
1 **Supplementary material**
2 **Optimized timing of parasitoid release: a mathematical model**
3 **for biological control of *Drosophila suzukii***

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8 This document contains supplementary material for the manuscript (Pfab et al, 2018).
9 Here we describe the model equations in detail and derive the parameters used.

10 **1 Framework**

11 Our model bases on the general approach by Nisbet and Gurney (1983). This approach al-
12 lows to model populations of insects with dynamically varying instar duration, which in our
13 case depend on the temperature of the environment. The method has proved useful in sev-
14 eral applications (McCauley et al, 2008; Nelson et al, 2013; Ewing et al, 2016). We extend
15 the basic model in a straightforward fashion to couple the dynamics of our two species, *D.*
16 *suzukii* and its parasitoid *T. drosophilae*. Our basic modeling parts are similar to the Ap-
17 pendix in (McCauley et al, 2008). The modeling parts are:

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<i>D. suzukii</i> densities (host)	
<i>E</i>	eggs
<i>L</i>	larvae
<i>U</i>	pupae
<i>A</i>	adults
<i>T. drosophilae</i> densities (parasitoid)	
<i>J</i>	juveniles
<i>P</i>	adults
Environment	
<i>C</i>	temperature
<i>F</i>	fruit availability

18

Functions and parameters (for stage $i = E, L, U, A, J, P$)		
Notation	Explanation	Reference
$\phi_i(C)$	background mortality rate	(11)-(12)-(14)-(15)
δ_i	total mortality rate	(2)
$g(C)$	speed of maturation	(10)
τ_i	time spent in the stage i	(6)
$f_A(C, F)$	rate of <i>D. suzukii</i> eggs deposited (rate per A and F)	(17)
$f_P(C, U)$	infestation rate of <i>T. drosophilae</i> (rate per P and U)	(19)
$\psi(F)$	competition coefficient for <i>D. suzukii</i> larva	(13)

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Fecundity, mortality and the duration of the different juvenile stages depend on the temperature, fruit availability and the population densities. The parameters and functions are taken from different sources, see Section 3. All together, the model is formulated as

$$\begin{aligned}
 \frac{dE(t)}{dt} &= R_E(t) - M_E(t) - \delta_E(t)E(t) \\
 \frac{dL(t)}{dt} &= M_E(t) - M_L(t) - \delta_L(t)L(t) \\
 \frac{dU(t)}{dt} &= M_L(t) - M_U(t) - \delta_U(t)U(t) \\
 \frac{dA(t)}{dt} &= M_U(t) - \delta_A(t)A(t) \\
 \frac{dJ(t)}{dt} &= R_J(t) - M_J(t) - \delta_J(t)J(t) \\
 \frac{dP(t)}{dt} &= M_J(t) - \delta_P(t)P(t).
 \end{aligned} \tag{1}$$

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24

The building parts are as follows. Mortality rates δ_i are composed of the temperature dependent background mortality rates ϕ_i , and competition and parasitism related terms (for *D.*

25 *suzukii* larvae and pupae). That is

$$\begin{aligned}
 \delta_E(t) &= \phi_E(C(t)) \\
 \delta_L(t) &= \phi_L(C(t)) + \psi(F(t))L(t) \\
 \delta_U(t) &= \phi_U(C(t)) + f(C(t), U(t))P(t) \\
 \delta_A(t) &= \phi_A(C(t)) \\
 \delta_J(t) &= \phi_J(C(t)) \\
 \delta_P(t) &= \phi_P(C(t))
 \end{aligned} \tag{2}$$

