit sampled was also placed individually into another cloth bag. All bags with fruit or soil were placed in plastic crates (32 × 24 × 12 cm) and taken to the Pest Biological Control Laboratory from the Planta Piloto de Procesos Industriales Microbiológicos y Biotecnología (PROIMI), in San Miguel de Tucumán. Fruits were removed from bags and individually placed in a plastic crate (20 × 15 × 5 cm) with a ½-cm layer of sterilised vermiculite Intersum® (Aislater S.R.L., Cordoba, Argentina) on the bottom as a pupation medium. Fruits and vermiculite were daily checked to remove drosophilid puparia. All puparia found inside pulp fruit, attached to the fruit rind or buried in the vermiculite were removed with a blunt-tip tweezer. Puparia were previously identified and then those of *D. suzukii* placed into 8 × 5 cm (diameter × height) voile cloth-covered plastic cups, with sterilised, moistened vermiculite on the bottom. Soil samples were removed from bags and sieved. Puparia thereby recovered were identified in order to select out those of *D. suzukii*. After that, all puparia were placed into cups described above. All cups were housed in a room at 25 ± 1°C, 75 ± 5% RH and 10:14 h L:D until adult *D. suzukii* and parasitoids emerged.

Drosophila suzukii puparia and adult parasitoids identification

Hauser's (2011) work was used to identify both the *D. suzukii* puparium and adult, and the Risbec's (1950) and Gibson's (2000) keys were used to identify pteromalid and diaprid adults, respectively. Voucher fly and parasitoid adult specimens were stored at the entomological collection of the Fundación Miguel Lillo, in San Miguel de Tucumán.

Data analyses

Numbers of recovered *D. suzukii* puparia, emerged adult flies and parasitoids, non-emerged parasitoids, non-emerged host puparia and parasitism, were used as response variables for statistical analyses. The parasitism percentage was calculated as the total number of emerged adult parasitoids and non-emerged parasitoids recovered from *D. suzukii* puparia sampled in a particular microhabitat (fruit or soil) and on a particular fruit species (peach or guava), and divided by the total number of host puparia recovered from those microhabitat and fruit species × 100. Given the lack of normality, data were ranked transformed prior to analyses (Conover and Iman 1981), but, untransformed data are shown as means (± SE) in tables and figures. All variable responses were analysed by one-way univariate general linear models (GLMs) with type III error at $p = 0.05$. This analysis allowed to identify significant effects of the fixed factor "host puparium origin related to tested fruit species", with four levels, namely, host puparia from peach fruit (= Fruit_Peach), host puparia from guava fruit (= Fruit_Guava), host puparia from soil next to peach (= Soil_Peach), and host puparia from soil next to guava (= Soil_Guava). Parasitism levels caused by a particular parasitoid species were analysed by two-way univariate GLMs. Fixed factors were "parasitoid species" with two levels, namely, species n° 1 and species n° 2, and "host puparium origin related to tested fruit species". Data from first and second collecting periods were separately analysed. Mean values were analysed by Tukey's honesty significant difference (HSD) test at $p = 0.05$. A Pearson product moment correlations at $p = 0.05$ was carried out to establish the level of relationship between the mean air temperature and the RH recorded during peach and guava fruiting periods. Air temperature, which it is correlated with RH, was chosen as a covariable when parasitim was analysed by one-way univariate GLMs. Temperature is a standard predictor of insect development dynamics (Terblanche et al. 2010). Statistical analyses were performed using STATISTICA software, version 10.0 (StatSoft Inc 2011).

Results

From 480 fruits, 50% feral guava and 50% feral peach, collected over two consecutive fruiting periods, 3437 *D. suzukii* puparia were recovered. A significantly higher number of *D. suzukii* puparia were found inside the fruit than buried in the soil underneath or close to the fruit sampled, with a significantly higher incidence on peach than on guava at both collecting periods (first collecting period: $F_{(3, 92)} = 60.495$, $p > 0.0001$; second collecting period: $F_{(3, 92)} = 68.919$, $p > 0.0001$) (Table 1). Overall, 78% of host puparia recovered were from fruit. The same pattern was recorded for the adult fly and parasitoid emergence in both surveying periods. Significantly, higher numbers of flies and parasitoids emerged from puparia recovered from fruit than from the soil, but predominantly from peach (first collecting period; adult flies: $F_{(3, 92)} = 90.830$, $p > 0.0001$, adult parasitoids: $F_{(3, 92)} = 34.001$, $p > 0.0001$; second collecting period, adult flies: $F_{(3, 92)} = 85.161$, $p > 0.0001$, adult parasitoids: $F_{(3, 92)} = 31.495$, $p > 0.0001$) (Table 1). However, significantly similar numbers of adult parasitoids were recovered from host puparia collected from both guava and peach fruits at the first sampling period (Table 1). Overall, 1163 and 566 emerged adult flies and parasitoids were recovered, respectively, from *D. suzukii* puparia. Additional 219 parasitoids were recovered from the dissection of non-emerged puparia. A significantly higher number of those parasitoids were from puparia recovered from the fruit than from soil (first collecting period: $F_{(3, 92)} = 15.746$, $p > 0.0001$; second

Table 1 Mean (± SE) numbers of *Drosophila suzukii* puparia and emerged adults, non-emerged host puparia, and emerged and non-emerged parasitoids recovered per sample from both infested peach and guava fruits, and from soil underneath or close to the fruit during two collecting periods, December 2016 - April 2017 and December 2017 - April 2018, in Horco Molle, Tucumán, northwestern Argentina

