



Trichopria drosophilae parasitizes *Drosophila suzukii* in seven common non-crop fruits

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Abstract

The invasive vinegar fly *Drosophila suzukii* not only infests and damages numerous fruit crops but also develops in many wild fruit species in semi-natural habitats. Biological control in these refuges could reduce *D. suzukii* populations and minimize their dispersal into fruit crops. We investigated parasitization of *D. suzukii* by the pupal parasitoid *Trichopria drosophilae* in seven common wild fruit species. Development and nutrient content of *D. suzukii* differed among the fruit species. Nevertheless, *T. drosophilae* significantly reduced *D. suzukii* numbers in all fruits. The development of *T. drosophilae* was affected by both the fruit species and the quality of the pupal host (size, nutrient content). In olfactometer assays, parasitoid females preferred infested fruits to an empty control and to most non-infested fruits, but spent an equal amount of time on the walking arena above the infested and non-infested fruits of *Rhamnus cathartica* and *Viscum album*. Our results show that *T. drosophilae* can utilize *D. suzukii* hosts from a variety of wild fruit species and therefore has the potential to be used as a control agent of *D. suzukii* in semi-natural habitats.

Keywords Energy budget · Host finding · Spotted-wing drosophila · Tritrophic system

Key message

- Non-crop fruits in semi-natural habitats could increase the risk of *Drosophila suzukii* infestations.
- We investigated the tritrophic effects of seven common non-crop fruits on the performance of *D. suzukii* and its native pupal parasitoid *Trichopria drosophilae*.
- The parasitoid significantly reduced *D. suzukii* numbers in all fruit species. Parasitoid offspring development was affected by the fruit species and the host quality.

- Our results underline the potential of *T. drosophilae* as a control agent of *D. suzukii* in semi-natural habitats.

Introduction

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae) is a vinegar fly of Southeast Asian origin that has invaded Europe and the Americas in the past decade (Asplen et al. 2015). Females lay their eggs in ripening fruits where larvae feed and develop. Along with the damage from secondary organisms that enter through the oviposition hole, this leads to the rapid decay of the fruits, which makes them unmarketable and results in severe losses in fruit production (Farnsworth et al. 2017; Mazzi et al. 2017).

Drosophila suzukii is a highly polyphagous organism that can develop in over 100 host plants, including many wild fruit species (Kenis et al. 2016; Lee et al. 2015; Poyet et al. 2015). The latter are found in natural and semi-natural habitats, and their fruiting seasons cover most of the year. Wild fruit species can therefore provide year-round food sources and oviposition sites for *D. suzukii* (Santoiemma et al. 2019). Control of *D. suzukii* by elimination of wild fruit species in semi-natural habitats is not an

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option because semi-natural habitats are valuable, i.e. they provide food and refuges for birds, pollinators, and natural enemies (Söderström et al. 2001; Tschumi et al. 2016). In addition, *D. suzukii* is highly mobile and able to disperse between habitats (Tait et al. 2018) and high levels of infestation have also been reported in landscapes lacking semi-natural habitats (Santoiemma et al. 2018). The Swiss agricultural landscape is characterized by small-scale mixed farming with scattered patches of semi-natural habitats (Rega et al. 2018). The control of *D. suzukii* in such a landscape where flies can regularly re-infest orchards (Hennig and Mazzi 2018; Tonina et al. 2018) is difficult. Furthermore, measures to control *D. suzukii* are often time consuming and expensive and currently depend to a large extent on the use of insecticides, which can have adverse effects on natural enemies and other non-target arthropods (Desneux et al. 2007; Haye et al. 2016).

There have been many efforts to identify native natural enemies for sustainable control of *D. suzukii* (Lee et al. 2019). Among the most promising organisms, the parasitoid *Trichopria drosophilae* Perkins (Hymenoptera: Diapriidae) successfully parasitizes the fly in laboratory experiments and, to some extent, in field trials (e.g. Wang et al. 2016; Rossi Stacconi et al. 2018, 2019; Gonzalez-Cabrera et al. 2019). It is a cosmopolitan species that is also present in the native range of *D. suzukii* (Daane et al. 2016). *Trichopria drosophilae* develops in the pupa of its hosts, i.e. at a time when fruits have already been damaged by larval feeding. It is therefore important to prevent the earlier generations of *D. suzukii* from increasing to large numbers on wild fruits by the use of parasitoids in semi-natural habitats (Rossi Stacconi et al. 2018).

In contrast to domesticated crops that have been selected for high nutrient content and reduced secondary metabolites (Chen et al. 2015), wild fruits presumably differ largely in both of these characteristics. The nutrient quality and defence compounds (toxins or other metabolites) of plants can affect the development and performance of both herbivores and their parasitoids (Ode 2006). As an endoparasitoid, *T. drosophilae* lives in very close association with its host and might be particularly affected by its host's food source. Yet, the potential effects of plant species on parasitoids of *D. suzukii* have, to our knowledge, not been studied.

In the current research, we used the tritrophic system of wild fruits–*D. suzukii*–*T. drosophilae* to investigate the effects of the fruits on *D. suzukii* and its parasitoid. We (1) tested effects of wild fruits on *D. suzukii* larval development; (2) measured the nutrient composition of emerging flies as a proxy of host quality for the parasitoids; (3) investigated the effects of wild fruits on *T. drosophilae* development, and

(4) observed the behaviour of adult parasitoid females in the proximity of infested and non-infested wild fruits.

Materials and methods

Insects

The colonies of *D. suzukii* and *T. drosophilae* were established and maintained as described in Knoll et al. (2017).

Drosophila suzukii individuals were collected in Zurich Affoltern, Switzerland, in 2013 and were since then (> 90 generations) reared on an artificial banana diet (400 g banana, 20 g agar–agar, 50 g brewer's yeast, 30 g wheat flour, 20 g saccharose, 4 g nipagin, and 1 L water) (Knoll et al. 2017). *Trichopria drosophilae* were collected with sentinel traps containing pupae of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) in Ticino, Switzerland, in 2015 and were since then (> 35 generations) reared with pupae of *D. melanogaster* that had developed on the above-mentioned diet (Knoll et al. 2017).

