

UNIVERSITY OF TRENTO

Faculty of Mathematics



DOCTORAL THESIS

**Mathematical models for host-parasitoid
interactions and biological control of
*Drosophila suzukii***

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Contents

Introduction	1
1 Multiple coexistence equilibria in a two parasitoid-one host model	4
Abstract	4
1.1 Introduction	4
1.2 The model	5
1.3 Preliminaries	7
1.4 Equilibrium states	8
1.4.1 When only the egg parasitoid is present	8
1.4.2 When only the larva parasitoid is present	9
1.4.3 When both parasitoids are present	9
1.5 Invasibility of stable equilibria	10
1.6 Applying distributions for the maturation delays	12
1.6.1 Simulations and stability	13
1.7 Discussion	16
Appendices	20
1.A Transition probabilities and expected duration of the stages	20
1.A.1 Transition probabilities $\Pi_1(P)$ and $\Pi_2(Q)$	20
1.A.2 Expectation values for the durations of different stages	21
1.B Computing f for some distributions	21
1.B.1 Constant durations	22
1.B.2 Two-value distribution	23
1.B.3 Exponential distribution	23
1.B.4 Shifted exponential distribution	24
1.B.5 Gamma distribution	24
1.B.6 Shifted gamma distribution	24
1.C Characteristic equation	25
1.C.1 A sufficient condition for instability	28
1.C.2 Instability of the coexistence equilibrium when maturation de- lays are constant	30
2 Optimized timing of parasitoid release: a mathematical model for biological control of <i>Drosophila suzukii</i>	32
Abstract	32
2.1 Introduction	33

2.2	Theory and calculations	34
2.3	Results	37
2.4	Discussion	42
	Appendices	46
2.A	Supporting Information: model details	46
2.A.1	Starting conditions	48
2.A.2	Parameters and functions	49
	Maturation delays	49
	Mortality	49
	Fecundity	52
3	Analysis of a semi-field experiment with <i>Drosophila suzukii</i> and its parasitoid <i>Trichopria drosophilae</i>	55
	Abstract	55
3.1	Introduction	55
3.2	Direct fits	56
3.2.1	Introduction	56
3.2.2	Estimating the rate with which the fruit is attacked and the population densities of <i>D. suzukii</i> adults	57
3.2.3	Estimating competition	59
3.2.4	Mathematical details	61
	Distribution for number of juveniles placed in fruit	61
	Expectation and variance for the number of flies emerging from one fruit	61
3.3	Modeling the population dynamics with differential equations	63
3.3.1	Sampling and positions in the experiment	63
3.3.2	The stage structure	63
3.3.3	Renewal equations	64
3.3.4	The differential equations	66
3.3.5	Weekly sampling procedure	67
3.3.6	Initial conditions	68
3.3.7	Fixed parameters	69
3.3.8	Likelihood function	69
3.3.9	Results	71
3.4	Discussion	71
	Final conclusions	76
	Acknowledgements	78
	Bibliography	79

Introduction

This thesis is composed of three chapters treating mathematical models for population dynamics of parasitoids and their hosts. The first chapter treats a class of such models theoretically. The second and third work focus on the population dynamics of the invasive fruit fly *Drosophila suzukii* and its parasitoids, which are thought to be useful for its biological control.

Parasitoids are insects whose larvae develop inside or attached to a host, which is finally killed. Most parasitoids are from the order *Hymenoptera* (wasps) or *Diptera* (flies). Parasitoids are globally widespread and they are thought to represent about 1/3 of all insect species. In many cases they are ecologically important because they can effectively control their host populations (Godfray, 1994). For that reason, various parasitoid species are used as agents in biological control programs of pest species (Cock et al., 2016). Such pests are often invasive species which arrived recently and have little natural enemies in their new habitat (Hoddle, 2004). While laboratory and field experiments are essential for identifying potential agents for biological control programs, mathematical models can help to understand the impact of such agents and how to make best use of them (Hamby et al., 2016).

The invasive fruit fly *D. suzukii* arrived in 2009 to Europe and America where it now inflicts considerable damage to the agriculture of soft shelled fruits as for example blueberry, raspberry and cherry (Asplen et al., 2015). In contrast to other fruit flies, *D. suzukii* can infest undamaged ripe fruit on the plant due to a specially formed ovipositor (Lee et al., 2011b). It is assumed that the pest can cause economical damage of yearly up to \$500 million in the Western US (Goodhue et al., 2011) and €3 million in the Province of Trento, Italy (De Ros et al., 2015). Currently, pest management relies heavily on pesticides but this practice is considered problematic (Roubos et al., 2014; Asplen et al., 2015). Biological control with parasitoids has been suggested as a promising alternative for confining the pest (Haye et al., 2016). Several indigenous larval and pupal parasitoids have been found to be able to infest *D. suzukii* in Europa and America (Rossi Stacconi et al., 2017b).

Chapter 1 is the most theoretical part of this thesis. It treats a model for the population dynamics of two parasitoid species attacking different juvenile stages of a common host (say eggs and larvae). The model has been introduced by Briggs et al. (1993), who investigated how multiple parasitoid species can coexist on a single host species. Such coexistence has been reported frequently but puzzled ecologists as it seems to contradict a principle of ecology stating that competing species cannot coexist on the same limiting resource (the host species in this case). The authors found,

that coexistence can be possible when there is sufficient variation in the duration of the hosts juvenile stages. In this case, the host population can be interpreted as two different resources: individuals with a relatively long egg stage and individuals with a relatively long larva stage – each benefiting the corresponding parasitoid and thus promoting coexistence. The work in this thesis shows additional analysis of the same model. It turns out, that coexistence equilibria are not necessarily unique in the model. Such multiple coexistence equilibria can lead to situations where stable coexistence is possible although one or both parasitoid species cannot invade an equilibrium of the host and the other parasitoid. This an example where –contrarily to a common assumption– mutual invisibility is not required for stable coexistence. The work also includes necessary conditions for the occurrence of such multiple coexistence equilibria. Finally an intuitive explanation for this phenomenon is discussed. Whether situations as described in this work do occur in nature is not clear yet, but generally understanding the interactions of different parasitoid species can be important when planing biological control programs; for example when deciding whether a single parasitoid species or multiple species should be released in order to control pest insects optimally.

Chapter 2 is dedicated to a question with potentially high practical relevance: at what time of the year should parasitoids be released to control *D. suzukii* most efficiently? Little is known about this question, and estimations span between early spring, with the idea to profit from a “bottleneck situation” of the population (Rossi Stacconi et al., 2017b), towards early summer, when the conditions are suitable for the parasitoid as temperatures are high and *D. suzukii* juveniles are widely available (Wiman et al., 2016). To account for the seasonality, the model includes temporal variation of both, temperature and availability of fruit suitable for the development of *D. suzukii*. Those environmental factors affect mortality, fecundity and development speed. The control agent chosen for this work is the promising pupal parasitoid *Trichopria drosophilae*. Parameters for *D. suzukii*, *T. drosophilae* and the environment are collected from various sources (Emiljanowicz et al., 2014; Tochen et al., 2014; Poyet et al., 2015; Shearer et al., 2016; Wang et al., 2016; Amiresmaeili, 2017; Rossi Stacconi et al., 2017b). The stage structure of the populations and the temperature dependence of the maturation delays are taken into account by using delay differential equations with variable time delays (Nisbet and Gurney, 1983; McCauley et al., 2008). Some parameters haven been fitted to match observed patterns of *D. suzukii* in the Province of Trento. For this work, *T. drosophilae* has been chosen as the biological control agent, but the results can be presumably transferred for other parasitoids with similar demands on the environment. The model results show clear suggestions: with the assumptions made, the parasitoids are optimally released at the end of spring or beginning of summer, when the *D. suzukii* population starts to grow sharply. The results do not support the hypothesis that release during early spring can be efficient. Releasing the parasitoids at a single event seems to be slightly more efficient than releasing the same amount of parasitoid at several

events, but latter method can increase the chance of successful biological control. In the discussion of the chapter, those results are examined together with possible implications of the key assumptions.

Chapter 3 describes the analysis of an experiment for biological control of *D. suzukii* with its parasitoid *T. drosophilae* in semi-field conditions (Rossi Stacconi et al., 2017a). The experiment was conducted in a closed greenhouse in which a known number of insects was released. Weekly fruit samples have been taken from the greenhouse and the number of infested fruits and emerging insect adults have been counted. This data is analyzed here in two different ways: directly with statistical methods, and indirectly by fitting a model based on differential equations. Results from this analysis are estimations for the growth rates, the competition for available fruit and the adult population densities, which were not measured directly in the experiments. Simulations of a modification of the experimental design suggest, that effectiveness of the parasitoid release could be increased when less fruit is removed from the greenhouse. This is explained with the relatively long developmental time of the parasitoids. Considering this effect, agricultural practices which could support the success of a parasitoid release are discussed.

Chapter 1

Multiple coexistence equilibria in a two parasitoid-one host model

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Abstract

Briggs et al., 1993 introduced a host-parasitoid model for the dynamics of a system with two parasitoids that attack different juvenile stages of a common host. Their main result was that coexistence of the parasitoids is only possible when there is sufficient variability in the maturation delays of the host juvenile stages. Here we analyse the phenomenon of coexistence in that model more deeply. We show that with some distribution families for the maturation delays, the coexistence equilibrium is unique, while with other distributions multiple coexistence equilibria can be found. In particular we find that stable coexistence does not necessarily require mutual invasibility.

1.1 Introduction

It is known that parasitoid species of the same host can coexist (Force, 1970; Price, 1970; Harvey et al., 2009). This observation seems to contradict a principle in ecology which predicts that competing species cannot coexist on the same limiting resource (Gause and Witt, 1935), though it has been shown that the principle holds under very stringent equilibrium conditions (Chesson and Case, 1986) and that competitors can coexist on the same biological resource along periodic solutions (Hsu et al., 1977; Armstrong and McGehee, 1980). Parasitoid species are a particularly interesting case, as various mechanisms that can promote parasitoid coexistence on the same host have been suggested (Price, 1970; Lane et al., 2006; Hackett-Jones et

al., 2009). Briggs (1993) started to investigate under which conditions parasitoids can coexist when they attack different juvenile stages of a common host. This investigation was continued by Briggs et al. (1993), who found that in their model coexistence at equilibrium is possible only when there is sufficient variability in the maturation delays of the juvenile stages. They suggested that when the variability is large enough, different host individuals can be interpreted as different resources: individuals with a relatively long egg phase support the egg parasitoid, and individuals with a relatively long larva phase support the larva parasitoid. In the present paper we re-analyse the model by Briggs et al. (1993) and find more complex patterns than those already identified: there may be multiple coexistence equilibria, and, contrary to conventional wisdom, stable coexistence does not require mutual invasibility. The model is presented in Section 1.2. In Sections 1.3, 1.4 and 1.5 we formulate the original results in our somewhat different notation and in Section 1.6 show that coexistence equilibria are not unique for many distributions of the maturation delays. Finally, in Section 1.7 we set our results in the context of other works, discuss their relevance for biological pest control, and propose questions for further investigation. A general introduction to parasitoid-host systems can be found, for instance, in the text book by Godfray (1994).

1.2 The model

The model describes a host with two juvenile stages E and L , and an adult stage A . We refer to the first juvenile stage as eggs and to the second juvenile stage as larvae but they can also represent other developmental stages as pupae or different instars. The egg stage is attacked by an egg parasitoid (whose density is denoted by P) while the larva stage is attacked by a larva parasitoid (density denoted by Q) with attack rates a_P and a_Q respectively. Non-infected host juveniles have random maturation delays which are distributed with probability density functions w_E and w_L . Infected hosts do not progress to the next stage but give rise to new parasitoids a constant time T_{JP} or T_{JQ} after the infection. Unlike the original paper, we do not explicitly introduce survival probabilities for the juvenile parasitoids, since these can be absorbed in the parameters c_P and c_Q for the expected number of parasitoids emerging from an infected host. All other host and parasitoid stages have constant (background) death rates d_E, d_L, d_A, d_P and d_Q . Adult hosts have a life time fecundity ρ (so ρd_A is the rate with which an adult produces offspring). The population dynamics are described by delay differential equations shown below. We adopt the notation used in the original paper but extend it when needed. For simplicity, the term maturing is used for eggs transforming to larvae as well as for larvae transforming to adults, although for eggs the term hatching might be more appropriate. The balance equations for the population densities are

$$\left\{ \begin{array}{l} \frac{dE(t)}{dt} = R_E(t) - M_E(t) - a_P P(t)E(t) - d_E E(t) \\ \frac{dL(t)}{dt} = M_E(t) - M_L(t) - a_Q Q(t)L(t) - d_L L(t) \\ \frac{dA(t)}{dt} = M_L(t) - d_A A(t) \\ \frac{dP(t)}{dt} = a_P c_P E(t - T_{JP})P(t - T_{JP}) - d_P P(t) \\ \frac{dQ(t)}{dt} = a_Q c_Q L(t - T_{JQ})Q(t - T_{JQ}) - d_Q Q(t) \end{array} \right. \quad (1.1)$$

where

$R_E(t) = \rho d_A A(t)$	host egg recruitment rate
$M_E(t) = \int_0^\infty R_E(t - x_E) S_E(x_E, t) w_E(x_E) dx_E$	host egg maturation rate = host larva recruitment rate
$M_L(t) = \int_0^\infty M_E(t - x_L) S_L(x_L, t) w_L(x_L) dx_L$	host larva maturation rate = host adult recruitment rate
with	
$S_E(x_E, t) = \exp\left(-\int_{t-x_E}^t (a_P P(y) + d_E) dy\right)$	probability for host eggs to survive from time $t - x_E$ to t
$S_L(x_L, t) = \exp\left(-\int_{t-x_L}^t (a_Q Q(y) + d_L) dy\right)$	probability for host larvae to survive from time $t - x_L$ to t

and

parameter	description
ρ	total lifetime fecundity of host adults
d_E	background mortality rate of host eggs
d_L	background mortality rate of host larvae
d_A	background mortality rate of host adults
d_P	background mortality rate of egg parasitoids
d_Q	background mortality rate of larva parasitoids
a_P	egg parasitoid attack rate
a_Q	larva parasitoid attack rate
c_P	expected number of egg parasitoids emerging from infected egg
c_Q	expected number of larva parasitoids emerging from infected larva
T_{JP}	duration of juvenile egg parasitoid stage
T_{JQ}	duration of juvenile larva parasitoid stage

and

function	description
w_E	probability density function for host egg maturation delay
w_L	probability density function for host larva maturation delay

1.3 Preliminaries

In order to investigate equilibrium states, we introduce some quantities that depend on constant parasitoid densities P and Q . Note first that eggs and larvae can have three different fates: they can die due to the background death rates d_E and d_L , they can be successfully attacked by parasitoids or they can progress to the next stage. We first state the formulae for the transition probabilities between the host stages and the expected durations in the different stages (for the full computations see 1.A).

The probability that a freshly emerged egg hatches into a larva is

$$\Pi_1(P) = \int_0^{\infty} w_E(\tau) e^{-(a_P P + d_E)\tau} d\tau \quad (1.2)$$

and the probability that a freshly hatched larva emerges as an adult is

$$\Pi_2(Q) = \int_0^{\infty} w_L(\tau) e^{-(a_Q Q + d_L)\tau} d\tau. \quad (1.3)$$

As shown in 1.A.2, the expected duration of the egg stage is

$$\Gamma_1(P) = \frac{1 - \Pi_1(P)}{a_P P + d_E}, \quad (1.4)$$

the expected duration of the larva stage (given that this stage is reached) is

$$\Gamma_2(Q) = \frac{1 - \Pi_2(Q)}{a_Q Q + d_L}, \quad (1.5)$$

and the expected duration of the adult stage (given that this stage is reached) is

$$\Gamma_3 = \frac{1}{d_A}. \quad (1.6)$$

We now can state the following relations, valid when the related population densities are constant:

The rate of eggs emerging, given constant adult density A , is by definition

$$R_E = \rho d_A A. \quad (1.7)$$

The constant egg density E is the product of the rate of eggs emerging and the expected duration of the egg stage (to verify set $\frac{dE}{dt} = 0$),

$$E = R_E \Gamma_1(P). \quad (1.8)$$

The constant larva density L is the product of three factors, viz., the rate of eggs emerging, the probability for an egg to mature to a larva and the expected duration of the larva stage, given that it is reached (to verify set $\frac{dL}{dt} = 0$),

$$L = R_E \Pi_1(P) \Gamma_2(Q). \quad (1.9)$$

The constant adult density A is the product of four factors, viz., the rate of eggs emerging, the probability for an egg to mature to a larva, the probability for a larva to mature to an adult and the expected life length of an adult (to verify set $\frac{dA}{dt} = 0$),

$$A = R_E \Pi_1(P) \Pi_2(Q) \Gamma_3. \quad (1.10)$$

The average number of offspring from a freshly laid egg (the basic reproduction number of the host) is the product of the average output of an adult ρ and the probability for an egg to mature to an adult,

$$R_0 = \rho \Pi_1(P) \Pi_2(Q). \quad (1.11)$$

At a nontrivial equilibrium the basic reproduction number R_0 equals one, as can be seen by plugging the definition of R_E into equation (1.10). The zero growth condition for host eggs (1.8) and larvae (1.9) can be combined by eliminating R_E . This yields

$$\frac{\Pi_1(P) \Gamma_2(Q)}{\Gamma_1(P)} = \frac{L}{E}. \quad (1.12)$$

1.4 Equilibrium states

1.4.1 When only the egg parasitoid is present

For the case that only the egg parasitoid is present, its equilibrium density P^* can be determined by plugging $Q = 0$ into the basic reproduction number R_0 , which is equal to 1 at equilibrium, i.e. by requiring

$$\rho \Pi_1(P^*) \Pi_2(0) = 1. \quad (1.13)$$

Assuming that $R_0 > 1$ for $P = 0$ and $Q = 0$, this equation has a unique root for P^* since R_0 approaches 0 strictly monotonically with increasing P .

The equilibrium state for the egg density is determined by the requirement of zero growth rate for (non-trivial) P . This, by setting $dP(t)/dt = 0$ and assuming constant population densities, leads to

$$E_P^* = \frac{d_P}{a_P c_P}. \quad (1.14)$$

The equilibrium larva density L_P^* in presence of only the egg parasitoid can be calculated from the relation (1.12),

$$L_P^* = E_P^* \frac{\Pi_1(P^*) \Gamma_2(0)}{\Gamma_1(P^*)}. \quad (1.15)$$

The host adult density can be obtained for all equilibrium systems by combining (1.7) and (1.8).

1.4.2 When only the larva parasitoid is present

In the same way as for the egg parasitoid, we can derive the equilibrium densities for the case that only the larva parasitoid is present. The equilibrium larva parasitoid density Q^* is determined through the equation

$$\rho \Pi_1(0) \Pi_2(Q^*) = 1 \quad (1.16)$$

and again this equilibrium density is unique. The equilibrium larva density is

$$L_Q^* = \frac{d_Q}{a_Q c_Q}, \quad (1.17)$$

and the equilibrium egg density is

$$E_Q^* = L_Q^* \frac{\Gamma_1(0)}{\Pi_1(0) \Gamma_2(Q^*)}. \quad (1.18)$$

1.4.3 When both parasitoids are present

According to equation (1.11) the host adult density is in equilibrium when the parasitoid densities satisfy

$$Q = \Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(P)} \right) \quad (1.19)$$

where Π_2^{-1} is the inverse function of Π_2 . Plugging (1.19) into (1.12) yields a condition for all host stages to be in equilibrium

$$f(P) = \frac{L}{E} \quad (1.20)$$

where $f : [0, P^*] \rightarrow \mathbb{R}^+$ is defined by

$$f(P) = \frac{\Pi_1(P)}{\Gamma_1(P)} \Gamma_2 \left(\Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(P)} \right) \right). \quad (1.21)$$

When both parasitoids coexist, the equilibrium egg and larva densities are determined by the requirement of zero growth rate for the egg and larva parasitoid respectively. Hence they are given by E_P^* and L_Q^* , and thus the egg parasitoid coexistence equilibrium P^{**} is determined by the condition

$$f(P^{**}) = \frac{L_Q^*}{E_P^*}. \quad (1.22)$$

The corresponding larva parasitoid density Q^{**} can be obtained by equation (1.19). Note that in the same way one can derive an equivalent function $g(Q) = L/E$ which

determines coexistence equilibria by $g(Q^{**}) = \frac{L_Q^*}{E_P^*}$, where

$$\begin{aligned} g(Q) &= \frac{\Pi_1\left(\Pi_1^{-1}\left(\frac{1}{\rho\Pi_2(Q)}\right)\right)}{\Gamma_1\left(\Pi_1^{-1}\left(\frac{1}{\rho\Pi_2(Q)}\right)\right)}\Gamma_2(Q) \\ &= \frac{\Gamma_2(Q)}{\Pi_2(Q)}\frac{1}{\rho\Gamma_1\left(\Pi_1^{-1}\left(\frac{1}{\rho\Pi_2(Q)}\right)\right)} \end{aligned} \quad (1.23)$$

with Π_1^{-1} being the inverse function of Π_1 . All further analysis could be carried out with either f or g but for simplicity we stick with the function f .

Turning back to the function f , we see that the shape of the function contains information on the multiplicity of coexistence equilibria. According to equation (1.22), multiple coexistence equilibria cannot arise if f is strictly monotonic. If on the other hand for some parameters f is not monotonic, we can always find values of the parameters c_P, c_Q, d_P or d_Q that give rise to multiple coexistence equilibria by shifting the critical horizontal $L_Q^*/E_P^* = d_Q a_P c_P / d_P a_Q c_Q$ until the graph of the function f (which does not depend on those parameters) is intersected multiple times. Each intersection yields a coexistence equilibrium. Similarly, the critical horizontal can be shifted using those parameters until there are no coexistence equilibria.

1.5 Invasibility of stable equilibria

When in the absence of parasitoids $R_0 > 1$, either parasitoid can establish a population. Often, a stable host-parasitoid equilibrium will be reached with R_0 set at 1 (Murdoch et al., 1987) and we follow Briggs et al., 1993 in examining when this equilibrium can be invaded by the other parasitoid. A case where the host and parasitoid populations settle into a periodic solution is examined numerically in the next Section.

It is not difficult to show that a stable equilibrium population with only the larva parasitoid can be invaded by the egg parasitoid when the egg parasitoid alone reduces the egg density more than the larva parasitoid alone, that is when

$$E_P^* < E_Q^*. \quad (1.24)$$

To demonstrate this, we compute the Malthusian parameter $\lambda = \lambda_P(E)$ for the egg parasitoid at constant egg density E . Namely, we linearise system (1.1) around the equilibrium, obtaining

$$\frac{dP(t)}{dt} = a_P c_P E P(t - T_{JP}) - d_P P(t) \quad (1.25)$$

where $E = E_Q^*$. We then assume

$$P(t) = e^{\lambda t} P(0) \quad (1.26)$$

and obtain

$$\begin{aligned}\lambda P(t) &= a_P c_P E P(t) e^{-\lambda T_{JP}} - d_P P(t) \\ \lambda &= E a_P c_P e^{-\lambda T_{JP}} - d_P.\end{aligned}\tag{1.27}$$

The egg parasitoid can invade a stable equilibrium community of the larva parasitoid and the host when this equation has a positive real root for $E = E_Q^*$, that is $\lambda_P(E_Q^*) > 0$. The claim that this requires $E_P^* < E_Q^*$ follows because the unique real root $\lambda_P(E)$ increases strictly monotonically with E and $\lambda_P(E_P^*) = 0$. (Note that we do not have to consider complex roots for λ since their real parts cannot exceed the real root.)

In the same way it can be seen that the larva parasitoid can invade a stable equilibrium population with only the egg parasitoid when

$$L_Q^* < L_P^*.\tag{1.28}$$

We speak of mutual invasibility of stable equilibria when

$$E_P^* < E_Q^* \text{ and } L_Q^* < L_P^*.\tag{1.29}$$

The value of the function f defined in (1.21) at the boundary of its domain, relative to the right hand side of (1.22), turns out to be related to the invasibility conditions. Indeed,

$$\begin{aligned}f(0) &= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 \left(\Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(0)} \right) \right) \\ &= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 \left(\Pi_2^{-1} (\Pi_2(Q^*)) \right) \\ &= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 (Q^*) \\ &= \frac{L_Q^*}{E_Q^*}\end{aligned}\tag{1.30}$$

and

$$\begin{aligned}f(P^*) &= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2 \left(\Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(P^*)} \right) \right) \\ &= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2 \left(\Pi_2^{-1} (\Pi_2(0)) \right) \\ &= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2 (0) \\ &= \frac{L_P^*}{E_P^*},\end{aligned}\tag{1.31}$$

which implies that the egg parasitoid can invade a stable equilibrium with the larva parasitoid alone when $f(0) < L_Q^*/E_P^*$ and the larva parasitoid can invade a stable equilibrium with the egg parasitoid alone when $f(P^*) > L_Q^*/E_P^*$.