Collecting period	Host fruit	Total no. of collected fruit (total weight)	Host puparia origin	Recovered puparia	Non-emerged puparia	Emerged adult flies	Emerged adult parasitoids	Non-emerged parasitoids
1st collecting period:								
Dec/16-Jan/17	Peach	120 (4.7)	Fruit	25.1 ± 1.9a	10.5 ± 0.9a	9.8 ± 0.9a	4.9 ± 0.6a	0.8 ± 0.2a
			Soil	8.5 ± 1.1c	6.0 ± 0.8b	1.6 ± 0.3c	1.0 ± 0.2b	0.1 ± 0.1b
Mar-Apr/17	Guava	120 (5.8)	Fruit	17.5 ± 1.4b	7.8 ± 0.6ab	6.3 ± 0.6b	3.4 ± 0.5a	0.9 ± 0.2a
			Soil	4.3 ± 0.7d	3.1 ± 0.4c	0.9 ± 0.2c	0.4 ± 0.1b	0.0 ± 0.0b
2nd collecting period:								
Dec/17-Jan/18	Peach	120 (4.9)	Fruit	42.2 ± 2.9a	19.4 ± 1.3a	15.1 ± 1.1a	7.8 ± 0.9a	3.9 ± 0.5a
			Soil	10.9 ± 1.1c	6.7 ± 0.7c	2.6 ± 0.4c	1.6 ± 0.3c	0.5 ± 0.1b
Mar-Apr/18	Guava	120 (6.1)	Fruit	27.1 ± 2.2b	12.8 ± 1.2b	10.5 ± 0.8b	3.7 ± 0.6b	2.7 ± 0.4a
			Soil	7.5 ± 0.7c	5.0 ± 0.5c	1.7 ± 0.4c	0.8 ± 0.2c	0.3 ± 0.1b

Mean values in the same column with dissimilar letter indicate significant differences (Tukey HSD test, $p = 0.05$). Post hoc analysis was performed for each collecting period collecting period: $F_{(3, 92)} = 52.799$, $p > 0.0001$) (Table 1). There were no significant differences between parasitoids not emerged from puparia collected from guava and peach fruits at both collecting periods (Table 1). There was no insect emergence from 1708 puparia. Significantly more non-emerged host puparia were disclosed from fruit samples than those from soil (first collecting period: $F_{(3, 92)} = 22.699$, $p > 0.0001$; second collecting period: $F_{(3, 92)} = 47.938$, $p > 0.0001$) (Table 1).

Three parasitoid species, *T. anastrephae*, *P. vindemiae*, both pupal parasitoids, and an unidentified species of *Leptopilina* Förster (Figitidae), a larval parasitoid, were recovered from the total number of *D. suzukii* puparia collected in the study area. Pupal parasitoids accounted for 99.8% of the total number of individuals collected, as only two specimens of *Leptopilina* sp. were found. *Trichopria anastrephae* was the most abundant parasitoid species, with 460 identified specimens, accounting for 72% of both pupal parasitoids. Of all *T. anastrephae* specimens, 94% were from host puparia found inside the fruit, whereas 61% of the 180 *P. vindemiae* specimens were from puparia collected directly from the fruit

Parasitism recorded on *D. suzukii* puparia recovered from fruit, either peach or guava, was significantly higher than that recorded from host puparia recovered from the soil next to the fallen fruit, at both the first and second collecting periods (first collecting period: $F_{(3, 92)} = 18.941$, $p > 0.0001$; second collecting period: $F_{(3, 92)} = 9.246$, $p = 0.0002$) (Fig. 1). The analysis showed the same parasitism pattern as previously described when the covariate "air temperature" was incorporated, which did not significantly influence parasitism (first collecting period: $F_{(3, 92)} = 18.921$, $p > 0.0001$, covariate, $F_{(1, 91)} = 1.211$, $p = 0.2741$; second collecting period: $F_{(3, 91)} = 9.212$, $p > 0.0001$, covariate, $F_{(1, 91)} = 1.846$, $p = 0.1776$). Air temperature and RH were positively correlated ($r = 0.98$, $N = 96$, $P < 0.0001$); therefore, RH did not influence parasitism during the study.

Significant differences in the *D. suzukii* parasitism were found when individual categorical factors, host puparium origin related to the fruit species and pupal parasitoid species and their interaction were analysed at both the first and second collecting periods (Table 2). Parasitism by *T. anastrephae* on *D. suzukii* puparia was significantly higher in those host puparia recovered from fruit than in those from soil parasitised by this diaprid (Fig. 2). In turn, *T. anastrephae* parasitised significantly more *D. suzukii* puparia on fruit than *P. vindemiae*. This pattern was evident in both study periods (Fig. 2). *Pachycrepoideus vindemiae* parasitised significantly more *D. suzukii* puparia on soil than *T. anastrephae* only in the first collecting period, whereas in the second study period there was no significant difference in the parasitism due to both parasitoid species on host puparia recovered from soil (Fig. 2).

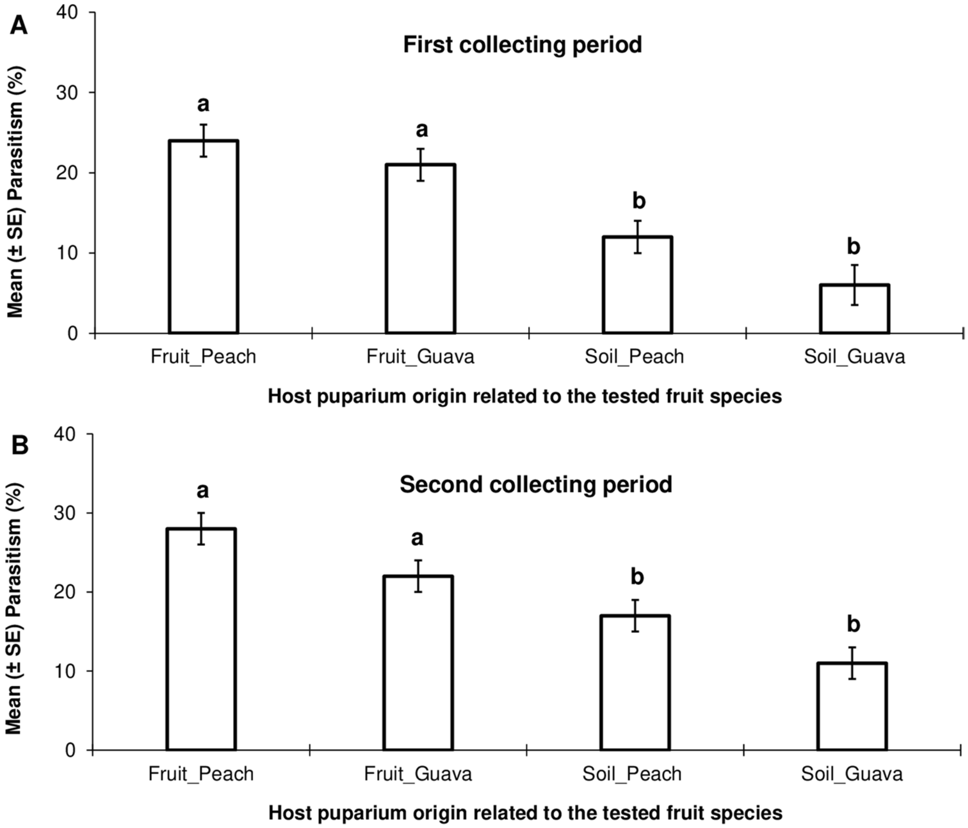

Fig. 1 Mean (± SE) parasitism percentages recorded from *Drosophila suzukii* puparia recovered from peach (*Prunus persica*) and guava (*Psidium guajava*) fruits, and from soil next to the fruit, during two collecting periods (**A** December 2016-April 2017; **B** December 2017-April 2018) in Horco Molle, Tucumán, northwestern Argentina. Bars with dissimilar letter indicate significant differences (Tukey HSD test, $p = 0.05$)

