Highlights

A general ODE-based model to describe the physiological age structure of ectotherms: description and application to *Drosophila suzukii*

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- Formulation of a novel physiologically-based model describing ectotherms.

- A system of ordinary differential equations describes the identifiable life stages.

- The model can describe the life cycle of most of the insect species.

- Four models existing in literature can be obtained as a special case of the novel model.

- *Drosophila suzukii* is considered as case study to validate the model with three-year field data.

A general ODE-based model to describe the physiological age structure of ectotherms: description and application to *Drosophila suzukii*

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Abstract

This paper introduces a novel general model based on Ordinary Differential Equations (ODEs) which is able to describe the population dynamics of a large class of insect pests. The proposed model is a physiologically-inspired generalization of a number of *ad hoc* models presented through the years in the literature. Its main feature is that it allows the systematic generation of a population model for a species by simply defining its key features, namely the sex ratio and the development, fertility, and mortality rates. The first part of the paper provides a detailed description of the model and shows that most ODE-based models existing in literature can be obtained as a special case of the proposed model. The second part of the paper shows an application of the model to the spotted wing drosophila *Drosophila suzukii*, which is a highly relevant pest in agriculture. The biological features of this species, i.e.,

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the sex ratio and the various rates, were retrieved from the existing scientific literature. The obtained model was validated using data from a three-year survey conducted in two experimental fields. Results show that the model described faithfully the experimental populations, although the simulations were performed completely in open-loop and without any adaptation of the parameters extracted from the existing literature.

1. Introduction

In recent years, thanks to the growing availability of different technologies, we are experiencing what is often defined as "the fourth agricultural revolution" [1]. The key concept of such revolution is the so-called "Precision agriculture" [2]. "Precision agriculture" is a concept that incorporates a series of technological and philosophical changes in the way agriculture is conceived.

The key feature of precision agriculture is that it aims at using the inputs (e.g., water and agrochemicals) only when and where they are actually needed [3]. The scientific community is investing a considerable amount of effort to make this vision become a reality. A large number of activities on the subject are currently ongoing at different levels [4]. To progress towards the precision agriculture paradigm, particular attention must be focused on plant protection against pests and diseases. In fact, a large portion of the agrochemicals is used to control insect pests and pathogens such as bacteria, fungi, or nematodes, and it is well-known that a indiscriminate use of these

substances is highly dangerous for the ecosystems [5]. Accordingly, to use them in a more selective way would dramatically reduce the environmental footprint of farming.

Several authors [6, 7] pointed out that, to do so, the development of technologies for the automated/semi-automated detection of pests and diseases is fundamental. However technology alone is not enough. This is due to at least two reasons: *i)* in agriculture measuring is economically expensive, and for many crops probably it will likely never be realistic to perform a continuous monitoring of all plants; *ii)* in order to plan effective treatments is important not only to measure the current status of the farm, but also to predict the future evolution of the infestations. Accordingly, in parallel with the technological research, it is fundamental to develop mathematical models able to describe and predict the evolution of the infestations [8]. Many scientists around the world are currently working on the mathematical modelling of insect pests population dynamics [8, 9, 10, 11]. Pest population models are particularly important when pest management is performed through the release of natural enemies, the use of which is rapidly growing among farmers and is one of the core aspects of the so-called Integrated Pest Management (IPM) framework. In fact, the effectiveness of IPM control strategies is strongly related to the pest life cycles, and to *when* the peak of the individuals belonging to the most susceptible stages occurs, which, to be determined, requires the use of sufficiently reliable mathematical models [12].

Insects, like most ectotherms, progress through their life stages with development speeds that are highly dependent on the environmental parame-

ters, temperature mainly [13]. This concept is well known by entomologists [8], at the point that several authors provided mathematical expressions to describe the development rate as a function of the temperature [14, 15, 16] (and references therein). The proliferation of mathematical expressions describing the relationship between ectotherms and environmental parameters such as temperature laid the foundations for the so-called "physiologically-based models". Conceptually a physiologically-based model can be defined as the union between "phenological models" and "population dynamics models" which means that they describe the development of ectotherm populations over time while considering the stage development driven by environmental factors. Most of the physiologically-based models are formulated using ordinary [17, 18, 19, 9, 20] and partial [21, 22, 23, 24, 25, 26, 27] differential equations (ODEs and PDEs, respectively). Note that, although most existing models present similarities, they are *ad hoc* models, each developed for specific insect species.

The aim of this work is to propose a general model able to describe the life cycle of most insect species of agricultural interest. The proposed model is a generalization of several existing models presented in the literature such as [17, 18, 19, 9, 20]. This means that all these models can be seen as special embodiments of the general model presented in this paper.

The proposed model formulation considers both a detailed description of the biological mechanisms of the ectotherms' populations development and a description of their age structure in terms of "identifiable life stages". Contrary to other species, such as mammals, insects have well defined and "identifiable" life stages. Accordingly, a natural way to represent their life

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cycle in mathematical form is through a system of coupled ODEs where each equation describes a clear and well identifiable part of the life cycle. Although some PDE-based models have been presented in the literature, ODEs are a much more natural way to describe the development of insect populations, and moreover are much simpler to handle and simulate. In the model we propose in this work the transitions between the various stages are summarized in terms of development, fertility, and mortality rates which, as mentioned before, are commonly studied in the entomological literature [28, 14, 29] and that are typically a function of the temperature and, possibly, of other external phenomena such as food availability [30, 31, 32] and photo-period [33].

We believe that the model proposed in this study provides a general framework that will allow the community to describe and simulate in a systematic and standardized way many insect populations. Indeed, to develop a model for a given insect species, it is enough to recover the development, fertility, and mortality rate functions specific to a species and plug them in our framework to obtain a new model.

To show the effectiveness and the flexibility of the proposed model, we will show that several models proposed in the literature for specific species can be actually seen as special cases for our model.

Furthermore, we propose a new (and highly relevant by itself) case study concerning the modelling of an invasive insect pest, the spotted wing drosophila *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae). For this insect the general model presented in this paper has been particularized using the development, fertility, and mortality rate functions and parameters available

in the literature. The simulations are then compared with data coming from a three-years data collection campaign on two different fields. Part of the used data were already published in [34] and part is published here for the first time. Interestingly, the open-loop simulations of the obtained model faithfully predict the measured data without any adaptation of the parameters.