26 The renewal rates R_i and the maturation rates M_i are

$$\begin{aligned}
 R_E(t) &= \beta_A(t)A(t) \\
 M_E(t) &= R_E(t - \tau_E(t))S_E(t) \frac{g(C(t))}{g(C(t - \tau_E(t)))} \\
 M_L(t) &= M_E(t - \tau_L(t))S_L(t) \frac{g(C(t))}{g(C(t - \tau_L(t)))} \\
 M_U(t) &= M_L(t - \tau_U(t))S_U(t) \frac{g(C(t))}{g(C(t - \tau_U(t)))} \\
 R_J(t) &= \beta_P(t)P(t) \\
 M_J(t) &= R_J(t - \tau_J(t))S_J(t) \frac{g(C(t))}{g(C(t - \tau_J(t)))}
 \end{aligned} \tag{3}$$

27 with the birth rates

$$\begin{aligned}
 \beta_A(t) &= \lambda_A h(C(t), F(t))F(t) \\
 \beta_P(t) &= \lambda_P f(C(t), U(t))U(t)
 \end{aligned} \tag{4}$$

28 where λ_A and λ_P are the sex ratios of *D. suzukii* and *T. drosophilae*, to take into account
 29 that only females lay eggs. The functions f and h include the temperature dependence of the
 30 fecundities and their leveling-off when there are many occasions for ovipositing. Further S_i
 31 are the stage survival probabilities for $i = E, L, U$ and J ,

$$S_i(t) = e^{-\int_{t-\tau_i(t)}^t \delta_i(\sigma) d\sigma}. \tag{5}$$

32 The maturation delays τ_i are given by the implicit relations

$$\Omega_i = \int_{t-\tau_i(t)}^t g(C(\sigma)) d\sigma \tag{6}$$

33 where $g(C)$ is the speed of maturation in dependence of the temperature. The speed of
 34 maturation is normalized to be 1 at its maximum, making Ω_i the minimum duration of the
 35 stage.

36 Under this assumption, we can apply a time-change to render the maturation delays
 37 constant. This technique is described in (McCauley et al, 2008; Nelson et al, 2013). Without
 38 going into detail, the transformation is

$$\tilde{t} = \int_0^t g(\sigma) d\sigma. \tag{7}$$

39 After this transformation the delays of the different stages become constant Ω_i , so that
 40 the system can be easily solved using readily available software (e.g. the MATLAB package

dde23 (Shampine et al, 2000)). We chose to use *Wolfram Mathematica* (Wolfram Research, 2016) to solve the system of delay differential equations (DDEs). After simulating the model under the transformation, we apply the inverse transformation to recover the dynamics in normal time. The *Mathematica* code is freely available on request.

The idea of transforming the time to render the delays constant can be seen as a continuous counterpart for discrete degree day models as the models for the dynamics of *D. suzukii* by (Wiman et al, 2014, 2016). Note that it would also be possible expressing the delays themselves through DDEs (Nisbet and Gurney, 1983; Johnson et al, 2015; Ewing et al, 2016) and use software which can solve DDEs with variable delays (e.g. the Fortran package DKLAGE6 (Thompson and Shampine, 2006), the Python package pyDDE, the MATLAB package ddesd (Shampine, 2005) and the R package PBSddesolve (Couture-Beil et al, 2013)).

2 Starting conditions

We start the system with only adult *D. suzukii*, assuming that no eggs are laid before. That is for $t < 0$, $A(t) = A_0$, while $E(t)$, $L(t)$, $U(t)$, $R_E(t)$, $M_E(t)$, $M_L(t)$ and $M_U(t)$ are all zero. To reduce the influence of the starting conditions, we run the simulations for an initial year which is disregarded.

Parasitoid adults are added in the same fashion after starting the simulation with *D. suzukii* alone. Given the time of the parasitoid release t_{intro} , we set for $t < t_{intro}$ the variables $J(t)$, $P(t)$, $R_J(t)$ and $M_J(t)$ to zero, and shift the adult parasitoid density at $t = t_{intro}$ to $P(t) = P_0$.