Table 2 Summary of two-way univariate general lineal models on the effect of the host puparia origin related to the tested fruit species (PuOr), the parasitoid species (PaSp) and their interaction on parasitism due to *Trichopria anastrephae* and *Pachycrepoideus vindemiae* on *Drosophila suzukii* puparia collected from both peach and guava fruits, and from soil next to fruit, during two collecting periods, December 2016 - April 2017 and December 2017-April 2018, in Horco Molle, Tucumán, northwestern Argentina

Collecting period	Source of variation	Statistical analysis outcome			
		df	Residuals *df*	*F*	*p*
1st collecting period (December 2016-April 2017)	PuOr	3	184	10.935	< 0.0001*
	PaSp	1	184	4.949	= 0.0273*
	PuOr × PaSp	3	184	22.146	< 0.0001*
2nd collecting period (December 2017-April 2018)	PuOr	3	184	10.031	< 0.0001*
	PaSp	1	184	15.269	= 0.0001*
	PuOr × PaSp	3	184	18.712	< 0.0001*

*Significant outcomes

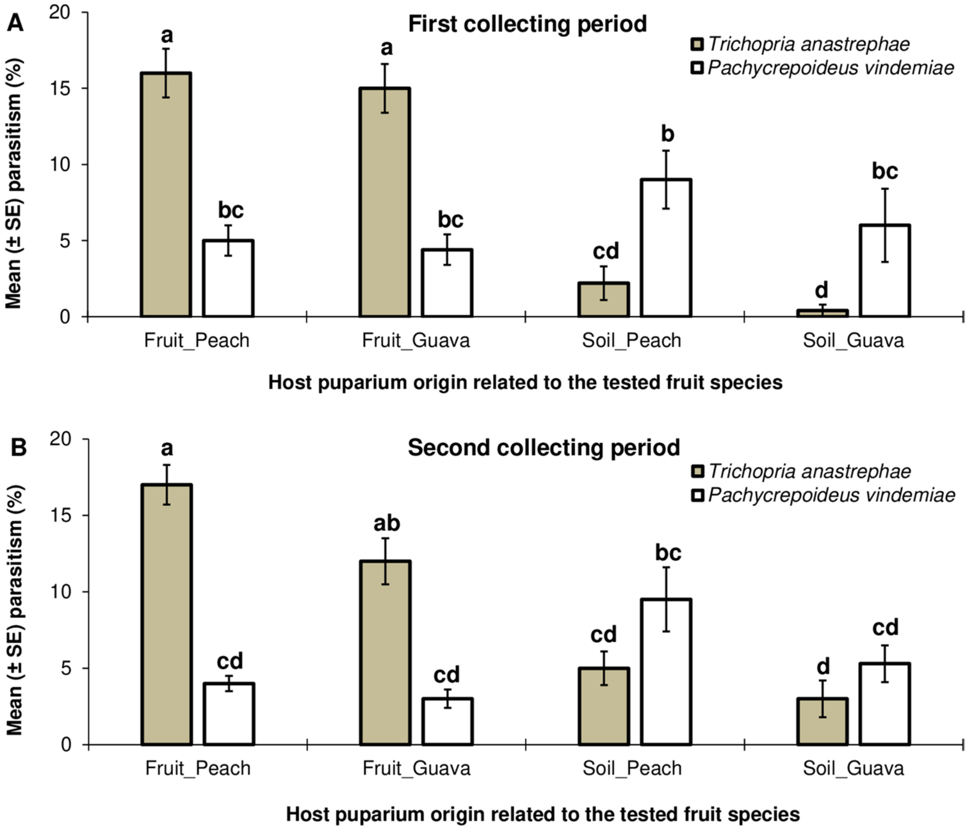

Fig. 2 Mean (± SE) parasitism on *Drosophila suzukii* by *Pachycrepoideus vindemiae* and *Trichopria anastrephae* based on the interaction between both parasitoid species and host puparium origin related to tested fruit species fixed factors, during two collecting periods (**A** December 2016-April 2017; **B** December 2017-April 2018) in Horco Molle, Tucumán, northwestern Argentina. Bars with dissimilar letter indicate significant differences (Tukey HSD test, $p = 0.05$)

Discussion

All integrated pest management programmes incorporate regular monitoring of the pest and its resident natural enemies in both crop and non-crop areas as critical tools for implementing a combination of pest management techniques for controlling the target pest (Garcia et al. 2022). These strategies are selected to minimise the extent of environmental degradation, reduce the impact of chemical inputs on humans and non-target organisms, improve on- and off-farm sustainability and reduce production costs to the farmer (Pretty and Bharucha 2015). Against this backdrop, results of the non-crop fruit field survey carried out in a protected wild forest area of the province of Tucumán, NW Argentina, highlight the combined role of two resident pupal parasitoids, *T. anastrephae* and *P. vindemiae*, as a natural regulating agent of the *D. suzukii* population in two host feral fruit species, *P. persica* and *P. guajava*. Particularly, the study provided three relevant findings on the trophic ecology of the non-crop fruit-*D. suzukii* - parasitoids system as follows: (1) the long-term use of both feral fruit species, *P. persica* and *P. guayava*, in non-crop areas as relevant alternative hosts by *D. suzukii*; (2) the importance of both *T. anastrephae* and *P. vindemiae* with regard to *D. suzukii* natural mortality and (3) the co-performance of the two pupal parasitoid species for targeting *D. suzukii* puparia located at different microhabitats.