All insects were kept and all experiments were conducted in climate chambers at 22° C, 70% RH, and 16:8 h L:D because both *D. suzukii* and *T. drosophilae* perform well at this temperature and light regime (Wang et al. 2018; Sánchez_Ramos et al. 2019).

Wild fruit species

The following wild fruits were collected in the field for use in the experiments: *Amelanchier ovalis* Medik. (Rosaceae), *Cornus mas* L. (Cornaceae), *Lonicera xylosteum* L. (Caprifoliaceae), *Mahonia aquifolium* (Pursh) Nutt. (Berberidaceae), *Rhamnus cathartica* L. (Rhamnaceae), *Sambucus nigra* L. (Adoxaceae), and *Viscum album* L. subsp. *album* (Santalaceae). All fruits were collected from at least five plants in the vicinity of Zurich. *Viscum album* was growing on two apple trees (*Malus* sp.) in the botanical garden of Zurich. We selected the indicated wild fruit species because they are common in Europe, are known hosts for *D. suzukii*, and differ in suitability for *D. suzukii* larval development (Kenis et al. 2016; Poyet et al. 2015).

The collection dates from each fruit species are reported in Table 1. Because the *S. nigra* fruits collected on the second date were already infested with *D. suzukii* eggs, umbels still containing unripe fruits were covered with cotton mesh bags tied to the stem to prevent *D. suzukii* oviposition before the third and fourth collection dates. Undamaged, ripening to ripe fruits were used for experiments on the day of collection, except that *V. album* fruits were stored for up to 19 days at 4° C before they were used in experiments.

Table 1 Experimental setup

Fruit species	Date of <i>D. suzukii</i> oviposition ^a	Number of fruit per sample	Number of eggs per fruit	Date when a <i>T. drosophilae</i> female was added for 24 h	Number of samples per treatment
<i>Amelanchier ovalis</i>	07.06.2017	12–13	1–6	20.06.2017	5
	14.06.2017	11–13	1–6	26.06.2017	6
	21.06.2017	11	1–7	02.07.2017	6 (Total: 17)
<i>Mahonia aquifolium</i>	21.06.2017	12	1–5	02.07.2017	1
	28.06.2017	14–15	1–6	10.07.2017	9
	03.07.2017	11–14	1–6	13.07.2017	10 (Total: 20)
<i>Lonicera xylosteum</i>	27.06.2017	10–13	1–6	17.07.2017	8
	04.07.2017	10–14	1–6	16.07.2017	10
	10.07.2017	10–20	1–4	20.07.2017	8 (Total: 26)
<i>Cornus mas</i>	17.07.2017	10–16	1–8	30.07.2017	5
	26.07.2017	13–14	1–7	09.08.2017	10
	01.08.2017	12–13	1–9	15.08.2017	9 (Total: 24)
<i>Rhamnus cathartica</i>	08.08.2017	25–26	1–3	21.08.2017	8
	15.08.2017	26	1–3	28.08.2017	11 (Total: 19)
<i>Sambucus nigra</i>	18.08.2017	35–36	1–2	24.08.2017	5
	24.08.2017	35–36	1–2	01.09.2017	4
	04.09.2017	34	1–2	14.09.2017	6
	18.09.2017	34	1–2	28.09.2017	7 (Total: 22)
<i>Viscum album</i>	25.01.2018	30–36	1–3	04.02.2018	9
	05.02.2018	25–31	1–3	15.02.2018	5
	12.02.2018	25–26	1–4	22.02.2018	6 (Total: 20)

^aFruits were collected on the day of *D. suzukii* oviposition, except that *V. album* fruits were stored at 4° C for the second and third date of *D. suzukii* oviposition

Effects of wild fruit on *D. suzukii* and *T. drosophilae*

All fruits were washed with tap water and placed in 1.3-L plastic cylinders containing a moist cotton pad, a droplet of honey, and ten females and two males of *D. suzukii*. The cylinders were covered with a plastic mesh. The *D. suzukii* females were allowed to oviposit for up to 24 h until they laid the desired number of eggs per fruit. The number of eggs per fruit was repeatedly checked by counting the eggs, visible by the respiratory filaments that protruded through the fruit skin, with the aid of a stereomicroscope (Zeiss Stemi SV11). A total of 40 eggs in a varying number of fruit (between 11 and 36 for large and small fruit, respectively) were used for each experimental replicate to compensate for differences in fruit size (Table 1). The replicates were randomly assigned to one of the following two treatments: 1) SUZ: to measure the quality of *D. suzukii* that developed in the wild fruits; and 2) TRI: to measure the tritrophic effects of wild fruits and *D. suzukii* hosts on *T. drosophilae*. When the first *D. suzukii* pupae appeared, one 3- to 5- day-old naïve mated female *T. drosophilae* was added to each replicate of the TRI treatment and allowed to parasitize the *D. suzukii* pupae for 24 h, but no parasitoids were added to the replicates of the SUZ treatment.

All replicates were stored in climate chambers under the previously described conditions.

The numbers of *D. suzukii* and *T. drosophilae* offspring were recorded daily, and emergence rates of *D. suzukii* were calculated as the total number of emerged flies divided by the total number of *D. suzukii* eggs. The sex of flies in the SUZ treatment and of parasitoids was recorded, and the percentage of female parasitoid offspring was calculated by dividing the number of females by the total number of offspring, multiplied by 100.

Drosophila suzukii offspring from the SUZ treatment were collected within 24 h of emergence, immobilized with CO₂, and individually weighed (Mettler Toledo MX5, ±0.002 mg). They were then stored separately in 1.5-mL plastic tubes and frozen at –20° C until their energetic components were analysed as described in the next section. *Trichopria drosophilae* offspring from the TRI treatment were collected within 24 h of emergence and stored individually in 1.5-mL tubes filled with 96% ethanol. Developmental times of fly and parasitoid offspring were calculated as the number of days from oviposition to adult emergence. On a few occasions, the 24-h checking interval for samples was missed; for these prolonged intervals, the intermediate time was used to calculate the developmental time. These

samples were excluded from weighing. The weight of *T. drosophilae* offspring was recorded as follows: the ethanol was removed from the tubes, and a piece of filter paper was added to each tube; the open tubes were then kept at 40° C for 2 h and at room temperature for another 22 h before each parasitoid was individually weighed (Mettler Toledo MX5, ± 0.002 mg).