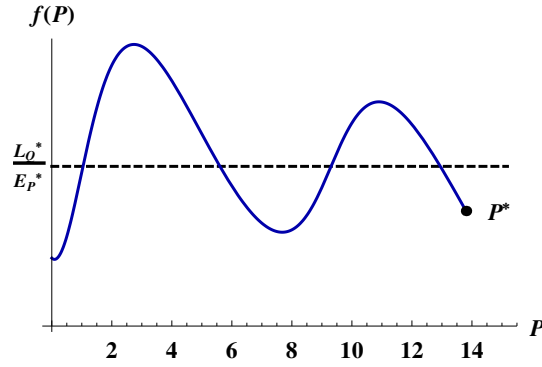


FIGURE 1.1: The graph of the function f which intersects the level L_Q^*/E_P^* when the egg parasitoid density corresponds to a coexistence equilibrium. The maturation delays are distributed with two discrete values each (see 1.B.2). Parameter values are $T_{E_1} = 0.2$, $T_{E_2} = 1.35$, $T_{L_1} = 0.75$, $T_{L_2} = 5$, $r_E = 0.5$, $r_L = 0.3$, $a_P = 2$, $a_Q = 0.2$, $d_E = 0$, $d_L = 0$, $\rho = 500$, $d_P = 8$, $d_Q = 0.175$, $c_P = 0.5$ and $c_Q = 0.5$

1.6 Applying distributions for the maturation delays

We apply several distributions for the maturation delays in order to analyze their influence on the multiplicity of coexistence equilibria. Among those are the constant-duration distribution, (shifted) exponential distribution and (shifted) gamma distribution, which have been introduced in the original paper of Briggs et al., 1993. Here the term 'shifted' refers to including minimal values for the maturation delays. Additionally we introduce a two-value distribution where the maturation delays assume one of two discrete values with certain probabilities.

It turns out that, among these distributions, only the constant-duration and the (non-shifted) exponential distribution yield at most one coexistence equilibrium. For those two distributions the function f is monotonic and therefore the critical horizontal L_Q^*/E_P^* can be crossed at most once. Elementary representations for f in those cases are shown in 1.B. For the case of constant maturation delays, f is decreasing and hence there is a coexistence equilibrium only if $f(0) > L_Q^*/E_P^* > f(P^*)$, implying that neither parasitoid can invade a stable equilibrium of the other parasitoid and the host. For the case of exponentially distributed maturation delays, f is increasing and hence, in the other way around, there must be mutual invasibility of stable equilibria for a coexistence equilibrium to exist.

For all the other distributions (two-value distribution, shifted exponential distribution and (normal or shifted) gamma distribution), we could numerically find parameters so that the graph of f crosses the critical horizontal line multiple times, giving rise to multiple equilibria. Fig. 1.1 shows an example where the graph of f crosses the critical horizontal line four times with two-value distributions for the maturation delays (see caption).

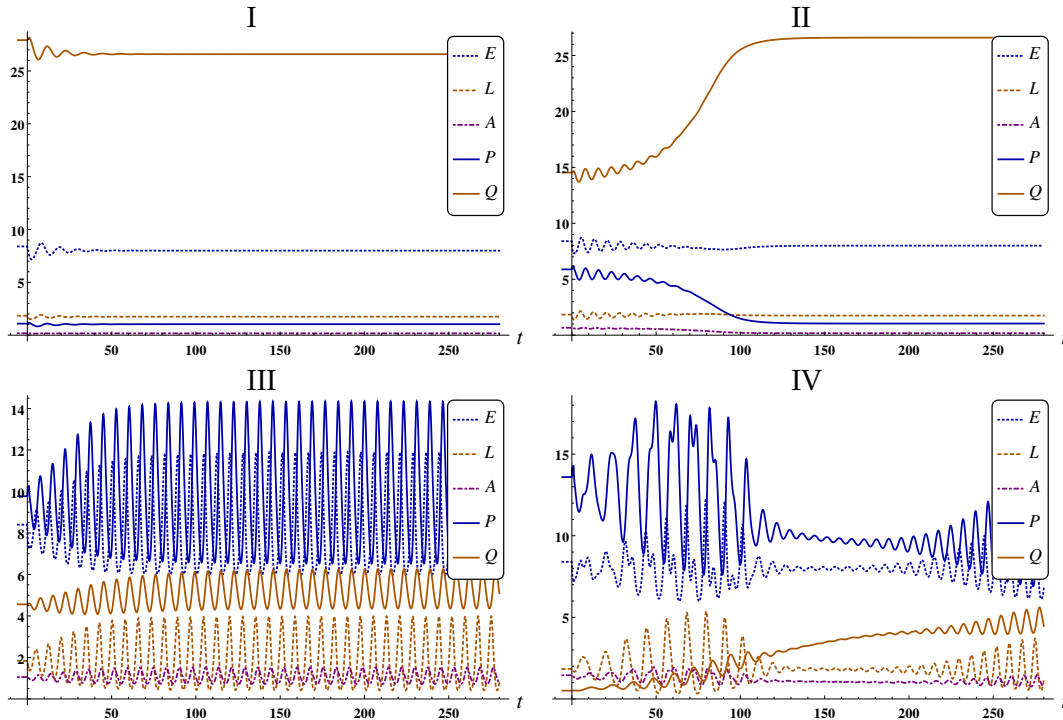


FIGURE 1.2: Time plots of population dynamics after small perturbations from equilibrium densities. The initial densities for $t \leq 0$ are constant and correspond to perturbations from the equilibrium densities indicated by the first (I), second (II), third (III) and fourth (IV) intersection of the graph of f with the critical horizontal in Fig. 1.1. The perturbations consist of increasing all equilibrium densities by 5%. Note that in plot (IV) the same attractor as in plot (III) seems to be approached. Distributions and parameter values are the same as in Fig. 1.1. Additionally $T_{JP} = 1$, $T_{JQ} = 1$ and $d_A = 0.3$

1.6.1 Simulations and stability

To see how the system behaves after a small perturbation from an equilibrium, we computed time plots with the software *Mathematica* shown in Fig. 1.2. The plots reveal that coexistence equilibria can be stable or unstable, possibly giving rise to oscillations around the equilibrium after perturbation. Bifurcation diagrams are shown in Fig. 1.3. The left panel shows how the parameter a_P shifts the horizontal in Fig. 1.1 without changing the function f , and thus we can observe how coexistence equilibria appear and disappear in pairs when changing the parameter. The right panel shows how the adult mortality d_A affects stability without changing the equilibrium values (since this parameter does not occur in the function f or in the level of the critical horizontal line). Low values for d_A seem to stabilize some equilibria while high values for d_A appear to destabilize all equilibria.

We further analyzed the dynamics for low values of the host adult death rate d_A . We show some simulations for that case in the (P, Q) -plane in Fig. 1.4. There we see that the population densities lie on the curve of equation $\Pi_1(P) \frac{\Gamma_2(Q)}{\Gamma_1(P)} = \frac{L_Q^*}{E_P^*}$ and move in a direction depending on the relative position of this curve and the

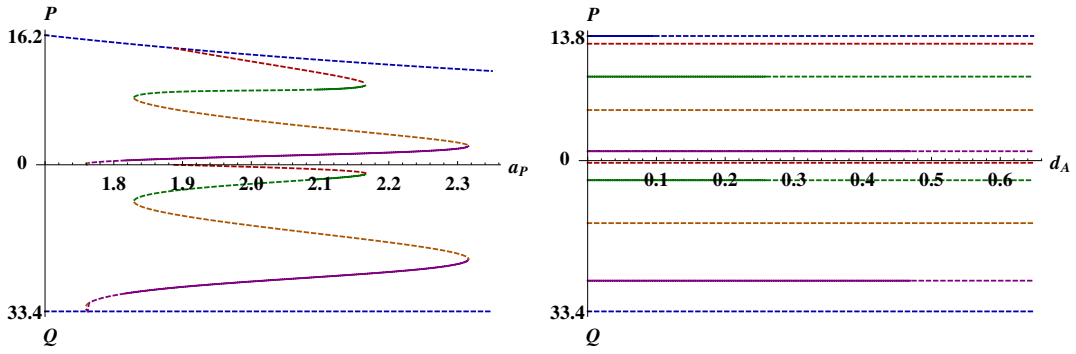


FIGURE 1.3: Bifurcation diagrams showing the equilibrium values for both parasitoid species. The upper vertical axis represents values for P and the lower vertical axis represents values for Q . The outermost lines represent equilibria with only one parasitoid species while the inner equilibria are true coexistence equilibria. Values for P and Q corresponding to the same coexistence equilibrium are drawn with the same color. Stability is indicated by solid (stable) and dashed (unstable) lines. For the stability analysis the eigenvalues of the characteristic equation were calculated with the MATLAB package eigAM/eigTMN by Breda et al., 2014. Parameter values are the same as in Fig. 1.1 and Fig. 1.2 (except axis parameters)

curve $\rho\Pi_1(P)\Pi_2(Q) = 1$. This can be justified through a time-scale argument that we just sketch here, leaving details to future work. For the argument note that $A(t)$ is a slow variable when d_A is low, what can be seen from the models definition (1.1); thus in the fast time-scale $E(t)$, $L(t)$, $P(t)$ and $Q(t)$ will evolve under a constant value for the rate of eggs emerging, see equation (1.7). Numerical evidence suggests that this reduced system always quickly converges to its (quasi)-equilibrium, where $E = E_p^*$, $L = L_Q^*$ and equations (1.8) and (1.9) hold, corresponding to the solid curve in the (P, Q) -plane in Fig. 1.4. Thus, on the slow time-scale, $A(t)$ changes according to the third equation of the system (1.1) with all other state variables at the quasi-equilibrium. It can be easily verified that $A(t)$ will increase or decrease according to whether the basic reproduction number R_0 from equation (1.11) is greater or smaller than 1, thus according to whether (P, Q) is above or below the dashed curve in Fig. 1.4. As at the quasi-equilibrium A and P are related by relation (1.8) with $E = E_p^*$, an increase [decrease] of $A(t)$ corresponds to an increase [decrease] of $P(t)$. This explains why the dynamics in the (P, Q) -plane is towards the right when the dashed curve is above the solid curve ($R_0 > 1$) and towards the left when the dashed curve is below. Since the intersections between the two curves correspond to values of (P, Q) where all state variables are at equilibrium, the previous graphical argument shows that, in the limit of $d_A \rightarrow 0$, an equilibrium is stable when the dashed curve crosses the solid curve from above, while it is unstable when the curves cross in the opposite way.

These findings can be transferred to the shape of the function $f(P)$. Indeed, it can be easily verified that the solid curve is below the dashed curve if and only if $f(P)$

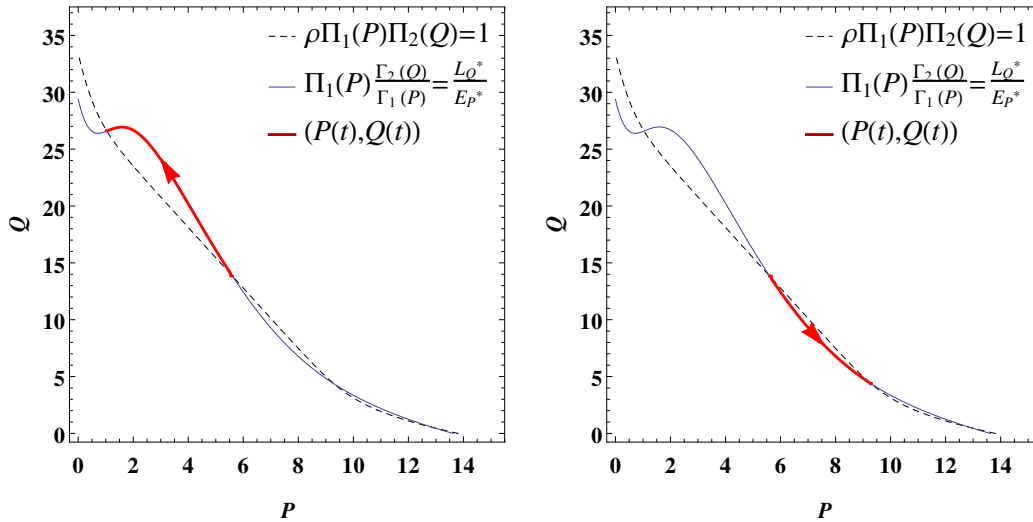
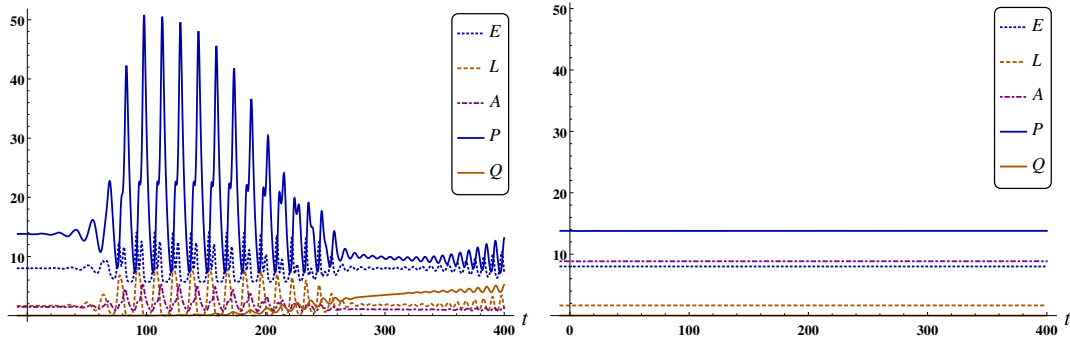


FIGURE 1.4: Parasitoid phase plane with time dynamics. Initial population densities (for $t \leq 0$) correspond to the second coexistence equilibrium from left in Fig. 1.1. Perturbation is introduced via the host adult densities, which are respectively to its equilibrium value decreased by 1% in the left panel and increased by 1% in the right panel. Host adult mortality rate is very low, $d_A = 0.001$. All other parameter values are as in Fig. 1.1 and 1.2

is below L_Q^*/E_P^* . Therefore the findings above imply that coexistence equilibria are stable, for d_A sufficiently small, when $f'(P^{**}) > 0$, while they are unstable when $f'(P^{**}) < 0$. The second statement appears to be true for all $d_A > 0$ but we give a formal proof only for the scenario with constant maturation delays in 1.C.2.

Further investigations of invasibility are illustrated with time plots in Fig. 1.5, where the larva parasitoid is introduced at very low density into an equilibrium system of egg parasitoid and host. This numerical example has important implications concerning invasion and coexistence which go beyond what was found by Briggs et al., 1993. One point is that the invasibility criteria stated in Section 1.5 do hold only for constant equilibria. If a single-parasitoid equilibrium is unstable with respect to the interaction of this parasitoid and the host, it has no sense to investigate its invasibility by the other parasitoid. Instead one should (numerically) find the single parasitoid-host attractor and investigate its invasibility (Metz et al., 1992). One may actually do this in one go by using the introduction of the second parasitoid as a way to perturb the unstable equilibrium as done in Fig. 1.5. As this figure reveals, oscillations may facilitate successful invasion in the sense that the second parasitoid is successful when the single parasitoid equilibrium is unstable ($d_A = 0.3$), while being unsuccessful in case it is stable ($d_A = 0.05$) since $L_P^* < L_Q^*$. By combining Fig. 1.5b with the right panel of Fig. 1.3 another conclusion emerges: non-invasibility of a stable single-parasitoid equilibrium does not exclude the possibility of stable equilibrium coexistence of the two parasitoids (indeed, for $d_A = 0.05$ we observe in Fig. 1.3 that simultaneously the equilibrium with only the egg parasitoid, and two coexistence equilibria are stable).



(A) For $d_A = 0.3$ the equilibrium of host and egg parasitoid is unstable and the larva parasitoid can invade through oscillations

(B) For $d_A = 0.05$ the equilibrium of host and egg parasitoid is stable and the larva parasitoid cannot invade

FIGURE 1.5: Time plots of population dynamics after introducing the larva parasitoid into an equilibrium system of egg parasitoid and host. The system is started with constant population densities for $t \leq 0$ corresponding to the equilibrium densities of egg parasitoid and host with additional a low density $Q = 0.01$ of the larva parasitoid. Distributions and parameter values are the same as in Fig. 1.1 and 1.2 with exception of a lower value for d_A in the right panel

1.7 Discussion

We found multiple (non-trivial) coexistence equilibria in a model for the population dynamics of two parasitoids attacking different juvenile stages of a common host. The model was introduced by Briggs et al. (1993) and it involves distributed maturation delays for the host juvenile stages. We have shown that, depending on the distributions of the maturation delays, multiple coexistence equilibria can arise. To our knowledge, this is the first documented example of multiple coexistence equilibria in a parasitoid-host model, as well as the first example for the multiplicity of coexistence equilibria to depend on the distribution of maturation delays.

Non steady-state attractors in parasitoid-host systems, in contrast, have received considerable attention before. Already the dynamics of the classical discrete-time model by Nicholson and Bailey (1935) are known to be oscillatory: one or both species go extinct after diverging oscillations around the unstable coexistence equilibrium. In a continuous-time parasitoid-host model by Murdoch et al. (1987), stability of a steady-state coexistence attractor can be facilitated by an invulnerable host stage. For modifications of this model, multiple non steady-state attractors have been found by Murdoch et al. (1992) and Murdoch et al. (1997), Briggs (1993) and Briggs et al. (1999). Particularly Briggs (1993) shows that such non steady-state attractors can lead to parasitoid coexistence in situations where no stable coexistence equilibrium is predicted. Further Sieber and Hilker (2011) report multiple (non-)equilibrium attractors in a single host population that is exploited by microparasites and predators. Beyond that, there is a well-developed body of theory on coexistence

in variable environments (deterministic and stochastic), see for example the works by Abrams (1984), Chesson (1994) and Li et al. (2016). Occurrence of oscillations in real parasitoid populations is documented by Godfray and Hassell, 1989, who offer a review on oscillations of host parasitoid systems in the tropics and corresponding discrete and continuous models.

In our model we found that equilibria can have different properties. Single parasitoid equilibria are potentially stable and non-invadable only when the host stage of the other parasitoid is reduced more strongly than what would be needed by the competitor to sustain. Similarly we found that two-parasitoid coexistence equilibria are "potentially stable" only when increasing a parasitoid species reduces its own host stage relatively to its competitors host stage when the competing parasitoid species is chosen accordingly so that the host stays at equilibrium. Coexistence equilibria for which this is not the case turned out to be always unstable. This can be interpreted as a manifestation of the principle that coexistence of competitors can be possible only when intraspecific competition is stronger than interspecific competition, see for example the review by Chesson (2000). For the potentially stable equilibria we found that stability can be always altered with the parameter d_A of host adult mortality (which does not change the equilibrium values due to the way the model is parameterized). Especially, we found that low values for d_A generally stabilize potentially stable equilibria. In the other way around we found that high values for d_A are always destabilizing. This is similar to the observations of Murdoch et al. (1987), who found for a similar single-parasitoid model that stable equilibria can exist only when there is a sufficiently long invulnerable adult stage of the host. We made several observations concerning invasibility and single-parasitoid equilibria in the model. One point is that in the presence of multiple coexistence equilibria, stable coexistence can occur without mutual invasibility. We described a situation where the parasitoids can coexist although the larva parasitoid cannot invade a stable equilibrium of egg parasitoid and host ($L_P^* < L_Q^*$). This is similar to the findings of Buonomo and Cerasuolo (2014) in a model for plants and parasites. Our example also shows that host juvenile densities can increase when an additional parasitoid is introduced since the equilibrium larva density with the egg parasitoid alone L_P^* is lower than the equilibrium larva density L_Q^* when both parasitoids coexist. Analogous examples can be found for situations where introducing the egg parasitoid increases the equilibrium egg density. These findings differ from those of other authors including Briggs (1993) and Briggs et al. (1993), who assume that stable coexistence requires mutual invasibility, and conclude that (in the absence of other mechanisms such as hyperparasitism) introducing a second parasitoid cannot lead to higher equilibrium densities of host juveniles. This is interesting in the light of the discussion whether single or multiple parasitoids should be introduced for optimal biological pest control, see for example the contributions by Ehler (1990) and Pedersen and Mills (2004). Furthermore we found that the invasibility criterion

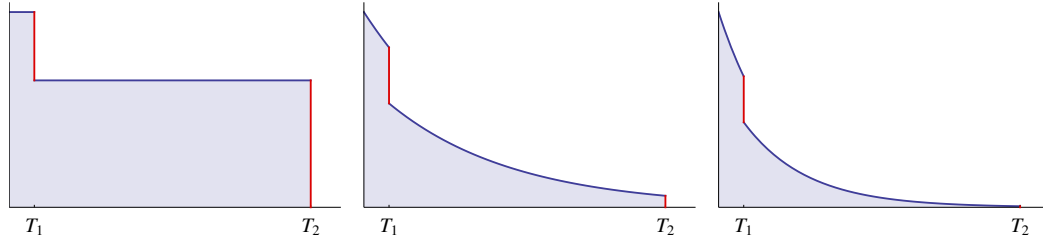


FIGURE 1.6: Age distribution of a host juvenile stage subjected to constant parasitism pressure $a_P P$ or $a_Q Q$ equal to 0, 0.2 or 0.4 (from left to right; note that there is no background death rate). The maturation delay for the stage is distributed by two discrete values T_1 and T_2 which occur with probabilities r and $1 - r$. The area under the curve represents the expectation value Γ_i for the time in this stage, while the sum of the lengths of the vertical bars at the times T_1 and T_2 represents the probability Π_i to reach the next stage. The ratio Γ_i/Π_i equals approximately 8.8, 9.5 and 7.9 from left to right, and thus first increases and then decreases with increasing parasitism. Parameter values are: $r = 0.35$, $T_1 = 1$, $T_2 = 12$

suggested by Briggs et al. (1993) is not generally valid when there are multiple coexistence equilibria. The original criterion states that a parasitoid species can invade only if its growth rate is positive at the equilibrium host density set by the resident parasitoid. We found however that if there are multiple coexistence equilibria, and the residents single-parasitoid equilibrium is not stable, invasion of the other parasitoid can take place through oscillations eventually leading to coexistence of both parasitoids. This is related to the findings on invasion in oscillating conditions by Armstrong and McGehee (1980), Bacaër and Guernaoui (2006), Greenman and Norman (2007) and Bate and Hilker (2013). Since in our model such situations occurred only when there are multiple coexistence equilibria we conjecture that this is indeed a necessary condition.

The question remains of when coexistence equilibria can arise generally and what is the connection to the maturation delays of the hosts. A literature search reveals that the occurrence of multiple equilibria in population models is generally connected to some non-linearity or non-monotonicity in the interaction of different species. Evidence for that can be found in several models based on ordinary differential equations. Pimenov et al. (2015) find that in a predator-prey model, multiple coexistence equilibria can arise when the prey changes its behavior in dependence of the predator density. Similarly Freeze et al., 2014 find multiple coexistence equilibria in a three species model where a super predator changes feeding behavior in dependence of its prey species densities. Buonomo and Cerasuolo (2014) find multiple coexistence equilibria in a model with host plants that react to parasitism in a non-linear way. We found in our model too that multiple coexistence equilibria can occur only when the host larva-egg proportion depends in a non-monotonic way on the density of one parasitoid while the other parasitoid density is kept so that the host stays at equilibrium. We have seen that this can never happen for two important special cases: constant and exponentially distributed maturation delays. For constant maturation

delays, increasing one parasitoid (and decreasing the other parasitoid accordingly) increases its own host stage relatively to the host stage of the competitor, which additionally implies that if there is a coexistence equilibrium, it is unstable and neither parasitoid can invade a stable population with the other parasitoid. Conversely for exponentially distributed maturation delays, increasing a parasitoid (and again decreasing the other parasitoid accordingly) reduces its host stage relatively to the host stage of the competitor, which additionally implies pairwise invasibility when there is a coexistence equilibrium. For all other distributions we investigated, the parasitoid densities can affect the hosts larva-egg proportion in a non-monotonic fashion giving rise to multiple coexistence equilibria. An illustration of how this can happen with the two-value distributions we used in our numerical examples is shown in Fig. 1.6. There we show the expected duration Γ_i of a juvenile stage and the probability Π_i to reach the next stage, both for different densities of the corresponding parasitoid. We see that increasing the parasitoid density first decreases Π_i heavily because only a small part of the hosts with long maturation delay reaches maturation, while further increasing the parasitoid density decreases Γ_i more strongly because parasitism still mainly affects hosts with a long maturation delay whose contribution to Π_i was already low. Such mechanisms can lead to a non-monotonic relation between the parasitoid densities and the hosts larva-egg proportion, what potentially gives rise to multiple coexistence equilibria. Note however that the ratio of a parasitoids host stage and the other parasitoids host stage is according to (1.21) and (1.23) not only proportional to Γ_i/Π_i but depends also on $\Gamma_j(\Pi_j^{-1}(\frac{1}{\rho\Pi_i}))$ (where j refers to the other parasitoids host stage); thus this graphical illustration is incomplete, but still, in our view, sheds some light on the mechanisms through which the distribution of maturation delays affects coexistence equilibria.