The first finding highlighted the importance of feral peach and guava as *D. suzukii* alternative exotic hosts in the NW, from their first record in wild vegetation areas between March and November 2016 (Escobar et al. 2018; Buonocore Biancheri et al. 2022). In fact, Rosaceae and Myrtaceae include the largest number of *D. suzukii* host fruit in Latin America, accounting for nearly 50% of all fruit species recorded as hosts of this novel invasive pest (Garcia et al. 2022). Evidently, both feral guava and peach play an important role in the maintenance of *D. suzukii* populations in environments with different wild vegetation disturbance levels, particularly when economically important crops, such as susceptible berries (Funes et al. 2018), are not present in the region. For example, both non-crop alternative hosts provide food and reproduction resources for *D. suzukii* population growth in NW Argentina, as shown in the current study. Thus, *D. suzukii* adults switch from peach, which fructifies between late spring and early summer, to guava, which bears ripe fruit from mid-summer to late autumn. This scenario may enable *D. suzukii* overwintering morphotype adults to be present in NW Argentina. Winter females are the ones that may infest berry crops at the beginning of spring, which leads eventually to the development of the first generation of summer morphotype adults (Panel et al. 2018; Kirschbaum et al. 2020).

With regard to the second finding, overall parasitism levels on *D. suzukii* recorded in the current study on feral guava and peach, which averaged 16 and 22%, respectively, were essentially caused by both *T. anastrephae* and *P. vindemiae*. These values outperform slightly the parasitism of *D. suzukii* by resident parasitoids reported for Europe and North America, which have remained below 10% for a long time (Jarret et al. 2022). Within a broader context, the two pupal parasitoid species were accountable for 12–18% and 19–23% of the total host puparia mortality in guava and peach, respectively. The remaining percentage of dead host puparia was mainly due to unknown causes and other organisms, such as mites, entomopathogens and, perhaps by some predators injuring puparia. The strong incidence of ants removing *D. suzukii* puparia from soil, such as documented by Woltz and Lee (2017), was not assessed in this study. However, it is likely that a high percentage of the unknown host mortality was due to the injury caused by parasitoid females when introducing the ovipositor into the host or to the host-feeding behaviour. In this regard, it has been found that *P. vindemiae* females are able to kill *D. suzukii* pupae due to the host-feeding behaviour (Bezerra da Silva et al. 2019). Because *P. vindemiae* has been recurrently recorded as an abundant species parasitizing tephritid and drosophilid puparia in both crop and wilderness areas of Tucumán (Turica and Mallo 1961; Ovruski 1995; Bunocore Biancheri et al. 2022), its impact on *D. suzukii* mortality may be even higher than that recorded using the parasitism rate alone. It is also noteworthy that *T. anastrephae* was the parasitoid species with the highest level of parasitism on *D. suzukii* in the surveyed area. The latter is highlighted because *T. anastrephae* is a native Neotropical parasitoid mainly associated with saprophytic drosophilids, although it has been recorded from tephritid puparia belonging to the *Anastrepha* genus (Ovruski et al. 2000; Garcia et al. 2020). That is, despite the lack of a co-evolutionary relationship in sympatry with *D. suzukii*, *T. anastrephae* has been successfully able to adapt to this novel pest immediately at the onset of its invasion and dispersal in NW Argentina. The cosmopolitan *P. vindemiae* has a distinctive background because it is a highly polyphagous parasitoid on Cyclorrapha Diptera (Wang and Messing 2004), which enables it to adapt easily on novel hosts species (Hogg et al. 2022). Therefore, the current study and the previous one by Buonocore Biancheri et al. (2022) have shown both pupal parasitoid species displayed a swift and successful host-parasitoid co-adaptation process. Nevertheless, both pupal parasitoid species are not apparently exerting a substantial regulating effect on the *D. suzukii* abundance. Although parasitism did not abruptly reduce the *D. suzukii* abundance, both pupal parasitoid species were relevant mortality agents in the surveyed area, which was recently invaded by this novel pest. Therefore, both *T. anastrephae* and *P. vindemiae* can be valuable components into a framework of biological control measures in combination with other *D. suzukii* management strategies (Garcia 2020b). Larval parasitoids, particularly figitid species, for which trophic relationship with *D. suzukii* has been genuinely proven (Reche et al. 2021; Gallardo et al. 2022b), have displayed too low parasitism on this exotic pest in NW Argentina. A strong immunological response of *D. suzukii* larvae against attack by indigenous larval parasitoids at sites invaded by this exotic pest may be the cause of the parasitism shortage (Wang et al. 2016).

The third finding corroborated the availability of both pupal parasitoids to attack *D. suzukii* puparia located either inside the fallen fruit or on the soil underneath it, or buried near the fruit. This ability of the parasitoids made it possible to cover at least two microhabitats in which the *D. suzukii* larvae develop their puparia. Thus, both *P. vindemiae* and *T. anastrephae* have a more extensive impact on the *D. suzukii* abundance. However, this combined action of the two pupal parasitoid species in both tested microhabitats may imply a competitive interaction between females for the same resource (the host puparium). Therefore, such mutual interference may influence the parasitoid species performance as regulating agents for the *D. suzukii* abundance. This has been shown in studies under lab conditions, in which *T. anastrephae* outperformed *P. vindemiae* in the ability to attack *D. suzukii* puparia (da Costa Oliveira et al. 2021). Similar competitive superiority was also recorded for *Trichopria drosophilae* Perkins, a parasitoid taxonomically and biologically related to *T. anastrephae* (Masner and Garcia 2002), when interacting with *P. vindemiae* in both lab and semi-field trials (Wolf et al. 2021). Laboratory functional response studies showed that *T. drosophilae* has a higher egg load than *P. vindemiae* which allows it to parasitise more *D. suzukii* puparia in less time (Kaçar et al. 2017). However, in ecosystems, sympatric species reduce competition by, among other actions, using different resources or habitats (Amarasekare 2003; Bonsall et al. 2002). This was tested for both parasitoids, which can reduce or avoid the negative effects of this interspecific interaction through the ability to discriminate hosts previously parasitised by the other species and/or through differentiated foraging behaviour patterns for targeting of available resources (Buonocore Biancheri et al. 2023). This divergence in foraging behaviour can be corroborated through parasitism levels caused by both parasitoid species according to the microhabitats tested in the present study. The results showed a tendency of *T. anastrephae* to forage and parasitise *D. suzukii* puparia located on the fruit. The preference of *T. anastrephae*, previously proven in field studies by Buonocore Biancheri et al. (2023), was also recorded for *T. drosophilae* in studies under lab (Wang et al. 2016), semi-field (Wolf et al. 2021) and field conditions (Trivellone et al. 2020). However, parasitism by *T. drosophilae* on *D. suzukii* puparia located on the soil was rather high. Previous studies (Buonocore Biancheri et al. 2023) suggested a preference of *P. vindemiae* to parasitise *D. suzukii* puparia in microhabitats away from inside the fruit when females are under an interference situation with *T. anastrephae* females. Interestingly, data from the current study demonstrated that *P. vindemiae* females exhibited a higher behavioural plasticity than *T. anastrephae* for locating host puparia, as they similarly parasitised *D. suzukii* puparia on both fruit and soil. Such ability of *P. vindemiae* females to forage over a wide range of microhabitats was also supported by studies in Switzerland (Wolf et al. 2021; Trivellone et al. 2020). The abovementioned authors revealed some preference of *P. vindemiae* females to forage on *D. suzukii* puparia located in fruit on the foliage, but at the same time, *T. drosophilae* displayed foraging preference for host puparia on fruit scattered on the soil. Host foraging plasticity spanning different microhabitats, coupled with high polyphagy, are likely behavioural strategies that enable *P. vindemiae* to avoid interference with resident competitors and to be plentiful in the surveyed area.

