

Understanding *Trichopria drosophilae* performance in laboratory conditions

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Abstract

The recent worldwide interest in the invasive pest *Drosophila suzukii* (Matsumura) has risen the interest to its biological control agents. Among the parasitoids, *Trichopria drosophilae* (Perkins) is a cosmopolitan species found in association with the pest in different countries. As different populations of the parasitoid can adapt to different geographical areas, this study is focused to deepen the effect of temperature and host on an Italian population. The performance of *T. drosophilae* was studied under controlled conditions at seven constant temperatures (5–40 °C), and on two hosts, the native *Drosophila melanogaster* (Meigen) and the invasive *D. suzukii*. Information on survival, oviposition and sex ratio were acquired for all temperatures. A GLM analysis showed the influence of temperature and host species on the biological parameters analysed. The best performance in terms of fertility and offspring production were obtained between 25 and 30 °C, while the upper thermal limit for the adult survival was identified at 40 °C. Finally, two equations useful to help predictive models have been obtained. We conclude that *T. drosophilae* has the potential to be efficiently mass-reared at 25 °C.

Key words: biological control, parasitoid, *Drosophila suzukii*, *Drosophila melanogaster*, offspring.

Introduction

Drosophila suzukii (Matsumura) (Diptera Drosophilidae), also known as the Spotted Wing Drosophila (SWD), is native to South East Asia and it represents one of the most destructive pests of small and stone fruits which has invaded North America and European countries since 2008 (Walsh *et al.*, 2011; Cini *et al.*, 2012). Unlike many drosophilids, *D. suzukii* females can lay eggs in ripening fruits pre-harvest, and larvae feed on the pulp inside the fruits reducing their quality and making them unmarketable. Insect invasiveness and its quickly spreading in the new invaded areas are due to egg-laying inside unripe cane fruits and stone fruits, to high reproductive capability, to numerous overlapping generations per year, and to a limited presence of natural enemies (Grassi *et al.*, 2012; Chabert *et al.*, 2012; Mazzetto *et al.*, 2015; Haye *et al.*, 2016). Since its introduction, many studies have been conducted, and many control strategies have been adapted in order to reduce its economic damage, especially on small fruits and cherries. Among control strategies, the use of natural enemies, in particular parasitoids, could reduce the dangerousness of *D. suzukii* by limiting its population. Different parasitoids belonging to four Hymenoptera families (Braconidae, Diapriidae, Figitidae and Pteromalidae) have been reported in association with *D. suzukii* in its native area, and also in invaded countries (Rossi Stacconi *et al.*, 2013; Miller *et al.*, 2015; Daane *et al.*, 2016; Mazzetto *et al.*, 2016; Knoll *et al.*, 2017). Among parasitoids, *Trichopria drosophilae* (Perkins) (Hymenoptera Diapriidae) has been reported several times in North America and Europe, and proved to be effective to attack either *D. suzukii* or *D. melanogaster* (Meigen) (Chabert *et al.*, 2012; Rossi Stacconi *et al.*, 2015; Gabarra *et al.*, 2015; Mazzetto *et al.*, 2016).

T. drosophilae is an idiobiont endoparasitoid special-

ized on frugivorous Drosophilidae (Fleury *et al.*, 2009; Chabert *et al.*, 2012; Wang *et al.*, 2016). The species attacks and develops in puparia of the common fruit flies, and lays egg into the hemocoel of the host (Carton *et al.*, 1986). Currently, this species is considered one of the best candidate parasitoids for biological control of *D. suzukii*. Field trials in Italy showed that *T. drosophilae* is widely spread all over the country, and has the potential for augmentative biological control of *D. suzukii* in open-field environment (Rossi Stacconi *et al.*, 2018; Mazzetto *et al.*, 2016). Laboratory studies were conducted both in Italy and in the USA in order to deepen the knowledge of the effects of temperature on the wasp performance. Rossi Stacconi *et al.* (2017) evaluated the performance of *T. drosophilae* at 15, 20, 25, 30 and 35 °C, while Wang *et al.* (2018) studied development and survival at 12, 16, 20, 24, 28, 30 and 31 °C. *T. drosophilae* was able to parasitize *D. suzukii* in a wide range of temperature (up to 35°C), with the best performance from 20 to 25 °C (Rossi Stacconi *et al.*, 2017). At lower temperatures (up to 15 °C), the species reported parasitization activity unlike other wasp species [e.g. *Pachycrepoideus vindemiae* (Rondani) and *Leptopilina heterotoma* Thomson]. Wang *et al.* (2018) reported similar data in California, but the wasp revealed a lower tolerance to high temperatures with no survival at or above 29.6 °C. Different results may suggest different adaptation of a local population. Also Chabert *et al.* (2012) found significant differences between populations with regard to both the degree of infestation and the success of parasitism.