Appendix

1.A Transition probabilities and expected duration of the stages

Here we derive formulas for the transition probabilities from egg to larva $\Pi_1(P)$ and from larva to adult $\Pi_2(Q)$, and for the expected duration of the egg, larva and adult stage, $\Gamma_1(P)$, $\Gamma_2(Q)$ and Γ_3 respectively. The calculations are valid for constant parasitoid densities P and Q . We use the following notations for the various random variables

random variable	density	description
X_E	$w_E(\tau)$	time needed for egg maturation
X_L	$w_L(\tau)$	time needed for larva maturation
K_E	$(a_P P + d_E)e^{-\tau(a_P P + d_E)}$	time until an egg dies or is infected (when it does not mature before), distributed exponentially
K_L	$(a_Q Q + d_L)e^{-\tau(a_Q Q + d_L)}$	time until a larva dies or is infected (when it does not mature before), distributed exponentially
K_A	$d_A e^{-\tau d_A}$	time until an adult dies, distributed exponentially

1.A.1 Transition probabilities $\Pi_1(P)$ and $\Pi_2(Q)$

When the parasitoid densities are constant, the probability for a freshly laid egg to mature to a larva is

$$\begin{aligned}
 \Pi_1(P) &= \mathbb{P}[X_E < K_E] \\
 &= \int_0^\infty \int_\tau^\infty w_E(\tau) (a_P P + d_E) e^{-(a_P P + d_E)\sigma} d\sigma d\tau \\
 &= \int_0^\infty w_E(\tau) e^{-(a_P P + d_E)\tau} d\tau,
 \end{aligned} \tag{1.32}$$

where we use the independence of X_E and K_E . Likewise the probability for a freshly hatched larva to mature to an adult is given by

$$\Pi_2(Q) = \mathbb{P}[X_L < K_L] = \int_0^\infty w_L(\tau) e^{-(a_Q Q + d_L)\tau} d\tau. \tag{1.33}$$

Obviously Π_1 and Π_2 decrease strictly monotonically to 0.

1.A.2 Expectation values for the durations of different stages

When the parasitoid densities are constant, the expected duration of the egg stage (which is either terminated by death of the egg or maturation to a larva) is for $a_P P + d_E \neq 0$

$$\begin{aligned}
\Gamma_1(P) &= \mathbb{E}[\min\{K_E, X_E\}] \\
&= \mathbb{E}[K_E | K_E \leq X_E] \mathbb{P}[K_E \leq X_E] + \mathbb{E}[X_E | X_E < K_E] \mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E | K_E \leq X_E] \mathbb{P}[K_E \leq X_E] \\
&\quad + (\mathbb{E}[K_E | X_E < K_E] - \mathbb{E}[K_E - X_E | X_E < K_E]) \mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E | K_E \leq X_E] \mathbb{P}[K_E \leq X_E] \\
&\quad + (\mathbb{E}[K_E | X_E < K_E] - \mathbb{E}[K_E]) \mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E] - \mathbb{E}[K_E] \mathbb{P}[X_E < K_E] \\
&= \frac{1}{a_P P + d_E} (1 - \Pi_1(P))
\end{aligned} \tag{1.34}$$

where we used that K_E is exponentially distributed.

For $a_P P + d_E = 0$ obviously

$$\Gamma_1(0) = \mathbb{E}[X_E]. \tag{1.35}$$

In the same way the expected duration of the larva stage (given that it is reached) can be calculated for constant parasitoid densities and $a_Q Q + d_L \neq 0$,

$$\Gamma_2(Q) = \mathbb{E}[\min\{K_L, X_L\}] = \frac{1}{a_Q Q + d_L} (1 - \Pi_2(Q)) \tag{1.36}$$

and for $a_Q Q + d_L = 0$

$$\Gamma_2(0) = \mathbb{E}[X_L]. \tag{1.37}$$

Note that the expectation values of K_E and K_L and thus Γ_1 and Γ_2 decrease strictly monotonically with the corresponding parasitoid densities.

The expected duration of the adult stage of a freshly emerged adult is

$$\Gamma_3 = \mathbb{E}[K_A] = \frac{1}{d_A}. \tag{1.38}$$

1.B Computing f for some distributions

Elementary representations for the function f from equation (1.21) can be found for some distribution families for the maturation delays. To facilitate the computations, we rearrange f by using the formulas for Γ_1 and Γ_2 derived in 1.A.2 (assuming that

$a_P P + d_E$ and $a_Q \Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(P)} \right) + d_L$ are non-zero),

$$\begin{aligned}
 f(P) &= \frac{\Pi_1(P)}{\Gamma_1(P)} \Gamma_2 \left(\Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(P)} \right) \right) \\
 &= \frac{\Pi_1(P)}{\frac{1-\Pi_1(P)}{a_P P + d_E}} \frac{1 - \Pi_2 \left(\Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(P)} \right) \right)}{a_Q \Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(P)} \right) + d_L} \\
 &= (a_P P + d_E) \frac{\Pi_1(P)}{1 - \Pi_1(P)} \frac{1 - \frac{1}{\rho \Pi_1(P)}}{a_Q \Pi_2^{-1} \left(\frac{1}{\rho \Pi_1(P)} \right) + d_L}.
 \end{aligned} \tag{1.39}$$

Now the following formulas for f in the special cases can be easily verified.

1.B.1 Constant durations

The maturation from egg to larva and from larva to adult takes a constant time T_E and T_L respectively. For this distribution

$$\begin{aligned}
 \Pi_1(P) &= e^{-(a_P P + d_E) T_E} \\
 \Pi_2(Q) &= e^{-(a_Q Q + d_L) T_L}
 \end{aligned} \tag{1.40}$$

and (for $d_E > 0$ and $d_L > 0$)

$$f(P) = \frac{T_L (a_P P + d_E) \left(\rho e^{-(a_P P + d_E) T_E} - 1 \right)}{\rho (\log(\rho) - (a_P P + d_E) T_E) (1 - e^{-(a_P P + d_E) T_E})}. \tag{1.41}$$

The function $f(P)$ decreases strictly monotonically in its domain $P \in [0, P^*]$ with $P^* = (\log(\rho) - d_L T_L - d_E T_E) / (T_E a_P)$ obtained by solving (1.13).¹ Therefore the arguments of Section 1.4.3 and 1.5 show that a coexistence equilibrium is necessarily unique and arises only when none of the parasitoids can invade an equilibrium population of the other parasitoid and the host. To prove the monotonicity of $f(P)$ we define $\gamma = (a_P P + d_E) T_E$ and $q = \log(\rho)$. The domain for P implies that $0 < \gamma < q$. Obviously $f(P)$ is decreasing if the following function $g(\gamma)$ is decreasing,

$$g(\gamma) = e^q \frac{T_E}{T_L} f(P) = \frac{\gamma (e^\gamma - e^q)}{(\gamma - q) (e^\gamma - 1)}. \tag{1.42}$$

To prove the desired monotonicity of $g(\gamma)$, we take the derivative by γ and show that $g_\gamma(\gamma) < 0$ for $0 < \gamma < q$. Differentiation yields

$$g_\gamma(\gamma) = \frac{e^\gamma (q + q\gamma - \gamma^2) + e^{q+\gamma} (q - q\gamma + \gamma^2) - qe^{2\gamma} - e^q q}{(\gamma - q)^2 (e^\gamma - 1)^2} \tag{1.43}$$

¹Note that for $d_E = 0$ or $d_L = 0$, the stated representation of $f(P)$ is undefined at the boundary of its domain but our result on monotonicity stays generally valid for the original function defined in (1.21). This can be verified by a simple limit argument.

and the numerator (now interpreted as a function of q for any $\gamma > 0$)

$$k(q) = e^\gamma (q + q\gamma - \gamma^2) + e^{q+\gamma} (q - q\gamma + \gamma^2) - qe^{2\gamma} - e^q q \quad (1.44)$$

determines the sign of $g_\gamma(\gamma)$. The first two derivatives of $k(q)$ by q are

$$\begin{aligned} k_q(q) &= e^{q+\gamma} (q - q\gamma + \gamma^2 + 1 - \gamma) - e^q(1 + q) - e^{2\gamma} + e^\gamma(\gamma + 1) \\ k_{qq}(q) &= e^q (e^\gamma (q - q\gamma + \gamma^2 - 2\gamma + 2) - q - 2). \end{aligned} \quad (1.45)$$

It can be easily seen that the equation $k_{qq}(q) = 0$ has only one solution for q . Therefore $k_q(q) = 0$ has at most two solutions and $k(q)$ has at most two (local) extrema.

Moreover, we see that $k(0) = k(\gamma) = 0$, that $k(q) \xrightarrow{q \rightarrow -\infty} \infty$ (the dominant term being qe^γ with coefficient $1 + \gamma - e^\gamma$), and that $k(q) \xrightarrow{q \rightarrow \infty} -\infty$ (the dominant term being qe^q with coefficient $e^\gamma(1 - \gamma) - 1$). Since $k_q(\gamma) = 0$, this implies $k(q) < 0$ for $q > \gamma$ (and actually $k(q) \leq 0$ for $q \geq 0$). This completes the proof that $f(P)$ decreases strictly monotonically.

1.B.2 Two-value distribution

The maturation delay from egg to larva and from larva to adult are each distributed with two distinct values that occur with certain probabilities. The transformation from egg to larva has length T_{E_1} with probability r_E and length T_{E_2} with probability $1 - r_E$. The transformation from larva to adult has length T_{L_1} with probability r_L and length T_{L_2} with probability $1 - r_L$. For this distribution

$$\begin{aligned} \Pi_E(P) &= r_E e^{(a_P P + d_E) T_{E_1}} + (1 - r_E) e^{(a_P P + d_E) T_{E_2}} \\ \Pi_L(Q) &= r_L e^{(a_Q Q + d_L) T_{L_1}} + (1 - r_L) e^{(a_Q Q + d_L) T_{L_2}}. \end{aligned} \quad (1.46)$$

Π_L^{-1} and therefore f have no elementary representations. The numerical example presented in Fig. 1.1 shows however that f can be non-monotonic and that therefore multiple coexistence equilibria can occur.

1.B.3 Exponential distribution

The maturation delays from egg to larva and from larva to adult are exponentially distributed with expectation $1/\lambda_E$ and $1/\lambda_L$ respectively. For this distribution

$$\begin{aligned} \Pi_1(P) &= \frac{\lambda_E}{a_P P + d_E + \lambda_E} \\ \Pi_2(Q) &= \frac{\lambda_L}{a_Q Q + d_L + \lambda_L} \end{aligned} \quad (1.47)$$

and

$$f(P) = \frac{a_P P + d_E + \lambda_E}{\rho \lambda_L}. \quad (1.48)$$

Obviously $f(P)$ increases strictly monotonically in this case. Therefore the arguments of Section 1.4.3 and 1.5 state that a coexistence equilibrium is necessarily unique and arises only in the case of mutual invasibility.

1.B.4 Shifted exponential distribution

The maturation delay from egg to larva and from larva to adult have shifted exponential distributions. They have a minimum duration of m_E and m_L respectively, followed by an additional time which is distributed exponentially with expectation $1/\lambda_E$ and $1/\lambda_L$ respectively. For this distribution

$$\begin{aligned}\Pi_E(P) &= e^{-(a_P P + d_E)m_E} \frac{\lambda_E}{a_P P + d_E + \lambda_E} \\ \Pi_L(Q) &= e^{-(a_Q Q + d_L)m_L} \frac{\lambda_L}{a_Q Q + d_L + \lambda_L}.\end{aligned}\tag{1.49}$$

Π_L^{-1} and therefore f have no elementary representations. Numerical calculations show that f can become non-monotonous and therefore multiple equilibria can arise.

1.B.5 Gamma distribution

The maturation delay from egg to larva and from larva to adult have gamma distributions with shape parameter p_E and p_L respectively and inverse scale parameter λ_E and λ_L respectively. For this distribution

$$\begin{aligned}\Pi_E(P) &= \left(\frac{\lambda_E}{a_P P + d_E + \lambda_E} \right)^{p_E} \\ \Pi_L(Q) &= \left(\frac{\lambda_L}{a_Q Q + d_L + \lambda_L} \right)^{p_L}.\end{aligned}\tag{1.50}$$

Π_L^{-1} and therefore f have elementary representations,

$$f(P) = \frac{(a_P P + d_E) \left((a_P P + d_E + \lambda_E)^{p_E} - \rho \lambda_E^{p_E} \right) \left(\frac{\lambda_E^{-p_E} (a_P P + d_E + \lambda_E)^{p_E}}{\rho} \right)^{1/p_L}}{\lambda_L \rho \left((a_P P + d_E + \lambda_E)^{p_E} - \lambda_E^{p_E} \right) \left(\left(\frac{\lambda_E^{-p_E} (a_P P + d_E + \lambda_E)^{p_E}}{\rho} \right)^{1/p_L} - 1 \right)}.\tag{1.51}$$

Numerical calculations show that f can become non-monotonous and therefore multiple equilibria can arise, see Fig. 1.7.

1.B.6 Shifted gamma distribution

The maturation delay from egg to larva and from larva to adult have shifted gamma distributions. They have a minimum duration of m_E and m_L respectively, followed by an additional time which is gamma distributed with shape parameter p_E and p_L

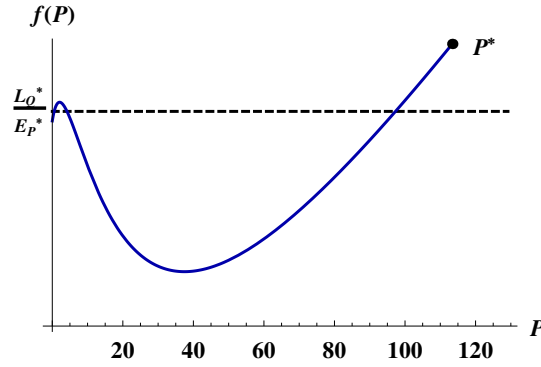


FIGURE 1.7: The graph of the function f with gamma distributed maturation delays. Parameter values are $p_E = 2$, $p_L = 5$, $\lambda_E = 1$, $\lambda_L = 1$, $a_P = 0.198$, $a_Q = 1$, $d_E = 0$, $d_L = 0$, $\rho = 550$, $d_P = 1$, $d_Q = 1$, $c_P = 1$ and $c_Q = 1$

respectively and inverse scale parameter λ_E and λ_L respectively. For this distribution

$$\begin{aligned}\Pi_E(P) &= e^{-(a_P P + d_E)m_E} \left(\frac{\lambda_E}{a_P P + d_E + \lambda_E} \right)^{p_E} \\ \Pi_L(Q) &= e^{-(a_Q Q + d_L)m_L} \left(\frac{\lambda_L}{a_Q Q + d_L + \lambda_L} \right)^{p_L}.\end{aligned}\tag{1.52}$$

Π_L^{-1} and therefore f have no elementary representations. As with the non-shifted gamma distribution, f can become non-monotonous and therefore multiple equilibria can arise.

1.C Characteristic equation

Here we derive a characteristic equation by considering a small perturbation from an equilibrium $(\bar{E}, \bar{L}, \bar{A}, \bar{P}, \bar{Q})$,

$$\begin{aligned}E(t) &= \bar{E} + e(t), \quad L(t) = \bar{L} + l(t), \quad A(t) = \bar{A} + a(t) \\ P(t) &= \bar{P} + p(t), \quad Q(t) = \bar{Q} + q(t)\end{aligned}\tag{1.53}$$

and assume that

$$\begin{aligned}e(t) &= h_E e^{\lambda t}, \quad l(t) = h_L e^{\lambda t}, \quad a(t) = h_A e^{\lambda t} \\ p(t) &= h_P e^{\lambda t}, \quad q(t) = h_Q e^{\lambda t}.\end{aligned}\tag{1.54}$$

The aim of the characteristic equation is to investigate stability of an equilibrium by the complex roots for λ . An equilibrium is stable when all roots have negative real parts while it is unstable when there are roots with positive real part, see (Diekmann

et al., 1995). In order to derive the characteristic equation, we define

$$\begin{aligned}
\bar{R}_E &:= \rho d_A \bar{A} \\
\gamma_E &:= a_P \bar{P} + d_E \\
\gamma_L &:= a_Q \bar{Q} + d_L \\
\bar{M}_E &:= \int_0^\infty \bar{R}_E e^{-x_E \gamma_E} w_E(x_E) dx_E \\
\bar{M}_L &:= \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} w_L(x_L) dx_L
\end{aligned} \tag{1.55}$$

and

$$\begin{aligned}
r_E(t) &:= R_E(t) - \bar{R}_E \\
&= \rho d_A A(t) - \bar{R}_E \\
&= \rho d_A (\bar{A} + a(t)) - \bar{R}_E \\
&= \rho d_A a(t)
\end{aligned} \tag{1.56}$$

and

$$\begin{aligned}
m_E(t) &:= M_E(t) - \bar{M}_E \\
&= \int_0^\infty R_E(t - x_E) S_E(x_E, t) w_E(x_E) dx_E - \bar{M}_E \\
&= \int_0^\infty (\bar{R}_E + r_E(t - x_E)) e^{-x_E \gamma_E} e^{-a_P \int_{t-x_E}^t p(y) dy} w_E(x_E) dx_E - \bar{M}_E \\
&= \int_0^\infty (\bar{R}_E + r_E(t - x_E)) e^{-x_E \gamma_E} \left(1 - a_P \int_{t-x_E}^t p(y) dy \right) w_E(x_E) dx_E - \bar{M}_E \\
&= \int_0^\infty r_E(t - x_E) e^{-x_E \gamma_E} w_E(x_E) dx_E \\
&\quad - \int_0^\infty \bar{R}_E e^{-x_E \gamma_E} a_P \int_{t-x_E}^t p(y) dy w_E(x_E) dx_E
\end{aligned} \tag{1.57}$$

where we use that $e^x \approx 1 + x$ for small x and that $r_E(t - x_E)p(y) \approx 0$. In the same way

$$\begin{aligned}
m_L(t) &:= M_L(t) - \bar{M}_L \\
&= \int_0^\infty m_E(t - x_L) e^{-x_L \gamma_L} w_L(x_L) dx_L \\
&\quad - \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} a_Q \int_{t-x_L}^t q(y) dy w_L(x_L) dx_L \\
&= \int_0^\infty \left(\int_0^\infty r_E(t - x_E - x_L) e^{-x_E \gamma_E} w_E(x_E) dx_E \right. \\
&\quad \left. - \int_0^\infty \bar{R}_E e^{-x_E \gamma_E} a_P \int_{t-x_E-x_L}^{t-x_L} p(y) dy w_E(x_E) dx_E \right) \cdot e^{-x_L \gamma_L} w_L(x_L) dx_L \\
&\quad - \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} a_Q \int_{t-x_L}^t q(y) dy w_L(x_L) dx_L.
\end{aligned} \tag{1.58}$$

Now we can state the derivatives

$$\begin{aligned}
\dot{e}(t) &= \dot{E}(t) = R_E(t) - M_E(t) - a_P E(t) P(t) - d_E E(t) \\
&= \bar{R}_E + r_E(t) - (\bar{M}_E + m_E(t)) - a_P (\bar{E} + e(t)) (\bar{P} + p(t)) - d_E (\bar{E} + e(t)) \quad (1.59) \\
&= r_E(t) - m_E(t) - a_P (\bar{E} p(t) + e(t) \bar{P}) - d_E e(t)
\end{aligned}$$

where we use that $\bar{R}_E - \bar{M}_E - a_P \bar{E} \bar{P} - d_E \bar{E} = 0$ and $e(t)p(t) \approx 0$. In the same way

$$\begin{aligned}
\dot{l}(t) &= m_E(t) - m_L(t) - a_Q (\bar{L} q(t) + l(t) \bar{Q}) - d_L l(t) \\
\dot{a}(t) &= m_L(t) - d_A a(t) \\
\dot{p}(t) &= c_P a_P (\bar{E} p(t - T_{JP}) + e(t - T_{JP}) \bar{P}) - d_P p(t) \\
\dot{q}(t) &= c_Q a_Q (\bar{L} q(t - T_{JQ}) + l(t - T_{JQ}) \bar{Q}) - d_Q q(t).
\end{aligned} \quad (1.60)$$

We introduce the notation

$$\begin{aligned}
\bar{\Pi}_1 &:= \Pi_1(\bar{P}) = \int_0^\infty e^{-x_E \gamma_E} w_E(x_E) dx_E \\
\bar{\Pi}_2 &:= \Pi_2(\bar{Q}) = \int_0^\infty e^{-x_L \gamma_L} w_L(x_L) dx_L \\
\bar{\Pi}_1(\lambda) &:= \Pi_1(\bar{P} + \frac{\lambda}{a_P}) = \int_0^\infty e^{-x_E (\gamma_E + \lambda)} w_E(x_E) dx_E \\
\bar{\Pi}_2(\lambda) &:= \Pi_2(\bar{Q} + \frac{\lambda}{a_Q}) = \int_0^\infty e^{-x_L (\gamma_L + \lambda)} w_L(x_L) dx_L
\end{aligned} \quad (1.61)$$

and obtain the following by plugging (1.54) into (1.59) and (1.60)

$$\begin{aligned}
\lambda h_E &= \rho d_A \left(h_A - h_A \bar{\Pi}_1(\lambda) + \bar{A} a_P h_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right) - a_P (\bar{E} h_P + h_E \bar{P}) - d_E h_E \\
\lambda h_L &= \rho d_A \left(h_A \bar{\Pi}_1(\lambda) - \bar{A} a_P h_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} - h_A \bar{\Pi}_1(\lambda) \bar{\Pi}_2(\lambda) + \bar{A} a_P h_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \bar{\Pi}_2(\lambda) \right. \\
&\quad \left. + \bar{A} a_Q h_Q \bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right) - a_Q (\bar{L} h_Q + h_L \bar{Q}) - d_L h_L \\
\lambda h_A &= \rho d_A \left(h_A \bar{\Pi}_1(\lambda) \bar{\Pi}_2(\lambda) - \bar{A} a_P h_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \bar{\Pi}_2(\lambda) - \bar{A} a_Q h_Q \bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right) - d_A h_A \\
\lambda h_P &= a_P c_P e^{-\lambda T_{JP}} (\bar{E} h_P + h_E \bar{P}) - d_P h_P \\
\lambda h_Q &= a_Q c_Q e^{-\lambda T_{JQ}} (\bar{L} h_Q + h_L \bar{Q}) - d_Q h_Q
\end{aligned} \quad (1.62)$$

where we divide on both sides by $e^{\lambda t}$ and use that $\bar{M}_E = \rho d_A \bar{A} \bar{\Pi}_1$. From the last two equations of (1.62) we can express h_p and h_q explicitly in terms of h_e and h_l as

$$\begin{aligned}
h_P &= h_E \Phi_P(\lambda) \quad \text{where} \quad \Phi_P(\lambda) = \frac{\bar{P} a_P c_P e^{-\lambda T_{JP}}}{\lambda + d_P - a_P c_P \bar{E} e^{-\lambda T_{JP}}} \\
h_Q &= h_L \Phi_Q(\lambda) \quad \text{where} \quad \Phi_Q(\lambda) = \frac{\bar{Q} a_Q c_Q e^{-\lambda T_{JQ}}}{\lambda + d_Q - a_Q c_Q \bar{L} e^{-\lambda T_{JQ}}}.
\end{aligned} \quad (1.63)$$

Using the solutions from (1.63) and the first two equations in (1.62) we can express h_E and h_L in the following form,

$$\begin{aligned}
h_E &= h_A \Phi_E(\lambda) \\
\text{where } \Phi_E(\lambda) &= \frac{\rho d_A (1 - \bar{\Pi}_1(\lambda))}{\lambda + d_E + a_P \bar{P} + \Phi_P(\lambda) \left(a_P \bar{E} - \rho d_A \bar{A} a_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)} \\
h_L &= h_A \Phi_L(\lambda) \\
\text{where } \Phi_L(\lambda) &= \frac{\rho d_A \left(\bar{\Pi}_1(\lambda) (1 - \bar{\Pi}_2(\lambda)) - \Phi_E(\lambda) \Phi_P(\lambda) \bar{A} a_P (1 - \bar{\Pi}_2(\lambda)) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}{\lambda + d_L + a_Q \bar{Q} + \Phi_Q(\lambda) \left(a_Q \bar{L} - \rho d_A \bar{A} a_Q \bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right)}. \tag{1.64}
\end{aligned}$$

Plugging h_P , h_Q , h_E and h_L in the third equation of (1.62) we have the characteristic equation in the form $G(\lambda) = 1$,

$$\begin{aligned}
G(\lambda) &= \\
\frac{\rho d_A}{\lambda + d_A} &\left(\bar{\Pi}_1(\lambda) \bar{\Pi}_2(\lambda) - \bar{A} a_P \bar{\Pi}_2(\lambda) \Phi_P(\lambda) \Phi_E(\lambda) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} - \bar{A} a_Q \bar{\Pi}_1 \Phi_Q(\lambda) \Phi_L(\lambda) \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right). \tag{1.65}
\end{aligned}$$

1.C.1 A sufficient condition for instability

The following observation can be helpful for proving instability of an equilibrium. It is easily verified that $G(\lambda) \xrightarrow{\lambda \rightarrow \infty} 0$. Hence if $G(0) > 1$ then there is a positive real root for the characteristic equation and the coexistence equilibrium is unstable. Therefore we investigate the structure of $G(0)$. First we see that

$$\begin{aligned}
\lim_{\lambda \rightarrow 0} \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} &= -\frac{d\bar{\Pi}_1/d\bar{P}}{a_P} \\
\lim_{\lambda \rightarrow 0} \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} &= -\frac{d\bar{\Pi}_2/d\bar{Q}}{a_Q}. \tag{1.66}
\end{aligned}$$