In conclusion, the results evidenced an interesting new system of trophic interactions in a non-crop area of NW Argentina between two exotic feral fruits widely abundant in the region, the recently introduced *D. suzukii* and two resident pupal parasitoids well adapted to the newly established host. Both peach and guava turned out to be important *D. suzukii* multiplier hosts, whereas both *P. vindemiae* and *T. anastrephae* contribute to the natural mortality of this invasive pest. Both pupal parasitoid species killed about one-quarter of the total *D. suzukii* puparia scattered in two different microhabitats, fruit and soil. This suggests targeting them when analyzing *D. suzukii* integrated management strategies, because *T. anastrephae* and *P. vindemiae* are promising *D. suzukii* biological control agents. The current incidence on the novel pest population by *T. anastrephae* and *P. vindemiae* may properly be managed to improve the *D. suzukii* mortality in natural settings with many alternative fruit hosts. A first advisable step may involve lab studies based on replicated experimental adaptation for increased developmental success rate of both pupal parasitoid species (Kruitwagen et al. 2018, Woltering et al. 2019, Jarret et al. 2022). A recommended second step may address conservation biological control (Barbosa 1998) in wilderness areas of the Yungas forest or in patches with mixed stands of native and introduced fruit species adjacent to commercial fruit crops. Non-crop habitats particularly provide *D suzukii* multiplication and overwintering sites as well as shelter and food (Schmidt et al. 2019). Both resident pupal parasitoids, *T. anastrephae* and *P. vindemiae*, can exert an interesting natural control of the *D. suzukii* population, based on the data provided in the current study. Therefore, wild vegetation areas, where insecticide use is precluded, may preserve and multiply resident *D. suzukii* parasitoids. Thus, as suggested by Aluja (1999) to control tephritid fruit flies by native parasitoids, keeping areas with native vegetation interspersed in large-scale fruit crops may be an approach to encourage conservation biological control. This procedure may be suitable in berry-producing regions of Argentina. In a further potential third step, when natural populations of pupal parasitoids are not large enough to suppress *D. suzukii* natural populations, the augmentative release from such agents may help to enhance their impacts. Thus, field trials in Italy showed that augmentative release of the diaprid *T. drosophilae* substantially reduced fruit damage by *D. suzukii* in both a managed closed (Rossi Staconi et al. 2018), and an unmanaged open cropping system (Rossi Staconi et al. 2019). Similarly, augmentative releases of *T. drosophilae* in Mexico in commercial crops of *Rubus fruticosus* L. reduced the *D. suzukii* population up to 50% *D. suzukii* (Gonzalez-Cabrera et al. 2019). Recently, augmentative releases of *P. vindemiae* reduced, but on a relatively small scale, *D. suzukii* populations in caneberry hoop houses in Minnesota, Oregon and California (USA) (Hogg et al. 2022). Those results suggest that augmentative releases of resident pupal parasitoids may reduce *D. suzukii* outbreaks (Wang et al. 2020). Consequently, developing biological control strategies for *D. suzukii* using local biocontrol agents seems achievable in berries-growing regions of Argentina, as elsewhere in the world.

Acknowledgements We thank Patricia Colombres and Guillermo Borchia for laboratory assistance and the authorities of the Sierra de San Javier Park, Universidad Nacional de Tucumán, for allowing us to collect fruits and providing local weather data.

Author contributions M.J.B.B., L.C.S., M.D.P., D.S.K., F.R.M.G., and S.M.O. conceived the research and wrote the manuscript. M.J.B.B. and M.D.P. conducted field surveys and laboratory work. M.J.B.B., L.C.S., M.D.P. and S.M.O. analysed data and conducted statistical analyses. All authors read and approved the manuscript.

Funding Support was provided by Fondo Nacional de Promoción Ciencia y Tecnología (FONCYT) from Agencia Nacional de Promoción Científica y Tecnológica de Argentina (ANPCyT) through grants PICT-2017–0512 and PICT-2020-01050.

Declarations

Conflict of interest The authors declare no competing interests.