As the temperature can greatly influence the biology and population of pest and parasitoid, and different populations of *T. drosophilae* could show different performance in relation to the temperature and the host, the purpose of the present research is to improve knowledge on this species with particular attention to an Italian

population. In detail, the objective is to update information on the thermal limits and on the development and fertility at different temperatures in association with *D. suzukii* and *D. melanogaster*. The parasitoid population used in this research was originally collected in Northern Italy, and was also used for field augmentative trials in Rossi Stacconi *et al.* (2018).

Materials and methods

Stock population

The colonies of *D. suzukii* and *D. melanogaster* were started from specimens emerged from raspberries and blackberries collected in Montanaso Lombardo, Lodi province, Northern Italy during summer 2013 (43°33'65.69"N 9°48'06.14"E). *T. drosophilae* colony was started from specimens emerged from infested fruit collected from the same location in Montanaso Lombardo in 2014.

Stock cultures of drosophilids and *T. drosophilae* were held in incubators under the condition of 25 ± 1 °C, L:D 16:8 and RH $70 \pm 5\%$. Both colonies of drosophilids were reared on a maize flour based artificial diet in 50 mL plastic centrifuge tubes (height 12 cm, diameter 3 cm). The artificial diet contained 1000 mL water, 15 g L⁻¹ yeast and 21 g L⁻¹ agar, supplemented with 90 g L⁻¹ sucrose, 180 g L⁻¹ semolina flour, 15 g L⁻¹ raisin, and 1.5 g L⁻¹ methyl 4-hydroxybenzoate (Regent Plus® >99.0% crystalline Sigma-Aldrich). Twice a week, fly adults were inserted into plastic tubes containing 25 mL of the diet, closed at the top by a fine mesh, and maintained for 2-3 days to obtain oviposition.

T. drosophilae colonies were reared separately on *D. suzukii* and *D. melanogaster*. Both populations were maintained on the artificial diet infested by drosophilid larvae and pupae. Adult parasitoids were removed after two weeks just before the new generation emergence.

Experimental temperatures

Development and reproductive parameters of *T. drosophilae* were studied at seven constant temperatures in controlled climate chambers: 5 ± 0.5 °C, 15 ± 0.5 °C, 20 ± 0.5 °C, 25 ± 0.5 °C, 30 ± 0.5 °C, 35 ± 0.5 °C and 40 ± 0.5 °C. The same relative humidity ($70 \pm 5\%$ RH) and photoperiod (L:D 16:8) were used for all treatments. Even if there is no evidence of any diapause for this parasitoid, the choice of a long photoperiod was to avoid diapause induction.

Adult survival and lifespan of *T. drosophilae*

Adult survival and lifespan of *T. drosophilae* were examined separately on adults emerged from *D. suzukii* and *D. melanogaster*. Ten one-day-old adults were held in plastic aerated transparent boxes (750 mL). Five replicates were studied at each temperature for males and females, separately. All adults were fed with 1:1 sugar-cane-water solution provided *ad libitum*. Containers were observed daily to check specimen survival. The mean death rate (DR₅₀) expressed as the time in which half of the population died, and the maximum period of survival at each temperature were calculated.

Development and offspring of *T. drosophilae*

T. drosophilae offspring production was tested on *D. suzukii* and *D. melanogaster* with 10 replicates per species at each temperature. Each replicate consisted of a couple of one-day-old *T. drosophilae* inserted in the plastic centrifuge tube (height 12 cm, diameter 3 cm) with the artificial diet previously infested by drosophilids (as described in the stock population paragraph). Tubes containing at least one hundred larvae were selected for the trial. Every week each couple of *T. drosophilae* was removed from the tube and transferred into a new one with the same characteristics, until female death. After adult removal, tubes were daily checked to verify the presence of newly emerged parasitoids, which were removed, counted and sexed. Tubes were discarded when emergence stopped for more than a week. Total number of offspring per female and sex ratio were calculated. As *T. drosophilae* is able to oviposit the day after emergence (Wang *et al.*, 2016), starting day of emergence (SDE) was considered as the time from parent introduction into the tubes to the first offspring emergence. The mean SDE value was obtained considering the first adult offspring emergence in each replicate. Mean developmental time was calculated for males and females emerged in each tube during the whole experimental period at each temperatures.