We will denote $\bar{\Pi}'_1 = d\bar{\Pi}_1/d\bar{P}$ and $\bar{\Pi}'_2 = d\bar{\Pi}_2/d\bar{Q}$. Then we calculate

$$\begin{aligned}
\Phi_P(\lambda) \Phi_E(\lambda) &= \Phi_P(\lambda) \frac{\rho d_A (1 - \bar{\Pi}_1(\lambda))}{\lambda + d_E + a_P \bar{P} + \Phi_P(\lambda) \left(a_P \bar{E} - \rho d_A \bar{A} a_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)} \\
&= \frac{\rho d_A (1 - \bar{\Pi}_1(\lambda))}{\frac{\lambda + d_E + a_P \bar{P}}{\Phi_P(\lambda)} + \left(a_P \bar{E} - \rho d_A \bar{A} a_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}. \tag{1.67}
\end{aligned}$$

Since $1/\Phi_P(\lambda) \xrightarrow{\lambda \rightarrow 0} 0$,

$$\lim_{\lambda \rightarrow 0} \Phi_P(\lambda) \Phi_E(\lambda) = \frac{\rho d_A (1 - \bar{\Pi}_1)}{a_P \bar{E} + \rho d_A \bar{A} \bar{\Pi}'_1}. \tag{1.68}$$

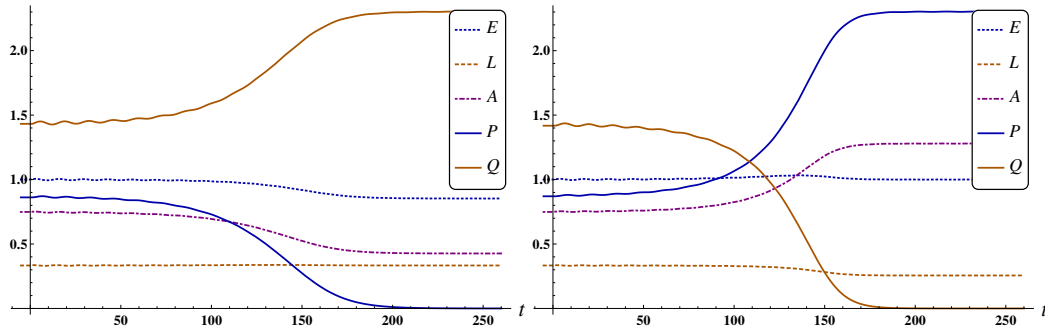


FIGURE 1.8: Time plots of population dynamics after small perturbations from equilibrium densities. Both maturation delays, from egg to larva and from larva to adult, have constant lengths T_E and T_L respectively. The initial densities for $t \leq 0$ are constant and correspond to perturbations from the unique set of coexistence equilibrium densities. In the left panel, the egg parasitoid density P is decreased by 1% and the larva parasitoid wins the competition. In the right panel, the larva parasitoid density Q is decreased by 1% and the egg parasitoid wins the competition. Parameter values are $T_E = 1$, $T_L = 1$, $a_P = 1$, $a_Q = 1$, $d_E = 0$, $d_L = 0$, $d_A = 0.2$, $\rho = 10$, $d_P = 1$, $d_Q = 1$, $c_P = 1$, $c_Q = 3$, $T_{JP} = 1$ and $T_{JQ} = 1$

In the same way

$$\begin{aligned} \Phi_Q(\lambda)\Phi_L(\lambda) &= \Phi_Q(\lambda) \frac{\rho d_A \left(\bar{\Pi}_1(\lambda)(1 - \bar{\Pi}_2(\lambda)) - \Phi_E(\lambda)\Phi_P(\lambda)\bar{A}a_P(1 - \bar{\Pi}_2(\lambda)) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}{\lambda + d_L + a_Q\bar{Q} + \Phi_Q(\lambda) \left(a_Q\bar{L} - \rho d_A\bar{A}a_Q\bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right)} \\ &= \frac{\rho d_A \left(\bar{\Pi}_1(\lambda)(1 - \bar{\Pi}_2(\lambda)) - \Phi_E(\lambda)\Phi_P(\lambda)\bar{A}a_P(1 - \bar{\Pi}_2(\lambda)) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}{\frac{\lambda + d_L + a_Q\bar{Q}}{\Phi_Q(\lambda)} + \left(a_Q\bar{L} - \rho d_A\bar{A}a_Q\bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right)}. \end{aligned} \quad (1.69)$$

Since $1/\Phi_Q(\lambda) \xrightarrow{\lambda \rightarrow 0} 0$,

$$\lim_{\lambda \rightarrow 0} \Phi_Q(\lambda)\Phi_L(\lambda) = \frac{\rho d_A(1 - \bar{\Pi}_2)(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}_1')}{(a_Q\bar{L} + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}_2')(a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}_1')}. \quad (1.70)$$

Now $G(0)$ can be simplified,

$$\begin{aligned} G(0) &= \rho \left(\bar{\Pi}_1\bar{\Pi}_2 + \bar{A}\bar{\Pi}_2\bar{\Pi}_1' \frac{\rho d_A(1 - \bar{\Pi}_1)}{a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}_1'} + \bar{A}\bar{\Pi}_1\bar{\Pi}_2' \frac{\rho d_A(1 - \bar{\Pi}_2)(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}_1')}{(a_Q\bar{L} + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}_2')(a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}_1')} \right) \\ &= \rho \left(\frac{\bar{\Pi}_2(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}_1')}{a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}_1'} + \bar{A}\bar{\Pi}_1\bar{\Pi}_2' \frac{\rho d_A(1 - \bar{\Pi}_2)(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}_1')}{(a_Q\bar{L} + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}_2')(a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}_1')} \right) \\ &= \rho \frac{(a_P\bar{E}\bar{\Pi}_1 + \rho d_A\bar{A}\bar{\Pi}_1')(a_Q\bar{L}\bar{\Pi}_2 + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}_2')}{(a_P\bar{E} + \rho d_A\bar{A}\bar{\Pi}_1')(a_Q\bar{L} + \rho d_A\bar{A}\bar{\Pi}_1\bar{\Pi}_2')}. \end{aligned} \quad (1.71)$$

1.C.2 Instability of the coexistence equilibrium when maturation delays are constant

We have seen in 1.B.1, that with constant maturation delays at most one coexistence equilibrium exists, and that if it exists, none of the parasitoids can invade an equilibrium population of the other parasitoid and the host. This observation and the simulations shown in Fig. 1.8 suggest that the coexistence equilibrium is unstable. We will now prove this conjecture by using the criteria from 1.C.1, which states that an equilibrium is unstable when the corresponding $G(0) > 1$. Using the formulations of 1.B.1 and 1.C.1, it is easily verified that with constant maturation delays $\bar{\Pi}'_1 = -a_P T_E \bar{\Pi}_1$ and $\bar{\Pi}'_2 = -a_Q T_L \bar{\Pi}_2$. Plugging into (1.71) yields with the notation $\Gamma_1(\bar{P}) = \bar{\Gamma}_1$ and $\Gamma_2(\bar{Q}) = \bar{\Gamma}_2$,

$$\begin{aligned} G(0) &= \rho \frac{(a_P \bar{E} \bar{\Pi}_1 - a_P T_E \rho d_A \bar{A} \bar{\Pi}_1)(a_Q \bar{L} \bar{\Pi}_2 - a_Q T_L \rho d_A \bar{A} \bar{\Pi}_1 \bar{\Pi}_2)}{(a_P \bar{E} - a_P T_E \rho d_A \bar{A} \bar{\Pi}_1)(a_Q \bar{L} - a_Q T_L \rho d_A \bar{A} \bar{\Pi}_1 \bar{\Pi}_2)} \\ &= \frac{\bar{\Gamma}_1 - T_E}{\bar{\Gamma}_1 - T_E \bar{\Pi}_1} \frac{\bar{\Gamma}_2 - T_L}{\bar{\Gamma}_2 - T_L \bar{\Pi}_2}, \end{aligned} \quad (1.72)$$

where we use $\bar{E} = \rho d_A \bar{A} \bar{\Gamma}_1$, $\bar{L} = \rho d_A \bar{A} \bar{\Pi}_1 \bar{\Gamma}_2$ and $\rho \bar{\Pi}_1 \bar{\Pi}_2 = 1$ according to equation (1.7), (1.8), (1.9) and (1.11). For both fractions in the last line of (1.72), the numerator is positive and the denominator is negative. To verify this, we deduce from equation (1.34) that

$$\begin{aligned} \bar{\Gamma}_1 &= \mathbb{E}[\min\{K_E, T_E\}] < T_E \text{ and} \\ \bar{\Gamma}_1 &= \bar{\Pi}_1 T_E + (1 - \bar{\Pi}_1) \mathbb{E}[K_E | K_E \leq T_E] > \bar{\Pi}_1 T_E, \end{aligned} \quad (1.73)$$

where K_E is an exponentially distributed random variable. In the same way $\bar{\Gamma}_2 < T_L$ and $\bar{\Pi}_2 T_L < \bar{\Gamma}_2$. To prove $G(0) > 1$, it is therefore enough to show that $\bar{\Gamma}_1 - T_E \bar{\Pi}_1 < T_E - \bar{\Gamma}_1$ and $\bar{\Gamma}_2 - T_L \bar{\Pi}_2 < T_L - \bar{\Gamma}_2$. To verify the first—and in the same way the second—inequality, we use $\bar{\Gamma}_1 = (1 - \bar{\Pi}_1)/(a_P \bar{P} + d_E)$ from equation (1.34), and argue

$$\begin{aligned} \bar{\Gamma}_1 - T_E \bar{\Pi}_1 < T_E - \bar{\Gamma}_1 &\Leftrightarrow \\ \frac{1 - \bar{\Pi}_1}{a_P \bar{P} + d_E} - T_E \bar{\Pi}_1 < T_E - \frac{1 - \bar{\Pi}_1}{a_P \bar{P} + d_E} &\Leftrightarrow \\ 1 - \bar{\Pi}_1 - \bar{\Pi}_1 (a_P \bar{P} + d_E) T_E < (a_P \bar{P} + d_E) T_E - 1 + \bar{\Pi}_1 &\Leftrightarrow \\ 1 - e^{-\gamma} - \gamma e^{-\gamma} < \gamma - 1 + e^{-\gamma} &\Leftrightarrow \\ \int_0^\gamma (x e^{-x}) dx < \int_0^\gamma (1 - e^{-x}) dx &\Leftrightarrow \\ x e^{-x} < 1 - e^{-x} \quad \forall x > 0 &\Leftrightarrow \\ 1 + x < e^x \quad \forall x > 0, \end{aligned} \quad (1.74)$$

where $\gamma = (a_P \bar{P} + d_E) T_E$. The last line of (1.74) is obviously true. This completes the proof that the coexistence equilibrium is unstable when the maturation delays are

constant.

Chapter 2

Optimized timing of parasitoid release: a mathematical model for biological control of *Drosophila suzukii*

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Abstract

1. The invasive fruit fly *Drosophila suzukii* is a major pest of soft fruit in Europe and the Americas. A promising method for containing the pest is biological control with parasitoids. Suitable parasitoid species have been identified, but still little is known on how to most efficiently carry out such an intervention. The timing of such parasitoid release can be crucial due to the strong seasonality of the pest. Here we analyze the question of optimal timing with a mathematical model. Parameters for *D. suzukii* and its pupal parasitoid *Trichopria drosophilae* are taken from various sources in the literature. The model accounts for seasonal changes of the temperature and the availability of fruit suitable for the development of *D. suzukii*.
2. Effectiveness of the intervention depends strongly on the timing of release. With the climate of North Italy and a typical seasonal pattern for the fruit abundance, optimal release timing is in June (when the *D. suzukii* population starts increasing sharply).

3. Our simulations did not confirm effectiveness of releasing parasitoids in early spring aiming to exploit a "bottleneck" situation where the pest population is at a low density.
4. A single parasitoid release event can be more efficient than multiple releases over a prolonged period. However the success of multiple releases may result in increases chances of successful biological control.
5. *Synthesis and applications*: We suggest a clear guideline for timing a parasitoid intervention, discussing the model assumptions and their implications. Our findings can be presumably transferred, after appropriate adjustments, to other parasitoid species with similar requirements. We hope our analysis will be useful for optimizing parasitoid release.

2.1 Introduction

The fruit fly *Drosophila suzukii* Matsumura arrived in 2008 to both, Europe and mainland America from its region of origin in East Asia (Hauser, 2011; Calabria et al., 2012; Cini et al., 2012; Cini et al., 2014; Deprá et al., 2014; Asplen et al., 2015; Fraimout et al., 2017). *D. suzukii* larvae develop in ripe fruit, but unlike most of its relatives it is able to oviposit in undamaged soft shelled fruit. Host plants include cherry, blueberry, raspberry, strawberry and various non-crop plants (Lee et al., 2011b; Atallah et al., 2014; Asplen et al., 2015; Kenis et al., 2016; Karageorgi et al., 2017). The ability to infest undamaged fruit makes it a serious problem in some agricultural areas (Bolda et al., 2010; Lee et al., 2011a; De Ros et al., 2013; Asplen et al., 2015). Conventional control programs are heavily reliant on pesticides, which are applied multiple times per season (Van Timmeren and Isaacs, 2013). This control strategy is believed to be effective but is associated with many problems. Some of these problems include ineffectiveness of the pesticides against larvae inside the fruits, adverse effects on natural enemies (Roubos et al., 2014), secondary pest resurgence (Klick et al., 2016), development of insecticide resistance, continuous immigration from population reservoirs (Klick et al., 2016), and unacceptably high pesticide residues (Asplen et al., 2015). Interestingly *D. suzukii* seems not to be a major problem in its region of origin, where it presumably does not reach extremely high population densities (Asplen et al., 2015). One reason might be the presence of adapted natural enemies, including most prominently diverse parasitoid wasps which develop inside the juvenile stages of *D. suzukii* (Mitsui et al., 2007).

Given the potential of parasitoid species to reduce their host population, they are considered for biological control programs of *D. suzukii* (Haye et al., 2016). Introducing the parasitoid species from the region of origin is considered in Europe and America (Daane et al., 2016; Haye et al., 2016), even though their release has yet to be authorized. Moreover, several indigenous parasitoids attack *D. suzukii* in the

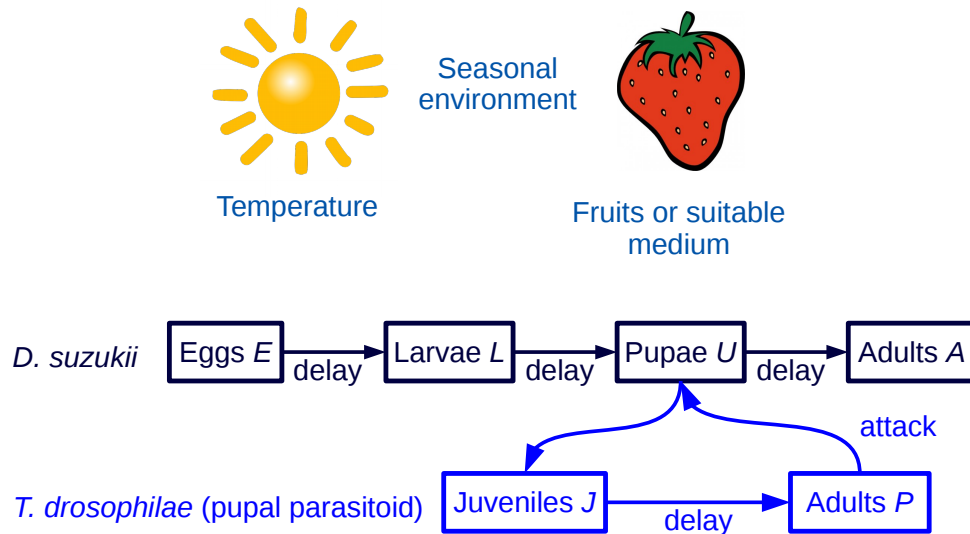


FIGURE 2.1: Flow chart for the stage structured model

invaded areas (Chabert et al., 2012; Rossi Stacconi et al., 2013; Gabarra et al., 2015; Miller et al., 2015; Mazzetto et al., 2016; Wang et al., 2016; Knoll et al., 2017). Among larval parasitoids, *Leptopilina heterotoma* Thomson has been observed to successfully develop on *D. suzukii*, even if its efficacy is strongly limited by the host immunoreaction (Rossi Stacconi et al., 2015). Among pupal parasitoids, *Pachycrepoideus vindemiae* Rondani and *Trichopria drosophilae* Perkins are the most common species attacking the pest. At the moment, the cosmopolitan *T. drosophilae* appears to be the most suitable species for implementing biocontrol programmes (Zhu et al., 2017; Rossi Stacconi et al., 2017b). Successful release is dependent, among other factors, on the use of parasitoid species, but also on targeting the most appropriate ecological time frame and habitat (Crowder, 2007). Mathematical models for population dynamics allow us to help determine most optimal timing for inundative releases of parasitoids (Shea and Possingham, 2000; Crowder, 2007; Hamby et al., 2016). In this work, we present such a model for *D. suzukii* and the parasitoid *T. drosophilae*. With this model we attempt to answer two questions: (a) when is the optimal time for releasing the parasitoids and (b) whether it is more effective to release them at a single event or at several events distributed over time. Our model takes into account the stage structure of the populations, and we collect parameters for both species and the seasonal environment from various sources. A brief introduction to the model and the results of the simulations are given in Section 2.2 and 2.3, and we discuss the implications in Section 2.4. The details of the model can be found in the supplementary material 2.A.

2.2 Theory and calculations

The population dynamics of *D. suzukii* and *T. drosophilae* are modelled through a system of delay differential equations analogous to similar models (Nisbet and Gurney,

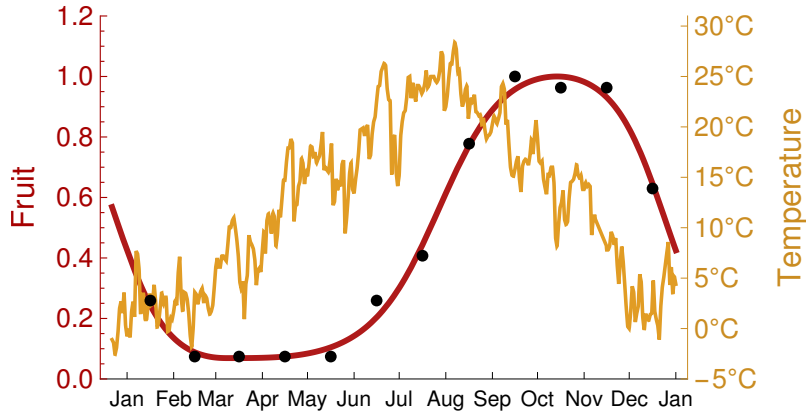


FIGURE 2.2: Number of host species suitable for *D. suzukii* development in northern France and daily mean temperature in S.Michele all'Adige, Italy (2014)

1983; Nelson et al., 2013; McCauley et al., 2008; Ewing et al., 2016). The equations are written out in the supplementary material 2.A.

D. suzukii structure consists of eggs (E), larvae (L), pupae (U) and adults (A), and that of *T. drosophilae* of juveniles (J) and adults (P). Transitions through life stages are presented within a simple biological control system flowchart in Fig. 2.1.

Fecundities, mortalities and developmental delays are assumed to depend on the environment. Our model accounts for two time-dependent environmental factors: the temperature $C(t)$ and the availability of fruit (or other suitable host medium) $F(t)$.

The temperature data has been measured at an elevation of 228 m a.s.l in S. Michele all'Adige, Province of Trento, North Italy (provided by Fondazione Edmund Mach). From these data we draw a continuous temperature curve $C(t)$ by two different methods to test whether they result in different conclusions. The first method was to obtain a generic expectation for the temperature profile by fitting a stretched and shifted sinusoidal curve over the course of one year. The second method was to obtain realistic curves for the different years by fitting piecewise linear functions to the daily mean temperature, see Fig. 2.2.

The function for the seasonal fruit availability $F(t)$ has been created with the data from Poyet et al., 2015, who report for each month the number of plant species carrying fruits suitable for *D. suzukii* in a region of northern France. We assume that the numbers of fruiting species also reflect the total availability of suitable host and create a continuous function by fitting a sinusoidal curve to the data, see Fig. 2.2.

For both species, the time spent in the juvenile stages depends on the temperature C . Following the approach of (Nisbet and Gurney, 1983), we model a temperature-dependent maturation rate, defined, for each stage, as the inverse of the length of the time spent in that stage. It turns out, that the maturation rates of the different stages scale very similarly with the temperature. We therefore use a single (Gaussian) function $g(C)$ for the maturation rate of all stages, and assume that insects in

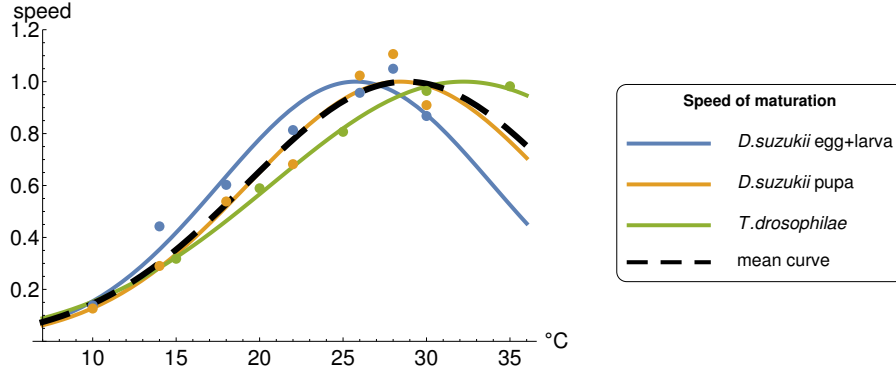
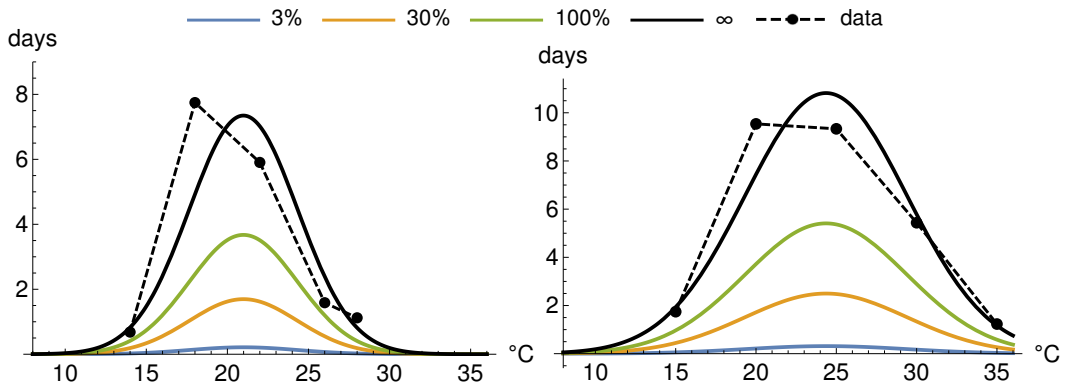


FIGURE 2.3: Maturation speed of different life stages of *D. sukukii* and its pupal parasitoid *T. drosophilae*



(A) Eggs laid per day by an adult female *D. sukukii* with different values for the fruit availabilities F (measured relatively to the maximum fruit available in the peak season)

(B) Host pupa infested per day by an adult female *T. drosophilae* with different values for the availability of pupae (measured relatively to the maximum of *D. sukukii* population size reached without intervention)

FIGURE 2.4: Daily fecundities

stage i (where $i = E, L, U$ or J) progress to the next stage when their maturation level reaches the value Ω_i . We normalize the maturation rate $g(C)$ so that it has a maximum value of 1, and thus Ω_i represent the minimum stage durations (at optimal temperature). Fig. 2.3 shows the fit of this model to delays measured in the laboratory (Tochen et al., 2014; Amiresmaeili, 2017).

Fecundity of adult *D. sukukii* depends on temperature C and fruit availability F through a multiplicative formula. Precisely, the dependence of the maximal fecundity on temperature follows a Gaussian function $\eta_A(C)$, fitted to available data. The dependence on fruit availability is through a Holling-type 2 function. The resulting formula for the realized fecundity is

$$\beta_A = \lambda_A \frac{\eta_A(C) \alpha_A F}{1 + \alpha_A F} \quad (2.1)$$

where $\lambda_A = 0.5$ is the sex-ratio (Emiljanowicz et al., 2014) and α_A is a parameter (the 'attack rate' of *D. sukukii* towards available fruit) to be adjusted. Fig. 2.4a shows

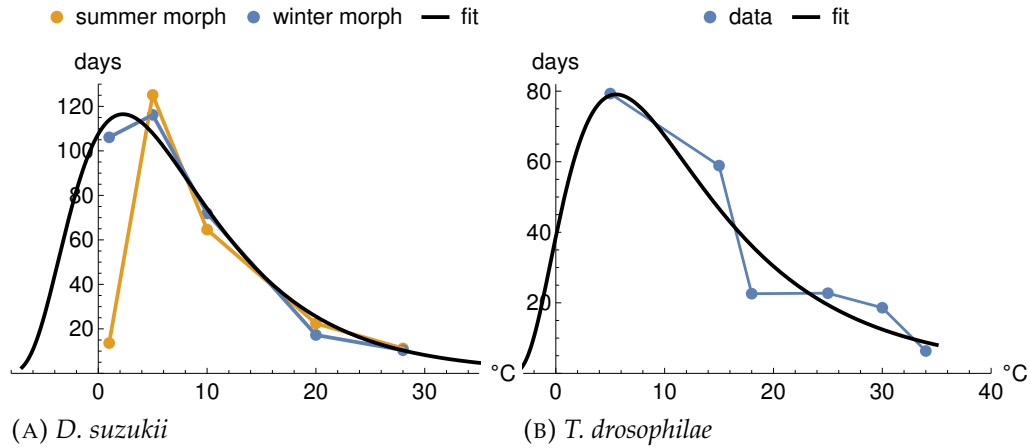


FIGURE 2.5: Average adult life length of *D. suzukii* and *T. drosophilae*

the dependence of fecundity on temperature for different levels of fruit availability together with laboratory data considered as estimates valid for unlimited resource availability.