References

Abram PK, Wang XG, Hueppelsheuser T et al (2022) A coordinated sampling and identification methodology for larval parasitoids of spotted-wing drosophila. J Econ Entomol 115:922–942. https://doi.org/10.1093/jee/toab237

Aluja M (1999) Fruit fly (Diptera: Tephritidae) research in Latin America: myths, realities, and dreams. Anais Soc Entomol Brasil 28:565–594. https://doi.org/10.1590/S0301-80591999000400001

Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis. Ecol Lett 6:1109–1122. https://doi.org/10.1046/j.1461-0248.2003.00530.x

Arno´ J, Sola M, Riudavets J, Gabarra R (2015) Population dynamics, non-crop hosts, and fruit susceptibility of *Drosophila suzukii* in Northeast Spain. J Pest Sci 89:713–723. https://doi.org/10.1007/s10340-016-0774-3

Asplen MK, Anfora G, Biondi A et al (2015) Invasion biology of spotted wing Drosophila (*Drosophila suzukii*): a global perspective and future priorities. J Pest Sci 88:469–494. https://doi.org/10.1007/s10340-015-0681-z

Atallah J, Teixeira L, Salazar R, Zaragoza G, Kopp A (2014) The making of a pest: The evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species. Proc Royal Soc B 281:20132840. https://doi.org/10.1098/rspb.2013.2840

Barbosa P (1998) Conservation biological control. Academic Press, New York, USA, p 396

Bezerra Da Silva CS, Price BE, Walton VM (2019) Water-deprived parasitic wasps (*Pachycrepoideus vindemmiae*) kill more pupae of a pest (*Drosophila suzukii*) as a water-intake strategy. Sci Rep 9:3592. https://doi.org/10.1038/s41598-019-40256-8

Bonsall MB, Hassell MP, Asefa G (2002) Ecological trade-offs, resource partitioning, and coexistence in a host–parasitoid assemblage. Ecology 83:925–934. https://doi.org/10.2307/3071902

Buonocore-Biancheri MJB, Núñez-Campero SR, Suárez L, Ponssa MD, Kirschbaum DS, Garcia FRM, Ovruski SM (2023) Implications of the niche partitioning and coexistence of two resident parasitoids for *Drosophila suzukii* management in non-crop areas. Insects 14:222. https://doi.org/10.3390/insects14030222

Buonocore-Biancheri MJB, Suárez L, Kirschbaum DS, Garcia FRM, Funes CF, Ovruski SM (2022) Natural parasitism influences biological control strategies against both global invasive pests *Ceratitis capitata* (Diptera: Tephritidae) and *Drosophila suzukii* (Diptera: Drosophilidae), and the Neotropical-native pest *Anastrepha fraterculus* (Diptera: Tephritidae). Environ Entomol 51:1120–1135. https://doi.org/10.1093/ee/nvac085

Conover WJ, Iman RL (1981) Rank transformation as a bridge between parametric and nonparametric statistics. Am Statist 35:124–129. https://doi.org/10.2307/2683975

da Costa OD, Stupp P, Martins LN, Wollmann J, Geisler FCS, Cardoso TDN, Bernardi D, Garcia FRM (2021) Interspecific competition in *Trichopria anastrephae* parasitism (Hymenoptera: Diapriidae) and *Pachycrepoideus vindemmiae* (Hymenoptera: Pteromalidae) parasitism on pupae of *Drosophila suzukii* (Diptera: Drosophilidae). Phytoparasitica 49:207–215. https://doi.org/10.1007/s12600-020-00843-2

Daane KM, Wang XG, Biondi A et al (2016) First exploration of parasitoids of *Drosophila suzukii* in South Korea as potential classical biological agents. J Pest Sci 89:823–835. https://doi.org/10.1007/s10340-016-0740-0

De Ros G, Grassi A, Pantezzi T (2020) Recent trends in the economic impact of *Drosophila suzukii*. In: Garcia FRM (ed) *Drosophila suzukii* Management. Springer Nature Cham, Switzerland, pp 11–28

Escobar LI, Ovruski SM, Kirschbaum DS (2018) Foreign invasive pests *Drosophila suzukii* (Matsumura) and *Zaprionus indianus* Gupta (Diptera: Drosophilidae) threaten fruit production in northwestern Argentina. Dros Info Serv 101:9–14

Fischbein D, Kun ME, Chillo V, Masciocchi M, Germano MD, Cardozo A, Martínez AS (2023) Resident hymenopteran parasitoids with potential drosophilid associations in Andean North Patagonia: implications for the biological control of the spotted wing Drosophila. Neotrop Entomol. https://doi.org/10.1007/s13744-023-01083-9

Funes CF, Escobar LI, Meneguzzi NG, Ovruski SM, Kirschbaum DS (2017) Occurrence of *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae) in organically grown *Rubus* spp. (Rosales: Rosaceae), in two very contrasting environments of northwestern Argentina. Fla Entomol 100:672–674. https://doi.org/10.1653/024.100.0330

Funes CF, Gallardo FE, Reche VA, Escobar LI, Ovruski SM, Kirschbaum DS (2023) Parasitoids associated with the invasive pest *Drosophila suzukii* (Diptera: Drosophilidae) in Argentina and their potential role as biological control agents of this pest in blueberry orchards. Acta Hortic 1357:385–391. https://doi.org/10.17660/ActaHortic.2023.1357.54

Funes CF, Kirschbaum DS, Escobar LI, Heredia AM (2018) La mosca de las alas manchadas, *Drosophila suzukii* (Matsumura): nueva plaga de las frutas finas en Argentina. Ediciones del Instituto Nacional de Tecnología Agropecuaria, Argentina https://repositoriosdigitales.mincyt.gob.ar/vufind/Record/INTADig_f738238070075dcbf05ee63daee431f8. Accessed 10 July 2023

Gabarra R, Riudavets J, Rodríguez GA, Pujade-Villar J, Arno´ J (2015) Prospects for the biological control of *Drosophila suzukii*. Biocontrol 60:331–339. https://doi.org/10.1007/s10526-014-9646-z

Gallardo FE, Funes CF, Reche V, Kirschbaum DS, Ovruski SM, Buffington ML (2022b) First record and distribution of *Ganaspis brasiliensis* (Hymenoptera: Figitidae: Eucoilinae), a parasitoid of *Drosophila suzukii* (Diptera: Drosophilidae) in

Argentina. Neotrop Entomol 51:164–169. https://doi.org/10.1007/s13744-021-00912-z

Gallardo FE, Reche VA, Margaría CB, Aquino DA, Ansa MA, Dettler MA, Vazquez F, Barrientos G, Santadino M, Martínez E, Riquelme-Virgala M (2022a) Survey of potential parasitoids (Hymenoptera) of *Drosophila suzukii* (Diptera: Drosophilidae) in Buenos Aires province, Argentina. Rev Soc Entomol Arg 81(1):71–78. https://doi.org/10.25085/rsea.810107

Garcia FRM (2020a) Introduction to *Drosophila suzukii* management. In: Garcia FRM (ed) *Drosophila suzukii* Management. Springer Nature Cham, Switzerland, pp 1–9