2. Materials and methods

2.1. Model overview and assumptions

In order to describe the main mechanisms of insects' development, the ectotherms' life cycle is divided into discrete age classes, each representing an "identifiable" life stage. As shown in Fig. 1, we consider an egg stage, a variable number of larval instars, and up to two adult stages. Note that adult stages are divided by sex, which is a highly important feature to describe insects where the two sexes have different characteristics.

To each stage it is associated a scalar state $x_i(t)$, $i = e, L_1, ..., L_n, A_m, A_{f,1}, A_{f,2}$ which represents the number of individuals in the population that at time t are in the stage i. Similarly to what is presented in other studies in the literature [22, 23], the flow of individuals entering and leaving each life stage is regulated by specific "rate functions" which are: *i)* specific for each species, and *ii)* relate the development, mortality and fertility rates to the environmental parameters (e.g., temperature, relative humidity, photo-period, food availability, etc.) and optionally to one or more states of the system.

As we will detail in the next subsections, this naturally leads to model the population development as a system of ODEs.

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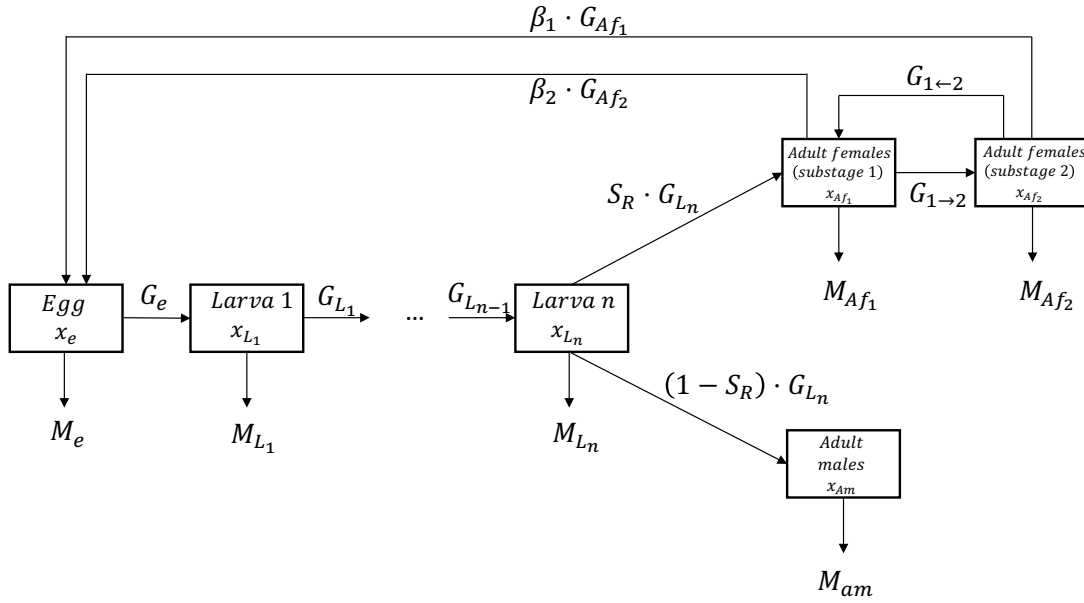Figure 1: Schematic representation of the life cycle

As already mentioned, to capture the specifics of certain insects, the adult stages in Fig. 1 are divided by sex and, moreover, the possibility that females can be in two different states (representing e.g., non-mated and mated or younger and older females) is taken into account. Note that, in line of principle, even more adult stages could be considered. However, to the best of our knowledge, no models using more than two adult stages have been presented so far in the literature nor we are aware of species for which more than 2 stages are necessary to describe the life of adult females. We believe that this two sexes - two female stages modelling is particularly important to represent multivoltine species, i.e., species having multiple generations in a single year (or in a single growing season) and allows to model, as special cases, a number of specific situations including:

- thelytokous parthenogenetic species, where populations are composed only by females (in this case $S_R = 1$ and no equations describing males are present);

- species where it is convenient to use the two female substages to distinguish between non-mated and mated females. In this case $\beta_2 = 0$. Note that it is also possible to model: *i)* females that mate and lay eggs multiple times in their life cycle ($G_{1\to2} \neq 0$), or *ii)* females that mate only once in their life cycle ($G_{1\to2} = 0$);

- species where it is convenient to divide the life of a female in two different stages with different fertility and mortality rates (in this case $\beta_1 \neq 0$, $\beta_2 \neq 0$, $G_{1\to2} = 0$).

In the rest of the text we will describe the ODEs for each stage of the proposed model. Note that in the literature the "rate" functions between stages are often characterized as functions of the temperature only [35, 36, 12, 14, 28], but there are cases where corrections to take into account other factors (e.g., relative humidity or rain) are used [18]. In this work we have chosen to write them as functions of the time to highlight that, in line of principle, they can be functions not only of the temperature but also of other environmental factors which, in turn, depend on time. For the sake of completeness we have also to mention that some of these rates (e.g., mortality rates and fertility rates) may also depend on some of the states of the population (to model, for instance, that overpopulation increases the mortality rate, see e.g., [20]). For the sake of notation compactness the potential dependence of the rate functions on the population states will not be

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152 explicitly reported in the rest of the this paper, unless explicitly needed.

2.2. Model formulation

154 Following the assumptions summarized in the above general overview, we
155 hereby introduce the general equations of our model. We wish to remind the
156 reader that being a general model, not all possible development paths that
157 the model is able to describe make sense for all insects, but that, depending
158 on the species, some of the development/fertility rates must be put to zero.
159 As usually done in the ecological literature, all over this paper we assume the
160 time measurement unit to be *days* and the rate functions to be expressed in
161 $\# \, of \, individuals/day$.

