Seasonal Fluctuation and Preference for Wild Fruits of Drosophila suzukii in Cultivated and Noncultivated Areas of Blackberry Crops

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Abstract

Spotted-wing Drosophila (SWD), Drosophila suzukii Matsumura (Diptera: Drosophilidae), is one of the most important pests of berry crops globally. Knowledge of the seasonal fluctuation of SWD population in cultivated and noncultivated areas of blackberry, in relation to preference for wild fruits, can contribute to the development of effective management strategies. In this study, the seasonal dynamics of SWD was determined in cultivated blackberry (Rubus sp.) and noncultivated areas. Moreover, the preference of SWD for wild fruits growing in the blackberry producing region in Michoacán, Mexico, was determined. From 2013 to 2015, field surveys were performed on the seasonal dynamics of SWD. Furthermore, to determine whether the wild and noncultivated plants in this region were hosts to SWD, choice and no-choice experiments were performed, using fruits, under laboratory conditions. The seasonal fluctuation of SWD was not only influenced by wild plant species as alternate hosts, but also by cultural practices, such as the mowing down of blackberry plants and the vegetation surrounding the blackberry crop. In addition to cultivated blackberry, Psidium guajava, Rubus adenotrichos, Spondias mombin, and Prunus serotina var. capuli are reported as new hosts for SWD in the study region. The results of this study will help develop sustainable regional management of this invasive pest in blackberry crops in Mexico.

Key Message

- Wild fruits and crop cultural practices influence seasonal fluctuations in SWD population.
- Preference for wild fruits of SWD influences the seasonal abundance in cultivated blackberries.
- SWD exploits a wide variety of noncrop host fruits outside of blackberry crops.
- Knowledge of the seasonal fluctuation of SWD population near blackberry crops contributes to developing IPM plans.

Introduction

Mexico is the main producer of blackberry (*Rubus* sp.; Rosaceae) globally, producing > 364,000 tons per year (SIAP 2019). Spotted wing Drosophila (SWD), *Drosophila suzukii* (Diptera: Drosophilidae) Matsumura, originally from east Asia, infests ripening soft-skinned fruits and is one of the most important pests of blackberry and other berry crops in Mexico, causing losses ranging from 40–80% (SENASICA 2019). Efficient management strategies are lacking for this species due to the lack of knowledge of its basic aspects. For example, the seasonal fluctuation of SWD in cultivated and noncultivated areas of blackberry, related to the preference for wild host fruits, is unknown.

A wide range of hosts allows SWD to move from cultivated to noncultivated areas (Lee et al. 2015; Poyet et al. 2015). Hosts of SWD include a wide variety of berries, grapes, plums, and peaches in both America and Europe (Yu et al. 2013; Cini et al. 2014; Harris et al. 2014). Hard fruits, such as loquat (*Eriobotrya japonica* Thunb.), fig (*Ficus carica* L.), apple (*Malus domestica* Borkh.), pear (*Pyrus* spp. L.), and guava *(Psidium guajava L.)* (Kinjo et al. 2013; Lasa et al. 2017), can be attacked if the skin is perforated or damaged by other insects (Mann and Stelinski, 2011). Other wild hosts, including Oregon grape (*Mahonia aquifolium* Pursh.), elderberry (*Sambucus* L.), currant (*Ribes* L.), dogwood (*Cornus kousa* Burg.), mulberry (*Morus* sp. L.), and salmonberry (*Rubus spectabilis* Pursh.) and various wild species of cranberry (*Vaccinium parvifolium* Smith) and *Prunus* L. on the California coast (Lee et al. 2015; Kenis et al. 2016; USDA.gov 2015) have also been reported. Therefore, noncultivated host plants are important for maintaining SWD populations (Asplen et al. 2015; Grant and Sial 2021).

SWD exhibits preference for fruits with certain characteristics (Rodriguez et al. 2019). Studies on susceptibility to SWD have been conducted with raspberry, wild blackberry, black cherry, guava, grape, and hawthorn (Burrack et al. 2013; Lee et al. 2011; Lasa et al. 2017; Elsensohn and Loeb 2018). However, studies on the roles of wild hosts, such as chokecherry, yellow mombin, and nance, in supporting the SWD population annually in subtropical and cool weather—typical of blackberry producing areas in Mexico—have not been conducted and how they influence the season dynamics on commercial blackberry crops under the forced production system (Kenis et al. 2016; Little et al. 2016).