In the same way, maximal parasitoid fecundity $\eta_P(C)$ is fitted to data available at different temperatures, and the realized fecundity β_P is assumed to depend additionally on the host density U , yielding

$$\beta_P = \lambda_P \frac{\eta_P(C) \alpha_P U}{1 + \alpha_P U} \quad (2.2)$$

where α_P needs to be adjusted (the 'attack rate' of *T. drosophilae* towards available *T. drosophilae* pupae), and the sex ratio is $\lambda_P = 0.53$ (Rossi Stacconi et al., 2017b). The resulting curves are shown in Fig. 2.4b together with the laboratory data.

Mortality of both species depends on temperature, and for *D. suzukii* larva it depends additionally on fruit availability and the number of competing larvae. For both species, average adult survival is modeled with a skewed Gaussian function. The fits to data from (Shearer et al., 2016) and (Amiresmaeili, 2017) are shown in Fig. 2.5. For *D. suzukii*, the phenotypic plasticity between summer and winter morph is accounted for by assuming that at all temperatures the flies exhibit the better adapted phenotype.

Further details on that and on other model assumptions can be found in the supplementary material 2.A. The model is implemented with *Wolfram Mathematica* (Wolfram Research, 2016) and the code is freely available on request.

2.3 Results

Fig. 2.7 shows a simulation of *D. suzukii* adult population dynamics for the years 2014-2016, superimposed with weekly average catches of *D. suzukii* adults from 22 traps in the Province of Trento (obtained from the Fondazione Edmund Mach, S.

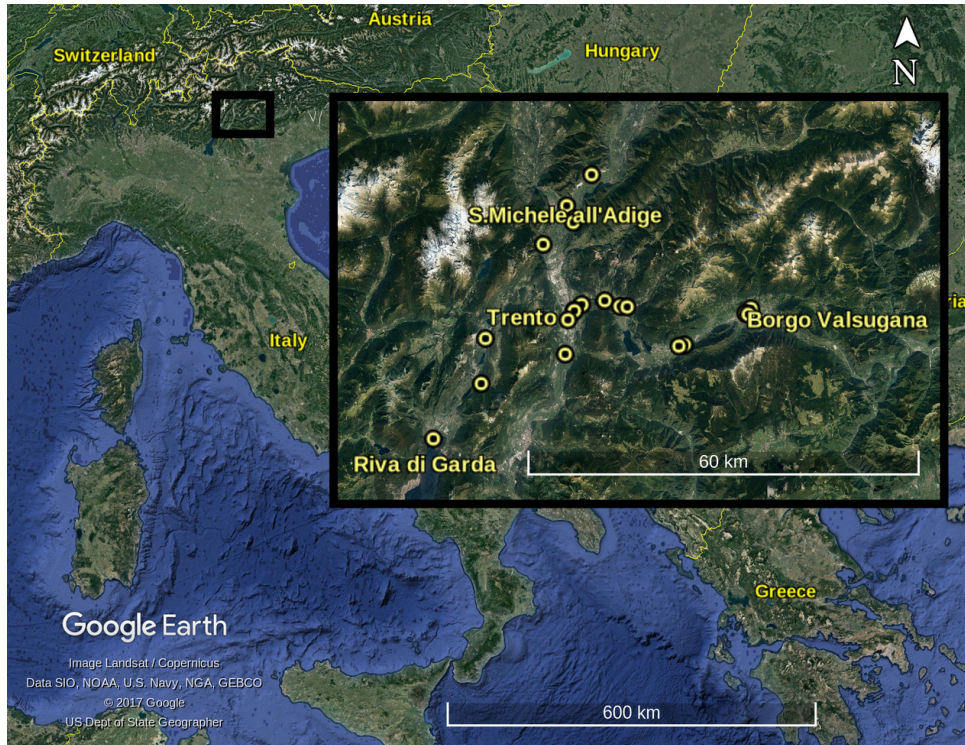


FIGURE 2.6: *D. suzukii* trap placement in the Province of Trento during 2014 to 2016

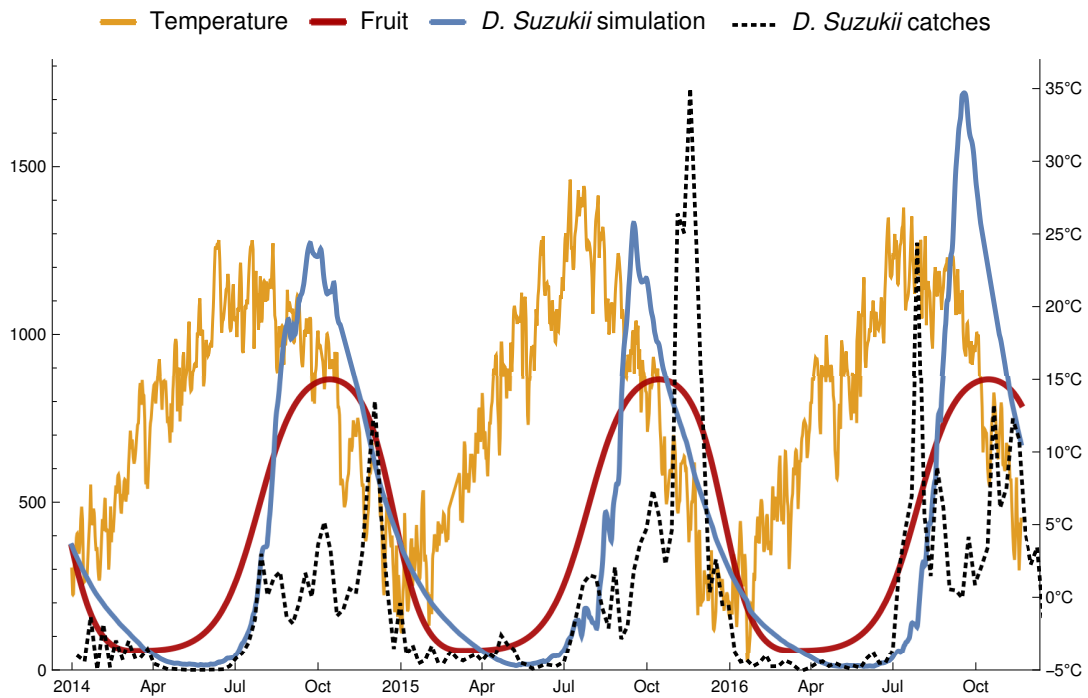


FIGURE 2.7: Simulated *D. suzukii* adult population size, mean *D. suzukii* trap catches and mean daily temperature from S. Michele, Province of Trento, Italy during 2014-2016

Michele all'Adige, Italy). Precisely, the traps are those maintained over all three years that are at an elevation below 500m a.s.l. (their elevations vary between 77m

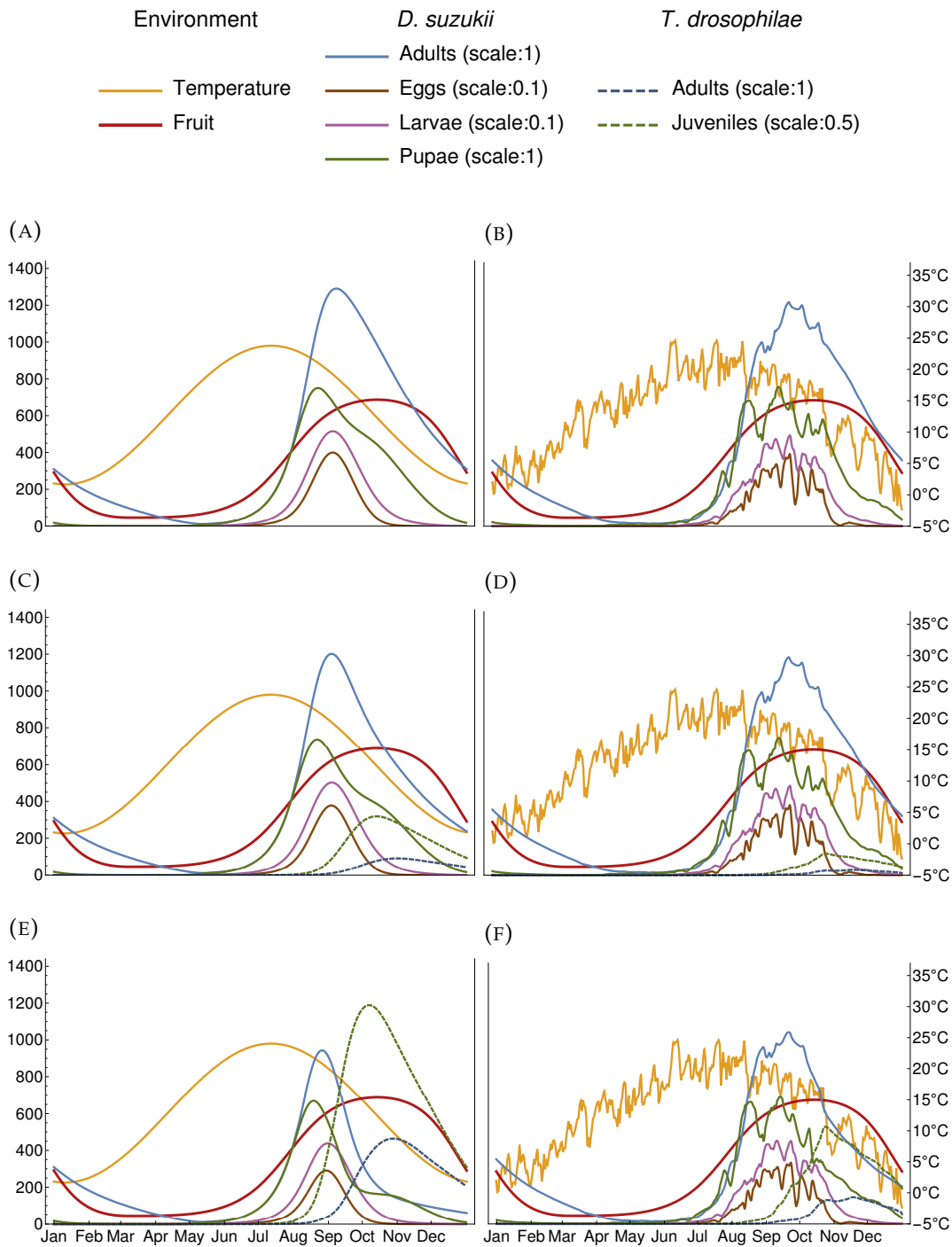


FIGURE 2.8: Simulated *D. suzukii* population size without (a, b) and with parasitoids introduced on 1 April (c, d) and 1 June (e, f). Figures a, c, and e (left) were created using the sinusoidal temperature curve and b, d, and f (right) interpolating the daily mean temperatures. Curves were created using weather data originally collected during 2014 in S. Michele all'Adige at 228 m a.s.l., Province of Trento. The number of released parasitoids corresponded to estimations of 0.05% of the yearly maximum of *D. suzukii* population size estimations reached without intervention.

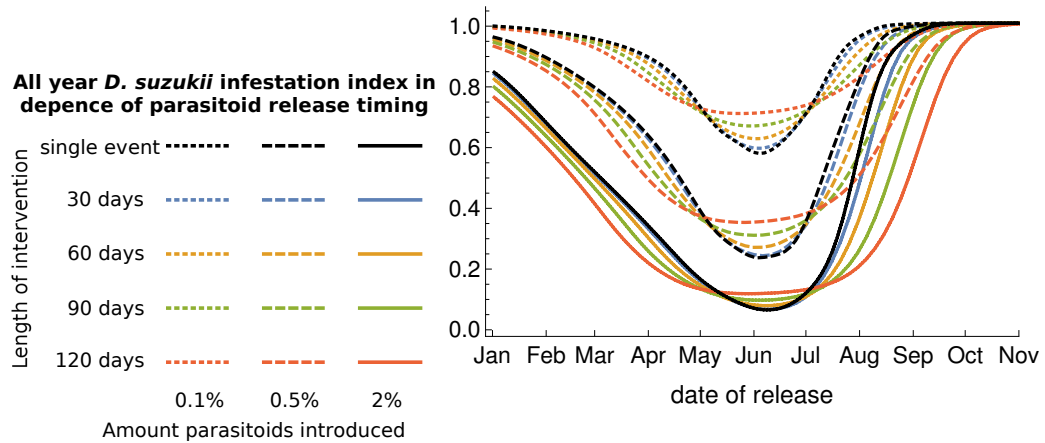


FIGURE 2.9: Effect of time of parasitoid introduction and amount of parasitoids introduced on all year *D. suzukii* infestation index (which is proportional to the total amount of *D. suzukii* eggs laid over the year). The temperature curve used is the generic sinusoidal fit. Dotted, dashed and straight lines correspond to an overall introduction of 0.1%, 0.5% and 2% of parasitoids compared to the yearly maximum of *D. suzukii* adults reached without parasitoid intervention. The blue lines correspond to a scenario where all parasitoids are released at a single event at the date given on the x-axis. The other lines correspond to an equally distributed parasitoid release around the date on the x-axis for 30, 60, 90 and 120 days

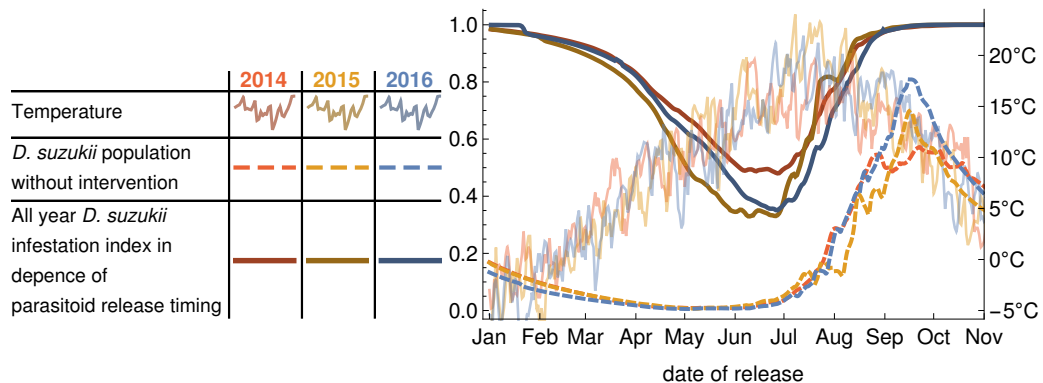


FIGURE 2.10: All year *D. suzukii* infestation index in dependence of the time of parasitoid introduction with the temperature curve from different years. A fixed amount of parasitoids (a quantity equal to 0.5% of peak density that would be reached by *D. suzukii* in absence of parasitoids in 2014) is released at a single event (the date on the x-axis). Thick dashed lines: population density of *D. suzukii* adults without parasitoid release. Thick straight lines: infestation index when parasitoids are introduced at the given date. Thin straight lines: temperature

and 489m a.s.l.). One of the locations is S. Michele all'Adige, the location of the weather station for the temperature data we use (see the map of the different trap locations in Fig. 2.6). Simulations and catch data have some differences, especially for the presence of large autumn peaks in catches, at a time when simulated densities are declining; possible reasons for such discrepancies are examined in the

discussion. However, the overall multi-year patterns of simulations and catch data roughly agree; thus, we deem the model reasonable enough to be used as a baseline for investigating the potential impact of parasitoid introductions.

Fig. 2.8 shows different scenarios for a one-year simulation, with and without parasitoid introduction. The temperature curve corresponds to the weather in S. Michele all'Adige in 2014, approximated by a sinusoid curve (left panels) or interpolated from daily mean temperatures (right panels). The upper plots show the densities of the different stages of *D. suzukii* in simulations without parasitoid introduction. In the other plots adult parasitoids are released on 1 April (central row) and on 1 June (bottom row).

Corresponding simulations on left and right panels differ somewhat: with the actually observed temperature (right side), *T. drosophilae* does not reach that high densities and is less reducing the *D. suzukii* population. Still, the patterns moving from top to bottom are extremely similar between the two columns: parasitoid release on 1 April has a smaller effect on the host population than parasitoid release on 1 June, with the latter reducing the peak adult *D. suzukii* density by around 35%. Parasitoid juvenile densities peak in all release scenarios between mid and end of October.

In order to better understand the influence of the timing the parasitoids are released, we measured success of an intervention by an “all year *D. suzukii* infestation index”, which is proportional to the *D. suzukii* eggs laid during the year. A low infestation index is assumed to indicate a successful intervention. We also experimented an alternative measure of infestation, aiming at assessing the damage caused to ripening fruit, and the results obtained with either measure are very similar.

Fig. 2.9 shows the effects of different scenarios of parasitoid release in terms of the “all year *D. suzukii* infestation index” compared to the no-intervention scenario. The scenarios differ in the amount of parasitoids released and in the time span over which the release is carried out. The total amount of parasitoids released corresponds to 0.1%, 0.5% and 2% of the peak density *D. suzukii* adults reach without parasitoid intervention. Those scenarios should represent generally different intensities of the introduction. Note that determining the number of parasitoids needed for successful biological control is out of our scope. To understand whether a single or multiple release events are more effective, we vary the time span of the introduction from a single event up to 120 days. In order to obtain more general results, we only considered the case of a sinusoidal temperature curve.

In all scenarios, the lowest infestation index was obtained by releasing the parasitoids in the first half of June, corresponding to the time when the *D. suzukii* population begins to grow. The optimal timing does not depend on the amount of parasitoids released, which however strongly affects the impact of the intervention. A single parasitoid release at the optimal time is slightly more effective than continuous release of the same amount of parasitoids over an extended period centered

around that date; however only a very long release period (several months) decreases the success substantially. On the other hand a continuous release increases the tolerance of a suboptimal timing.

We also examined how much optimal timing changes from year to year: Fig. 2.10 shows the infestation index in dependence of the date of a single parasitoid release using the daily mean temperature data of the years 2014 to 2016. For each simulation, the model is started with a fixed amount of *D. suzukii* adults at the beginning of the preceding year. The simulations suggest that, depending on the year, the optimal date for an introduction may lie between early to late June.

2.4 Discussion

Our findings suggest that the success of a biological control strategy of *D. suzukii* by means of the pupal parasitoid *T. drosophilae* depends strongly on the time when the parasitoids are released. With our assumptions on the fruit availability and the climate of the Province of Trento (northern Italy), the optimal time of release is estimated to lie around the beginning of summer in June, when the *D. suzukii* population begins to grow. Simulations of the population dynamics can be seen in Fig. 2.7 and 2.8, and the main results on the timing of parasitoid interventions are shown in Fig. 2.9 and 2.10.

Generally choosing the right time for a parasitoid intervention is about finding a balance between an early and a late release. On one hand, the intervention should be late enough in the season so that *D. suzukii* has started reproducing since only the pupal stage is attacked by the parasitoid. On the other hand, the intervention should be early enough to augment the parasitoid density and decimate the *D. suzukii* population before crops are becoming susceptible. An early intervention could possibly benefit from a “bottleneck” effect by intervening when the pest population has a low density. For other control methods based on pesticides, such an early intervention has been suggested to be effective already in late winter to early spring (Rossi Stacconi et al., 2016). However our simulations do not confirm that for biological control with parasitoids. This is to be expected since parasitoids –in contrast to pesticides– need sufficiently warm conditions and target only a juvenile stage of the pest species, which is present only after the population starts reproducing (Wiman et al., 2016). Yet early parasitoid is tested in the field (MVRS - personal communication) and our results need to be interpreted carefully, as the model is only a simplified picture of reality and it is based on a range of assumptions – which can also depend on local factors. In the following, we shall discuss some key assumptions and their possible implications on the conclusions.

A crucial factor for the population dynamics of *D. suzukii* is the availability of fruit or other suitable host material. In our model, fruit availability affects adult fecundity as well as larval competition. However, fruit availability can be difficult to estimate and it strongly depends on the location. In our model, we estimate fruit availability

by the monthly number of plant species carrying suitable fruits. This might not adequately represent the total amount of fruit, especially considering the large fruit abundance in agricultural areas. An exploration of alternative scenarios suggests, that the most important factor for timing a parasitoid release is the onset of fruit becoming largely available. Basically the parasitoids can attack *D. suzukii* as soon as it starts reproducing, given that the temperatures are not too low. In our scenario this occurs at the beginning of summer, but depending on the local crops the optimal timing for releasing parasitoids can be earlier or later.

For our model we consider only two environmental factors: temperature and fruit availability. We chose those factors because they are main drivers of the population dynamics, and because they have clear seasonal patterns in most climatic zones – allowing us to draw general conclusions independently of yearly variations. However, other environmental factors could play a role too, including, for instance, weather influences as wind, rain and humidity (Tochen et al., 2016). All these factors can influence the optimal timing for releasing parasitoids. It is difficult to reach general conclusions, but one should clearly seek suitable weather conditions for releasing parasitoids.

We also assume, for the sake of simplicity, that environment is homogeneous and affects all individuals in the same way. However, in nature the environment is heterogeneous on many scales. For example, individuals can avoid extreme temperatures by finding shelter under leaf piles or by seasonal migration between different altitudes (Tait et al., 2016; Rossi Stacconi et al., 2016). Similarly, resources –as fruits suitable for the development of *D. suzukii*– are distributed heterogeneously in time and space (for example due to different ripening times). Obviously, optimal parasitoid release depends on such local factors. A related question is, whether the spread of *D. suzukii* can be limited effectively at the beginning of the season by intervening at a source population, i.e. close to the overwintering habitat (Klick et al., 2016). In order to answer such questions, a (stochastic) spatially-structured model could be helpful.

To estimate the optimal timing for releasing the parasitoids, we assume to have full information about the (future) development of the environment. In reality however predictions have limited accuracy, and stochasticity needs to be considered. Thus for the practice it can be beneficial to distribute the parasitoid release over several events. This is in accordance with our theoretical results which suggest that distributing the release increases the tolerance for the timing of the intervention.

Understanding the way *D. suzukii* overwinters (Rossi Stacconi et al., 2016) is a key for its successful control. Current research has revealed the existence of a specially adapted winter morph with largely increased tolerance towards low temperatures at the cost of a reduced fecundity (Kaçar et al., 2015; Shearer et al., 2016). The morph is induced by cold temperatures during juvenile development in autumn (Toxopeus et al., 2016), and the flies are thought to reproduce during spring giving rise to the first new generation (Rossi Stacconi et al., 2016). There are data on the temperature

tolerance of the two morphs (Shearer et al., 2016), but no quantitative information is available on the fecundity of the winter morph or on the environmental cues for shifting between the two morphs. In order to still capture the broad temperature tolerance of *D. suzukii* without increasing the number of unknown parameters of the model, we thus simply assumed that the whole population is always adapted to the current environment. However, this will not accurately reflect reality. A comparison between simulations and catch data (see Fig. 2.7) suggests that the model may underestimate adult mortality at the end of autumn, and conversely underestimating reproduction in spring; if so, this might be a possible reason justifying a parasitoid release earlier than predicted by the current model. More data on the fecundity of the winter morph and on the transitions between morphs could be valuable to better assess this possibility.

When trying to control *D. suzukii* populations, it is important to understand when and where the population is growing, and how its stage distribution is composed. The population has been extensively surveyed in the Province of Trento (Italy), where it deals serious damage to the local fruit production. Comparing catch data and model simulation in Fig. 2.7, we see that the overall temporal patterns coincide. However, catches are lower than simulations in summer and higher in autumn. The discrepancy cannot be simply explained by increased mortality due to high temperatures – we ran additional simulations with intra-daily temperature fluctuations, and thus higher mortality in hot days, but found no relevant differences in the outcome. Other factors responsible for the low catch numbers during summer could be low humidity and seasonal migration towards cooler habitats at higher altitudes. We however believe, that an important reason is simply that the vinegar baited traps are less attractive during summer due the high fruit abundance. Indeed, analysis of weekly catches in orchards generally show higher numbers of adults after the harvest (Rossi Stacconi et al., 2016). We overall deem the model realistic enough, since it reproduces well the begin of the yearly *D. suzukii* outbreak – which seems to be the most important event for timing the parasitoid intervention.

In our model, we neglect the complex ecological web in which both species are embedded. These include various predators, parasitoids and other drosophilids which can be infested by *T. drosophilae*. Such third species can have a wide range of effects on the populations and possible control efforts. For example additional hosts for the parasitoid can be disadvantageous when they dilute the parasitoid attacks on other hosts, or beneficial by helping to increase the parasitoid density. If in this example, additional hosts reproduce earlier in the season than *D. suzukii*, those could justify an earlier release in order to augment parasitoid densities in the field. It seems difficult to draw general conclusions on the impact of further species, but specific cases could be analyzed with support of simulations that extend our approach including other species.