Energy budget analyses

To measure the protein, lipid, carbohydrate, and glycogen contents of female and male *D. suzukii* that had developed in the different wild fruit species, the method of Foray et al. (2012) was used with some minor adaptations. Details are described in the Online Resource 1.

Behavioural assays

To test whether females of *T. drosophilae* respond to infested and non-infested wild fruits, behavioural assays were conducted in a circular four-chamber olfactometer of 20 cm diameter (according to Steidle and Schöller 1997, see Online Resource 1: Fig. A1) that is divided into four equal-sized chambers. The samples containing fruit were placed in one (infested fruit only) or two opposite (infested vs. non-infested fruit) chambers. The chambers were covered with a fine metal gauze, such that the parasitoids could move freely above the samples without contacting them. An open 1.5-mL tube containing one parasitoid (a 3- to 5-day-old naïve mated female) was inserted into the centre of the olfactometer; the female parasitoids were placed in the tubes 30–60 min before the assays. The olfactometer was then covered with a glass plate and was placed in a white plastic basin and lit from above to evenly distribute the light.

Two setups were tested: (1) infested fruit vs. an empty control (no choice) and (2) infested fruit vs. non-infested fruit (choice). Infested fruit containing *D. suzukii* pupae were obtained as described above, and non-infested fruit were of the same age and batch as the infested fruit. Three to eight fruit were used per chamber, depending on fruit size. Individual parasitoid females were observed for 300 s, and the observation time began when the female left the tube. The time it walked over each chamber was recorded (Noldus, the Observer XT). If a female spent more time walking over a test chamber compared to the opposite chamber, we considered this to be a response to olfactory cues. Each female was used only once. If a female did not leave the tube for 50 s or moved for less than 150 s during the observation time, it was excluded from the analysis. After each parasitoid observation, the olfactometer

was turned by 90°. After three females were observed, the fruits were exchanged and the olfactometer was cleaned with 70% ethanol. The experiment was repeated with every fruit batch from the different collection dates. For each fruit species and setup, 18–24 females were observed except that only 11 females were observed in the choice assay with *R. cathartica*.

Statistical analyses

All analyses were conducted with R version 3.4.4 (R Core Team 2018). The number of *D. suzukii* that emerged from the wild fruits was analysed with a generalized linear model (GLM, quasipoisson distribution) with treatment (SUZ vs. TRI) and fruit species as explanatory variables. The same model was used to analyse the number of parasitoid offspring, but with fruit species and sex as explanatory variables. Weights of *D. suzukii* and parasitoid offspring were analysed with linear models (LM) with fruit species and sex as explanatory variables. A linear mixed-effects model (LMER) with collection date as a random factor and fruit species and sex as explanatory variables was used to analyse the developmental time of *D. suzukii* offspring. Developmental time of parasitoid offspring was separately analysed for each sex with a Kruskal–Wallis test because residuals were not normally distributed in fitted models. Protein and lipid contents of *D. suzukii* adults were analysed with a generalized (GLMER) and linear mixed-effects model, respectively, with assay plate as a random factor and with fruit species and sex as explanatory variables. Glycogen content was analysed separately for each sex with a Kruskal–Wallis test because the residuals were not normally distributed. Outliers (data points outside the $1.5 \times$ interquartile range) were removed from the nutrient content data before analyses. Multiple comparisons after the Kruskal–Wallis tests were run with the function *kruskalmc* (package *pgirmess*, Giraudoux 2018). For the fitted models, Tukey multiple comparisons were used as post hoc tests. If interactions between fruit species and sex were significant, post hoc analyses were run separately for each sex.

A principal component analysis (PCA) was run with the function *prcomp* (package *stats*) and was visualized with the function *ggbiplot* (package *ggbiplot*, Vu 2011). All energetic components (protein, lipid, glycogen, and carbohydrate contents) as well as weight and developmental time of *D. suzukii* offspring that emerged from wild fruits were used as explanatory variables.

The time that female parasitoids spent walking over infested fruit vs. no fruit (no choice) and over infested fruit vs. non-infested fruit (choice) was analysed with Wilcoxon signed rank tests.

Results

Drosophila suzukii development in wild fruits in the absence of *T. drosophilae*

Emergence rates and number of *D. suzukii* offspring

The average emergence rate of *D. suzukii* in replicates without parasitoids (SUZ) ranged from 8% (*R. cathartica*) to 52% (*C. mas*). Fly emergence was significantly lower from *R. cathartica* and *S. nigra* than from the other fruits (GLM followed by Tukey multiple comparisons, Fig. 1a, dark boxes, Online Resource 1: Table A1).

Weight of offspring

The analysis of the weight (and developmental time, see below) of *D. suzukii* offspring did not include data from *A. ovalis* because only a small number of flies were collected from that fruit species within 24 h of emergence. Offspring weight was significantly affected by fruit species (LM, $F(df=5)=271.65$, $p \leq 0.001$, Fig. 1b, Online Resource 1: Table A1) with females being heavier than males, ($F(df=1)=82.22$, $p \leq 0.001$). There was a significant interaction between fruit species and sex ($F(df=5)=4.97$, $p \leq 0.001$). The heaviest flies emerged from *V. album*, and the lightest from *L. xylosteum* (Tukey multiple comparisons, for females and males separately, Fig. 1b).

Developmental time of *D. suzukii* offspring

Fruit species significantly affected the developmental time of *D. suzukii* offspring (LMER with collection date as a random factor, $X^2(df=5)=3528.96$, $p \leq 0.001$, Fig. 1c). Development was longest in *C. mas* and shortest in *S. nigra* (Tukey multiple comparisons, Fig. 1c, Online Resource 1: Table A1). There was a difference between the sexes ($X^2(df=1)=6.56$, $p=0.011$), with developmental time slightly shorter for males than females, but the interaction between fruit species and sex was not significant ($X^2(df=5)=1.42$, $p=0.922$).