Data analyses

SPSS® Statistic (Version 24 for Windows, SPSS Inc. Chicago, IL, USA) was used to analyse all data. To test significant differences (ANOVA test), prior to analyses, all data were examined with the Levene's test for homogenous distribution, and with Shapiro-Wilk test for normal distribution. Log transformation and non-parametric tests were used if necessary. A general linear model (GLM) was used to test the effect of temperatures and hosts on *T. drosophilae* fertility, and to evaluate the interaction between these two parameters. Tukey-Kramer's Honestly Significant Difference (HSD) multiple comparisons test was applied to compare mean values. Kaplan-Meier survival curve analysis (Kaplan and Meier, 1958) was used to compare the survival rate among different experimental groups (host species, sex and temperatures) in adults; Log rank, Breslow and Tarone-Ware tests were then applied to evaluate differences. A value of $P < 0.05$ was considered statistically significant.

Starting from mean developmental time and mean offspring production per temperature, regression curves were interpolated to find equations representing the development and the reproduction capability of *T. drosophilae* at different temperatures.

Results

Adult survival and lifespan

T. drosophilae adults could survive at temperatures between 5 °C and 35 °C for several days, while at 40 °C they lived less than 4 hours (table 1).

Adult survival rate varied according to temperature, sex and host species (table 1). The log rank, Breslow,

Table 1. Longevity of *T. drosophilae* adults emerged from *D. suzukii* and *D. melanogaster* at seven temperatures expressed as the mean survival period and as the day of death of the half of the population (DR₅₀).

Temp. (°C)	Host											
	<i>D. suzukii</i>						<i>D. melanogaster</i>					
	Mean period (days ± SE)		DR ₅₀		Maximum		Mean period (days ± SE)		DR ₅₀		Maximum	
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
5	46.80 ± 2.88	82.25 ± 5.41	37	64	139	196	81.7 ± 5.5	75.26 ± 6.16	80	72	189	169
15	54.40 ± 4.68	60.36 ± 3.78	40	68	126	101	39.23 ± 2.22	50.76 ± 3.85	38	43	74	94
20	33.01 ± 1.0	44.76 ± 0.86	32	40	59	90	30.00 ± 1.3	42.01 ± 1.9	28	35	50	71
25	23.12 ± 1.13	25.77 ± 1.65	25	24	37	64	21.04 ± 1.37	35.36 ± 2.13	21	40	47	59
30	13.02 ± 0.87	20.23 ± 0.79	11	21	24	30	16.20 ± 1.21	19.92 ± 1.24	16	20	34	34
35	7.64 ± 0.43	8.2 ± 0.46	10	8	14	20	5.68 ± 0.34	5.79 ± 0.23	1	5	13	10
40	< 4h	< 4h	< 4h	< 4h	-	-	< 4h	< 4h	< 4h	< 4h	-	-

and Tarone-Ware statistics evidenced significant differences among adult survival at different temperatures belonging to the same sex and emerging from the same host species (log-rank $P < 0.001$, Breslow $P < 0.001$, Tarone-Ware $P < 0.001$ for all data). Female and male longevity declined gradually with the increasing temperatures until 35 °C. Maximum survival of *T. drosophilae* emerged from *D. suzukii* ranged from 20 to 196 days in females, and from 14 to 139 days in males at 35 °C and 5 °C, respectively. Females emerged from *D. melanogaster* survived at the maximum from 10 to 169 days, and males from 13 to 189 days at 35 °C and 5 °C, respectively. Kaplan-Meier statistic evidenced that females obtained from both host species survived significantly longer than males (Log rank, Breslow, and Tarone-Ware with $P < 0.05$); an exception was for the specimens emerged from *D. melanogaster* at 5 °C and 30 °C where the survivorship of both sexes was the same (Log rank, Breslow, and Tarone-Ware with $P > 0.05$).

The same test applied to compare the survival of females emerged from *D. suzukii* to those emerged from *D. melanogaster* showed similar survival at all temperatures (Log rank, Breslow, and Tarone-Ware with $P > 0.05$).