162 *Egg stage.* We denote by $x_e(t)$ the number of individuals in the egg stage at
163 time t. The variation of $x_e(t)$ over time depends on: *i)* the number of new
164 eggs produced by adult females, which is a function of the number of adult
165 females in the two stages, denoted by $x_{A_{f_i}(t)}$, $(i = 1, 2)$, of the fertility rates
166 $\beta_i(t)$, $(i = 1, 2)$ and the development rates $G_{A_{f_i}}(t)$, $(i = 1, 2)$, *ii)* the number
167 of eggs which moves to the first larval instar stage, given by the current
168 population and the development rate function $G_e(t)$ at time t, and *iii)* the
169 number of eggs which leaves the stage due to mortality, which is based on the
170 mortality rate function $M_e(t)$. Accordingly, the egg stage can be expressed
171 by the following ODE:

$$\frac{d}{dt}x_e(t) = G_{A_{f_1}}(t)\beta_1(t)x_{A_{f_1}}(t) + G_{A_{f_2}}(t)\beta_2(t)x_{A_{f_2}} - G_e(t)x_e(t) - M_e(t)x_e(t).$$
$$(1)$$

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¹⁷² *Larval stages.* Larval stages are usually composed by a series of identifiable

¹⁷³ instars, whose number varies from species to species. Although in many

¹⁷⁴ models all larval instars are mathematically represented by a single stage

¹⁷⁵ [37, 38, 18], the proposed model allow to generalize to an arbitrary number

¹⁷⁶ of instars. In general we believe that, if the larval instars are "identifiable",

¹⁷⁷ each of them should be treated as a single stage. Thus, contrary to previous

¹⁷⁸ works, in this work the larval stage is described by n chained equations corre-

¹⁷⁹ sponding to the number of larval instars. We denote by $x_{L_i}(t)$ the number of

¹⁸⁰ individuals belonging to the ith larval instar at time t. The variation of $x_{L_i}(t)$

¹⁸¹ over time depends on: *i)* the number of individuals coming from the previous

¹⁸² stage, which is a function of the populations of the stage $x_{L_{i-1}}$ ($x_e(t)$ for the

¹⁸³ first larval instar) and the development rate function $G_{L_{i-1}}(t)$ ($G_e(t)$ for the

¹⁸⁴ first larval instar), *ii)* the number of individuals that after maturation moves

¹⁸⁵ towards the next stage, which depends on the corresponding development

¹⁸⁶ rate function $G_{L_i}(t)$ at time t, and *iii)* the number of individuals that leave

¹⁸⁷ the stage due to mortality, given by the current number of individuals $x_{L_i}(t)$

¹⁸⁸ and the mortality rate function $M_{L_i}(t)$. Mathematically this is described by

¹⁸⁹ the ODE

$$\frac{d}{dt}x_{L_i}(t) = G_{L_{i-1}}(t)x_{L_{i-1}}(t) - G_{L_i}(t)x_{L_i}(t) - M_{L_i}(t)x_{L_i}(t), \ i = 1,...,n, \quad (2)$$

¹⁹⁰ where L_0 denotes the egg stage, i.e. $L_0 = e$. Note that in this model the

¹⁹¹ last larval stage (i.e., $x_{L_n}(t)$) typically refers either to pupa or to the last

¹⁹² nymphal stage, depending on the species under study.

193 *Adult males.* Since the reproduction is a process that does not involve the
194 preimaginal stages, for the sake of simplicity, the distinction between sexes
195 is introduced only on the equations describing adults. Accordingly, when
196 the individuals leave the last larval stage they are distributed between adult
197 males and females in proportion to the sex ratio S_R. In many species this
198 parameter can be considered constant with good approximation, but in the
199 case of species which change their sex ratio depending on the period of the
200 year and of environmental and biological parameters (e.g., [39]), S_R can be
201 considered as a function of the time $S_R(t)$. As a convention, we will denote
202 with $S_R(t)$ the proportion of females within the population. The proportion
203 of males is the complement $1 - S_R(t)$.

204   Accordingly to this discussion, let us introduce the variable $x_{A_m}(t)$ which
205 represents the number of adult males at time t. With a similar reasoning
206 to equations (1) and (2), the variation on the number of adult males $x_{A_m}(t)$
207 depends on: *i)* the number of individuals coming from the last larval instar,
208 which is based on $x_{L_n}(t)$, the current number of individuals at that stage, the
209 corresponding development rate function $G_{L_n}(t)$ and the sex ratio $1 - S_R(t)$,
210 and *ii)* the number of adults males that leave the stage due to mortality which
211 is based on the current number of individuals $x_{A_m}(t)$ and the mortality rate
212 function for this stage, i.e. $M_{A_m}(t)$. Mathematically:

$$\frac{d}{dt}x_{A_m}(t) = (1 - S_R(t))\, G_{L_n}(t)x_{L_n}(t) - M_{A_m}(t)x_{A_m}(t). \qquad (3)$$

213 *Females Stage 1.* As already mentioned, in this model the adult females life-
214 stage is described by up two substages. Depending on the species, these two
215 substages can represent different things. For instance they can be used to

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describe two classes of age with different reproduction/mortality rates, or can be used to distinguish between non-mated and mated females. The number of female individuals in the adult stage 1 is denoted by $x_{A_{f_1}}$. One of the inflows of individuals is the portion of the larvae that become females and enter the Female Stage 1 accordingly to the sex ratio $S_R(t)$. Another inflow of individuals is, for the species for which it makes sense (e.g. for species where females after oviposition are again fertile), the flow of individuals that from the Female Stage 2 moves back to the Female Stage 1. This flow is proportional to the transition rate $G_{1 \leftarrow 2}(t)$. For species for which this is not the case, $G_{1 \leftarrow 2}(t) = 0$. The number of individuals leaving the class is the sum of the portion of individuals developing to the next stage accordingly to the transition rate function $G_{1 \rightarrow 2}(t)$ and the ones that die accordingly to the mortality rate function $M_{A_{f_1}}(t)$. Mathematically, the equation describing the Female Stage 1 is:

$$
\begin{aligned}
\frac{d}{dt} x_{A_{f_1}}(t) = \quad & S_R(t)G_{L_n}(t)x_{L_n}(t) - G_{1 \rightarrow 2}(t)x_{A_{f_1}}(t) - M_{A_{f_1}}(t)x_{A_{f_1}}(t) + \\
& + G_{1 \leftarrow 2}(t)x_{A_{f_2}}(t).
\end{aligned}
\tag{4}
$$

Female Stage 2. The variation on the number of individuals $x_{A_{f_2}}(t)$ in this stage depends on: *i)* the inflow of females from Female Stage 1 accordingly to the transition rate function $G_{1 \rightarrow 2}(t)$, *ii)* the number of females in Female Stage 2 that moves back to Female Stage 1 (where it makes sense) proportionally to the transition rate $G_{1 \leftarrow 2}(t)$, *iii)* the number of females which leave the stage due to mortality, proportionally to the mortality rate function $M_{A_{f_2}}(t)$. Mathematically:

$$\frac{d}{dt}x_{A_{f_2}}(t) = \quad G_{1\to2}(t)x_{A_{f_1}}(t) - M_{A_{f_2}}(t)x_{A_{f_2}}(t) - G_{1\leftarrow2}(t)x_{A_{f_2}}(t). \qquad (5)$$

In the case this stage is not needed for the description of a specific species, it is enough to set $G_{1\to2}(t) = 0$.