Energy budget

The protein, lipid, glycogen, and carbohydrate content of *D. suzukii* offspring were significantly affected by fruit species (Table 2, Online Resource 1: Figs A2–A5). Flies from *A. ovalis* were removed from the analyses. *Drosophila suzukii* protein content was highest with *V. album* and lowest with *L. xylosteum* (GLMER, $X^2(df=5)=892.76$, $p \leq 0.001$); the interaction between fruit species and sex

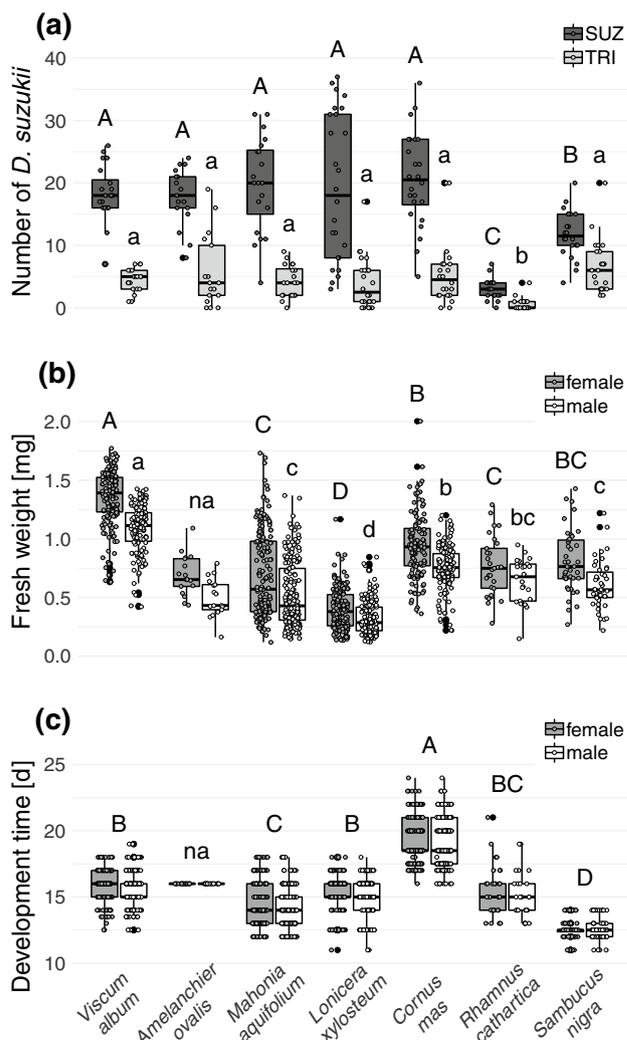


Fig. 1 *Drosophila suzukii* offspring that developed in different wild fruit species: **a** number of flies that emerged from infested fruits in the absence of *T. drosophilae* (SUZ) and in the presence of *T. drosophilae* (TRI); **b** fresh weight (mg) and **c** developmental time (days) of *D. suzukii* offspring (SUZ). Each dot represents a replicate (**a**) or an individual fly (**b**, **c**). Different letters indicate significant differences at the 5% level. **b**, **c** Offspring from *A. ovalis* were not included in the analysis (na)

was not significant ($X^2(df=5)=5.94$, $p=0.312$). Across all fruits, female flies contained more protein than male flies ($X^2(df=1)=38.19$, $p \leq 0.001$). The lipid content also differed depending on the fruit species (GLMER, $X^2(df=5)=554.31$, $p \leq 0.001$) and the sex of the flies ($X^2(df=1)=32.42$, $p \leq 0.001$), and the interaction between fruit species and sex was significant ($X^2(df=5)=18.22$, $p=0.003$). For both sexes, *D. suzukii* lipid content was highest with *V. album* and lowest with *L. xylosteum* and *S. nigra*. Glycogen content in both sexes was significantly affected by fruit species (Kruskal–Wallis; females: $H(df=5)=115.9$, $p \leq 0.001$; males: $H(df=5)=78.0$,

Table 2 Protein, lipid, glycogen, and carbohydrate contents (μg) per female and male *D. suzukii* adults that developed in different wild fruit species

Fruit species	Sex	Energy compartment (μg^{fly})										
		Protein		Lipid		Glycogen		Carbohydrate				
			<i>n</i>		<i>n</i>		<i>n</i>		<i>n</i>		<i>n</i>	
<i>Viscum album</i>	F	94.22 ± 4.25	44	A	318.95 ± 10.69	47	A	56.51 ± 3.03	43	A	6.13 ± 0.60	43
	M	81.99 ± 4.30	50		260.27 ± 9.53	50	a	45.07 ± 2.48	48	a	4.00 ± 0.32	46
<i>Amelanchier ovalis</i>	F	49.61 ± 3.44	15	na	162.64 ± 12.09	16	na	16.49 ± 1.39	14	na	3.36 ± 0.74	14
	M	43.28 ± 5.95	17		87.90 ± 9.42	17		13.83 ± 1.55	15		9.50 ± 2.44	16
<i>Mahonia aquifolium</i>	F	49.93 ± 2.33	43	B	201.20 ± 8.04	47	B	29.89 ± 1.79	43	B	3.37 ± 0.48	40
	M	42.54 ± 2.41	52		145.26 ± 5.67	50	b	27.21 ± 1.83	51	b	2.51 ± 0.38	45
<i>Lonicera xylosteum</i>	F	25.96 ± 1.53	52	C	121.17 ± 6.68	54	C	22.15 ± 1.37	53	B	1.28 ± 0.18	50
	M	23.09 ± 1.15	47		112.78 ± 7.64	48	cd	20.36 ± 1.16	46	b	0.94 ± 0.16	46
<i>Cornus mas</i>	F	41.68 ± 2.06	47	B	191.66 ± 6.73	49	B	64.52 ± 6.01	44	A	9.96 ± 1.40	46
	M	36.31 ± 1.46	44		161.51 ± 8.79	48	b	38.82 ± 2.74	46	a	5.57 ± 0.70	40
<i>Rhamnus cathartica</i>	F	51.77 ± 4.47	29	B	178.60 ± 11.89	29	B	24.44 ± 2.08	29	B	4.08 ± 0.53	26
	M	38.19 ± 3.17	23		125.37 ± 10.06	24	bc	21.23 ± 2.00	24	b	2.28 ± 0.39	22
<i>Sambucus nigra</i>	F	49.83 ± 3.32	39	B	111.29 ± 6.75	40	C	25.77 ± 1.57	39	B	1.49 ± 0.22	33
	M	35.08 ± 1.67	39		97.44 ± 6.57	42	d	22.91 ± 1.33	41	b	1.12 ± 0.21	39