Studies have reported that the population dynamics of SWD is related to the season and availability of ripe fruits in cultivated and noncultivated areas (i.e., riparian systems, ornamental trees, forest) (Tonina et al. 2018, Tait et al. 2020, Hwang et al. 2020). The studies have been performed in crops such as raspberry, blueberry, and cherry (Klick et al. 2016; Wang et al. 2016; Cahenzli et al. 2018; Briem et al. 2018), but not with blackberry grown under forced production systems in subtropical areas. Therefore, it is of interest to know how wild vegetation in areas surrounding commercial blackberry crops influence the population dynamics of SWD throughout the blackberry growing season. Moreover, in this crop, it is unclear how cultural practices, such as plant mowing, a necessary practice at the beginning of the season, influence population density.

This study hypothesizes that in the absence of commercial production of blackberry, the SWD population increases in areas with alternate hosts, which maintain its population. When cultivated blackberry fruit starts ripening in production season, SWD population starts getting established on commercial plots. However, population density is also influenced by cultural practices, such as crop mowdown. Therefore, the objectives of this study were to determine the seasonal fluctuation of SWD in cultivated blackberry and noncultivated areas and to determine the preference of SWD for fruits grown in the wild and in blackberry producing region in Michoacán, Mexico.

Materials And Methods

Experimental setup

Experiment 1. Seasonal fluctuation of SWD in cultivated and noncultivated areas of blackberry

Establishment and execution of the experiments

The seasonal fluctuation of SWD was determined in blackberry cultivated and noncultivated areas in Los Reyes, Ziracuaretiro, Tacambaro, and adjacent localities (referred to as zones 1, 2, and 3, respectively) of the Michoacán state, from 2013 to 2015. For this purpose, 1 L clear plastic cups, containing 200 mL of apple cider vinegar (Clemente Jacques, Sabormex, S. A. de C. V., Mexico City), with 10 holes (5-mm diameter) made in a zigzag fashion (Lee 2012), were used as traps. The traps were placed in commercial orchards of blackberry, at the borders of blackberry orchards, in forest areas and non-target wild fruits at different altitudes, 1100–2800 m above sea level, separated approximately 3 km (Fig. 1). In blackberry cultivation areas producing under different levels of management and technology, 27 monitoring traps were located within blackberry commercial plots (7 were in zone 1, 9 in zone 2, and 11 in zone 3). Additionally, 42 traps were located in forested areas (16, 10, and 16 in zones 1, 2, and 3, respectively) (Fig. 1). All traps were replaced every 10–14 d and refilled with 200 mL of apple cider vinegar. The contents were poured separately into the corresponding closed 0.5 L plastic container for transport to the laboratory for fly counting.

Separation and counting of adult SWD flies from other captured flies were performed under a stereomicroscope (CARL ZEISS; Model DV4) based on morphology (Ashburner et al., 2005). The total number of SWD (males and females) was counted, added to prepare the graphs of fluctuation weekly, and transformed to monthly catches.

Experiment 2. Preference For Wild Fruits

SWD rearing

To establish the rearing of SWD, blackberry fruits infested with larvae and pupae were collected from Los Reyes Michoacán, México (19º 36´54´´ N, -102º 20´, 09´´ W). In the laboratory, the blackberry fruits were placed for one week in a ventilated plastic box (30 × 20 × 9 cm) under room conditions until adults emerged. The laboratory rearing of SWD was initiated with these adults, which were considered generation zero (F_0). The adults were placed in wooden cages with walls made of acetate sheets and gauze, each containing *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) artificial diet developed by Guerrero (2011) in small glass jars (5 cm in diameter and 6 cm in height). The artificial diet of agar (10 g), sugar (135 g), and beer yeast (72.5 g) also served as an oviposition substrate and as feed for the larvae until pupation. SWD was reared under room conditions of 25°C ± 2°C, 60% ± 2% relative humidity.