Model summary.. The overall system can be written as the following system of ODEs:

$$
\begin{cases}
\dfrac{d}{dt}x_e(t) = G_{A_{f_1}}(t)\beta_1(t)x_{A_{f_1}}(t) + G_{A_{f_2}}(t)\beta_2(t)x_{A_{f_2}}(t) - G_e(t)x_e(t) - M_e(t)x_e(t) \\[2em]
\dfrac{d}{dt}x_{L_1}(t) = G_e(t)x_e(t) - G_{L_1}(t)x_{L_1}(t) - M_{L_1}(t)x_{L_1}(t) \\[2em]
\qquad \vdots \qquad\quad \vdots \qquad\quad \vdots \qquad\quad \vdots \qquad\quad \vdots \\[2em]
\dfrac{d}{dt}x_{L_n}(t) = G_{L_{n-1}}(t)x_{L_{n-1}}(t) - G_{L_n}(t)x_{L_n}(t) - M_{L_n}(t)x_{L_n}(t) \\[2em]
\dfrac{d}{dt}x_{A_m}(t) = (1 - S_R(t)) \cdot G_{L_n}(t) \cdot x_{L_n}(t) - M_{A_m}(t)x_{A_m}(t) \\[2em]
\dfrac{d}{dt}x_{A_{f_1}}(t) = \quad S_R(t)G_{L_n}(t)x_{L_n}(t) - G_{1\to2}(t)x_{A_{f_1}}(t) - M_{A_{f_1}}(t)x_{A_{f_1}}(t) + \\[1em]
\qquad\qquad\qquad +G_{1\leftarrow2}(t)x_{A_{f_2}}(t) \\[2em]
\dfrac{d}{dt}x_{A_{f_2}}(t) = \quad G_{1\to2}(t)x_{A_{f_1}}(t) - M_{A_{f_2}}(t)x_{A_{f_2}}(t) - G_{1\leftarrow2}(t)x_{A_{f_2}}(t)
\end{cases}
$$

$$(6)$$

A list of the variables and functions with their description is reported in Table 1.

Remark. As mentioned before, the development, mortality and fertility rates can be in general not only functions of environmental parameters (temperature, humidity, food availability, etc.) but also of the system state. Common dependencies are: *i)* in the mortality and development rates to represent that overpopulation increases the mortality rate and slows down the development rates, see e.g. the logistic map [40], and *ii)* in the fertility rates (or equivalently in the rate $G_{1 \to 2}(t)$ if the substage 2 describes mated females) to consider that the probability of a female to procreate depends in general on the adult males population density [41]. However it must be remarked that, for many species of agricultural interest, these dependencies on the state can be omitted. The reason is that, for what concerns the dependency of the rates on overpopulation, because of the abundance of food and because of control policies, in agriculture is extremely rare that insect populations reach "overpopulation" numbers [42]. Note that these kinds of phenomena are instead quite common in forestry [43, 44] and urban areas [42], where treatments are usually not allowed or not convenient. For what concerns the dependency of fertility/mating rates with the concentration of males, for most species this is a saturated function that above a certain male concentration becomes "practically" a constant [45]. Although important in line of principle, for most species this dependency is not well studied and is neglected as it has an effect only for very low population densities, or where the number of males

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is much smaller with respect to the female population [45]. For most species of agricultural interest this situation does not occur frequently (usually it just happen at the very beginning of the growing season after overwintering) and is often neglected in the literature. Note that, in the case the rate functions do not depend on the state, model (6) becomes a Linear Time-Varying system.

2.3. Connection with existing ODE-based physiologically-based models

In this section we show, with no seek of completeness, how some relevant physiologically-based models in the existing literature can be seen as special cases of model (6).

ODE model from Banks et al. [9]. This model was introduced by Banks et al. [9] to describe a population of *Homalodisca vitripennis*. The insect's life cycle was divided in three macro stages, namely eggs x_e, a combined nymphal stage x_N and adults x_A. The mathematical model, as presented in the original work, is the following:

$$
\begin{cases}
\dfrac{dx_e}{dt} = b(T_{t-270})x_A - \left(r_e(T_{t-270}) + d_e\right)x_e \\[2em]
\dfrac{dx_N}{dt} = r_e(T_{t-270})x_e - \left(r_N(T_{t-270}) + d_N\right)x_N \\[2em]
\dfrac{dx_A}{dt} = r_N(T_{t-270})x_N - d_A(T_{t-270})x_A
\end{cases}
\tag{7}
$$

where T_{t-270} is the temperature in $^\circ C$ at time $t-270$ days, d_e, d_N and d_A are the mortality rate functions, r_e and r_N are the development rate functions,

282 and finally $b(T_{t-270})$ is the fertility rate function. Model (7) can be obtained

283 as a particular case of model (6) making the following positions: *i)* the

284 number of preimmaginal stages is $n = 1$, *ii)* there are no males represented

285 by the model, namely the equation describing males in the model (6) is

286 omitted, *iii)* the transition rates $G_{1\leftarrow 2}(t)$ and $G_{1\rightarrow 2}(t)$ are set to zero, and

287 *iv)* the sex ratio $S_R(t) = 1$, given that the males are not included within

288 the model. In addition, only one female substage is considered (the substage

289 1), accordingly the equation related to $x_{A_{f_2}}(t)$ is omitted (6), $\beta_2(t) = 0$ and

290 $\beta_1(t) = b(T_{t-270})$. For a summary please refer to Table 2.

291 *ODE model from Nance et al. [18].* The model was introduced by Nance

292 et al. [18] with the aim to represent *Aedes albopictus* population dynamics.