Values are mean ± SE. Different letters indicate significant differences between the fruit species (within each energetic compartment) at the 5% level. Protein content was analysed with a generalized linear mixed-effects model with negative binomial distributions followed by Tukey multiple comparisons. For lipid content, a linear mixed-effects model was used, and Tukey multiple comparisons were run separately for males and females because of a significant interaction between fruit species and sex. Glycogen content was analysed separately for each sex with a Kruskal–Wallis Test and was followed by multiple comparisons using the *kruskalmc* function (package *pgirmess*). Flies that emerged from *A. ovalis* were not analysed (na). Carbohydrate content was not analysed because many flies did not contain any carbohydrates

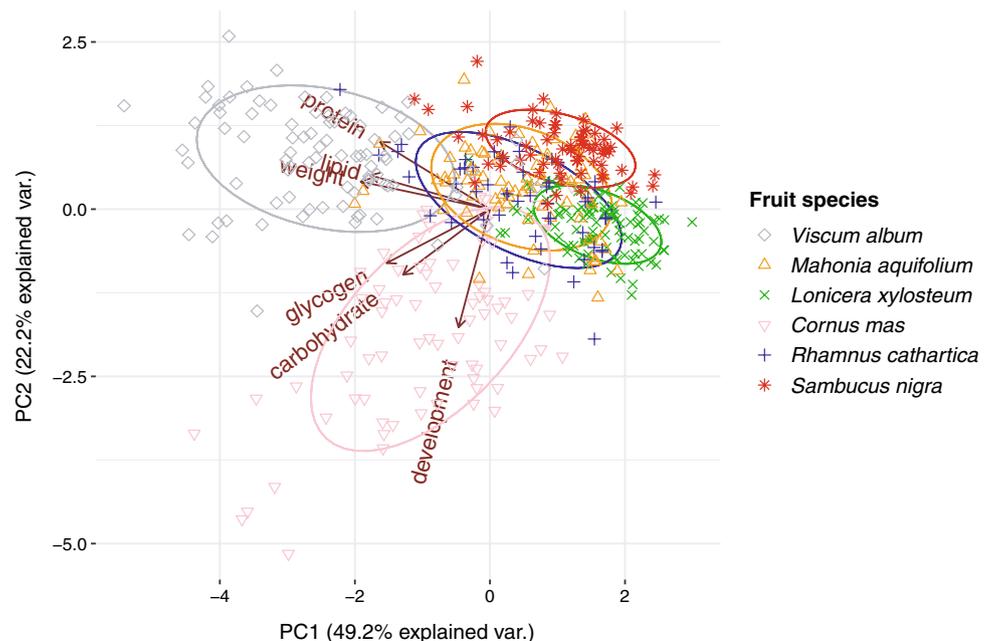
$p \leq 0.001$). For females and males, *D. suzukii* glycogen content was significantly higher with *V. album* and *C. mas* than with the other fruits.

The carbohydrate content was low in flies from most fruit species, and many flies did not contain measurable levels

of carbohydrates. As a consequence, these data were not statistically analysed.

Figure 2 shows the output of the PCA of the energy budget. The first two principal components explained 71.4% of the variation and grouped the fruit species according to

Fig. 2 Principle component analysis of energetic contents (protein, lipid, glycogen, and carbohydrate), weight, and developmental time of *D. suzukii* adults that emerged from six wild fruit species



the nutrient content, weight, and developmental time of the emerged flies. Weight was strongly linked with lipid content (and to a lesser degree with protein content) and high measures in these best characterized flies from *V. album*. Flies from *C. mas* were separated from the offspring from other fruits by their long developmental time and high carbohydrate content. Flies from *S. nigra* were mainly characterized by a short developmental time and low nutrient content. Flies from *L. xylosteum* had a low weight and low nutrient contents. Flies from *R. cathartica* and *M. aquifolium* overlapped to a large extent and had intermediate values for most characteristics.

Tritrophic system: interactions among wild fruits, *D. suzukii*, and *T. drosophilae*

Reduction in *D. suzukii* numbers

The number of *D. suzukii* offspring developing in wild fruits was significantly lower with the parasitoid (TRI) than without the parasitoid (SUZ) (GLM, $X^2(df=1) = 62.45$, $p \leq 0.001$, Fig. 1a). On average, the reduction in *D. suzukii* was 78% in *V. album*, 67% in *A. ovalis*, 80% in *M. aquifolium*, 79% in *L. xylosteum*, 76% in *C. mas*, 67% in *R. cathartica*, and 42% in *S. nigra*. The number of *D. suzukii* offspring in TRI replicates was also significantly affected by the fruit species ($X^2(df=6) = 136.45$, $p \leq 0.001$, Fig. 1a, light boxes) and by the interaction between fruit species and treatment ($X^2(df=6) = 20.66$, $p = 0.002$). In TRI, significantly fewer flies emerged from *R. cathartica* than from other fruits (Tukey multiple comparisons, Fig. 1a). The average emergence rate of *D. suzukii* in TRI ranged from 1.6% (*R. cathartica*) to 16.6% (*S. nigra*).