Experimental Setup

Wild fruits as potential SWD hosts

To determine whether wild fruits collected from the field were SWD hosts, choice and no-choice experiments were conducted in the laboratory using blackberry (*Rubus adenotrichos* Schltdl.; Rosaceae), yellow mombin (*Spondias mombin* L.; Anacardiaceae), loquat (*E. japonica* Thunb.; Rosaceae), hawthorn (*Crataegus pubescens* Steud.; Rosaceae), nance (*Byrsonima crassifolia* L.; Malpighiaceae), wild guava (*P. guajava* L.; Myrtaceae), black cherry (*Prunus serotina* subsp. *capulí* McVaugh; Rosaceae), and wild grape (*Vitis tiliifolia* Humb. & Bonpl. ex Schult.; Vitaceae). Excluding the fruits of hawthorn and loquat, which were collected from an experimental field at the Centro Regional Universitario Centro Occidente of the Universidad Autónoma Chapingo, Morelia, Michoacán (Mexico), all fruits were collected around the main blackberry crop production areas in Tacambaro, Ziracuaretiro, and Los Reyes, in the state of Michoacán, Mexico. The identification of plants containing the wild fruits was based on a reference guide (Rzedowski and Calderon 2005).

The wild fruits selected were ripe, with no apparent insect infestation or mechanical injury. The fruits were either used for experiments the day after collection or stored at 4°C for ≤ 5 d. Before use, the fruits were disinfected for 1 min with 70% ethyl alcohol and placed on Styrofoam plates (20cm × 20 cm).

Choice test. Twenty fruits from each of the eight wild fruit species and cultivated blackberry were placed on 20 cm × 20 cm-Styrofoam trays and exposed, inside a wooden frame cage (60 cm × 60 cm × 70 cm) covered with organza fabric, to 20 females and 20 males of SWD (5-d-old) for 24 h. Then, the fruits were removed from the cages and the number of eggs laid per fruit was counted using a stereomicroscope (CARL ZEISS; Model DV4). Subsequently, the fruits were kept at room temperature and checked every 5 d to count pupae and adults. To ensure that the fruits were not infested from the field, a Styrofoam tray with fruits was placed inside a wooden cage, but without adults, as a control. This experiment was performed in 7 cages (replications), and the entire experiment was performed two times.

No-choice test. This test was performed using the procedure described for choice test, with the exception that fruit species were exposed to SWD separately, to determine whether each fruit could be an alternate host for oviposition. A total of 20 fruits of one species were placed on a tray per cage and exposed to 20 females and 20 males of SWD (5-d-old) for 24 h. Six cages (30 cm × 30 cm × 30 cm) were used (replications) for each fruit species.

Data analysis

To examine fluctuations in SWD population in the three zones during the two years (three growing seasons) of sampling, data from each sampling time were standardized to fly per trap per week (ftw) and then to fly per trap per month. With these data, population fluctuation was determined per month in the two years of study under different conditions. ANOVA analysis was performed on the data obtained from choice and no-choice tests and variables were evaluated with SAS statistical software (Ver. 9.4) using Proc Generalized Linear Mixed Models (GLIMMIX), considering each fruit species as the treatment and fruit and cage (repetition) as random effects. To fit the GLIMMIX model, the Laplace approximation method was used. A negative binomial distribution with the log link function was assumed because the data involved counts (e.g., number of eggs, pupae, and adults) (Gbur et al. 2012). Because several zero values were obtained, analysis was performed with a transformation of $x + 0.5$. A Tukey–Kramer ($\alpha = 0.05$) mean comparison was performed for each variable. Estimates and standard errors on the mean scale were obtained by selecting the *ilink* option (inverse link scale). All statistical analyses were performed using the SAS/STAT statistical software package (SAS Studio https://www.sas.com/).

Results

Experiment 1. Seasonal fluctuations in SWD population in cultivated and noncultivated areas

In the areas evaluated, a pattern of population density could be determined during the three seasons that seasonal fluctuation was followed. Higher peaks were observed at the end of spring and during summer in the three regions studied between May and July, independent of the area studied (Fig. 2a–c). Furthermore, it was possible to observe that the SWD population increased in the border areas of the commercial blackberry crop between January and March.

Catches of SWD in the commercial plots of blackberry

In the three locations evaluated, the number of SWD catches in the commercial plots of blackberry increased sharply from November to February. Furthermore, in the Tacambaro area, the fluctuation in crop populations was similar (Fig. 2c). The population increased in the months of October and November, with a peak in December and again in April and May, similar to the rest of the sampled areas. The populations tended to increase on the borders as they were reduced inside the crop. A slight increase was obtained in November and December. In Los Reyes, more adult SWD were captured in the three environments evaluated, compared with those in Ziracuaretiro and Tacambaro, where differences were observed between the sampled areas in the three environments (Fig. 2a–c).