293 Also in this case the population was divided in three macro stages: eggs

294 E, larval stages I and adult females. The latter, contrary to the model of

295 Banks et al. (7) is divided in two substages: the non-mated females A_h and

296 the mated females A_g. The resulting system of four ODEs is written in the

297 original paper as

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$$\begin{cases} \dfrac{dE}{dt} = \left(1 - \dfrac{E}{k_E(1+\alpha P)}\right)\gamma_{A_g}\beta A_g - (\mu_E + f_E(t))\,E \\[2em] \dfrac{dI}{dt} = f_E(t)E - (m_I(t) + f_I(t))\,I \\[2em] \dfrac{dA_h}{dt} = f_I(t)I - (m_A(t) + \mu_r + f_{A_h}(t))\,A_h + \gamma_{A_g}A_g \\[2em] \dfrac{dA_g}{dt} = f_{A_h}(t)A_h - \left(m_A(t) + \mu_r + \gamma_{A_g}\right)A_g \end{cases} \qquad (8)$$

Model (8) can be derived from our model (6) making the following positions (see also Table 2): *i)* the equation describing egg populations in the model (8) can be obtained by the equation (1) considering $\beta_1(t) = 0$ and $\beta_2(t) = \left(1 - \frac{E}{k_E(1+\alpha P)}\right)\beta$, since Nance et al indicate with $f_E(t)$ and μ_E the egg's development and mortality rates, respectively; *ii)* the number of larval instars is $n = 1$; *iii)* there are no males in the model, hence the adult male state and the associated equation is omitted; *iv)* the transition rate $G_{1\leftarrow2}(t) = \gamma_{A_g}$, while $G_{1\rightarrow2}(t) = f_{A_h}(t)$; *v)* the sex ratio $S_R(t) = 1$, since males are not represented in the model; *vi)* the adult mortality rate is the sum of two terms, namely $M_{A_{f_1}}(t) = M_{A_{f_2}}(t) = m_A(t) + \mu_r(t)$.

ODE model from Manetsch [17] and Vansickle [19]. The model, known by the name of Distributed Delay Model, represents the ectotherms life cycle considering a series of h age classes not corresponding directly to the identifiable life stages. Mathematically, it is presented as follows:

17

$$
\begin{cases}
\dfrac{d}{dt}Q_1(t) = h \cdot G(t) \cdot \left[Q_0(t) - Q_1(t) \left(1 + \dfrac{1}{h \cdot G(t)} \cdot AR(t) \right) \right] \\[4mm]
\dfrac{d}{dt}Q_2(t) = h \cdot G(t) \cdot \left[Q_1(t) - Q_2(t) \left(1 + \dfrac{1}{h \cdot G(t)} \cdot AR(t) \right) \right] \\[2mm]
\qquad \vdots \qquad \quad \vdots \qquad \quad \vdots \\[2mm]
\dfrac{d}{dt}Q_h(t) = h \cdot G(t) \cdot \left[Q_{h-1}(t) - Q_h(t) \left(1 + \dfrac{1}{h \cdot G(t)} \cdot AR(t) \right) \right]
\end{cases}
\tag{9}
$$

where $Q_i(t)$ indicates the number of individuals in the i-th age class, $G(t)$ is the development rate function and $AR(t)$ is the mortality rate function. Model (9) can be obtained from model (6) making the following positions (Table 2): *i)* there are no males represented by the model, accordingly the equation (3) is omitted, *ii)* only larval stages are considered, with a number $n = h$, accordingly the egg (1), females of substage 1 (4) and females of substage 2 (5) equations are not present, *iii)* development and mortality rates are the same in all the equations, namely $M_{L_i}(t) = AR(t)$ and $G_{L_i}(t) = h \cdot G(t)$, respectively.

ODE model from Otero et al. [20]. This model was introduced by Otero et al. [20] with the aim to simulate populations of *Aedes aegypti*. The model divides the life cycle of the species in a total of five stages: eggs E, larvae L, pupae P, young adult females A_1, and adult females A_2. Also in this case the model does not consider the male population. Mathematically was presented in the original work [20] as follows:

$$
\begin{cases}
\dfrac{dE}{dt} = egn\left(ovr_1 \cdot A_1 + ovr_2 \cdot A_2\right) - m_e \cdot E - elr\left(1 - \gamma(L)\right)E \\[4ex]
\dfrac{dL}{dt} = elr\left(1 - \gamma(L)\right)E - m_L \cdot L - \alpha \cdot L^2 - lpr \cdot L \\[4ex]
\dfrac{dP}{dt} = lpr \cdot L - m_P \cdot P - par \cdot P \\[4ex]
\dfrac{dA_1}{dt} = par \cdot ef \cdot \dfrac{P}{2} - m_a \cdot A_1 - ovr_1 \cdot A_1 \\[4ex]
\dfrac{dA_2}{dt} = ovr_1 \cdot A_1 - m_a \cdot A_2
\end{cases} \tag{10}
$$

The model (10) can be obtained from model (6) considering the following positions reported also inTable 2: $i)$ the model does not describe male populations, accordingly the state and the equation describing males are omitted; $ii)$ the number of preimmaginal stages is $n = 2$, namely larva, L, and pupa P; $iii)$ the adult females are divided in two gonotrophic cycles, A_1 and A_2, where reproduction is allowed. The development rates are $G_{A_{f_1}}(t) = ovr_1$ and $G_{A_{f_2}}(t) = ovr_2$, respectively; $iv)$ the average number of eggs laid is provided by the same oviposition rate $\beta_1(t) = \beta_2(t) = egn$; $v)$ the egg development rate depends also on the population density of larvae L, $G_e(t) = elr\left(1 - \gamma(L)\right)$; $vi)$ larvae and pupae develop with respective rates $G_{L_1}(t) = lpr$ and $G_{L_2}(t) = par$; $vii)$ the sex ratio is $S_R(t) = \frac{1}{2}ef$, while the transition rates are $G_{1 \leftarrow 2}(t) = 0$ and $G_{1 \rightarrow 2}(t) = ovr_1$, respectively; $viii)$ the mortality rates are: $M_e(t) = m_e$, $M_{L_1}(t) = m_L - \alpha L$, $M_{L_2}(t) = m_P$,

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$$M_{A_{f_1}}(t) = M_{A_{f_2}}(t) = m_a.$$

2.4. Case study: the spotted wing drosophila Drosophila suzukii

In this section we show that the proposed model (6) can be used to define a new model for a pest of high agricultural interest simply by using development, fertility, and mortality rates available in the literature. The effectiveness and the open-loop predictivity of the resulting model is demonstrated against data collected between 2017 and 2019 in different locations.

2.4.1. Biology and development, fertility and mortality rate functions

The spotted wing drosophila *Drosophila suzukii* is a harmful pest worldwide. In most countries it represents an invasive species of more or less recent introduction. It originates from Asia, more specifically from Japan [46], and given its capability to adapt to different territories and climates it is now present in North and South America [47] and in Europe [48], where it was firstly detected in Spain [49] and Italy [50] about one decade ago.

D. suzukii is characterised by a high polyphagy and by a short generation time, which lead to up to 15 generations in a year [49]. Soft fruit plantations (cherry strawberry, blueberry, apples, peaches, grapes and more in general *Prunus* and *Rubus* spp.) [51, 52] are the most affected crops. Contrary to other fruit flies, the spotted wing drosophila can lay eggs on ripening fruits using its particular serrated ovipositor [53].