Parasitoid offspring

Parasitoid offspring emerged from *D. suzukii* hosts from all wild fruit species, but offspring numbers differed among fruit species (GLM with quasipoisson distribution, $X^2(df=6) = 104.43$, $p \leq 0.001$, Fig. 3a, Online Resource 1: Table A2). Significantly fewer parasitoids emerged from *R. cathartica* than from the other fruits (Tukey multiple comparisons). In all fruit species, significantly more female than male offspring were produced ($X^2(df=1) = 274.49$, $p \leq 0.001$). The percentage of parasitoid offspring that were female ranged from 72% (*V. album*) to 80% (*R. cathartica*) and was not affected by fruit species ($X^2(df=6) = 4.82$, $p = 0.568$).

Replicates in which no parasitoid offspring emerged were removed from the analysis. This was the case with the following fruit species (number of replicates): *R. cathartica* (five), *S. nigra* (four), *A. ovalis* (two), and *L. xylosteum* (one). There were no all male broods, indicating that all

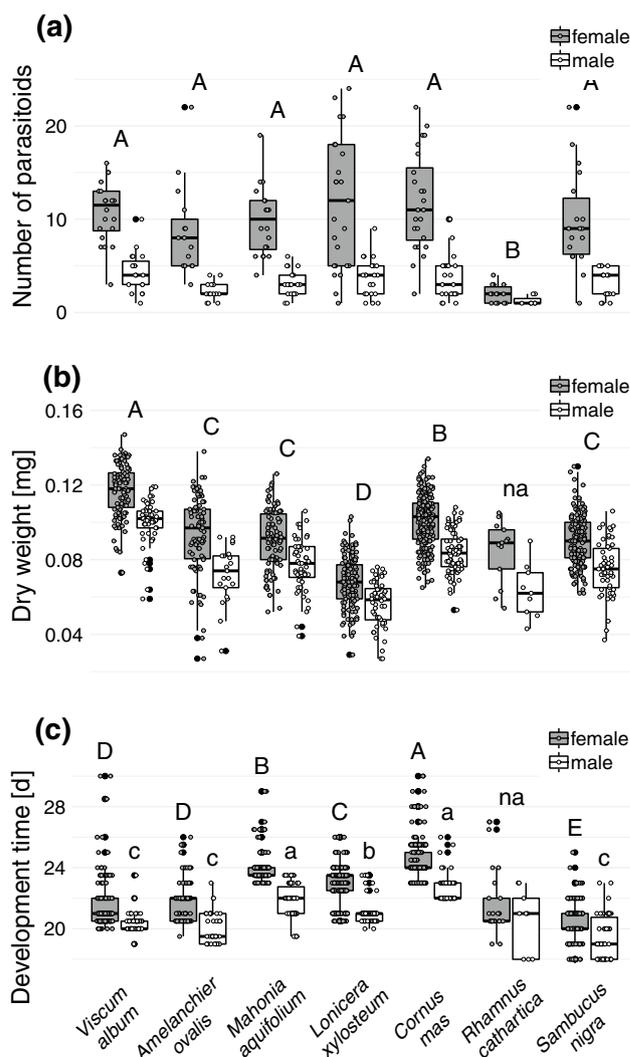


Fig. 3 *Trichopria drosophilae* offspring from pupae of *D. suzukii* that developed in different wild fruit species: **a** number of parasitoids; **b** dry weight (mg), and **c** developmental time (days). Each dot represents a replicate (**a**) or an individual parasitoid (**b**, **c**). Different letters indicate significant differences at the 5% level. Weight and developmental time were not analysed for *R. cathartica* because only a few parasitoids emerged

parasitoid females added at the start of the experiment were mated.

Weight of parasitoid offspring

The dry weight of parasitoid offspring differed significantly according to the fruit species in which their hosts had developed (LM, $F(df=5) = 207.60$, $p \leq 0.001$, Fig. 3b, Online Resource 1: Table A2). Female parasitoids were significantly heavier than males ($F(df=1) = 267.17$, $p \leq 0.001$), and there was no interaction between fruit species and sex ($F(df=5) = 1.32$, $p \leq 0.253$). The heaviest

parasitoids emerged from *D. suzukii* in *V. album*, and the lightest ones from *D. suzukii* in *L. xylosteum* (Tukey post hoc test, Fig. 3b). *R. cathartica* was not included in the analysis of weight (and developmental time, see below) because only very few parasitoids emerged from these fruit.

Developmental time of parasitoid offspring

Developmental time of female parasitoids was longest in *D. suzukii* from *C. mas* followed by *D. suzukii* from *M. aquifolium* and was shortest in *D. suzukii* from *S. nigra* (Kruskal–Wallis, females: $H(df=5) = 796.5$, $p \leq 0.001$, followed by kruskalmc post hoc test, Fig. 3c, Online Resource 1: Table A2). Males developed faster than females, and the differences between the fruit species were similar to those for females but less pronounced (males: $H(df=5) = 243.14$, $p \leq 0.001$, Fig. 3c).

Behavioural assays

Parasitoid females walked significantly longer over the olfactometer chambers containing any fruits infested by *D. suzukii* than over chambers without fruits (Wilcoxon signed rank test, Fig. 4a).

When offered infested vs. non-infested fruit, parasitoid females walked significantly longer over infested than over non-infested fruit in five of the seven tested wild fruit species, but the duration was not significantly different with *V. album* or *S. nigra* (Wilcoxon signed rank test, Fig. 4b).

Discussion

Our results show that *T. drosophilae* parasitizes *D. suzukii* and significantly reduces fly numbers in a variety of common wild fruits. However, the performance of both the fly host and the parasitoid significantly differed among the fruits.

Effects of wild fruits on *D. suzukii* development

The development of herbivorous insects can be affected by the nutrients available in their host plants but also by secondary plant compounds (Gols 2014). The latter may function as feeding deterrents, digestion inhibitors, or toxins (Schoonhoven et al. 2005). The number, weight, and developmental time of *D. suzukii* offspring were affected by the species of wild fruit. The most suitable fruit for *D. suzukii* development was *V. album*, i.e. the flies that emerged from *V. album* were the heaviest and had a relatively short developmental time. *Viscum album* bears fruit from winter to early spring, a time when most insects have not yet emerged, which probably explains why only a few insect species are associated with *V. album* (Briggs 2011). Consequently, *V. album* may not have evolved strong insect defences.