Catches of SWD in marginal areas

More SWD adults were captured in the marginal areas in both Los Reyes and Ziracuaretiro (Fig. 2a–c) than in blackberry commercial crops. The presence of SWD in the marginal areas remained at the highest levels in Los Reyes Michoacán, from November to March and from May to July. In Ziracuaretiro, SWD was detected in November and December; in Tacambaro, the highest peaks were recorded from November to February and May to August. The Tacambaro area showed a similar pattern throughout, except in cultivated areas where a slight increase was observed in April.

SWD suzukii population density in forest areas

The forests in the three areas, the abundance of adult SWD was lower than that at sites of cultivated blackberry and marginal areas. In this area, the highest average catches were recorded in July and August of the sampled seasons and from November to December 2013 (Fig. 2a–c).

Proportion of female and male SWD captured per season

The abundance of adult SWD, as well as that of the females, varied between environments throughout the year. In particular, in winter, females were less abundant (20%) than males, when the SWD population is present in forest areas. In summer and spring, females and males were equally abundant (50% females and 50% males), with females being more abundant than males, as seen in the borders and blackberry crops in Los Reyes (Fig. 3a–c).

Experiment 2. Preference Of Wild And Noncultivated Fruits By Swd

Choice experiments

Oviposition

Data from choice experiments indicated significant differences between the number of eggs laid inside the fruits ($F = 106.16$, $P = 0.001$). SWD females oviposited the highest number of eggs in cherry and guava, compared with blackberry, grape, yellow mombin, and nance (Fig. 4a). Eggs were not found in loquat and hawthorn fruits.

Pupae per fruit

ANOVA analysis revealed significant differences between fruits ($F = 31.84$, $P < 0.001$). Guava was most suitable for pupal development, followed by black cherry. Fewer pupae developed in blackberry and yellow mombin. When the flies had choice, pupae did not develop in nance, loquat, grape, and hawthorn (Fig. 4c). These data indicate that guava is the most preferred host for SWD, followed by black cherry and yellow mombin, as it allowed the pupa to eventually become an adult.

No-choice Experiments

Oviposition

Significant differences were present between the bioassayed fruits ($F = 111.49$, $P = 0.0001$). Most oviposition was observed in blackberry (Fig. 4b), followed by black cherry, whereas no significant differences were observed between yellow mombin, guava, nance, loquat, and hawthorn. No eggs were laid on grape, indicating that it is not attractive to SWD under the conditions tested.

Pupae per fruit

Significant differences were present between the bioassayed fruits ($F = 169.48$, $P = 0.001$). Most pupae developed in blackberry, followed by yellow mombin, guava, and black cherry (Fig. 4d). In loquat, data indicated that in the absence of choice, SWD can lay eggs and even complete its development, albeit at low rates compared with blackberry, but not in hawthorn, nance, and wild grape, which were unattractive to the insect (Fig. 4d).

Discussion

The SWD population fluctuated throughout the blackberry growing season. Cultural practices, such as pruning and defoliation, and host plants surrounding the commercial plots influenced population fluctuation. Higher peaks were found at the edges of the orchards after the blackberry plantations were mowed down, in the vegetative growth and green fruit stage of development. Fluctuation peaked in forest areas in summer when the blackberry crop is not producing, but coincided with the presence of wild fruits in the ripening stage.

The peaks in summer are likely related to the end of the blackberry producing season, when packing houses close down and growers leave the crop unattended for 2 or 3 weeks before defoliating the plant again to start the new production season. During this period, population densities increase in wild fruits in the forest, sustaining the populations, until the fruits of commercial production start ripening.

These results indicate that during the low production season of blackberry, SWD populations increase in areas with alternative hosts for maintenance and increase again when commercial production of blackberry begins. Notably, SWD populations are more abundant in the margins of the crop, and increase further from the end of April until the end of July.

During this period, most of the cultivated area is in defoliation, a cultural practice used by growers, as part of the forced production system, that allows them to obtain 2–3 harvests per season. This activity takes place between November and March. Furthermore, this greater abundance could be because in marginal areas, growers do not frequently apply any products to control this pest. SWD can be protected in these areas and escape insecticides sprayed on the crops (Arno et al. 2016; Pelton et al. 2016; Evans et al. 2017; Santoiemma et al. 2018). Therefore, the marginal areas surrounding commercial blackberry provided wintering habitats; refuge during cold, warm, or dry periods; and sources of food for the growth of the SWD population (Cahenzli et al. 2018; Tonina et al. 2018).