The damages produced are mainly due to the oviposition and to the larval feeding, which makes the fruits unmarketable. Larvae, more specifically, develop on the ripening fruits feeding the endocarp tissue, and possibly opening

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access points for secondary pathogens responsible of relevant diseases, such as fungi and bacteria.

This insect is characterised by a sexual dimorphism, from where its common name spotted wing drosophila derives: males have two black spots on the wings [47, 54]. This feature represents an important factor for the field monitoring as it allows to more rapidly distinguish them from other similar species. Unlike males, females are, at first sight, closely similar to other *Drosophila* species [49], and the differentiation requires optical instruments such as microscopes to analyse the ovipositor [34]. Hence, to simplify the monitoring activities, the data collection for this species typically focuses only on males.

In this work we propose a model for the life cycle of the spotted wing drosophila consisting of an egg stage, three larval instars, pupa stage, and adult stages. Accordingly, the total number of equations in the model (6) is 8: one for the egg stage, four for the larval stages (pupa is considered as the last larval instar), and one for the adult males, non-mated females, and mated females, respectively.

Due to its harmfulness, the dependence of *D. suzukii* development, fertility and mortality rates on temperature has been studied by several authors [55, 56, 57, 58, 59]. An exhaustive overview about the main rate functions commonly used to represent the biological features of the spotted wing drosophila can be found in Winkler et al. [60]. Accordingly, the literature provides all the information needed to build a specific model using the proposed general model (6).

The first expression introduced is the development rate function. Rossini

et al. [34] tested different functions using the data provided in Tochen et al. [55], assessing that the Briére [61] function (11) was a very good function to describe the relationship between *D. suzukii* development rate and environmental temperature. Mathematically, the Briére function is defined as:

$$G(t) = a \cdot T(t) \cdot (T(t) - T_L)(T_M - T(t))^{\frac{1}{m}},\qquad(11)$$

where a and m are empirical parameters, T_L and T_M are the lower and upper temperature thresholds below and above which the development of the species theoretically does not occur. It is worth to remind the reader that the development rate is defined as the inverse of the development time [62, 63, 64, 65]. Even though the spotted wing drosophila is one of the most studied pests, there is not sufficient information to estimate the parameters of the function (11) for each life stage. Accordingly, this leads to the unavoidable simplification of considering only one development rate function for all the stages.

An estimation of the "accidental" mortality, dependent on the temperature, was proposed by Asplen et al. [57], who interpolated the data provided by Dalton et al. [58], Kinjo et al. [59] and Tochen et al. [55] with a second order polynomial function. However, this approximation tends to overestimate the mortality in temperature ranges where the development of the species can still be considered near the optimum. Hence, for the purpose of this work we decided to use a more detailed function. In particular in this work we considered the fourth order polynomial function

$$M\left[T(t)\right] = a_1\ \left[T(t)\right]^4 + b_1\left[T(t)\right]^3 + c_1\ \left[T(t)\right]^2 + d_1\ \left[T(t)\right] + e_1. \qquad (12)$$

Equation (12) is commonly known as the "bathtub" function and is widely used to represent the dependence of the mortality on temperature [66], since it is able to describe the low mortality rates in the optimal temperature ranges and the rapid increase as the thermal thresholds of the species are reached. The coefficients a_1, b_1, c_1, d_1 and e_1 in (12) are empirical parameters which, in this study, are estimated based on the rates provided in a highly detailed study published by Ryan et al. [53]. The Python scripts used to compute the parameters of (12) are publicly available at the GitHub page `https://github.com/Niboros91/Ectotherms-ODE-based-model`. The quality of this polynomial fitting in representing the data from Ryan et al. [53] has been assessed with a χ^2-test and considering the coefficient of determination R^2. The values of these measures, and of the parameters, are reported in Table 3.

Similarly to what we did for the development rate function (11), the same mortality rate will be used for all the stages ranging from egg to pupa. However, an additional consideration is necessary for all the adult stages. Referring to the equations (3), (4) and (5), it is possible to notice that there is not an explicit reference to the development rate. Accordingly, the respective mortality rates should take into account of the mortality due to ageing (i.e., the development rate), leading to the following modifications:

$$
\begin{cases}
M_{A_m}(t) = G(t) + M\left[T(t)\right] \\[2mm]
M_{A_{f_1}}(t) = G(t) + M\left[T(t)\right] \\[2mm]
M_{A_{f_2}}(t) = G(t) + M\left[T(t)\right]
\end{cases}
\tag{13}
$$

where $M\left[T(t)\right]$ and $G(t)$ are expressed by the functions (12) and (11), respectively. In other words, we are considering the mortality rate in the "terminal life stages" as the sum of the "natural" mortality (ageing) and the "accidental" mortality (due, for the sake of simplicity, to temperature).

For the temperature-dependent birth rate function β_2 we consider the equation provided by Ryan et al. [53], who fitted their experimental data with the following Gaussian-like function:

$$
\beta_2\left[T(t)\right] =
\begin{cases}
\alpha\left[\dfrac{\gamma+1}{\pi\lambda^{2\gamma+2}}\left(\lambda^2 - \left(\left[T(t)-\tau\right]^2 + \delta^2\right)\right)^{\gamma}\right] & if\ T_{min} < T(t) < T_{max} \\[4mm]
0 \quad otherwise.
\end{cases}
\tag{14}
$$

This birth rate function (14) expresses the number of eggs produced per day by the adult mated females as a function of the temperature. T_{min} and T_{max} represent the lower and upper temperature thresholds where the oviposition occurs, while α, γ, λ, δ and τ are empirical parameters. Since for the case under study the adult females substages are defined as non-mated and mated, we set $\beta_1 = 0$.

To the best of our knowledge, $D.suzukii$ females can mate only once in their life cycle. Accordingly, the transition rate $G_{1\leftarrow 2}(t) = 0$. For the rate $G_{1\rightarrow 2}(t)$ the function $G_{1\rightarrow 2}(t) = 1 - M\left[T(t)\right]$ was selected. The reason why

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this is not a function of the number of males in the population is that, as already stated in the Section 2.2, in average conditions the probability that a female meets a male is considered constant.

The last parameter to be defined is the sex ratio $S_R(t)$. This value has been reported by Emiljanowicz et al. [56] as $S_R = 0.5$ (i.e., males:females = 1:1), and for the purposes of this work can be considered in first approximation constant, even though it is known that it might in theory change in particular environmental conditions [67].