Considering offspring weight, *C. mas* was also a good food source for *D. suzukii* larvae, but the flies took significantly longer to develop on *C. mas* fruit than on all of the other fruits. The slow development could be attributed to iridoid glycosides in *C. mas* (Deng et al. 2013), which have been reported to prolong the development of insect larvae (Dobler et al. 2011).

The lightest *D. suzukii* emerged from *L. xylosteum*. Plant defences could be responsible for this because *Lonicera* species generally contain varying amounts of phenolics and iridoid glycosides that act as defence against leaf herbivores,

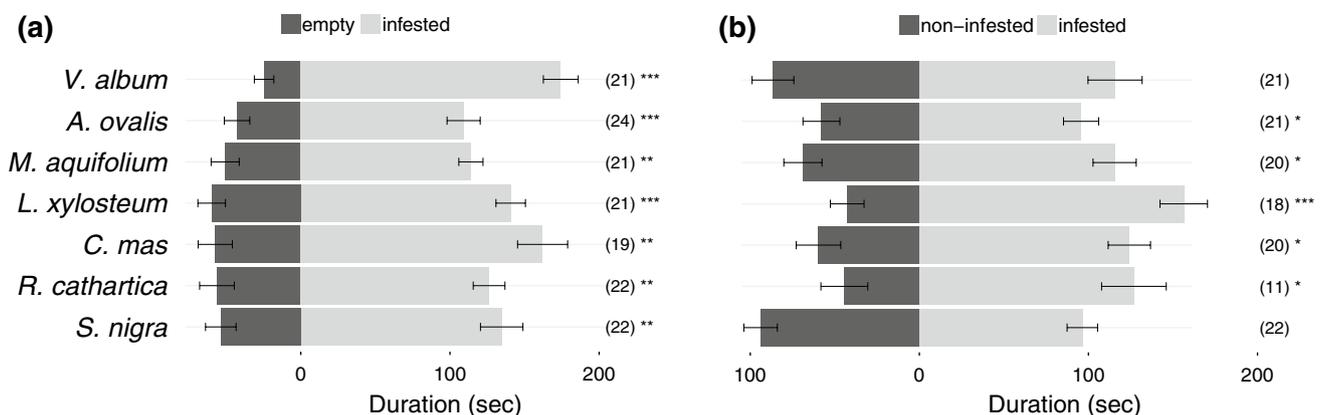


Fig. 4 Length of time that parasitoid females spent walking over olfactometer chambers with (a) no fruits vs. infested fruits, and over chambers with (b) non-infested fruits vs. infested fruits. Values are

mean \pm SE. The sample size is indicated in the brackets. *, **, and *** indicate a significant difference at the 5, 1, and 0.1% level, respectively (Wilcoxon signed rank tests)

and because *L. xylosteum* is particularly well protected against herbivores (Lieurance et al. 2015). However, we cannot rule out an influence of larval competition in samples of this fruit because many *L. xylosteum* fruits used in our experiment were already infested by the fruit fly *Rhagoletis cerasi* (Linnaeus) (Diptera: Tephritidae).

Significantly fewer flies emerged from *S. nigra* than from the other fruits (except *R. cathartica*). This is consistent with the results of the laboratory assays of Poyet et al. (2015), who reported a low suitability of *S. nigra* fruit for *D. suzukii*. Lee et al. (2015), however, observed a very low to high *D. suzukii* infestation in field-collected *S. nigra* fruit in the USA and Kenis et al. (2016) reported a high level of infestation in *S. nigra* fruit collected in Europe. Only a few insect species are associated with *S. nigra*, which has been attributed to secondary metabolites (i.e. lectins) (Atkinson and Atkinson 2002) that could also have affected the survival of *D. suzukii* larvae in our study. Although *S. nigra* fruits were smaller than the other fruits in the current study, the flies that emerged were of intermediate weight and thus did not appear to have suffered from food limitation.

Offspring that emerged from *M. aquifolium* and *R. cathartica* were intermediate in weight and developmental time. However, only very few flies emerged from *R. cathartica*. Poyet et al. (2015) observed that although some *D. suzukii* larvae developed in *R. cathartica* fruit, no adult offspring emerged. *Rhamnus cathartica* might therefore act as a natural sink, attracting *D. suzukii* females to lay eggs without supporting larval development. The low suitability of these fruit might be due to high contents of the secondary metabolite emodin, which has insecticidal properties (Izhaki 2002). Alternatively, emergence of adults from *R. cathartica* fruit may have been limited by the desiccation of the fruit and the fruit's hard skin (personal observation).

Across all wild fruits, *D. suzukii* weight and developmental time were not correlated. Both the heaviest offspring (from *V. album*) and the lightest offspring (from *L. xylosteum*) had intermediate developmental times, while the flies with the fastest development (in *S. nigra*) and slowest development (in *C. mas*) were intermediate in weight. In addition, the weights of male and female flies were differently affected by the fruit species as indicated by the significant interaction between fruit species and sex. During larval development in fruit flies, the allocation of nutrients to reproduction is assumed to differ between the sexes (Kaspi et al. 2002), and this could also be the case for *D. suzukii*.

Nutrient contents in *D. suzukii* offspring from wild fruits

Lipids, proteins, glycogen, and carbohydrates are the key energetic resources that insects need for maintenance and reproduction (Rivero and Casas 1999; Jervis et al. 2008).