3 Parameters and functions

3.1 Maturation delays

The stage durations at various constant temperatures are taken for *D. suzukii* from (Tochen et al, 2014) (using the delays for females in Table 1 and 2 there) and for *T. drosophilae* from (Rossi Stacconi et al, 2017) (using the delays for females in Table 2 there). The data corresponds to the egg-larva stage and the pupal stage of *D. suzukii*, and the entire juveniles stage of *T. drosophilae*. We use the data separately to define the speed of maturation $g_i(C)$ for stage i as the inverse of the stage duration, and we fit its temperature dependence by a Gaussian bell curve of the shape

$$g_i(C) = \frac{1}{\Omega_i} e^{-\left(\frac{\mu_{g_i} - C}{\sigma_{g_i}}\right)^2} \quad (8)$$

where Ω_i is the minimum duration of a stage (at constant optimal temperature $C = \mu_{g_i}$). The fit is obtained by the least square method in logarithmic scale. We approximate the speed of maturation of the different stages with a general speed function $g(C)$

$$g_i(C) \approx \frac{1}{\Omega_i} g(C) \quad (9)$$

where

$$g(C) = e^{-\left(\frac{\mu_g - C}{\sigma_g}\right)^2} \quad (10)$$

with μ_g and σ_g being the averages of the values we found for μ_{g_i} and σ_{g_i} , see Fig. 3. After the fit we divide the egg-larva stage of *D. sukuzii* into egg and larva stage using the proportions measured by Emiljanowicz et al (2014) at constant temperature (in Table 5 there). The finally obtained parameter values are $\Omega_E = 1.3$, $\Omega_L = 5.3$, $\Omega_U = 4.3$, $\Omega_J = 16.9$, $\mu_g = 28.9$ and $\sigma_g = 13.7$.

3.2 Mortality

Mortality rates depend on the temperature. Note that experiments on the mortality of *D. sukuzii* differ sometimes considerably in their outcomes (Kinjo et al, 2014; Tochen et al, 2014; Jakobs et al, 2015; Stephens, 2015; Shearer et al, 2016; Ryan et al, 2016; Enriquez and Colinet, 2017).

D. sukuzii adults

We use the data on the adult life span of *D. sukuzii* from (Shearer et al, 2016) (medium life span of females from Figure 3 there). There the life length has been measured for two different different phenotypes of *D. sukuzii*: a summer morph and a winter morph, which are induced by high and low temperatures respectively during juvenile development. For the sake of simplicity, we assume that the flies always exhibit the most favorable phenotype and thus we take for each temperature the value of the better adapted phenotype. We fit the average life lengths with a log-transformed Gaussian curve by the least square method in logarithmic scale (see Fig. 5a). This form turned out to fit the data best after testing different formulas. We then use the inverse of that curve as the mortality rate, i.e.

$$\phi_A(C) = \frac{1}{\varepsilon_{\phi_A}} e^{\left(\frac{\log[C+s] - \log[\mu_{\phi_A} + s]}{\sigma_{\phi_A}} \right)^2} \quad (11)$$

with $s = 8$. The obtained parameter values are $\varepsilon_{\phi_A} = 117.4$, $\mu_{\phi_A} = 2.6$ and $\sigma_{\phi_A} = 0.79$. For the simulations we assume that mortality in the wild is twice as large as in the laboratory due to predation from species different to *T. drosophilae*, and additional weather influences as wind, rain, humidity etc. The factor 2 for increased mortality in the wild is presumably a conservative estimate; though we found no information about mortality of *D. sukuzii* in the wild, two recent papers suggest that mosquito mortality in the wild is around 4 times higher than under laboratory conditions (Cianci et al, 2013; Marini et al, 2016).

Note that the tolerance curve at lower temperatures is mostly guessed because we could not find clear data for long-time survival of winter morph *D. sukuzii* adults at very low temperatures, although some efforts have been made into this direction (Ryan et al, 2016; Enriquez and Colinet, 2017).