Numbers of offspring produced on presented hosts

Offsprings of *T. drosophilae* were obtained from 15 °C to 30 °C on *D. suzukii* and *D. melanogaster*. No progeny was obtained at 5 °C, 35 °C and 40 °C (table 2).

According to GLM, host species did not influence total offspring ($F = 1.094$; $df = 1, 63$; $P = 0.300$) while influenced female offspring ($F = 2.971$; $df = 1, 63$; $P = 0.050$). The sex ratio of *T. drosophilae* from *D. suzukii* was close to 1:1 at all temperatures, while on *D. melanogaster* was 1:1 only at 30 °C (table 2). On the contrary, temperatures significantly affected total offspring ($F = 6.656$; $df = 3, 61$; $P = 0.001$) but did not influence the number of female offspring ($F = 2.054$; $df = 3, 61$; $P = 0.117$). Finally, the interaction between host species and temperature did not result in a significant difference ($F = 0.163$; $df = 3, 63$; $P = 0.921$).

The highest number of offspring emerged from both host species at 25 °C (74.62 ± 24.13 and 70.87 ± 12.33 offsprings from *D. suzukii* and *D. melanogaster*, respectively).

The starting day of emergence (SDE) significantly diminished ($F = 836.48$; $df = 3$; $P < 0.001$) when the temperature increased from 52.33 ± 1.16 to 16.10 ± 0.14 days on *D. suzukii* and from 64.27 ± 1.14 to 15.85 ± 0.18 days on *D. melanogaster*. The comparison of the mean starting day of emergence from the two host species at the same temperature did not result in a significant difference (table 2).

As shown in table 2, the oviposition period shortened with increasing temperature, passing from seven weeks at 15 °C to two weeks at 30 °C on *D. suzukii* and from three weeks to two weeks on *D. melanogaster*.

To evaluate the trend of offspring production, two

Table 2. Mean (± SE) number of progeny per female, daily emergence, starting day of emergence (SDE), 50% and 90% of adult emergence (Et₅₀ and Et₉₀), % of female offspring (± SE), and maximum reproductive period of mated *T. drosophilae* on two different hosts *D. suzukii* and *D. melanogaster* ($n = 10$ for each temperature). Different letters mean significant differences (ANOVA, $P < 0.05$).

Host	Temperature (°C)	Mean progeny/female	Mean of daily emergence	SDE (day)	Et ₅₀ (day)	Et ₉₀ (day)	% female offspring	Maximum reproductive period
<i>D. suzukii</i>	15	30.86±4.88 a	0.36±0.17 a	52.33±1.16 c	28	49	51.12±7.71 a	7 weeks
<i>D. suzukii</i>	20	44.01±6.88 a	0.73±0.24 a	28.99±1.21 b	8	19	51.27±4.66 a	4 weeks
<i>D. suzukii</i>	25	74.62±24.13 b	1.57±0.24 a	16.28±0.59 a	10	15	53.92±5.33 a	3 weeks
<i>D. suzukii</i>	30	61.45±11.33 b	3.39±0.32 b	16.10±0.14 a	6	11	49.38±7.06 a	2 weeks
<i>D. melanogaster</i>	15	26.00±6.03 a	4.11±0.07 b	64.27±1.14 c	15	31	29.68±7.09 b	3 weeks
<i>D. melanogaster</i>	20	38.39±7.58 a	0.48±0.33 a	31.10±0.25 b	4	12	29.13±6.00 b	3 weeks
<i>D. melanogaster</i>	25	70.87±12.33 b	1.27±0.27 a	18.72±0.96 a	5	11	28.82±14.65 b	2 weeks
<i>D. melanogaster</i>	30	57.78±11.24 b	1.82±0.30 a	15.85±0.18 a	3	9	52.15±7.42 a	2 weeks

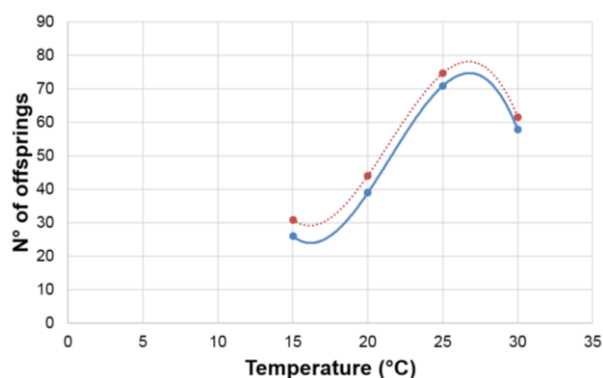


Figure 1. Trend of the mean offspring production at different temperatures on *D. suzukii* (dotted line) and *D. melanogaster* (solid line).