In the forest, SWD adults were less abundant than at sites of cultivated blackberry and marginal areas. This could be because in forest areas, the reproductive success of SWD is low in available wild fruits. Compared to cultivated fruits, wild fruits could contain secondary metabolites that affect larval survival (Wink 1988). In this area, the highest average catches were recorded in July and August, which coincide with the wettest months of the year, and from November to December 2013, when the lowest temperatures are recorded. During this period, most of the cultivated areas are in the defoliation stage or vegetative growth period, but there is little variability of noncultivated fruit species that allow the insect to survive for a long time. However, in wooded areas, wild blackberry was in full production and the fruit ripening stage, which also happened with black cherry (*P. serotina* subsp. capul Mc Vaugh), which allowed the insect to sustain its population as well until the ripening of cultivated blackberry began. SWD can use olfactory cues to migrate from the adjacent forest to crop fields during fruit ripening (Keesey et al. 2015; Cahenzli et al. 2018).

In the forest, the lowest abundance of adult SWD and female SWD was observed (20% less). By contrast, in marginal areas and blackberry crops, females and males were equally abundant (50% females and 50% males), with females surpassing males, as seen in Los Reyes. Females were less abundant than males in the forest, possibly because it was winter and they were overwintering.

SWD females are less abundant in winter because they are more sensitive than males to low temperatures (Arno et al. 2016). SWD females overwinter in reproductive diapause in winter and resume their reproductive activity as soon as temperatures become favorable (~ 21°C) (Tochen et al. 2014; Arno et al. 2016). However, it is likely that in tropical and subtropical conditions, SWD populations do not enter diapause, and populations sustain over the year on wild fruits, which are always available in different regions of the state (Funes et al. 2018).

Overall, the diversity of flies (including SWD) in forested areas was higher than that in cultivated areas, which is not surprising given the intensity of pesticide application in cultivated blackberry. No attempt was made to identify the other fly species.

Studies have documented that SWD population dynamics is greatly related to season and the availability of ripe fruits in different environments (Wang et al. 2016). Tonina et al. (2018) reported that the population dynamics of SWD is related to the phenological stages of the crop; when host cherry plants were not suitable for reproduction (i.e., without ripe fruit), SWD preferred to fly to other environments (i.e. forest margin) with ripe fruits. Consistently, in this study, when cultivated blackberry do not produce in summer, the SWD population moves to the edges of orchards and forest areas to obtain ripe fruits. However, it is in adjacent areas to the blackberry crop that *D. suzukii* becomes more abundant. Wang et al. (2016), reported that in cherry orchards, the SWD population was the highest near harvest (June) and declined thereafter, as the fly population moved to other crop (e.g., citrus) or noncrop habitats (i.e., riparian systems) to obtain ripe fruits. These results are different from those of this study. In this study, the SWD population increased in blackberry crops toward the end of the production season rather than at the beginning. This greater abundance at the end of the harvest season is because at this time, the blackberry production season is ending and growers stop applying pesticides; therefore, the fly population increases on berries that are no longer harvested. Subsequently, populations tend to increase in the borders as they decrease inside the crop. Harris et al. (2014) reported that SWD migration from the crops to adjacent environments occurs in the hottest and coldest months, which is consistent with the findings of this study.

The population dynamics of SWD could also be explained by the preference of SWD for wild fruits, which are present at different times of the year (Spring–Summer: black cherry, blackberry, nance, grapes, yellow mombin, guava, and loquat; Autumn–Winter: blackberry, guava and hawthorn). Choice and no-choice tests indicated that the most attractive wild or uncultivated fruit for SWD in order of preference was wild blackberry, guava, black cherry, yellow mombin, and loquat. These fruits could contribute to the survival of SWD populations in summer when the commercial production of blackberry has paused.

In the case of nance fruit, wild grape and hawthorn were not suitable for the development of this pest. SWD can lay eggs inside or outside fruits, such as hawthorn and nance, but the larvae do not develop, probably because hawthorn has a hard consistency, which prevents larvae from feeding on the fruit (Kinjo et al. 2013).

In wild grape, eggs were laid in low proportions, but no larvae were observed, except those near the peduncle of the fruit. Interestingly, hawthorn and loquat did not receive oviposition when the fruits were together in the same cage. Therefore, these fruits could not contribute to sustain SWD populations; however, because these plants produce during the fall and winter, when commercial blackberry production is at its peak, SWD can continue its life cycle in commercial plantings. Although these fruits are not SWD hosts, they were reported to be resources with high genetic potential that must be conserved and used in a sustainable way (Garcia-Mateos et al. 2013; Guzman and Segura 2016).