Juvenile *D. sukuzii*

The juvenile mortality of *D. sukuzii* rate is assumed to depend on temperature and competition when fruit availability is limited. For the temperature dependent background mortality rate, we use the same function $\phi_V(C)$ for all three juvenile stages of *D. sukuzii*. The function is derived from the stage survival probabilities and stage durations of males and females from (Tochen et al, 2014) (from Table 2 and Table 3 there; survival can be deduced

116 from the sample size in this table by using that all replicates were started with 50 females
117 and 50 males). This data is fitted by a Gaussian function of the form

$$\phi_V(C) = \frac{1}{\varepsilon_{\phi_V}} e^{\left(\frac{C - \mu_{\phi_V}}{\sigma_{\phi_V}}\right)^2} \quad (12)$$

118 and we obtain the parameter values $\varepsilon_{\phi_V} = 42.6$, $\mu_{\phi_V} = 17.0$ and $\sigma_{\phi_V} = 13.2$ by the least
119 square method.

120

121 This function is the only mortality term for the egg stage. For the larva stage we include
122 an additional term, which accounts for competition. As juveniles consume fruit, we assume
123 that this term depends inversely proportional on fruit availability, without loss of generality

$$\psi(F) = \frac{1}{F}. \quad (13)$$

124 Any constant in front of the formula (13) can be absorbed in a scaling factor of host
125 densities. For the plots, the population densities obtained in the simulations have been
126 scaled to roughly match observed catch data. For the pupal stage there is an additional
127 mortality term due to parasitism, $f(C(t), U(t))P(t)$, which is described below in Section 3.3.

128

129 Adult *T. drosophilae*

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131 Data on life length of *T. drosophilae* adults at different temperatures are presented by
132 Amiresmaeili (2017), see Fig. 5b. To fit a mortality curve to that data, we proceed as for *D.*
133 *suzukii* adults (dropping the data point for the survival of *T. drosophilae* at the maximum
134 tested temperature because all insects died before the first census and this would conflict
135 with the least square fit in logarithmic scale). We use the function

$$\phi_P(C) = \frac{1}{\varepsilon_{\phi_P}} e^{\left(\frac{\log[C+s] - \log[\mu_{\phi_P} + s]}{\sigma_{\phi_P}}\right)^2} \quad (14)$$

136 where we assume that $s = 5$, since *T. drosophilae* is thought to be more sensitive towards cold
137 temperatures than *D. suzukii* (MVRS - Personal communication). The obtained parameter
138 values are $\varepsilon_{\phi_P} = 79.1$, $\mu_{\phi_P} = 5.5$ and $\sigma_{\phi_P} = 0.88$.

139 Note that survival at low temperatures is guessed because we could not find data
140 measured at cold conditions. For the simulations, we again doubled the mortality to account
141 for the difference between laboratory experiments and field survival.

142

143 Juvenile *T. drosophilae*

144

145 Juvenile mortality of *T. drosophila* has been measured by Wang et al (2016) at 23 °C
146 (from the average in Fig. 2 with high host abundance there – note that the reported mortality
147 of unexposed hosts has to be added to the values in this figure). Using the stage duration
148 from the same work (from the average value in Fig. 3 there), we obtain the mortality rate
149 $\phi_J(23) = 0.011$ at this temperature. For different temperatures we assume that the juvenile
150 parasitoid mortality $\phi_J(C)$ scales with temperature as the juvenile mortality of *D. suzukii*
151 and obtain