We measured the nutrient contents in *D. suzukii* offspring that emerged from wild fruits as a proxy of the quality of the flies as hosts for the parasitoids. Protein and lipid contents were highest in flies from *V. album*. Fruit from *L. xylosteum*, in contrast, produced flies with a low lipid content and with the lowest protein content. Most *D. suzukii* offspring from the other wild fruits contained intermediate levels of nutrients. The nutrient levels measured in our study were equal or higher than those reported in other studies. For example, freshly emerged *D. suzukii* that were reared on an artificial diet contained about 24 µg of lipids, 5 µg of glycogen, and 10 µg of total sugars (Tochen et al. 2016). Adult *D. suzukii* that emerged from an artificial diet and that fed on blossoms, fruit, or sugars contained 21–42 µg of lipids, 5–88 µg of glycogen, and 4–186 µg of carbohydrates (Wong et al. 2018). Relative to these earlier studies, the lipid contents in our study were higher, ranging from 88 to 319 µg, and glycogen and carbohydrate contents were similar (14–64 µg and 1–10 µg, respectively). We did not find comparable protein measurements for *D. suzukii* in the literature, but the protein content in *D. melanogaster* males was 67 µg in a previous report (Oudman et al. 1992) compared to 23–94 µg in our study. The measurement methods differed, however, in the cited studies vs. the current study, which may have contributed to differences in results.

The PCA analysis revealed that *D. suzukii* weight and lipid content were strongly linked. Lipids play an important role in insect metabolism and are utilized for flight, egg production, and survival of starvation (Arrese and Soulages 2010). The nutrient content of *D. suzukii* adults alone does not explain the variation in weight and developmental time between the fruit species. Secondary compounds in the fruit species probably contributed to this variation and may have interacted with dietary microbes that apparently affect *D. suzukii* development (Gols 2014; Bing et al. 2018).

Tritrophic effects of wild fruits and host quality on *T. drosophilae*

Trichopria drosophilae reduced the number of *D. suzukii* in all of the tested wild fruit species. Based on the emergence rate of *D. suzukii*, the parasitoids had about 20 pupae available for parasitism in all fruits except *S. nigra* and *R. cathartica*. Because *T. drosophilae* females carry > 40 mature eggs within 4 h of emergence and can parasitize at least 20 hosts within 24 h (Wang et al. 2016; Kaçar et al. 2017), we cannot rule out the possibility that some of the female parasitoids in our assays were host-limited.

The host plant of herbivores can affect natural enemies directly via plant secondary compounds or indirectly via host quality (Ode 2019). In our experiments, the weights of the parasitoid offspring were related to the weights of the *D. suzukii* hosts. This is common in solitary pupal

parasitoids, for which the available nutrients are limited to the host pupa (Harvey 2005). Developmental time of the parasitoid, in contrast, was only partially linked to the developmental time of *D. suzukii*. While developmental times of both flies and parasitoids were fastest in *S. nigra* fruits and slowest in *C. mas* fruits, developmental times differed between flies and parasitoids in the other fruits. Growth rates of *T. drosophilae* also varied depending on the fruits: parasitoids that emerged from the heaviest *D. suzukii* hosts in *V. album* were among the fastest to develop, indicating good quality hosts. Conversely, parasitoids that emerged from the lightest hosts (from *L. xylosteum*) developed relatively slowly, which could be attributed to host quality and/or effects of secondary plant metabolites.

At the adult stage, most parasitoid species including *T. drosophilae* lack the ability to store lipids (Visser and Ellers 2008). In addition, *T. drosophilae* adults do not resorb eggs or feed on hosts and only consume sugar-based diets (Carton et al. 1986; Ellers et al. 2011). Therefore, lipids and proteins are exclusively acquired during larval development, and hosts with high lipid and protein contents should improve the fitness of adult parasitoids (Jervis et al. 2008). Because lipid and protein contents were relatively high in *D. suzukii* from all fruits, the quality of hosts in all fruits was probably sufficient for *T. drosophilae*. Indeed, the percentage of female parasitoid offspring was high in all fruit species (72–80%), and a high percentage of females indicates good host quality (Benelli et al. 2017). Future studies should assess whether good host quality also leads to *T. drosophilae* females with high fecundity.

Behavioural assays with *T. drosophilae*

The ability of a parasitoid to find its hosts will obviously affect its efficacy as a biological control agent and is often mediated by volatile compounds emitted by the host food (plants), the host, and/or an interaction of the two (Vet and Dicke 1992). *Trichopria drosophilae* parasitizes pupae of *Drosophila* that are located in decaying, fermenting fruits. Our results show, that infested fruits elicit a response in the parasitoid females. In the olfactometer, females preferred to walk over chambers containing infested fruits as compared to empty controls. In most cases they preferred infested fruits to non-infested fruits indicating that fruit odours alone are not sufficient for host location in these fruits. This is in line with results obtained from a larval parasitoid of *Drosophila* that also preferred *D. suzukii*-infested to non-infested fruits (Biondi et al. 2017). Host emitted volatiles are not likely to play a major role in *T. drosophilae* host location since they depend on antennal contact to recognize the host and oviposit into it (Romani et al. 2002). Therefore, the cues eliciting the responses in our assay probably resulted from the interaction of the host food, the host, and host-associated

microorganisms (Vet & Groenewold 1990). The specific volatiles that play a role in host location are not known yet and should be analysed in further studies. In *V. album* and *S. nigra*, however, *T. drosophilae* females showed no preference for infested over non-infested fruit, and their host location ability might thus be impaired in these fruits. Given that *V. album* appears to be a high quality food source for *D. suzukii* and the fly can reproduce and develop at low temperatures (Tochen et al. 2014; Tonina et al. 2016), *V. album* could serve as an early season oviposition site (Briem et al. 2016). The ability of *T. drosophilae* to locate *D. suzukii* in *V. album* fruits would therefore be desirable.

Conclusions

Drosophila suzukii shows a high level of plasticity when developing in different fruit species. *Trichopria drosophilae* can clearly utilize *D. suzukii* hosts in all of the tested wild fruits even though the quality of *D. suzukii* as a host for the parasitoid varied among the fruit species. To target the *D. suzukii* populations in semi-natural habitats near crops, researchers should investigate the host finding and parasitization efficacy of *T. drosophilae* in those habitats.

Author contributions

JC, JR, and SW conceived and designed research; SW and SB collected the data; SW led the analysis and writing of the manuscript. All authors contributed to the drafts and approved the manuscript.

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Data availability Data is available at figshare: <https://doi.org/10.6084/m9.figshare.11317961>.

Compliance with ethical standards

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

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