Garcia FRM (2020b) Basis for area-wide management of *Drosophila suzukii* in Latin America. In: Garcia FRM (ed) *Drosophila suzukii* management. Springer Nature Cham, Switzerland, pp 93–110

Garcia FRM, Lasa R, Funes CF, Buzzetti K (2022) Drosophila suzukii management in Latin America: current status and perspectives. J Econ Entomol 115:1008–1023. https://doi.org/10.1093/jee/toac052

Garcia FRM, Ovruski SM, Suárez L, Cancino J, Liburd OE (2020) Biological control of tephritid fruit flies in the Americas and Hawaii: a review of the use of parasitoids and predators. Insects 11:662. https://doi.org/10.3390/insects11100662

Garrido SA, Cichón LI, Lago JD, Gallardo FE, Navarro MD (2018) Primer registro de *Leptopilina boulardi* (Hymenoptera: Figitidae) asociado a *Drosophila suzukii* (Diptera: Drosophilidae) en el Alto Valle de Río Negro y Neuquén, Patagonia, Argentina. Rev Soc Entomol Arg 77:22–27. https://doi.org/10.25085/rsea.770202

Gibson GAP (2000) Illustrated key to the native and introduced Chalcidoid parasitoids of filth flies in America North of Mexico (Hymenoptera: Chalcidoidea). http://res2.agr.ca/ecorc/apss/chalkey/keyintro.htm (accessed on 20 October 2000)

Gonzalez-Cabrera J, Moreno-Carrillo G, Sanchez-Gonzalez JA (2019) Single and combined release of *Trichopria drosophilae* (Hymenoptera: Diapriidae) to control *Drosophila suzukii* (Diptera: Drosophilidae). Neotrop Entomol 48:949–956. https://doi.org/10.1007/s13744-019-00707-3

Hauser MA (2011) Historic account of the invasion of *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) in the continental United States, with remarks on their identification. Pest Manag Sci 67:1352–1357. https://doi.org/10.1002/ps.2265

Haye T, Girod P, Cuthbertson AGS, Wang XG, Daane KM, Hoelmer KA, Baroffio C, Zhang JP, Desneux N (2016) Current SWD IPM tactics and their practical implementation in fruit crops across different regions around the world. J Pest Sci 89:643–651. https://doi.org/10.1007/s10340-016-0737-8

Hogg BN, Lee LC, Rogers MA, Worth L, Nieto DJ, Stahl JM, Daane KM (2022) Releases of the parasitoid *Pachycrepoideus vindemmiae* for augmentative biological control of spotted wing drosophila, *Drosophila suzukii*. Biol Control 168:104865. https://doi.org/10.1016/j.biocontrol.2022.104865

Jarrett BJM, Linder S, Fanning PD, Isaacs R, Szucs M (2022) Experimental adaptation of native parasitoids to the invasive insect pest, *Drosophila suzukii*. Biol Control 167:104843. https://doi.org/10.1016/j.biocontrol.2022.104843

Kaçar G, Wang XG, Biondi A, Daane KM (2017) Linear functional response by two pupal Drosophila parasitoids foraging within single or multiple patch environments. PLoS ONE 12:e0183525. https://doi.org/10.1371/journal.pone.0183525

Kenis M, Tonina L, Eschen R, van der Sluis B, Sancassani M, Mori N, Haye T, Helsen H (2016) Non-crop plants used as hosts by *Drosophila suzukii* in Europe. J Pest Sci 89:735–748. https://doi.org/10.1007/s10340-016-0755-6

Kirschbaum DS, Funes CF, Buonocore-Biancheri MJ, Suárez L, Ovruski SM (2020) The biology and ecology of *Drosophila suzukii* (Diptera: Drosophilidae). In: Garcia FRM (ed) *Drosophila suzukii* Management. Springer Nature Cham, Switzerland, pp 41–91

Krüger AP, Scheunemann T, Vieira JGA, Morais MC, Bernardi D, Nava DE, Garcia FRM (2019) Effects of extrinsic, intraspecific competition and host deprivation on the biology of *Trichopria anastrephae* (Hymenoptera: Diapriidae) reared on *Drosophila suzukii* (Diptera: Drosophilidae). Neotrop Entomol 48:957–965. https://doi.org/10.1007/s13744-019-00705-5

Kruitwagen A, Beukeboom LW, Wertheim B (2018) Optimization of native biocontrol agents, with parasitoids of the invasive pest *D. suzukii* as an example. Evol Appl 11:1473–1497. https://doi.org/10.1111/eva.12648

Lee JC, Dreves AJ, Cave AM, Kawai S, Isaacs R, Miller JC, van Timmeren S, Bruck DJ (2015) Infestation of wild and ornamental noncrop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). Ann Entomol Soc Am 108:117–129. https://doi.org/10.1093/aesa/sau014

Lue CH, Mottern JL, Walsh GC, Buffington ML (2017) New record for the invasive spotted wing drosophila, *Drosophila suzukii* (Matsumura, 1931) (Diptera: Drosophilidae) in Anillaco, western Argentina. Proc Entomol Soc Wash 119(1):146–150. https://doi.org/10.4289/0013-8797.119.1.146

Masner L, García JL (2002) The genera of Diapriinae (Hymenoptera, Diapriidae) in the New World. Bull Am Mus Nat 268:1–138. https://doi.org/10.1206/0003-0090(2002)2682.0.CO;2

Morgan P, Patterson R, Labrecque G, Weidhaas D, Benton A (1975) Suppression of field population of housefly with *Spalangia endius*. Science 189:388–389. https://doi.org/10.1126/science.1145207

Ovruski SM (1995) Pupal and larval-pupal parasitoids (Hymenoptera) obtained from *Anastrepha* spp. and *Ceratitis capitata* (Dipt. Tephritidae) pupae collected in four localities of Tucumán province, Argentina. Entomophaga 40:367–370. https://doi.org/10.1007/BF02373724

Ovruski SM, Aluja M, Sivinski J, Wharton R (2000) Hymenopteran parasitoids on fruit infesting Tephritidae (Diptera) in Latin America and the Southern United States: diversity, distribution, taxonomic status and their use in fruit fly biological control. Integr Pest Manag Rev 5:81–107. https://doi.org/10.1023/A:1009652431251