T. drosophilae is not the only parasitoid wasp known to attack *D. suzukii*. Other parasitoids include species resident in the area of origin of *D. suzukii* (Mitsui et al., 2007),

as well as species resident in the newly invaded areas (Rossi Stacconi et al., 2015). It was not in the scope of this work to compare efficacy of different parasitoids, and neither to examine whether a single species or multiple species should be introduced. However, we believe that our findings can be transferred widely for other parasitoid wasps, as they have similar needs on the environment. This also includes parasitoids attacking other juvenile stages than pupae, since the different juvenile stages appear in the field virtually at the same time when *D. suzukii* is reproducing. In summary, we believe that the present analysis yields useful insights for designing optimal strategies of parasitoid release. However, only experience can validate our predictions. Currently parasitoid release is being tested in the field (MVRS - Personal communication) and the tools developed in the current work may be useful in their analysis. We hope that our study will help to improve integrated pest management of *D. suzukii*.

Appendix

2.A Supporting Information: model details

Our model bases on the general approach by Nisbet and Gurney (1983). This approach allows to model populations of insects with dynamically varying instar duration, which in our case depend on the temperature of the environment. The method has proved useful in several applications (McCauley et al., 2008; Nelson et al., 2013; Ewing et al., 2016). We extend the basic model in a straightforward fashion to couple the dynamics of our two species, *D. suzukii* and its parasitoid *T. drosophilae*. Our basic modeling parts are –similarly to the Appendix in (McCauley et al., 2008)–

<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

Functions and parameters (for stage $i = E, L, U, A, J, P$)		
Notation	Explanation	Reference
$\phi_i(C)$	background mortality rate	(2.13)-(2.14)-(2.16)-(2.17)
δ_i	total mortality rate	(2.4)
$g(C)$	speed of maturation	(2.12)
τ_i	time spent in the stage i	(2.8)
$f_A(C, F)$	rate of <i>D. suzukii</i> eggs deposited (rate per A and F)	(2.19)
$f_P(C, U)$	infestation rate of <i>T. drosophilae</i> (rate per P and U)	(2.21)
$\psi(F)$	competition coefficient for <i>D. suzukii</i> larva	(2.15)

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 2.A.2. With those building parts the model is formulated as

$$\begin{aligned}
\frac{dE(t)}{dt} &= R_E(t) - M_E(t) - \delta_E(t)E(t) \\
\frac{dL(t)}{dt} &= M_E(t) - M_L(t) - \delta_L(t)L(t) \\
\frac{dU(t)}{dt} &= M_L(t) - M_U(t) - \delta_U(t)U(t) \\
\frac{dA(t)}{dt} &= M_U(t) - \delta_A(t)A(t) \\
\frac{dJ(t)}{dt} &= R_J(t) - M_J(t) - \delta_J(t)J(t) \\
\frac{dP(t)}{dt} &= M_J(t) - \delta_P(t)P(t)
\end{aligned} \tag{2.3}$$

where the mortality rates δ_i are composed of the temperature dependent background mortality rates ϕ_i , and competition and parasitism related terms (for *D. sukukii* larvae and pupae). That is

$$\begin{aligned}
\delta_E(t) &= \phi_E(C(t)) \\
\delta_L(t) &= \phi_L(C(t)) + \psi(F(t))L(t) \\
\delta_U(t) &= \phi_U(C(t)) + f(C(t), U(t))P(t) \\
\delta_A(t) &= \phi_A(C(t)) \\
\delta_J(t) &= \phi_J(C(t)) \\
\delta_P(t) &= \phi_P(C(t))
\end{aligned} \tag{2.4}$$

The renewal rates R_i and the maturation rates M_i are

$$\begin{aligned}
R_E(t) &= \beta_A(t)A(t) \\
M_E(t) &= R_E(t - \tau_E(t))S_E(t) \frac{g(C(t))}{g(C(t - \tau_E(t)))} \\
M_L(t) &= M_E(t - \tau_L(t))S_L(t) \frac{g(C(t))}{g(C(t - \tau_L(t)))} \\
M_U(t) &= M_L(t - \tau_U(t))S_U(t) \frac{g(C(t))}{g(C(t - \tau_U(t)))} \\
R_J(t) &= \beta_P(t)P(t) \\
M_J(t) &= R_J(t - \tau_J(t))S_J(t) \frac{g(C(t))}{g(C(t - \tau_J(t)))}
\end{aligned} \tag{2.5}$$

with the birth rates

$$\begin{aligned}
\beta_A(t) &= \lambda_A h(C(t), F(t))F(t) \\
\beta_P(t) &= \lambda_P f(C(t), U(t))U(t)
\end{aligned} \tag{2.6}$$

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

$$S_i(t) = e^{-\int_{t-\tau_i(t)}^t \delta_i(\sigma) d\sigma}. \quad (2.7)$$

The maturation delays τ_i are given by the implicit relations

$$\Omega_i = \int_{t-\tau_i(t)}^t g(C(\sigma)) d\sigma \quad (2.8)$$

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

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

$$\tilde{t} = \int_0^t g(\sigma) d\sigma. \quad (2.9)$$

After this transformation the delays of the different stages become constant Ω_i , so that 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; Wiman et al., 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 DKLAG6 (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.A.1 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 $M_U(t)$ and all being 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 $P(t) = P_0$.

2.A.2 Parameters and functions

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 there) and for *T. drosophilae* from (Rossi Stacconi et al., 2017b) (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

$$g_i(C) = \frac{1}{\Omega_i} e^{-\left(\frac{\mu_{g_i} - C}{\sigma_{g_i}}\right)^2} \quad (2.10)$$

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 $g(C)$

$$g_i(C) \approx \frac{1}{\Omega_i} g(C) \quad (2.11)$$

where

$$g(C) = e^{-\left(\frac{\mu_g - C}{\sigma_g}\right)^2} \quad (2.12)$$

with μ_g and σ_g being the averages of the values we found for μ_{g_i} and σ_{g_i} , see Fig. 2.3. After the fit we divide the egg-larva stage of *D. suzukii* 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 $\Omega_E = 1.3$, $\Omega_L = 5.2$, $\Omega_U = 4.1$, $\Omega_J = 16.9$, $\mu_g = 28.8$ and $\sigma_g = 13.6$.

Mortality

Mortality rates depend on the temperature. Different researches have been made on the temperature tolerance of *D. suzukii* with rather different outcomes for adult (Tochen et al., 2014; Jakobs et al., 2015; Stephens, 2015; Shearer et al., 2016; Ryan et al., 2016; Enriquez and Colinet, 2017), and for juveniles (Tochen et al., 2014; Kinjo et al., 2014).

D. suzukii adults:

We use the data on the adult life span of *D. suzukii* 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. suzukii*: 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. 2.5a). 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.

$$\phi_A(C) = \phi_{A_{min}} e^{\left(\frac{\log[C+s] - \log[\mu_{\phi_A} + s]}{\sigma_{\phi_A}}\right)^2} \quad (2.13)$$

with $s = 10$. The obtained parameter values are $\phi_{A_{min}} = 0.0085$, $\mu_{\phi_A} = 2.3$ and $\sigma_{\phi_A} = 0.73$. In the simulations we assumed 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. suzukii* 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. suzukii* adults at very low temperatures, although some efforts have been made into this direction (Ryan et al., 2016; Enriquez and Colinet, 2017).

Juvenile *D. suzukii*:

The juvenile mortality of *D. suzukii* rate is assumed to depend on temperature, but also to be affected by competition when fruit availability is limited. For the temperature dependent background mortality rate $\phi_V(C)$ of all three *D. suzukii* juvenile stages, we use the stage survival probabilities and stage durations of males and females from (Tochen et al., 2014) (from Table 2 there; survival can be deduced from the sample size in this table by using that all replicates were started with 50 females and 50 males). This data is fitted by a Gaussian function of the form

$$\phi_V(C) = \phi_{V_{min}} e^{\left(\frac{C - \mu_{\phi_V}}{\sigma_{\phi_V}}\right)^2} \quad (2.14)$$

and we obtain the parameter values $\phi_{V_{min}} = 0.02$, $\mu_{\phi_V} = 14.7$ and $\sigma_{\phi_V} = 11.7$ by the least square method.

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

$$\psi(F) = \frac{1}{F}. \quad (2.15)$$

Any constant in front of (2.15) can be absorbed in a scaling factor of host densities. For the plots, the population densities obtained in the simulations have been scaled to roughly match observed catch data.

For the pupal stage there is an additional mortality term due to parasitism, $f(C(t), U(t))P(t)$, which is described below in 2.A.2.

Adult *T. drosophilae*:

Data on life length of *T. drosophilae* adults at different temperatures are presented by Amiresmaeli (2017), see Fig. 2.5b. To fit a mortality curve to that data, we proceed as for *D. suzukii* adults (dropping the data point for the survival of *T. drosophilae* at the maximum tested temperature because all insects died before the first census and this would conflict with the least square fit in logarithmic scale). We find a function

$$\phi_P(C) = \phi_{P_{min}} e^{\left(\frac{\log[C+s] - \log[\mu_{\phi_P} + s]}{\sigma_{\phi_P}} \right)^2} \quad (2.16)$$

where we assume that $s = 5$, since *T. drosophilae* is thought to be more sensitive towards cold temperatures than *D. suzukii* (MVRS - Personal communication). The obtained parameter values are $\phi_{P_{min}} = 0.013$, $\mu_{\phi_A} = 5.5$ and $\sigma_{\phi_A} = 0.88$.

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

Juvenile *T. drosophilae*:

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

$$\phi_J(C) = \frac{\phi_J(23)}{\phi_V(23)} \phi_V(C). \quad (2.17)$$

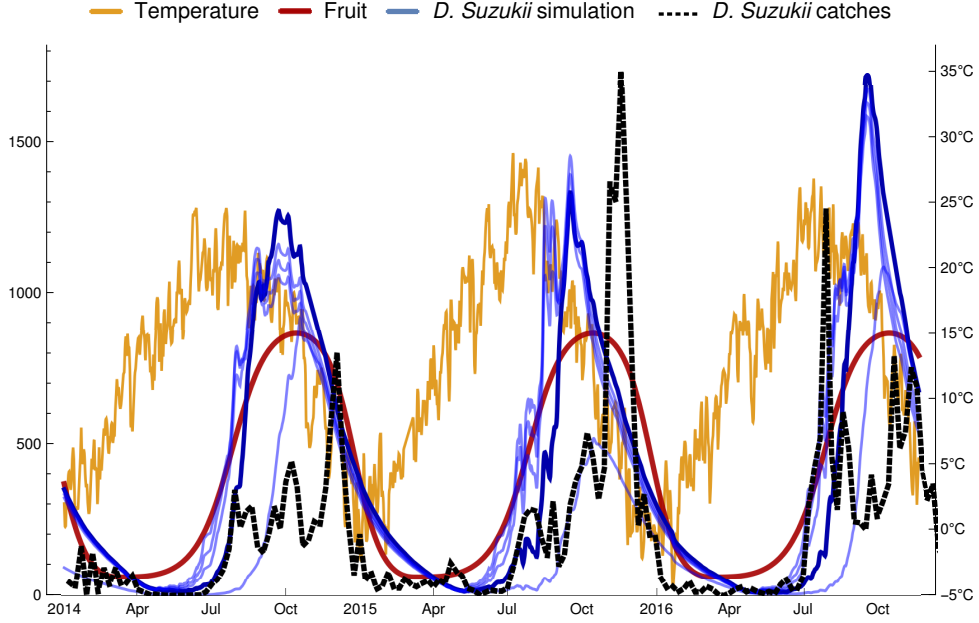


FIGURE 2.11: Simulated *D. suzukii* adult population size, mean *D. suzukii* trap catches and mean daily temperature from S.Michele all'Adige, Italy, during 2014-2016. Different courses of the simulation correspond to different values for the *D. suzukii* attack rate, $\alpha_A = 0.5, 1, 2, 3$ and 5 . The thick curve corresponds to the attack rate we use for further simulations, $\alpha_A = 1$

Fecundity

D. suzukii:

We assume that the daily fecundity of *D. suzukii* depends on two factors: the temperature C and the fruit availability F . To estimate the fecundity at high fruit availability we use the lifetime fecundity from Tochen et al. (2014) (using the data measured on cherry, Table 3 there). From this data we calculate the daily fecundity by using the average life length from the same paper, see Fig. 2.4 (using the data measured on cherry, Table 1 there). The daily fecundity is then fitted by a Gaussian curve

$$\eta_A(C) = \eta_{A_{max}} e^{-\left(\frac{\mu_{\eta_A} - C}{\sigma_{\eta_A}}\right)^2}. \quad (2.18)$$

We obtain the parameter values $\eta_{A_{max}} = 7.3$, $\mu_{\eta_A} = 21.0$ and $\sigma_{\eta_A} = 4.7$ by the least square method in logarithmic scale.

For the fruit dependence we assume a type 2 functional response with attack rate α_A . 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

$$\beta_A = \lambda_A \frac{\eta_A(C)\alpha_A}{1 + \alpha_A F} F = f_A(C, F) F \quad (2.19)$$

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

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. 2.11 with observed catches in the traps, we chose $\alpha_A = 7$ 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 on fecundity and sex ratio (Emiljanowicz 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. 2.4. For the daily fecundity with high pupa abundance, we use the data of (Rossi Stacconi et al., 2017b) (from Figure 4 there). This data is fitted by a Gaussian like curve

$$\eta_P(C) = \eta_{P_{max}} e^{-\left(\frac{\mu_{\eta_P} - C}{\sigma_{\eta_P}}\right)^2} \quad (2.20)$$

and we obtain the parameter values $\eta_{P_{max}} = 10.8$, $\mu_{\eta_P} = 24.4$ and $\sigma_{\eta_P} = 7.1$ 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

$$\beta_P = \lambda_P \frac{\eta_P(C)\alpha_P}{1 + \alpha_P U} U = f_P(C, U) U \quad (2.21)$$

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

where the sex ratio $\lambda_P = 0.53$ is obtained from (Rossi Stacconi et al., 2017b) (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., 2017b). Note also that different experiments suggest quite different values for the fecundity. On one hand, the experiments in (Rossi Stacconi et al., 2017b) 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.

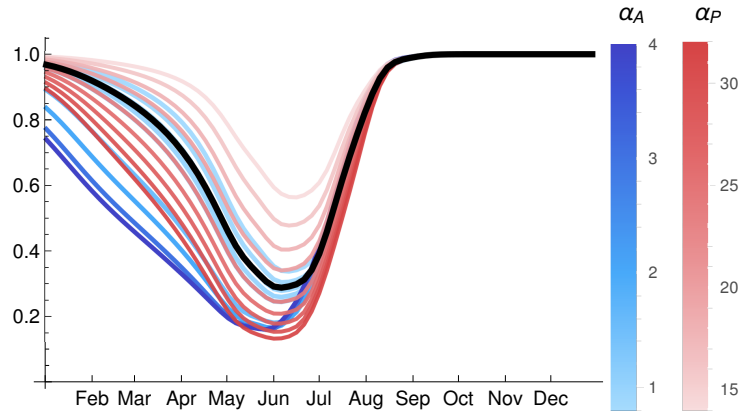


FIGURE 2.12: *D. suzukii* infestation index in dependence of the time of parasitoid introduction with different parameter values for the attack rates of *D. suzukii* versus fruit, α_A , and of *T. drosophilae* versus *D. suzukii*, α_P . The thick black line corresponds to the values we used for the other simulations, $\alpha_A = 1$ and $\alpha_P = 24$. For the other lines we changed the values for one of the parameters with α_A between 0.8 and 4, and α_P between 14 and 32. Parasitoids are released at a single event. The amount of parasitoids released corresponds to 0.5% of the maximum of *D. suzukii* population size estimations reached without intervention (and $\alpha_A = 1$)

To choose a value for the parasitoid attack rate α_P , we assume that the parasitoids reach half of their potential fecundity during the peak season of *D. suzukii* peak season. The obtained value is $\alpha_P = 24$.

Sensitivity analysis for α_A and α_P

As the attack rates of *D. suzukii* and *T. drosophilae*, α_A and α_P , cannot be reliably estimated from laboratory experiments, we conducted a sensibility analysis on their influence. For this analysis, we use different values of this two parameters to repeat in Fig. 2.12 a simplified version of Fig. 2.9 (this figure shows our main objective, the optimal timing for introducing the parasitoid). It turns out, that the parasitoid attack rate, α_P , has virtually no influence on the optimal timing – what is assuring since this parameter could be only guessed roughly. The attack rate of *D. suzukii*, α_A , has a slightly stronger influence. High values suggest an earlier parasitoid release than low values. The reasons is that with higher values for α_A the simulated *D. suzukii* population is growing earlier in the season, see Fig 2.11. This again is reassuring since we adjusted the parameter α_A to fit the onset of the yearly *D. suzukii* outbreak.

Chapter 3

Analysis of a semi-field experiment with *Drosophila suzukii* and its parasitoid *Trichopria drosophilae*

Abstract

An experiment on biological control of the invasive fruit fly *Drosophila suzukii* with its parasitoid *Trichopria drosophilae* is analyzed. The population size, growth rate and the impact of larva competition is estimated for *D. suzukii* directly from data on the proportion of infested fruit. Further data on the number of insects emerging from sampled fruit is used to fit a model based on differential equations for the population dynamics of both species. We obtain estimates of attack rates, of the competition within *D. suzukii* juveniles and of adult population sizes. We find that effectiveness of the parasitoid release might be reduced due to the sampling of fruit and contained juveniles because of the long developmental time of the parasitoid compared to its host. Agricultural practices which could support the success of a parasitoid release are discussed.

3.1 Introduction

The invasive fruit fly *Drosophila suzukii* arrived recently to Europa and America (Asplen et al., 2015). It is continuing to spread and deals considerable damage to the agriculture of soft shelled fruit. Different to other fruit flies, it can infest intact fruit on the plants due to a specially formed ovipositor. Biological control with parasitoids has been suggested as a promising method to confine the pest (Daane et al., 2016; Rossi Stacconi et al., 2017b). However it is still difficult to infer what could be the effect of a large-scale release of parasitoids. In this respect, a very insightful experiment has been carried out on the population dynamics of *Drosophila suzukii* and the local pupal parasitoid *Trichopria drosophilae* in semi-field conditions by Rossi Stacconi et al. (2017a). The full experimental procedure is described in the original work. Here we report only the elements essential for building an appropriate

model. The experiment were conducted in a greenhouse growing raspberry in S. Michele all'Adige (Italy) from 4 August to 22 September, 2016. The greenhouse was divided into three compartments of 50m² with 10 raspberry plants each (5 plants of the variety Tulameen and 5 plants of the variety Heritage). In each compartment a different treatment was applied.

- treatment T0: only *D. suzukii* was introduced. Precisely, 1 couple of flies per m² (1 male and 1 female) was released on 5 August.
- treatment T1: *D. suzukii* release as for T0. Additionally, 0.5 couples of *T. drosophilae* per m² were released each on 4 August and on 11 August.
- treatment T2: identical releases as for T1, but the compartment was additionally equipped with special cages (*augmentoria*) intended to help the parasitoids reproducing. We do not analyze this experiment here.

Weekly fruits have been sampled from different sampling locations (directly from the plants and from two ground positions with differently aged fruits). We describe two different methods to analyze the data of the experiments. In section 3.2, we use direct statistical methods to analyze the experiment with *D. suzukii* alone (treatment T0). The data is used to estimate the population growth rate, the effect of larval competition, and the adult population density which has not been measured directly in the experiment. In section 3.3, we model the population dynamics with differential equations and fit the model parameters to the data of the experiments with and without parasitoid release (treatments T0 and T1). For some parameters, we use values obtained by experiments in the literature. The remaining parameters are estimated with a Monte Carlo Markov Chain approach. The model is used to understand the population dynamics of *D. suzukii* and its parasitoid. We show prognosis for longer time spans and for a modification of the model design, where individuals emerging from the samples are kept in the greenhouse instead of removing them. Finally we discuss the analysis and possible implications on biological control programs in section 3.4.

3.2 Direct fits

3.2.1 Introduction

Here we use direct statistical methods to analyze the data from the compartment in the greenhouse in which only *D. suzukii* was introduced (treatment T0). We look at the measurements obtained from 100 fruits collected from the plants. Each fruit was examined individually to verify whether it had been infested by *D. suzukii*. The fruits were then incubated and the number of emerging flies was counted. The obtained data are

week i	0	1	2	3	4	5
fruits infested d	0	24	79	88	92	91
emerging flies h	0	92	279	414	473	439

The data of the 5 replicates (with each 20 fruits) are shown in Fig. 3.1 together with mean values.

3.2.2 Estimating the rate with which the fruit is attacked and the population densities of *D. suzukii* adults

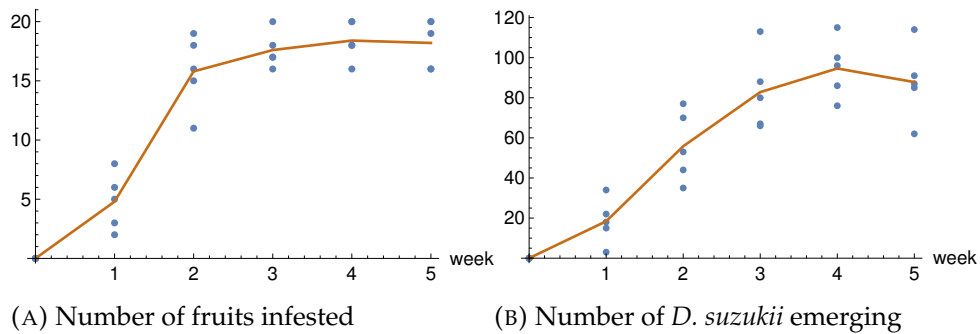


FIGURE 3.1: Experiment with *D. suzukii* alone: measurements from 20 fruits collected randomly from the plants. The data points correspond to the five replicates and the curves correspond to the mean values

We first estimate the probability p_i that a fruit randomly collected in week i is infested by *D. suzukii*. Using that every week $s = 100$ fruit has been collected, the number D_i of infest fruit is binomially distributed. The likelihood function with the observed value d_i thus is

$$P[D_i = d_i] = \binom{s}{d_i} p_i^{d_i} (1 - p_i)^{s-d_i} \quad (3.1)$$

The maximum likelihood estimator is $p_i = \frac{d_i}{s}$. We will use this estimator to derive a direct proxy for the *D. suzukii* population density. This proxy is the rate α_i with which fruit is attacked by *D. suzukii* during week i . We assume, that the α_i are constant during each week and set up a model for the dynamics of infested fruit F_+ and non-infested fruit F_0 . For that, we use the attack rate α_i and assume that fruit matures on the plant at a rate ρ and drops to the ground at rate δ . The system is

$$\begin{aligned} F_0' &= \rho - (\alpha_i + \delta)F_0 \\ F_+' &= \alpha_i F_0 - \delta F_+ \end{aligned} \quad (3.2)$$

We assume that the proportion of infested fruit is close to the (quasi-)equilibrium (\bar{F}_0, \bar{F}_+) . With this equilibrium, we can express the probability p_i for a fruit to be infested as

$$\begin{aligned}
 p_i &= \frac{\bar{F}_+}{\bar{F}_0 + \bar{F}_+} \\
 &= \frac{\alpha_i}{\alpha_i + \delta}
 \end{aligned}
 \tag{3.3}$$

Using the maximum likelihood estimator for $p_i = \frac{d_i}{s}$, we find a maximum likelihood estimator for the weekly attack rate α_i relatively to the rate fruit drops,

$$\begin{aligned}
 \frac{\alpha_i}{\delta} &= \frac{p_i}{1 - p_i} \\
 &= \frac{d_i}{s - d_i}
 \end{aligned}
 \tag{3.4}$$

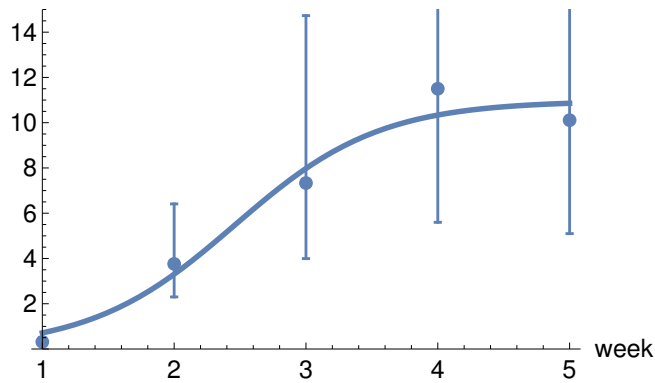


FIGURE 3.2: Maximum likelihood estimators for α_i/δ , a proxy for adult density in the different weeks (dots) fitted with a logistic growth curve

The obtained estimates for α_i/δ for each week are shown in Fig. 3.2. The values are, together with 95% (Clopper Pearson) confidence intervals,

α_1/δ	α_2/δ	α_3/δ	α_4/δ	α_5/δ
0.32	3.8	7.3	11.5	10.1
(0.19-0.51)	(2.3-6.4)	(4.0-14.7)	(5.6-27.4)	(5.1-22.8)

The attack rate can be assumed to be proportional to the density of *D. suzukii* adults. Thus we can estimate, that the population has increased by around 30 times during the course of the experiment. As the obtained estimates suggest that the population is approaching an equilibrium, we fit a logistic growth model for the number of adult *D. suzukii* flies. Namely we assume that the population A is described by the differential equation

$$A'(t) = rA(t) \left(1 - \frac{A(t)}{k} \right)
 \tag{3.5}$$

As we assumed that the attack rate α is proportional to the adult density A , we can plug in $A = c\frac{\alpha}{\delta}$ (with a proportionality constant c) and fit the model to the weekly data points for $\frac{\alpha_i}{\delta}$, see Fig. 3.2. We obtain for the growth rate in absence of competition $r = 0.26$ (per day).