Studies have reported that wild blackberry and guava are susceptible to SWD, but hawthorn, wild grape, or loquat are not, which coincides with the results of this study (Lasa et al. 2017; Elsensohn and Loeb 2018; Weißinger et al. 2019). Moreover, the susceptibility of wild blackberry (*Rubus fruticosus L*., *Rubus caesius L*., and *Rubus allegheniensis* Porter) to SWD is very high (202 adults per year) under field conditions in Italy, the Netherlands, Switzerland, and central New York (Kenis et al. 2016; Elsensohn and Loeb 2018). These results are consistent with those of this study, where the most infested fruit was wild blackberry (70%). Lasa et al. (2017) reported that under both laboratory and field conditions, 23% and 74% guava fruit was infested by SWD, respectively, in Veracruz, México. These results differ slightly from those of this study in that guava was less infested with SWD (~ 10%), considering pupae per fruit in choice and no-choice experiments. Differences between the results could be because the studies were performed under different conditions.

By contrast, it has been indicated, from both field surveys and laboratory studies, that autumn glory hawthorn showed no evidence of being susceptible to SWD. In addition, wild grape (*Vitis* spp. L.) and loquat (*E. japonica*) collected from the edges of strawberry and cherry fields, were also not susceptible to SWD (Lee et al. 2015; Renkema et al. 2018; Wang et al. 2019), as found in this study, with these fruits collected outside blackberry fields.

In the case of black cherry (*P. serotina* var. *capuli*) SWD infestation (10%) was lower than that reported for black cherry (70%) by Poyet et al. (2014), in France. However, there are no reports on the preference for yellow mombin and nance fruits.

In this study, wild blackberry, guava, and black cherry were the most preferred by SWD possibly because these fruits have higher volatile emission rates (Urbaneja-Bernat et al. 2021). These fruits possess optimal nutrients (sugar content) for the development of *D. suzukii*, better quality (firmness, pH), few defensive metabolites (Lee et al. 2011; Bellamy et al. 2013; Rodriguez et al. 2019), and attractive colors. Yellow mombin and loquat are likely to be used more frequently by SWD in the absence of higher quality host options (wild blackberry, guava, black cherry) in noncultivated areas (Diepenbrock et al. 2016; Takahara and Takahashi 2017). However, these aspects were not evaluated in this study and warrant further investigation.

The findings of this study showed that SWD exploits a wide variety of noncrop host fruits outside of blackberry crops, because of all the noncultivated fruits studied (8 species), 5 were used by SWD as hosts.

Thus, taking all studies together, and considering the growing season of each fruit, when cultivated blackberry is not in production (July–August), SWD can sustain its populations on wild blackberry growing in forest areas and noncultivated areas. Wild blackberries begin ripening from February, but peak production occurs in summer, when cultivated blackberry is not in harvest season. During this period, black cherry is in fruit ripening period. These trees grow naturally and produce substantial amounts of fruits that drop and serve as substrates for SWD to complete its cycle. Furthermore, in this period, noncultivated guavas are ripening, which are not collected and drop.

In conclusion, the results clearly indicate how SWD populations sustain themselves in blackberry production areas on wild and noncultivated fruits present in borders and forest areas surrounding commercial blackberry crops. These results should contribute to the design of a more effective, integrated and sustainable pest management program to manage this exotic pest, not only on a local scale, but also on a regional scale. A management strategy to control SWD populations would involve protecting the natural enemies of SWD in both uncultivated and cultivated areas (Ballman and Drummond 2017).

As SWD continues expanding its range globally, it will encounter new and potentially novel hosts in a range of different environments. Understanding host selection under field conditions and factors influencing that selection in detail in the laboratory will allow researchers to assess host risk and potential impact (Burrack et al. 2013).

Declarations

Author Contributions Angel Rebollar-Alviter designed and conceptualized the study, conducted data analyses, coordinated the study, and wrote the first draft versions of the paper. Ornella Barreto-Barriga participated in the writing of the original draft. Erick Flores-González collected and organized field data. Monserrat Pérez-Pérez and Ana Celestina Juárez-Gutierrez helped to conduct preference and no-preference experiments. Bernardino Ibarra-Bautista helped in field samplings and data collection. Samuel Pineda-Guillermo helped conceptualize choice and no-choice experiments and reviewed the final draft of the manuscript. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Data availability The data sets generated during and/or analyzed during the study are available from the corresponding author on reasonable request.