similar regression lines were obtained interpolating the mean value of total offspring per female at each temperature. The equation obtained for *D. suzukii* was $y = -0.0817x^3 + 5.2484x^2 - 105.53x + 708.57$, and the one for *D. melanogaster* was $y = -0.0854x^3 + 5.5034x^2 - 111.05x + 741.67$ (where x is the temperature and y is the number of offsprings) ($R^2 = 1$ for both) (figure 1).

Developmental time

According to GLM, developmental time was significantly influenced by the temperature ($F = 6.656$; $df = 3$, 552 ; $P = 0.001$) but not by the host species ($F = 1.005$; $df = 1$, 555 ; $P = 0.250$) (table 3). The developmental time significantly diminished from 15 to 25 °C, while similar results were observed at 25 and 30 °C. Developmental time ranged from a minimum of 16.13 ± 0.13 days for males on *D. melanogaster* at 30 °C to a maximum of 70.23 ± 1.21 days for females on *D. melanogaster* at 15 °C. The regression analysis applied to mean data at different temperatures allowed to obtain two similar regression lines with $R^2 = 1$ for both host species: the equations were $y = -0.0144x^3 + 1.2954x^2 - 39.03x + 411.46$ for *D. melanogaster* and $y = -0.0045x^3 + 0.596x^2 - 22.781x + 285.98$ for *D. suzukii* (where x is the temperature and y is the developmental time expressed in days) (figure 2).

Discussion

This study provides a comprehensive assessment of the influence of temperature and host on the biological parameters of a population of *T. drosophilae*. Collecting data on parasitoid survival and fecundity is essential to understand the population dynamics of the parasitoid as these parameters affect the host/parasitoid equilibrium. Researches on the biology of natural enemies under controlled conditions can contribute to deepen information for future researches in fields (Lupi *et al.*, 2017). However, it is necessary to state that field situation under varying temperatures can differently affect the biological answer of a species (Wang *et al.*, 2018).

According to adult survival, we found that the parasitoid is able to easily survive until 35 °C. The highest temperature tested (40 °C) resulted in the death of the parasitoid only after few hours. This was also confirmed by Amiresmaeli *et al.* (2015) in experiments conducted in a blackberry and raspberry field in Guanzate (CO) (Northern Italy, $45^{\circ}42'43.01''N$ $9^{\circ}00'47.12''E$) with the same population: no *T. drosophilae* emerged from fruits and sentinel traps when the temperature was higher than 35 °C for some hours. Even if the parasitoid was able to survive for some days at 35 °C, neither oviposition nor progeny was observed, unlike what reported by Rossi Stacconi *et al.* (2017). In addition, the Californian popu-

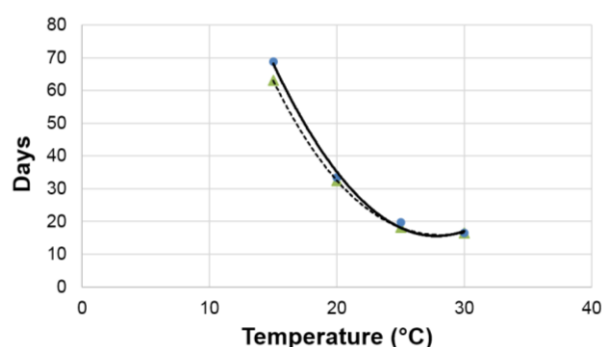


Figure 2. Trend of mean developmental time at different temperatures on *D. suzukii* (dotted line) and *D. melanogaster* (solid line).

Table 3. Mean developmental time of *T. drosophilae* from egg to adult of males, females and cohort (males + females) in days (\pm SE) on *D. suzukii* and *D. melanogaster*. Different letters mean significant differences among species (ANOVA, $P < 0.05$).