$$\phi_J(C) = \frac{\phi_J(23)}{\phi_V(23)} \phi_V(C). \quad (15)$$

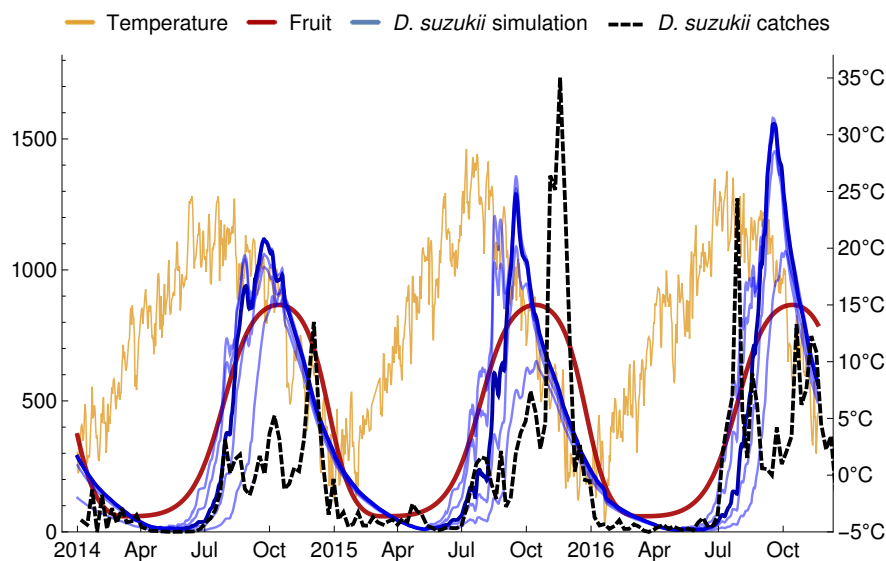


Fig. A1: Simulated *D. suzukii* adult population size, mean *D. suzukii* trap catches and mean daily temperature from S.Michele all'Adige, Province of Trento, Italy during 2014-2016. Different courses of the simulation correspond to different values for the *D. suzukii* attack rate $\alpha_A = 1, 1.5, 2, 4$ and 10 . The thick curve corresponds to the attack rate we use for the other simulations, $\alpha_A = 2$

152 3.3 Fecundity

153 *D. suzukii*

154

155 We assume that the daily fecundity of *D. suzukii* depends on two factors: the temperature
 156 C and the fruit availability F . To estimate the fecundity at high fruit availability we use the
 157 lifetime fecundity from Tochen et al (2014) (using the data measured on cherry, Table 3
 158 there). From this data we calculate the daily fecundity by using the average life length from
 159 the same paper, see Fig. 4 (using the data measured on cherry, Table 1 there). The daily
 160 fecundity is then fitted by a skewed Gaussian curve

$$\eta_A(C) = \eta_{A_{max}} e^{-\begin{cases} \kappa_A & \text{if } C \leq \mu_{\eta_A} \left(\frac{\mu_{\eta_A} - C}{\sigma_{\eta_A}} \right)^2 \\ 1 & C > \mu_{\eta_A} \end{cases}} \quad (16)$$

161 We choose $\kappa_A = 3$ as a reasonable value for skew parameter, and obtain the parameter
 162 values $\eta_{A_{max}} = 4.8$, $\mu_{\eta_A} = 19.6$ and $\sigma_{\eta_A} = 6.4$ by the least square method in logarithmic
 163 scale.

164

165 For the fruit dependence we assume a type 2 functional response with attack rate α_A .
 166 Additionally we include the adult sex ratio $\lambda_A = 1/2$ (Emiljanowicz et al, 2014). Summing

up, the fecundity rate is assumed to be of the form

$$\beta_A = f_A(C, F)F$$

$$\text{with } f_A(C, F) = \lambda_A \frac{\eta_A(C)\alpha_A}{1 + \alpha_A F}. \quad (17)$$

In order to have an order-of-magnitude estimate for α_A , we computed simulations of the system with only *D. suzukii* for different values of α_A . By comparing those simulations in Fig. A1 with observed catches in the traps, we chose $\alpha_A = 2$ as a reasonable reference value.

Note that this is a simplified way to model the fecundity of *D. suzukii*, neglecting possible details as reduced fecundity of the winter morph (Wallingford et al, 2016) and effects of female age and larval diet on fecundity and sex ratio (Emiljanowicz et al, 2014; Tochen et al, 2014).