Ethical approval The manuscript is original and has not been previously published or considered for publication elsewhere.

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Figures

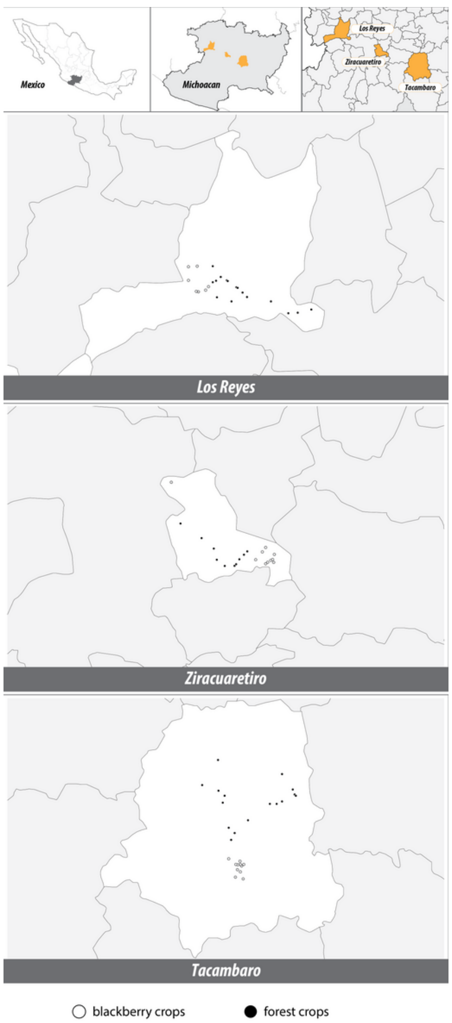

Figure 1

Map of Mexico and Michoacán state showing (above) the area of study and the location of the cultivated (blackberry crops) and noncultivatedareas (forest crops) in Los Reyes, Ziracuaretiro, and Tacambaro (Referred as zones 1, 2, and 3, respectively).

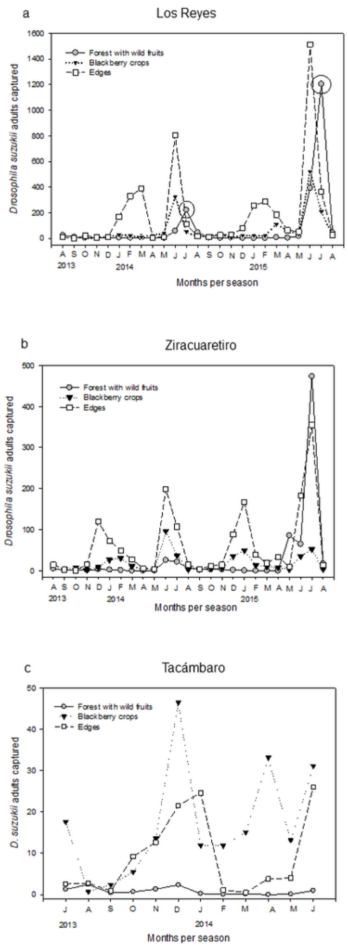

Figure 2

SWD population fluctuation (means ± SE) in cultivated and noncultivated areas in (a) Los Reyes, (b) Ziracuaretiro from August 2013 to August 2015, and (c) Tacambaro from July 2013 to July 2014. SWD: Spotted-wing Drosophila.