Host	Temperature (°C)	Egg-adult ♂ (days)	Egg-adult ♀ (days)	Egg-adult cohort/males + females (days)
<i>D. suzukii</i>	15	62.90 \pm 1.32 a	63.24 \pm 1.33 a	63.07 \pm 0.93 a
<i>D. suzukii</i>	20	32.16 \pm 0.51 b	33.15 \pm 0.27 b	32.5 \pm 0.23 b
<i>D. suzukii</i>	25	17.33 \pm 0.22 c	18.93 \pm 0.27 c	18.13 \pm 0.20 c
<i>D. suzukii</i>	30	16.23 \pm 0.23 c	16.79 \pm 0.22 c	16.56 \pm 0.16 c
<i>D. melanogaster</i>	15	67.72 \pm 1.14 a	70.23 \pm 1.21 a	68.74 \pm 0.85 a
<i>D. melanogaster</i>	20	33.15 \pm 0.29 b	34.12 \pm 0.15 b	33.5 \pm 0.30 b
<i>D. melanogaster</i>	25	19.34 \pm 0.30 c	20.30 \pm 0.28 c	19.71 \pm 0.43 c
<i>D. melanogaster</i>	30	16.13 \pm 0.13 c	16.75 \pm 0.13 d	16.54 \pm 0.11 c

lation of *T. drosophila* showed a different thermal profile, as *T. drosophilae* was not even able to develop at 30 °C (Wang *et al.*, 2018). However, different studies (Walsh *et al.*, 2011; Tochen *et al.*, 2014) showed that also *D. suzukii* is less active at temperatures above 30 °C (Kinjo *et al.*, 2014). Thus, the thermal profile of the pest and the parasitoid is synchronized. These results confirm that *T. drosophilae* appears as a good candidate for the control of the invasive *D. suzukii*.

The lowest temperature tested (5 °C) allowed the survival of the adults up to six months or nearly, without any egg deposition. This is the only study that considers this low temperature in laboratory conditions, as in Rossi Stacconi *et al.* (2017) the lowest experimental temperature was 15 °C, and in Wang *et al.* (2018) it was 12 °C. Considering this long survival period at 5 °C, further research is needed to evaluate the lowest thermal limit of *T. drosophilae*, and to deepen the knowledge of the parasitoid overwintering habits in different climatic areas. However, the capability to survive at 5 °C for such a long time suggests that the parasitoid is able to survive as adult in winter at least in milder climates.

Host species did not influence the offspring number, and this confirms information provided by Mazzetto *et al.* (2016) through choice experiments. However, sex ratio of the resultant progeny was different between the two hosts: the female proportion was 49% or higher on *D. suzukii* than on *D. melanogaster*, with the exception at 30 °C. The haplodiploid mother is assumed to control her sex ratio (proportion of male eggs) with a physiological mechanism as a function of host size, since female offspring are usually allocated to larger hosts (Assem, 1971; Godfray, 1994). As in the present research, *T. drosophilae* oviposited more males in the pupae of *D. melanogaster*, which are usually smaller than those of *D. suzukii* (Wang *et al.*, 2016). Therefore, it is necessary to deepen information on male and female emergence in relation to pupal size to evaluate if sex ratios can be regulated by the “mother”.

The research provides also for the first time the lifetime progeny of *T. drosophilae* on a wide range of temperatures on two drosophilid hosts. The results in this research showed that the parasitoid has a higher fertility than that obtained in other researches (Wang *et al.*, 2016). Therefore, it appears as a good candidate to be used in biological control programs. Besides, as no significant differences occurred between the two hosts examined in developmental time and offspring production, both *Drosophila* species seem appropriate to be used for the rearing of *T. drosophilae*. However, since the parasitoid showed a balanced sex ratio on *D. suzukii*, this host could be more suitable for commercial mass rearing of this parasitoid.

Comparing the parasitoid developmental time obtained in this research with the one of *D. suzukii* (Tochen *et al.*, 2014), it results that both species have similar developmental periods at 25 °C and 30 °C. At lower temperatures, *T. drosophilae* takes significantly more days to emerge than *D. suzukii*. Thus, for a biological control strategy, it appears necessary to introduce *T. drosophilae* in spring as soon as possible to allow its

settlement and an efficient control. Finally, the identification of two equations that perfectly fit laboratory data can greatly help in obtaining information on developmental time and progeny at different temperatures. This acquisition can support the development of predictive models on the trend of population and thus helping decision-making in different geographical areas.

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