T. drosophilae

We assume that the daily fecundity of *T. drosophilae* depends on temperature C and on the density of host pupae U , see Fig. 4. For the daily fecundity with high pupa abundance, we use the data of (Rossi Stacconi et al, 2017) (from Figure 4 there). This data is fitted by a skewed Gaussian curve

$$\eta_P(C) = \eta_{P_{max}} e^{-\begin{cases} \kappa_P & \text{if } C \leq \mu_{\eta_P} \left(\frac{\mu_{\eta_P} - C}{\sigma_{\eta_P}} \right)^2 \\ 1 & C > \mu_{\eta_P} \end{cases}}. \quad (18)$$

We use $\kappa_P = 3$ as a reasonable value for the skew parameter, and obtain the parameter values $\eta_{P_{max}} = 11.2$, $\mu_{\eta_P} = 22.0$ and $\sigma_{\eta_P} = 8.9$ by the least square method in logarithmic scale.

Using again a type 2 functional response with attack rate α_P we obtain the fecundity rate

$$\beta_P = f_P(C, U)U$$

$$\text{with } f_P(C, U) = \lambda_P \frac{\eta_P(C)\alpha_P}{1 + \alpha_P U} \quad (19)$$

where the sex ratio $\lambda_P = 0.53$ is obtained from (Rossi Stacconi et al, 2017) (using the total numbers of emerging individuals in Table 2 there).

Again this functional form neglects several biological details, such as changing sex ratios, age-dependence of the fecundity and other physiological factors (Rossi Stacconi et al, 2017). Note also that different experiments suggest quite different values for the fecundity. On one hand, the experiments in (Rossi Stacconi et al, 2017) suggest that the daily fecundity is lower over a longer time span and additionally decreases with the age of the parasitoid. On the other hand, experiments in (Kaçar et al, 2017) suggest much higher values for the short-term daily fecundity. The values we use are between those two extremes, so we believe they are reasonable estimates.

The parasitoid attack rate α_P cannot be reliably estimated from laboratory experiments, so we guessed it roughly by assuming that the parasitoids reach half of their potential fecundity during the peak season of *D. suzukii* peak season. The obtained value is $\alpha_P = 23$. As this guess could be potentially misleading, we did a sensitivity analysis for its impact. For this analysis, we use different values of the parameter and repeat in Fig. A2 a simplified version of Fig. 10 (this figure shows our main objective, the influence of the parasitoid

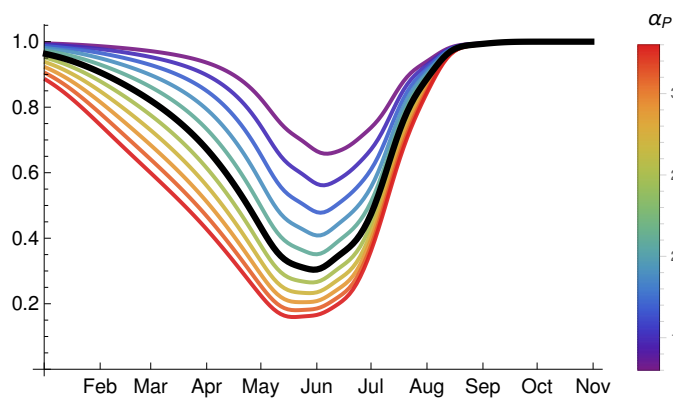


Fig. A2: *D. suzukii* infestation index in dependence of the time of a single parasitoid introduction. The different lines correspond to different parameter values for the attack rate α_P of *T. drosophilae*. The thick black line corresponds to the value we used for the other simulations, $\alpha_P = 23$. The amount of parasitoids released equals 0.2% of the maximum *D. suzukii* adult population size reached without intervention.

203 release timing on the success of the intervention). As one can expect, choosing a higher
 204 value for α_P increases the success of the intervention. Also, higher values slightly anticipate
 205 the optimal release timing, but the beginning of June is a reasonable choice in all scenarios.
 206

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