3.2.3 Estimating competition

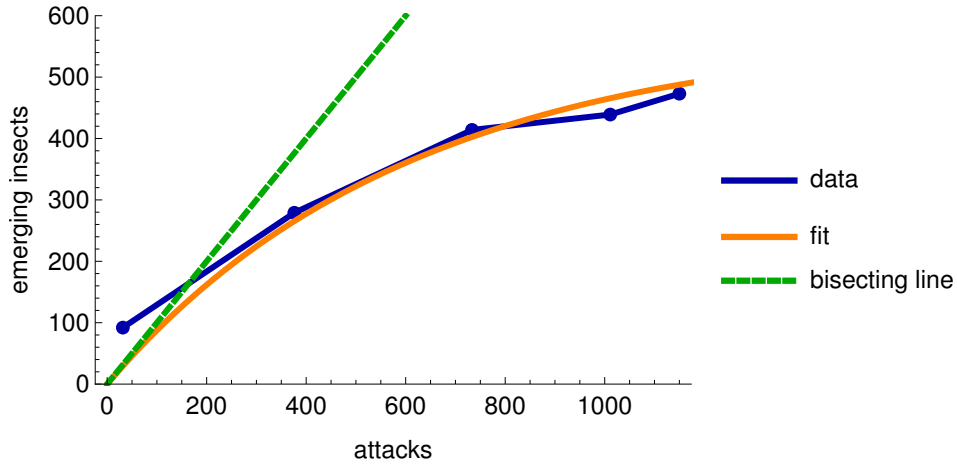


FIGURE 3.3: Blue: Observed number of emerging insects from 100 fruits versus the number of attacks (estimated from the number of infested fruits). Orange: the expectation of emerging insects given the number of infested fruits (including competition). Green: bisecting line. See the main text for details

Now we try to analyze how juveniles compete for fruit. We assume, that the rate with which fruit is attacked is independent of how often the fruit has been attacked before. The probability that a randomly in week i collected fruit has been attacked $K_i = k$ times is then according to Section 3.2.4

$$P[K_i = k] = p_i^k (1 - p_i) \quad (3.6)$$

This describes a geometric distribution and thus the expectation for the total number of attacks for a fruit collected in week i is

$$E[K_i] = \sum_{k=1}^{\infty} k P[K_i = k] = \frac{p_i}{1 - p_i} \quad (3.7)$$

The expectation for how often the $s = 100$ fruit collected in week i have been attacked is thus

$$sE[K_i] = s \frac{p_i}{1 - p_i} \quad (3.8)$$

where the p_i are calculated as described before from the weekly proportion of infested fruits d_i .

However with more juveniles contained in one fruit, the survival probability of the juveniles will decrease (and the fruit might be less attractive for oviposition). We assume that at each attack an egg is placed into the fruit (until a maximal number of eggs in the fruit is reached), and that the survival probability for a juvenile in a fruit in which k eggs were laid is given by

$$e^{-\gamma k} \quad (3.9)$$

where γ represents the competition coefficient. Thus the number of flies M_i emerging from a fruit containing $K_i = k_i$ juveniles can be assumed to be binomially distributed with the success probability calculated by the number of competitors,

$$P[M_i = m | K_i = k] = \binom{k}{m} (e^{-\gamma k})^m (1 - e^{-\gamma k})^{k-m} \quad (3.10)$$

Expectation $E[M_i]$ and Variance $V[M_i]$ of M_i can be computed by using conditioned probabilities, see Section 3.2.4.

We have data for the weekly emergence from $s = 100$ fruits. According to the central limit theorem, the random variable for the total numbers H_i of emerging insects can be assumed to be approximately normal distributed with expectation and variance

$$\begin{aligned} E[H_i] &= sE[M_i] \text{ and} \\ V[H_i] &= sV[M_i] \end{aligned} \quad (3.11)$$

Using the weekly data on emerging insects h_i , a maximum likelihood estimator for the competition parameter γ can be obtained by maximizing

$$\prod_{i=1}^5 f(E[H_i], V[H_i]; h_i) \quad (3.12)$$

where $f(E, V; \cdot)$ is the density of a normal distribution with expectation E , variance V .

The obtained maximum likelihood estimator for the competition parameter is

$$\gamma = 0.045 \quad (0.039 - 0.050) \quad (3.13)$$

where the numbers in brackets correspond to a 95% confidence interval calculated by the likelihood ratio theorem. The maximum average number of emerging insects per fruit can be estimated as

$$\max_k k e^{-\gamma k} = \frac{1}{\gamma e} = 8.2 \quad (3.14)$$

In Fig. 3.3, we compare the number of emerging insects h_i from the weekly collected $s = 100$ fruits with the expectation for how often this fruit has been attacked, $sE[K_i]$, and the "competition corrected" expectation for the number of emerging insects, $E[H_i]$. Note, that if the competition coefficient γ would be zero (and thus survival would be always close to unity), then $sE[K_i] = E[H_i]$ and the data points could be expected to be close to the bisecting line. The figure suggests, that the model fits the data well with our estimation for the competition coefficient. The only strongly outlying data point corresponds to the first week, where juveniles emerged clustered

from a few fruits (even stronger clustered than one would expect when neglecting competition, as the data point is above the bisecting line).

3.2.4 Mathematical details

Distribution for number of juveniles placed in fruit

Here we prove the formula in equation (3.6) for the probability that a randomly in week i collected fruit received $K_i = k$ juveniles when competition is neglected. The idea is to find the equilibrium of a system of ODEs describing the densities of fruit F_k which was attacked k times, and calculate recursively the proportion of fruit attacked k times as $\frac{\bar{F}_k}{\sum_{i=0}^{\infty} \bar{F}_i}$. The system is equivalent to the system (3.2) but fruits in the class of infested fruits are distinguished according to how often they have been attacked, that is the equation for F'_0 stays unchanged and

$$F'_k = \alpha F_{k-1} - (\alpha + \delta) F_k \text{ for } k > 0 \quad (3.15)$$

Note that $\sum_{i=0}^{\infty} \bar{F}_i = \frac{\rho}{\delta}$. Using the equilibrium of the system, we find

$$\begin{aligned} P[K_i = k] &= \frac{\bar{F}_k}{\sum_{i=0}^{\infty} \bar{F}_i} \\ &= \left(\frac{\alpha_i}{\alpha_i + \delta} \right)^k \left(\frac{\delta}{\alpha_i + \delta} \right) \\ &= p_i^k (1 - p_i) \end{aligned} \quad (3.16)$$

Expectation and variance for the number of flies emerging from one fruit

Here we find the expectation and variance of the number M_i of insects emerging from a single fruit used in equation (3.11).

Expectation

$$\begin{aligned} E[M_i] &= \sum_{k=1}^{\infty} E[M_i | K_i = k] P[K_i = k] \\ &= \sum_{k=1}^{\infty} e^{-\gamma k} k P[K_i = k] \\ &= \sum_{k=1}^{\infty} e^{-\gamma k} k p_i^k (1 - p_i) \\ &= (1 - p_i) \sum_{k=1}^{\infty} k (e^{-\gamma} p_i)^k \\ &= (1 - p_i) \frac{e^{-\gamma} p_i}{(1 - e^{-\gamma} p_i)^2} \end{aligned} \quad (3.17)$$

Variance

$$\begin{aligned}
V[M_i] &= E[M_i^2] - E[M_i]^2 \\
&= \left(\sum_{k=1}^{\infty} E[M_i^2 | K_i = k] P[K_i = k] \right) - E[M_i]^2 \\
&= \left(\sum_{k=1}^{\infty} (V[M_i | K_i = k] + E[M_i | K_i = k]^2) P[K_i = k] \right) - E[M_i]^2 \\
&= \left(\sum_{k=1}^{\infty} \left(ke^{-\gamma k} (1 - e^{-\gamma k}) + (ke^{-\gamma k})^2 \right) p_i^k (1 - p_i) \right) - \left((1 - p_i) \frac{e^{-\gamma} p_i}{(1 - e^{-\gamma} p_i)^2} \right)^2 \\
&= \frac{e^{\gamma} (1 - p_i) p_i \left(\frac{(e^{6\gamma} + 2e^{\gamma} p_i^3 - p_i^3 - e^{2\gamma} p_i^2 + 2e^{3\gamma} p_i - 3e^{4\gamma} p_i)(e^{\gamma} - p_i)^2}{(e^{2\gamma} - p_i)^3} - e^{\gamma} (1 - p_i) p_i \right)}{(e^{\gamma} - p_i)^4}
\end{aligned} \tag{3.18}$$

3.3 Modeling the population dynamics with differential equations

This model approach seeks to reproduce the observed data with a system of differential equations. The demographic parameters have been obtained from the literature, while parameters related to the attack rates and the sampling procedure are fitted from the data using a Monte Carlo Markov Chain approach.

3.3.1 Sampling and positions in the experiment

Our model aims to reproduce not only the population dynamics of host and parasitoid, but also the features of the sampling procedure from which the observed data have been obtained. Every week 100 fruit (or a comparable mass of fruit material) is taken from three positions. The first position corresponds to picking fruit directly from the plant. The second position contains fruits which dropped from the plants during the most recent week. These fruits are collected from plates positioned under the plants in the greenhouse. The plates are emptied during the sampling procedure once a week and a remaining part of the fruit is moved to a third sampling position: containers which are left open in the greenhouse for sampling in the coming week. This third sampling position corresponds to fruit remaining on the ground for longer time. All ground samples are taken together with larvae or pupae dropped out of the fruits. The fruit not used for sampling remains in the greenhouse. In our model, we reproduce this sampling scheme by defining 4 different positions through which all fruit (which is not previously removed for sampling) passes. This is convenient and effectively equivalent to the real experimental design, where only a part of the fruits enters the sampling cycle and the other part of the fruit remains directly on the ground. The pattern how fruit is moved in our model is shown in Fig. 3.4. Fruit is maturing on the plants (position 1) from where it drops to the ground (position 2). Once a week all fruit on the greenhouse ground is moved from position 2 to another place on the ground (position 3). At the same time, fruit previously at position 3 is moved to the last compartment on the ground, where it remains (position 4). The model explicitly accounts for the weekly removal of fruit for sampling.

3.3.2 The stage structure

Population densities are measured per m^2 . Juveniles of *D. suzukii* are divided into an egg-larva stage E and a pupa stage U . The pupa stage can be attacked by *T. drosophilae* and is then counted as parasitoid juveniles J . All juvenile stages are assumed to be contained in fruits. The fruit availability is modeled explicitly by tracking the number of times a fruit has been visited by *D. suzukii* adults. Adults of *D. suzukii*, A , and of *T. drosophilae*, P , do not belong to a specific position as they can move freely in the greenhouse. A flow diagram for the stage dynamics is shown in Fig. 3.5. The building blocks of the model are shown in Table 3.1.

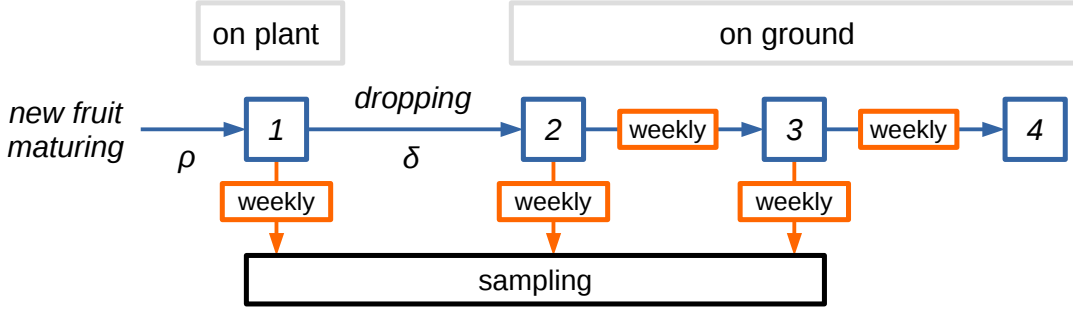


FIGURE 3.4: Flow chart for the movement of fruit and the contained juveniles of *D. suzukii* and *T. Drosophilae*. New fruits are maturing at rate ρ . Uninfested and infested fruit is dropping at rate δ_0 and δ_1 respectively. Fruit is collected weekly from different positions

3.3.3 Renewal equations

The stage dynamics of the different stages X are governed by renewal equations R_X . Those equations determine the rates at which the stages are entered and left (plus the changes due to parasitism and change of the position).

Newly recruited juveniles We only track juveniles which eventually do mature to an adult of *D. suzukii* or *T. drosophilae*. As in section 3.2, we assume that survival of all juveniles contained in a fruit decreases exponentially with the number of competitors. Using the competition parameter γ , the expected number of *D. suzukii* adults to emerge from a fruit visited k times is

$$q_k = ke^{-\gamma k} \quad (3.19)$$

The density of fruits in position i visited k times is denoted by $F_{i,k}$. Assuming the *D. suzukii* adults attack fruits at rate β , the rate successful *D. suzukii* eggs are laid in position i thus is

$$R_{E_i} = \sum_{k=0}^{n-1} \beta A F_{i,k} (q_{k+1} - q_k) \quad (3.20)$$

The maximum number n of visits to a fruit is chosen so as to ensure that $q_{k+1} - q_k$ is positive. That is

$$n = \max\{k \in \mathbb{N} : q_k > q_{k-1}\} = \left\lfloor \frac{e^\gamma}{e^\gamma - 1} \right\rfloor \quad (3.21)$$

T. drosophilae adults are assumed to infest host pupae with attack rate ϵ . Thus new parasitoid juveniles appear in position i at rate

$$R_{J,i} = \epsilon P U_i \quad (3.22)$$

Maturation of juvenile stages The model accounts for the maturation delays of the juvenile stages, which follow stochastic distributions. To ease computations we keep

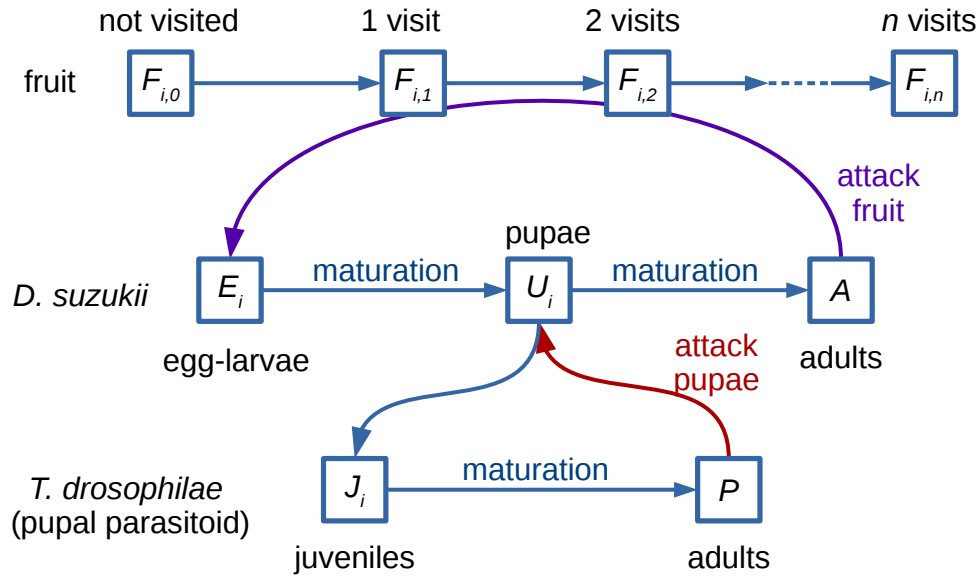


FIGURE 3.5: Flow chart for the dynamics of the model. $F_{i,k}$ is the density of fruit in position i visited k times by $D. suzukii$ adults. E_i , U_i and A are the densities of $D. suzukii$ egg-larvae, pupae and adults. J_i and P are the densities of $T. drosophilae$ juveniles and adults. The different positions i for fruit and the juveniles contained are shown in Fig. 3.4

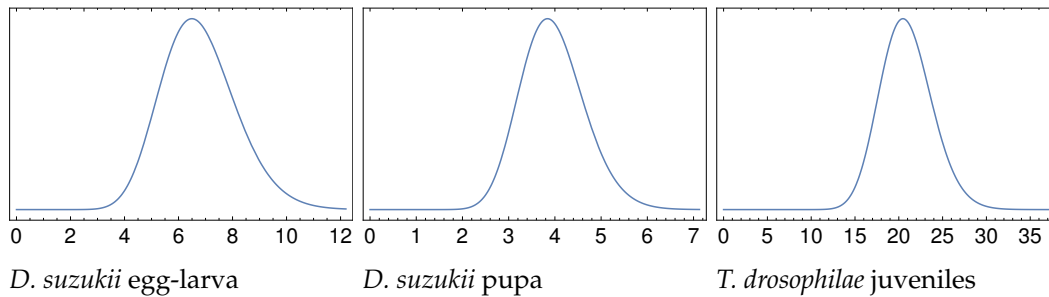


FIGURE 3.6: Distributions for maturation delays (in days, at 25°C or 26°C)

the model within the framework of ordinary differential equations and implement these distributions by dividing the juvenile stage X into k_X sub-stages, and letting individuals mature from each of them with constant rate λ_X . This makes the maturation delay of the complete stage follow an Erwald distribution (the convolution of independent and identical exponentially distributed random variables). Values for the mean μ_X and variance σ_X^2 of the maturation delays can be found in the literature. Using these data and the formulas for the expectation and variance of an Erwald distribution, $\frac{k_X}{\lambda_X}$ and $\frac{k_X}{\lambda_X^2}$ respectively, and taking into account that k_X needs to be an integer, we obtain the parameter values

$$k_X = \text{round} \left(\frac{\mu_X^2}{\sigma_X^2} \right) \quad (3.23)$$

$$\lambda_X = \frac{k_X}{\mu_X}$$

Position i	
1	on plant
2	newly dropped on ground
3,4	on ground for longer time
State variables	
<i>D. suzukii</i> densities (host)	
E_i	egg-larvae
U_i	pupae
A	adults
<i>T. drosophilae</i> densities (parasitoid)	
J_i	juveniles
P	adults
Fruit	
$F_{i,k}$	fruit visited k times
Parameters	
δ_0	dropping rate of non-infested fruit
δ_1	dropping rate of infested fruit and contained juveniles
β	attack rate of <i>D. suzukii</i> on fruit
ϵ	attack rate of <i>T. drosophilae</i> on host pupae
μ_X	expectation for duration of juvenile stage $X = E, U, J$
σ_X^2	variance for duration of juvenile stage $X = E, U, J$
ω_X	mortality rate for adults $X = A, P$

TABLE 3.1: The building blocks for the differential equation model

For a critical examination of this distribution, see (Blythe et al., 1984). The obtained functions are shown in Fig. 3.6.

The sub-stages are passed at rate λ_X . Thus the recruitment rates for pupae and adults of *D. suzukii*, and adults of *T. drosophilae* are given by the rate individuals mature out of the last sub-stage of the preceding juvenile stage. That is

$$\begin{aligned}
 R_{U_i} &= \lambda_L L_{i,k_L} \\
 R_{A_i} &= \lambda_U U_{i,k_U} \\
 R_{P_i} &= \lambda_J J_{i,k_J}
 \end{aligned} \tag{3.24}$$

3.3.4 The differential equations

To formulate the differential equations, it is convenient to use the indicator function

$$\mathbb{1}_x = \begin{cases} 1 & \text{if } x \text{ is true} \\ 0 & \text{if } x \text{ is not true} \end{cases} \tag{3.25}$$

Infested fruit and the juveniles contained drop from the plant (that is move from position 1 to position 2) at rate δ_1 . We define

$$D = \delta_1 (\mathbb{1}_{\{i=2\}} - \mathbb{1}_{\{i=1\}}) \tag{3.26}$$

Now the differential equations for the juvenile sub-stages are

$$\begin{aligned}
E'_{i,z} &= \mathbb{1}_{\{z=1\}} R_{E,i} + E_{i,z} D + \lambda_E (\mathbb{1}_{\{z \geq 2\}} E_{i,z-1} - E_{i,z}) \\
U'_{i,z} &= \mathbb{1}_{\{z=1\}} R_{U,i} + U_{i,z} D + \lambda_U (\mathbb{1}_{\{z \geq 2\}} U_{i,z-1} - U_{i,z}) - \epsilon P U_{i,z} \\
J'_{i,z} &= \mathbb{1}_{\{z=1\}} R_{J,i} + J_{i,z} D + \lambda_J (\mathbb{1}_{\{z \geq 2\}} J_{i,z-1} - J_{i,z})
\end{aligned} \tag{3.27}$$

Hereby we included, that pupae U can be parasitized and is then moved to the parasitoid juvenile stage. The total density of stage $X_i = E_i, U_i, J_i$ is given by the sum of all k_X sub stages

$$X_i = \sum_{z=1}^{k_X} X_{i,z} \tag{3.28}$$

Thus for the overall changes of the juvenile stages the differential equations simplify to

$$\begin{aligned}
E'_i &= R_{L,i} - R_{U,i} + E_i D \\
U'_i &= R_{U,i} - R_{A,i} + U_i D - R_{J,i} \\
J'_i &= R_{J,i} - R_{P,i} + J_i D
\end{aligned} \tag{3.29}$$

Note that there is no mortality for juveniles as we track only juveniles that will reach an adult stage. Competition for fruit is accounted for in the renewal equation (3.20). The differential equations for the adult stages are composed of the juveniles maturing from all positions, and the mortality rates ω_A and ω_P

$$\begin{aligned}
A' &= \sum_{i=1}^4 R_{A_i} - \omega_A A \\
P' &= \sum_{i=1}^4 R_{P_i} - \omega_P P
\end{aligned} \tag{3.30}$$

Fruits $F_{i,k}$ are distinguished by their position i and the number of times k they have been visited by *D. suzukii* adults A . Each fruit is assumed to be visited by *D. suzukii* adults at rate βA independently of how often it was visited before (unless the maximum number of visits n is reached). New mature fruit appear on the plants at rate ρ . They then drop from the plant (moving from position 1 to position 2) at rates δ_0 and δ_1 for non-infested and infested fruit respectively. All together the fruit dynamics are given by

$$\begin{aligned}
F'_{i,k} &= \mathbb{1}_{\{k=0 \wedge i=1\}} \rho + \beta A (\mathbb{1}_{\{k>0\}} F_{i,k-1} - \mathbb{1}_{\{k<n\}} F_{i,k}) \\
&\quad + (\mathbb{1}_{\{k>0\}} \delta_1 + \mathbb{1}_{\{k=0\}} \delta_0) (\mathbb{1}_{\{i=2\}} - \mathbb{1}_{\{i=1\}}) F_{1,k}
\end{aligned} \tag{3.31}$$

3.3.5 Weekly sampling procedure

The weekly sampling procedure is carried out at time $t = 7, 14, 21, \dots$. The samples consist of $s = 100$ fruit from position $i = 1, 2$ and 3 each. This corresponds to $\zeta = 2$ fruits per m^2 from each position (as the greenhouse compartments have 50

m²). Thus from each of those three positions, a proportion of $\frac{\zeta}{F_i}$ of fruit and all contained juveniles is removed for sampling. Here

$$F_i = \sum_{k=0}^n F_{i,k} \quad (3.32)$$

is the total number of fruit in position i .

After taking the samples, the state variables $X_i = E_{i,z}, U_{i,z}, J_{i,z}$ and $F_{i,k}$ are thus changed according to the samples removed and the scheme described in Section 3.3.1. That is

$$\begin{aligned} X_4 &\rightarrow X_4 + X_3 \left(1 - \frac{\zeta}{F_3}\right) \\ X_3 &\rightarrow X_2 \left(1 - \frac{\zeta}{F_2}\right) \\ X_2 &\rightarrow 0 \\ X_1 &\rightarrow X_1 \left(1 - \frac{\zeta}{F_1}\right) \end{aligned} \quad (3.33)$$

3.3.6 Initial conditions

The initial density for fly adults is

$$A(0) = 1 \quad (3.34)$$

All juvenile densities are zero at the beginning. In treatment T0 no parasitoids are introduced. In treatment T1 parasitoids are released twice, once at the beginning of the experiment and once after the first week. That is

$$\begin{aligned} P(0) &= 0.5 \\ P(7) &\rightarrow P(7) + 0.5 \end{aligned} \quad (3.35)$$

At the beginning the densities for the non-infested fruit compartments are

$$\begin{aligned} F_{1,0}(0) &= \phi \\ F_{2,0}(0) &= 0 \\ F_{3,0}(0) &= \zeta \\ F_{4,0}(0) &= 0 \end{aligned} \quad (3.36)$$

Hereby, the initial condition for the fruit in position 1 (on the plant) is a parameter ϕ to be adjusted. The initial condition for the fruit in position 3 reflects the assumption, that the fruit on the ground is just enough to allow for the sampling in the following week. All compartments for infested fruit are zero at the beginning.

3.3.7 Fixed parameters

Estimations for the durations of the juvenile stages and the mortality of the adult stages have been taken from the literature. Those factors depend on the temperature. The average temperature outside the greenhouse was 21°C according to data from Fondazione Edmund Mach (S. Michele all'Adige, Italy). We assumed that the temperature in the greenhouse was constant and 4 – 5°C warmer than that.