For the sake of completeness, this section is concluded reporting, in Table 3, all the numerical values of the parameters that have been included in the model (6) to simulate *D. suzukii*.

2.5. Numerical scheme for equation solutions

Since all the rate functions for the developed model depend only on the environmental factors and not on the states, (6) is a Linear Time-Varying system that can be rewritten as

$$\dot{x}(t) = A(t)x(t) \tag{15}$$

where

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$$A(t) = \begin{bmatrix}
M_e(t) & -G_e(t) & 0 & \cdots & 0 & 0 & 0 & \beta_1(t)GA_{f_1}(t) + \beta_2(t)GA_{f_2}(t) \\
0 & G_e(t) & -G_{L_1}(t) - M_{L_1}(t) & 0 & \cdots & 0 & 0 & 0 \\
0 & G_{L_1}(t) & -G_{L_2} - M_{L_2}(t) & \ddots & \cdots & 0 & 0 & 0 \\
0 & \vdots & \ddots & \ddots & 0 & \vdots & \cdots & 0 \\
0 & 0 & 0 & 0 & (1 - S_R(t)) \cdot G_{L_n}(t) & -MA_m(t) & 0 & 0 \\
0 & 0 & 0 & 0 & S_R(t) \cdot G_{L_n}(t) & 0 & -MA_{f_1}(t) - G_{1\to2}(t) & G_{1\leftarrow2}(t) \\
0 & 0 & 0 & 0 & 0 & 0 & G_{1\to2}(t) & -G_{1\leftarrow2}(t) - MA_{f_2}(t)
\end{bmatrix}$$

(16)

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is the transition matrix containing all the rate functions and parameters introduced in the previous subsections.

As it is common in this kind of models, the dependency on the temperature should be considered in the average sense, rather than as an instantaneous temperature. Accordingly we will consider average daily temperatures. Because of this, assuming a sampling time T_s that is an integer fraction of one day, (15) is equivalent to the following discrete-time system

$$x(t + T_s) = e^{A_t T_s} x(t) \tag{17}$$

where A_t denotes the transition matrix (16) with the temperatures measured at time t. In this study the sampling time is set equal to $T_s = 1\,day$. From (17) the state of the population at the next sampling time $t + T_s$ can be obtained based on the current state $x(t)$ and the computed transition matrix A_t. All the code to simulate these equations, including the parameters and the daily average temperatures for the different growing seasons in exam, have been encoded in a Matlab script (vers. R2018b) and is publicly available at the GitHub page `https://github.com/Niboros91/Ectotherms-ODE-based-model`.

2.5.1. Field trials for model validation

To assess the predictive capability of the presented model, the experimental dataset of Rossini et al. [34] will be considered. [34] reports a three-year experiment (2017-2019) in an experimental cherry orchard located in Montelibretti (Lazio, Italy) and a two-year experiment (2018-2019) in a second cherry orchard located in Monterotondo (Lazio, Italy). The dataset provides

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the dynamics of adult male flies during the cherry growing season, in the period April-July. In this work we complement the existing dataset with new unpublished data collected in the winter 2018 (from July to December 2018). These data are particularly precious for the validation of the model because they allow to simulate and validate more generations in different seasons of the same year.

The experimental orchards have a surface of 2000 square meters and are cultivated with local mixed cherry varieties. We will denote the two experimental fields as "Montelibretti field" and "Monterotondo field", maintaining the same nomenclature used in Rossini et al. [34].

Overall, the data collection covers the period from 20 April to 28 June, from 19 April to 15 December and from 12 April to 18 July in the years 2017, 2018 and 2019, respectively. Three Droso-Trap (Biobest, Waterloo Belgium) lured with Droskidrink (Azienda Agricola Prantil, Priò, Trento, Italy) were deployed in each field, and inspected weekly.

Because of the easier distinguishability of the adult males, the population profile was obtained only for this sex.

Daily temperature values were obtained by averaging 24 measurements in 24 hours provided by the ARSIAL agency (Regional Agency for the Development of Innovation and Agriculture in Lazio) [68]. The most interested readers are referred to [34] for further information about the experimental trial.

Simulations and field data can be compared following the procedure already discussed in other works such as [69, 28, 70, 71, 72, 73] and combine the use of the χ^2 function and of the coefficient of determination R^2. Notably,

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the χ^2 function is used as indicator of the distance among the n points of the simulated and field populations. According to this assumption, hence, the lower is the value of the function, more simulations and field data are overlapped. However, it may happen that in case of high population densities even a small difference between high values can provide high χ^2 values. Accordingly, the coefficient of determination R^2 is introduced to confirm the reliability of the estimations provided by χ^2. An R^2 value close to 1, hence, will indicate a high reliability of the simulations in representing field data.
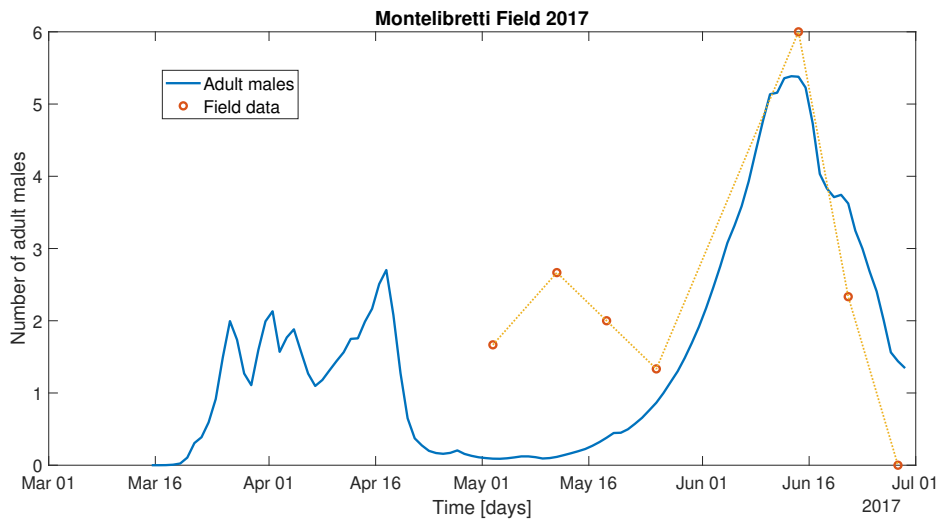
3. Results

Figure 2: Development of adult males: comparison between simulations and field data.

In this section we show the results of the open-loop simulation and compare them with the data available from the experimental fields.