Panel ADC, Zeeman L, van der Sluis BJ, van Elk P, Pannebakker BA, Wertheim B, Helsen HHM (2018) Overwintered *Drosophila suzukii* are the main source for infestations of the first fruit crops of the season. Insects 9:145. https://doi.org/10.3390/insects9040145

Pretty J, Bharucha ZP (2015) Integrated pest management for sustainable intensification of agriculture in Asia and Africa. Insects 6:152–182. https://doi.org/10.3390/insects6010152

Reche V, Gallardo FE, Funes CF, Escobar LI, Ovruski SM, Kirschbaum DS (2021) A new species of *Dieucoila* (Hymenoptera Figitidae) associated with *Drosophila suzukii* (Diptera Drosophilidae) in Argentina. Bull Insectol 74:11–18 http://sedici.unlp.edu.ar/handle/10915/119946

Risbec J (1950) La Faune Entomologique des Cultures au Sénégal et au Soudan: II. Contribution à L'étude des Proctotrupidae (Serphiidae). [s.l.], (Travaux du Laboratoire d'Entomologie du Secteur Soudanais de Recherche Agronomique–Station de Bambey); Gouvernement Général de l'Afrique Occidentale Française, 638p

Rossi Stacconi MV, Amiresmaeili N, Biondi A, Carli C, Caruso S, Dindo ML et al (2018) Host location and dispersal ability of the cosmopolitan parasitoid *Trichopria drosophilae* released to control the invasive spotted wing drosophila. Biol Control 117:188–196. https://doi.org/10.1016/j.biocontrol.2017.11.013

Rossi Stacconi MV, Grassi A, Ioriatti C, Anfora G (2019) Augmentative releases of *Trichopria drosophilae* for the suppression of early season *Drosophila suzukii* populations. BioControl 64:9–19. https://doi.org/10.1007/s10526-018-09914-0

Schliserman P, Aluja M, Rull J, Ovruski SM (2014) Habitat degradation and introduction of exotic plants favor persistence of invasive species and population growth of native polyphagous fruit fy pests in a Northwestern Argentinean mosaic. Biol Invasions 16:2599–2613. https://doi.org/10.1007/s10530-014-0690-5

Schliserman P, Aluja M, Rull J, Ovruski SM (2016) Temporal diversity and abundance patterns of parasitoids of fruit-infesting Tephritidae (Diptera) in the Argentinean Yungas: implications for biological control. Environ Entomol 45:1184–1198. https://doi.org/10.1093/ee/nvw077

Schmidt JM, Whitehouse TS, Green K, Krehenwinkel H, Schmidt-Jeffris R, Sial AA (2019) Local and landscape-scale heterogeneity shape spotted wing drosophila (*Drosophila suzukii*) activity and natural enemy abundance: implications for trophic interactions. Agric Ecosyst Environ 272:86–94. https://doi.org/10.5061/dryad.52c2k52

StatSoft, Inc. 2011. STATISTICA (data analysis software system), version 10.0. https://www.statsoft.com.

Terblanche JS, Nyamukondiwa C, Kleynhans E (2010) Thermal variability alters climatic stress resistance and plastic responses in a globally invasive pest, the Mediterranean fruit fly (*Ceratitis capitata*). Entomol Exp Appl 137:304–315. https://doi.org/10.1111/j.1570-7458.2010.01067.x

Trivellone V, Meier M, Cara C, Pollini Paltrinieri L, Gugerli F, Moretti M, Wolf S, Collatz J (2020) Multiscale determinants drive parasitization of Drosophilidae by Hymenopteran parasitoids in agricultural landscapes. Insects 11:334. https://doi.org/10.3390/insects11060334

Turica A, Mallo RG (1961) Observaciones sobre la poblacion de las Tephritidae y sus endoparásitoss en algunas regiones citrícolas argentinas. Rev Inform Invest Desarrollo Agrobioindustrial (IDIA) 6:145–161

Wang XG, Kaçar G, Biondi A, Daane KM (2016) Foraging efficiency and outcomes of interactions of two pupal parasitoids attacking the invasive spotted wing drosophila. Biol Control 96:64–71. https://doi.org/10.1016/j.biocontrol.2016.02.004

Wang XG, Lee JC, Daane KM, Buffington ML, Hoelmer KA (2020) Biological control of *Drosophila suzukii*. CAN Reviews 15. https://doi.org/10.1079/PAVSNNR202015054

Wang XG, Messing RH (2004) Two different life history strategies determine the competitive outcome between *Dirhinus giffardii* and *Pachycrepoideus vindemmiae*, ectoparasitoids of cyclorrhaphous Diptera. Bull Entomol Res 94:473–480. https://doi.org/10.1079/BER2004318

Wolf S, Barmettler E, Eisenring M, Romeis J, Collatz J (2021) Host searching and host preference of resident pupal parasitoids of *Drosophila suzukii* in the invaded regions. Pest Manag Sci 77:243–252. https://doi.org/10.1002/ps.6013

Wollmann J, Schlesener DCH, Ferreira MS, Garcia MS, Costa VA, Garcia FRM (2016) Parasitoids of drosophilidae with potential for parasitism on *Drosophila suzukii* in Brazil. Dros Info Serv 99:38–42

Wollmann J, Schlesener DCH, Mendes SR, Kruger AP, Martins LN, Bernardi F, Garcia MS, Garcia FRM (2020) Infestation index of *Drosophila suzukii* (Diptera: Drosophilidae) in small fruit in southern Brazil. Arq Inst Biol 87:1–9. https://doi.org/10.1590/1808-1657000432018

Woltering SB, Romeis J, Collatz J (2019) Influence of the rearing host on biological parameters of Trichopria drosophilae, a potential biological control agent of *Drosophila suzukii*. Insects 10:183. https://doi.org/10.3390/insects10060183

Woltz JM, Lee JC (2017) Pupation behavior and larval and pupal biocontrol of *Drosophila suzukii* in the field. Biol Control 110:62–69. https://doi.org/10.1016/j.biocontrol.2017.04.007

Zheng Y, Song ZW, Zhang YP, Li DS (2021) Ability of *Spalangia endius* (Hymenoptera: Pteromalidae) to parasitize *Bactrocera dorsalis* (Diptera: Tephritidae) after Switching Hosts. Insects 12:613. https://doi.org/10.3390/insects12070613