We fit the distributions for the maturation delays for *D. suzukii* to the data from (Tochen et al., 2014) (at 26°C on cherry for females), and for *T. drosophilae* from (Rossi Stacconi et al., 2017b) (at 25°C for females). Using the means μ_X and the standard deviations σ_X (estimated from the standard error and the sample size) in those works, we obtain the rate parameters λ_X and shape parameters k_X (which is equivalent to the number of sub-stages) as described in equation (3.23). For *T. drosophilae* the obtained shape parameter was very large (and thus making the simulations too computationally intensive) so we reduced it to 50 and calculated the rate parameter using the mean μ_X . The parameter values are

Maturation delay parameters		
stage X	rate λ_X	sub-stages k_X
E (<i>D. suzukii</i> egg-larvae)	3.4	24
U (<i>D. suzukii</i> pupae)	8.3	33
J (<i>T. drosophilae</i> juveniles)	2.4	50

Adult mortality of both species was calculated as the inverse of the average life length from the same works (under the same conditions).

Mortality parameters	
$\omega_A = 1/12.8$	mortality rate of <i>D. suzukii</i> adults
$\omega_P = 1/22.7$	mortality rate of <i>T. drosophilae</i> adults

3.3.8 Likelihood function

The parameters γ , β , ρ , ϵ , δ_0 , δ_1 and ϕ are estimated with a Monte Carlo Markov Chain (MCMC) method.

The weekly data have been obtained for each $s = 100$ fruits from three positions: directly from the plants (position 1) and from the ground positions 2 and 3. In the first experiment (treatment T0), the obtained measures are

week i	1	2	3	4	5	6	7
fruits infested $y^{T0,F}$ from plant	24	79	88	92	91	-	-
emerging flies $y^{T0,D1}$ from plant	92	279	414	473	439	-	-
emerging flies $y^{T0,D3}$ from pos. 3	261	366	388	514	448	465	523

The measures obtained in the second experiment (treatment T1) are

week i	1	2	3	4	5	6	7
fruits infested $y^{T1,F}$ from plant	25	61	72	87	88	-	-
emerging flies $y^{T1,D1}$ from plant	120	294	383	423	462	-	-
emerging flies $y^{T1,D2}$ from pos. 2	290	310	364	454	428	422	488
emerging flies $y^{T1,D3}$ from pos. 3	205	346	343	383	369	344	375
emerging parasitoids $y^{T1,P2}$ from pos. 2	2	8	6	9	2	13	3
emerging parasitoids $y^{T1,P3}$ from pos. 3	17	48	42	68	51	51	72

The likelihood functions are composed by binomial distributions for the numbers of infested fruits (with sample size $s = 100$ and the "success probability" given by the proportion of non-infested fruit compared to total fruit) and Poisson distributions for the number of insects emerging from the samples (with the expectation value given by the average number of juveniles per $s = 100$ fruits). We write the probability mass functions as

$$\begin{aligned} Bin(m, p) &= \binom{s}{m} p^m (1-p)^{s-m} \\ Poi(m, \lambda) &= e^{-s\lambda} \frac{(s\lambda)^k}{k!} \end{aligned} \quad (3.37)$$

The samples are given by the densities in the compartments right before they are moved according to equation (3.33).

The data Y^{T0} of the experiment without parasitoids (treatment T0) is used for the likelihood function

$$\begin{aligned} \mathcal{L}_1(Y^{T0}|\theta) &= \prod_{i=1}^5 \left(Bin \left(y_i^{T0,F}, \frac{\sum_{k=1}^n F_{1,k}(7i)}{\sum_{k=0}^n F_{1,k}(7i)} \right) Poi \left(y_i^{T0,D1}, \frac{E_1(7i) + U_1(7i)}{\sum_{k=0}^n F_{1,k}(7i)} \right) \right) \\ &\cdot \prod_{i=1}^7 \left(Poi \left(y_i^{T0,D3}, \frac{E_3(7i) + U_3(7i)}{\sum_{k=0}^n F_{3,k}(7i)} \right) \right) \end{aligned} \quad (3.38)$$

The data Y^{T1} of the experiment with parasitoids (treatment T1) is used for the second likelihood function

$$\begin{aligned} \mathcal{L}_2(Y^{T1}|\theta) &= \prod_{i=1}^5 \left(Bin \left(y_i^{T1,F}, \frac{\sum_{k=1}^n F_{1,k}(7i)}{\sum_{k=0}^n F_{1,k}(7i)} \right) Poi \left(y_i^{T1,D1}, \frac{E_1(7i) + U_1(7i)}{\sum_{k=0}^n F_{1,k}(7i)} \right) \right) \\ &\cdot \prod_{i=1}^7 \left(Poi \left(y_i^{T1,D2}, \frac{E_2(7i) + U_2(7i)}{\sum_{k=0}^n F_{2,k}(7i)} \right) Poi \left(y_i^{T1,D3}, \frac{E_3(7i) + U_3(7i)}{\sum_{k=0}^n F_{3,k}(7i)} \right) \right) \\ &\cdot \prod_{i=1}^7 \left(Poi \left(y_i^{T1,P2}, \frac{J_2(7i)}{\sum_{k=0}^n F_{2,k}(7i)} \right) Poi \left(y_i^{T1,P3}, \frac{J_3(7i)}{\sum_{k=0}^n F_{3,k}(7i)} \right) \right) \end{aligned} \quad (3.39)$$

The joint likelihood function of the two experiments $Y = \{Y^{T0}, Y^{T1}\}$ is

$$\mathcal{L}(Y|\theta) = \mathcal{L}_1(Y^{T_0}|\theta)\mathcal{L}_2(Y^{T_1}|\theta) \quad (3.40)$$

We use the Metropolis-Hastings algorithm to estimate the parameters (Gilks et al., 1995). That is, we start with some initial parameter values and repeat simulating the model. For each run, new “candidate” parameters are drawn by a normal distribution with means from the last “accepted” parameter values and some given variances. The accepted parameter values θ_A are at the beginning equal to the start values. After each step they are replaced by the current candidate parameters θ with probability

$$\min \left\{ 1, \frac{\mathcal{L}(Y|\theta)}{\mathcal{L}(Y|\theta_A)} \right\} \quad (3.41)$$

3.3.9 Results

The parameter values obtained by the MCMC method are shown in Fig. 3.7. The parameter values with the highest likelihood are used for simulations which are shown together with the corresponding sample values in Fig. 3.8. Plots of the simulated population densities over an extended time span are shown in Fig. 3.9. As a modification of the model, we assumed that no fruit and juveniles were removed for sampling from the greenhouse. Simulations for the proportion of fruit infested are shown in Fig. 3.10. The maximum likelihood estimators found for the parameters are

γ	β	ρ	ϵ	δ_0	δ_1	ϕ
0.052	0.55	0.65	0.15	0.0061	0.29	4.4

3.4 Discussion

We described two different methods to analyze the data of the experiment.

In Section 3.2, we use direct statistical methods to analyze the treatment with only *D. suzukii* released and no parasitoids. We use only a part of the data –precisely the measures taken from fruits collected directly from the plants– to reduce uncertainties due to the sampling procedure. We obtain an estimation for the development of the adult *D. suzukii* population size. According to the estimation, the population has grown during the course of the experiment from 1 couple of adults per m² to about 30 couples per m². The intrinsic growth rate of the population (in the absence of competition) is estimated to be $r = 0.26$. This corresponds to a doubling time of $\log(2)/r = 2.7$ days. The estimation is comparable to laboratory data from Tochen et al. (2014), who report $r = 0.22$ and 0.21 at temperatures of 22°C and 26°C respectively (which is a realistic range for the mean temperature in the greenhouse). We further use the data of the experiment to estimate the strength of juvenile competition in the fruits. We estimated that, with maximal infestation, an average of about 8 insects can emerge per raspberry fruit.

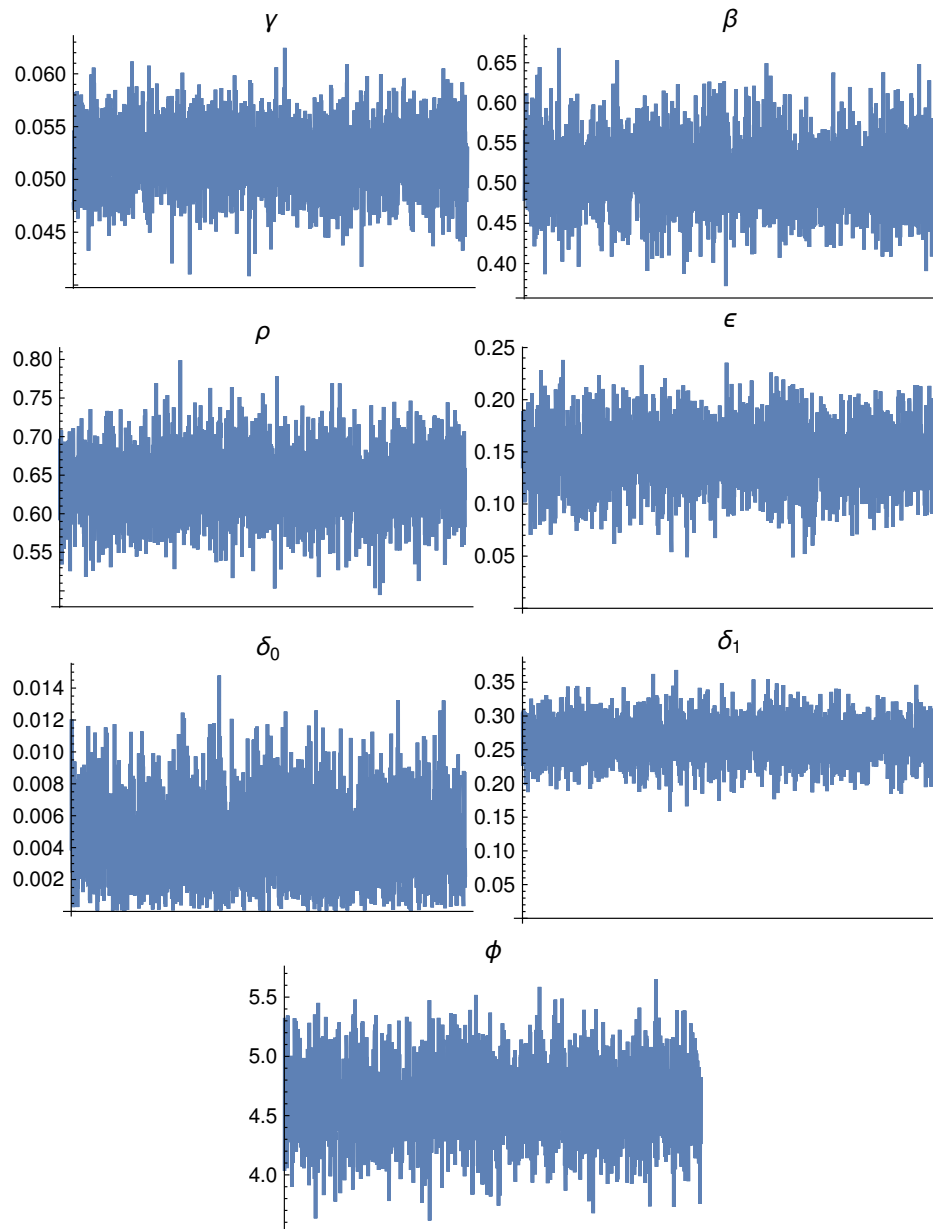


FIGURE 3.7: Parameters obtained by MCMC

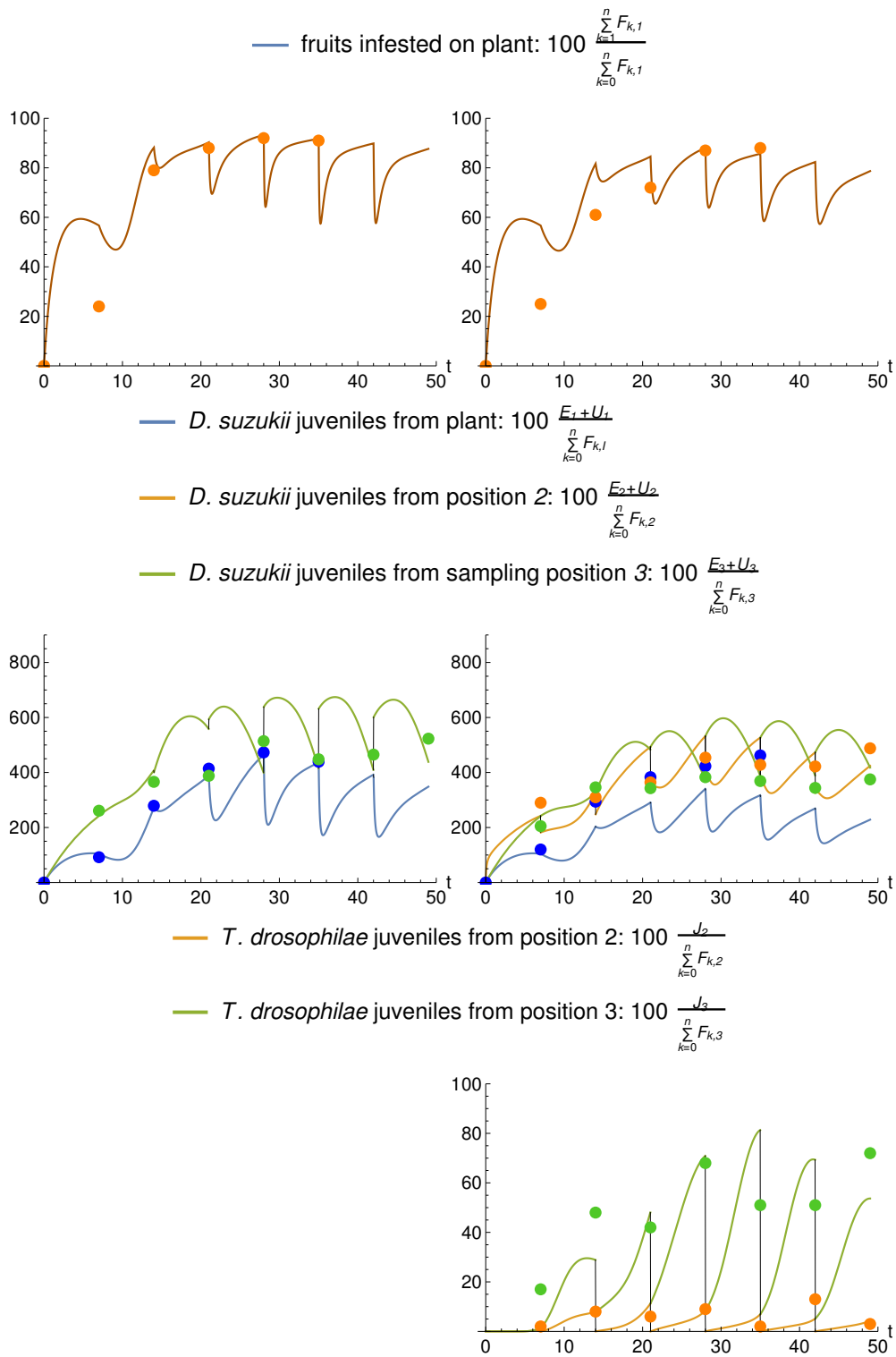


FIGURE 3.8: Simulations and experimental data without (left, treatment T0) and with parasitoids (right, treatment T1)

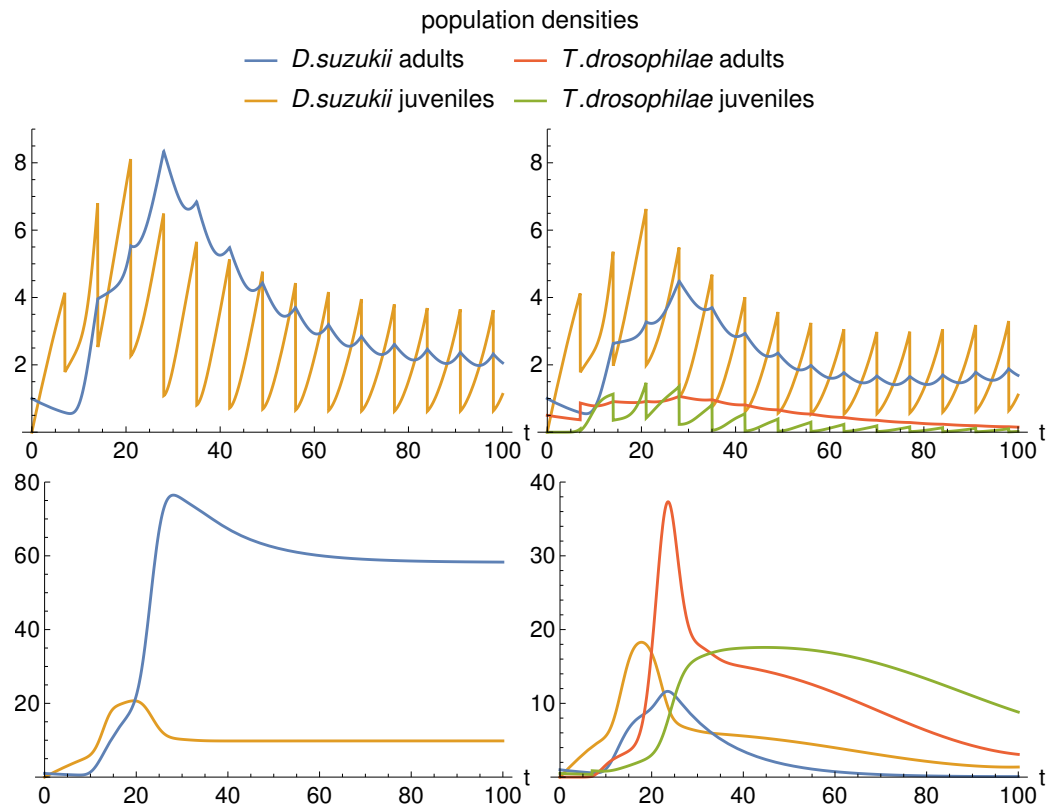


FIGURE 3.9: Simulation without (left, treatment T0) and with parasitoids (right, treatment T1) for an extended time span. Upper panels: fruit and juveniles are removed for sampling. Lower panels: all fruit and juveniles are kept in the greenhouse. *D. suzukii* juveniles are scaled down by factor 5. Note the different scales on the y-axes

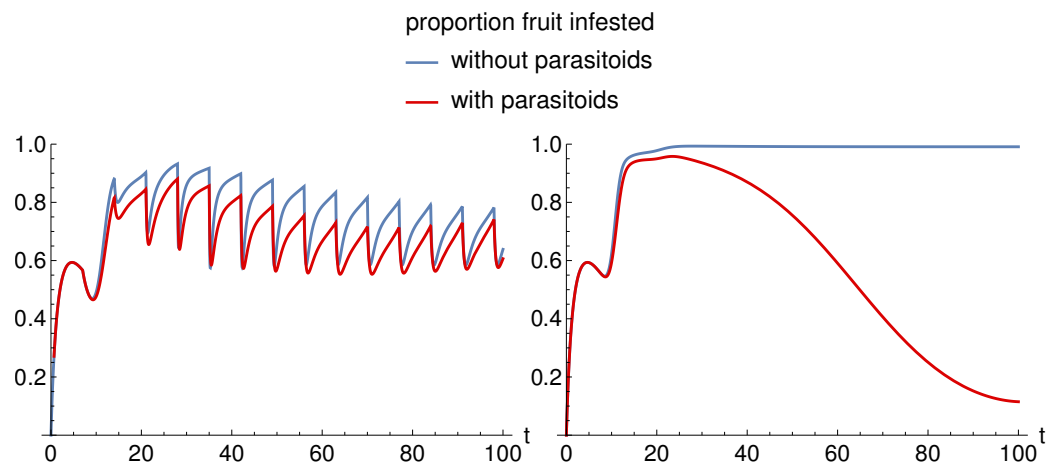


FIGURE 3.10: Simulated proportion of infested fruit for longer time span. Left: removing fruit and juveniles from the greenhouse for sampling. Right: keep all fruit and juveniles in the greenhouse

In Section 3.3, we use the experiments with and without parasitoid release to fit the parameters of a model for the population dynamics. The estimates for the competition coefficients are quite comparable with the previous estimation. On the other hand, the estimates for adult densities are different both quantitatively and qualitatively (in Fig. 3.9 adult density is estimated to decrease after week 4, while Fig. 3.2 suggests it was growing to an equilibrium). A reason for this discrepancy could be due to the relatively low estimate for the rate at which new ripe fruits appear. Also the assumption that fruits are either totally attractive (ripe) or unattractive (unripe) to *D. suzukii* may be an oversimplification which can lead to discrepancies between the models and reality (Lee et al., 2011b).

With the parameters found, the model suggests that a significant part of the fruit and contained juvenile insects is removed for sampling. To understand what effect this removal of fruits can have, we show simulations of the original model and a modification where no fruits are removed in Fig. 3.9 and 3.10. Without parasitoid release, the *D. suzukii* adult density is reduced strongly by the removal. However in the simulations with parasitoid release, the removal of fruits affects the parasitoids much stronger than its host. The parasitoid intervention has almost no effect when fruits are removed, while it reduces the infestation drastically when all fruits remain in the greenhouse. This can be explained by the longer developmental time of the parasitoids, which makes them more sensible to the removal of fruit and the contained juveniles. The effect clearly depends on how much fruit is removed relatively to the total amount of fruit available. We had no direct data for the fruit availability and relied on a maximum likelihood technique to estimate the rate it is maturing on the plants. Besides temporal variations, this rate might be considerably higher than we estimated (Daubeny and Anderson, 1991; Myers, 1993). To test our hypothesis, one could alter the current experimental design so that the insects emerging from the samples are released back to the greenhouse. In practice, so called *augmentoria* could help to increase parasitoid densities (Deguine et al., 2011). Such *augmentoria* are cages equipped with nets through which only the parasitoid can pass but not the much larger *D. suzukii*. Fruits infested by *D. suzukii* are placed in the cages so they can be attacked by parasitoids which offspring then can emerge from the cage. In fact, a third treatment with *augmentoria* has been tested in the greenhouse. In this treatment some fruit was collected from the ground and placed in the *augmentoria*. However the results did not differ substantially from the treatment with normal parasitoid release, and we do not analyze it in this work. Still the limited effectiveness of *augmentoria* in the experiment does not necessarily disprove our hypothesis, as in both treatments the same amount of fruit was removed from the greenhouse. Experiments where a given amount of fruit is for one treatment removed and for another treatment put into *augmentoria* could be valuable to understand whether such techniques can be effective for controlling *D. suzukii* in the practice.

Final conclusions

Mathematical models can make us look differently at biological systems. This can sometimes lead to real surprises. In fact, I experienced such surprises during the preparation of each work in this thesis. Interestingly, it were exactly those – at the beginning puzzling – observations, from which I learned most and which finally shaped the thesis.

In the first work, the moment of surprise was when trying to solve a seemingly easy exercise. The exercise was to prove uniqueness of the coexistence equilibrium in a model for two competing parasitoid species. Looking for this proof felt somehow much harder than expected - until finally numerical trials revealed the true nature of the problem: the assumption itself was misleading, as coexistence equilibria are not necessarily unique in this model. What first seemed an odd observation then turned out to be related to the deeper connection between coexistence, invasibility and competition.

In the second work, the surprise was the outcome of a model for the release of parasitoids in agriculture. The model was used to study how a parasitoid release should be timed for optimally controlling the invasive fruit fly *Drosophila suzukii*. Initially it seemed convincing, that releasing parasitoids would be most efficient in early spring with the idea to target the pest population when it is at a low density. However, the model is far from verifying this expectation. In fact, it suggests that the optimal timing for a parasitoid release is around the begin of summer, when the *D. suzukii* population increases sharply. The model underlines two key factors for the success of a parasitoid release: the temperature of the environment should be warm enough for the parasitoid to be active, and the pest population should be reproducing so that the parasitoids can find the vulnerable juvenile stage.

Also the third work shows a surprising observation concerning the use of parasitoids for controlling *D. suzukii*. The work analyzes an experiment in which *D. suzukii* and a parasitoid species were released in a greenhouse, from which then fruit was sampled regularly to obtain different measures. After incubating these samples, quite a lot of parasitoids emerged, but strangely the success of the intervention seemed limited as still most of the fruit collected were infested by *D. suzukii*. However, a model might give a simple answer to this puzzling observation: it may be, that the sampling procedure actually removed a large part of the fruit grown in the greenhouse, so that the parasite juveniles attached to this fruit could no more emerge in the greenhouse due to their long developmental time (differently to the host juveniles, which develop faster). Additional simulations suggest, that the intervention

could have been much more effective if no fruit would have been removed or if the insects emerging from the samples would have been released back into the greenhouse. The same mechanism might be relevant when parasitoids are used to protect frequently harvested crops. In such circumstances, it could be counter-intuitively beneficial to leave infested fruit in the field so that new parasitoids can emerge from it. A better alternative might be to place the infested fruit into so called augmentoria, which are cages equipped with fine nets through which only the parasitoid can pass but not the larger host. In this way, emerging host adults are trapped inside the augmentoria, while emerging parasitoids can pass through the nets and continue to control the pest population.

All together, I hope that these works are not only interesting but will also help to improve biological control of *D. suzukii* or similar pest species. I am convinced that mathematical models as those presented here can support the development of integrated pest management strategies, which can protect crops in an effective and environment friendly way.

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