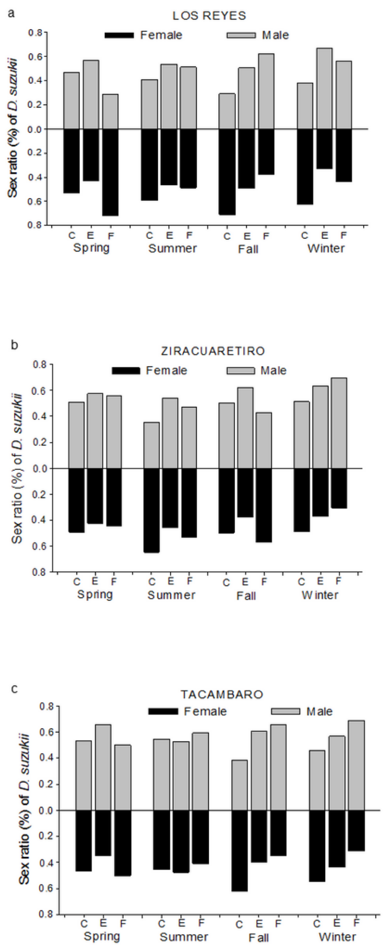

Figure 3

Percentage (means) of female and male SWD captured per season: Spring (March–May), Summer (June–September), and Fall (October–November) inside blackberry crops (c = crops) and outside (E = edges, F = forest with wild fruits) in (a) Los Reyes, (b) Ziracuaretiro,and (c) Tacambaro. SWD: Spotted-wing Drosophila.

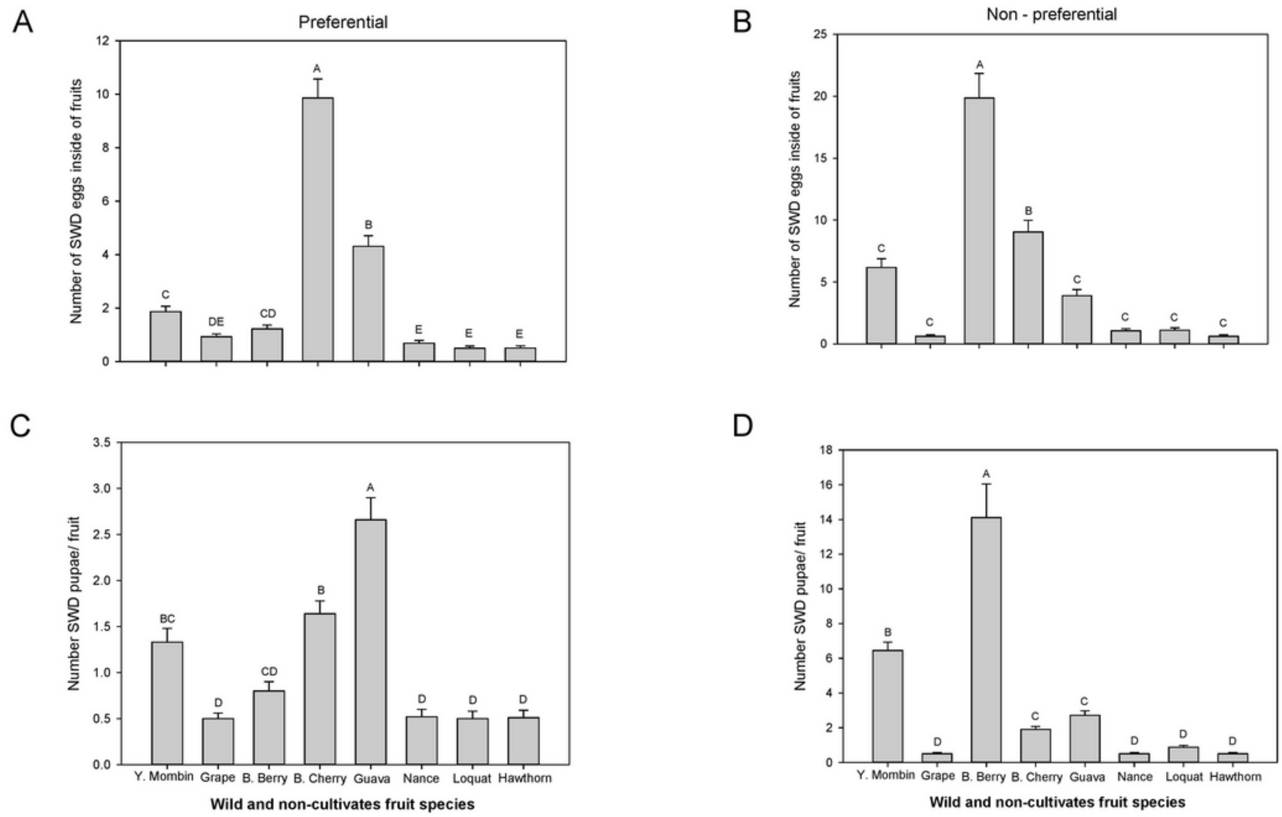

Figure 4

Oviposition and pupae in wild fruits (means ± SE) in choice and no-choice election tests (a–d). Means with the same letter are not significantly different (Tukey's test; α = 0.05).