The first year of survey, 2017, was the year where only data from the Montelibretti field were available (Fig. 2). The field population in this year

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was on the whole low, reporting three peaks on 25 April, 14 May and 15 June, respectively. The day zero for the simulations was fixed to 15 March. The highest peak was reported on the 15 June. The first simulated peak (i.e., half of March - end of April) was slightly anticipated with respect to the field data. Despite the low population density assessed, the reliability of the model has been confirmed by the χ^2 and R^2 values reported in Table 4.

The year 2018 was the most complete regarding the data availability, and it allows to show the long term behaviour of the model. In both fields, the day zero for the simulations was fixed to 15 April.
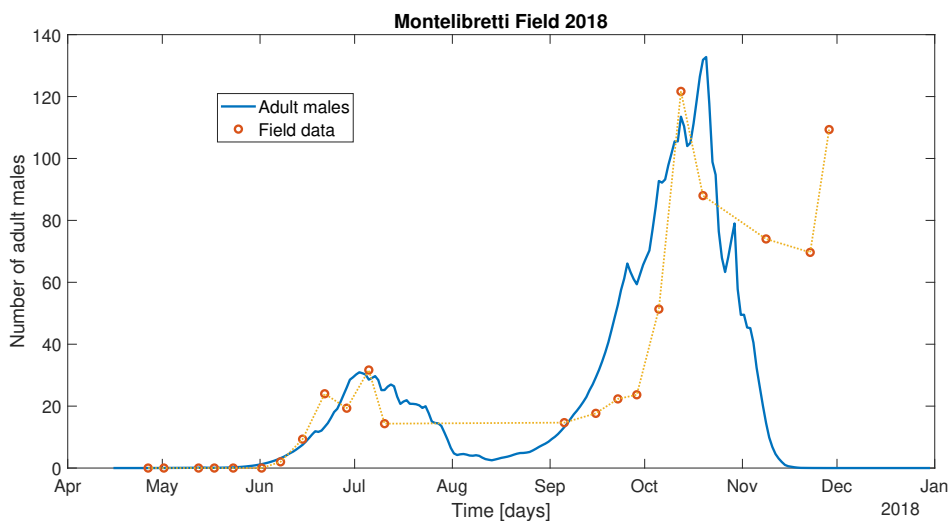
Figure 3: Development of adult males: comparison between simulations and field data.

In the Montelibretti field (Fig. 3) the experimental population reported two close peaks on 26 June and 12 July, while the simulation reported only a single peak centered on 2 July. In the hottest period of the season (late July-August) the model indicated a population density close to zero, which started to rise again at the end of September. Even though the early au-

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tumnal generation of the experimental population increased slightly slower with respect to the simulations, both peaks were centered on the same day, 19 October.
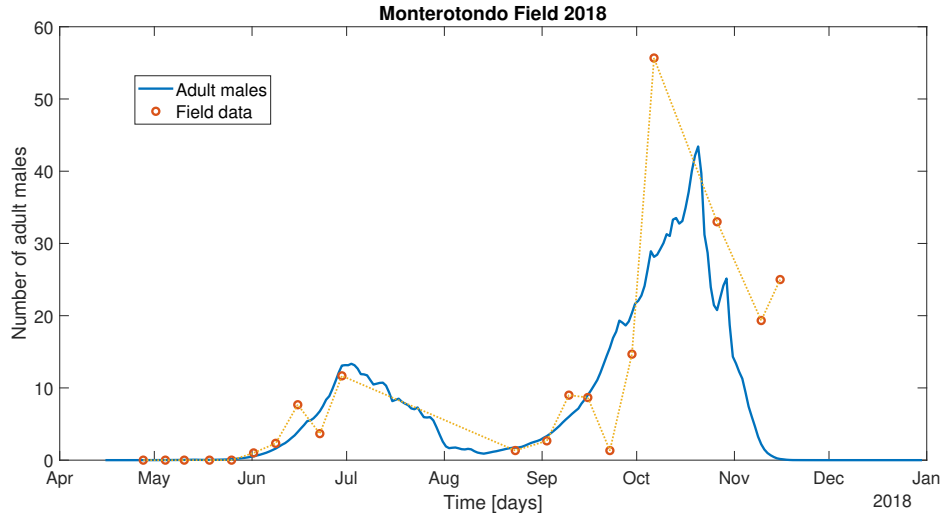

Figure 4: Development of adult males: comparison between simulations and field data.

A similar situation was assessed at the Monterotondo field (Fig. 4), where in the first part of the year two peaks were reported at the experimental population, on 5 and 19 July, while the model provided a single peak centered on 21 July. The behavior during the hottest period of the season was the same assessed at the Montelibretti field, with a more pronounced increase occurring at the beginning of October. In the second part of 2018 both the experimental and simulated populations reported a single peak, centered on 26 October and 8 November, respectively.

The numerical consistence of the simulations in representing the field data (Table 4) confirmed the overall reliability of the model for the 2018 season, also.
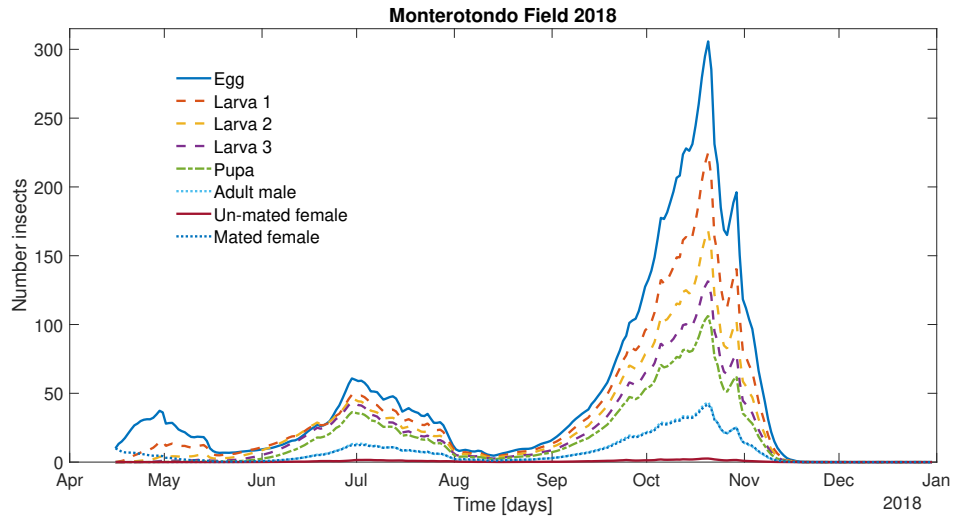
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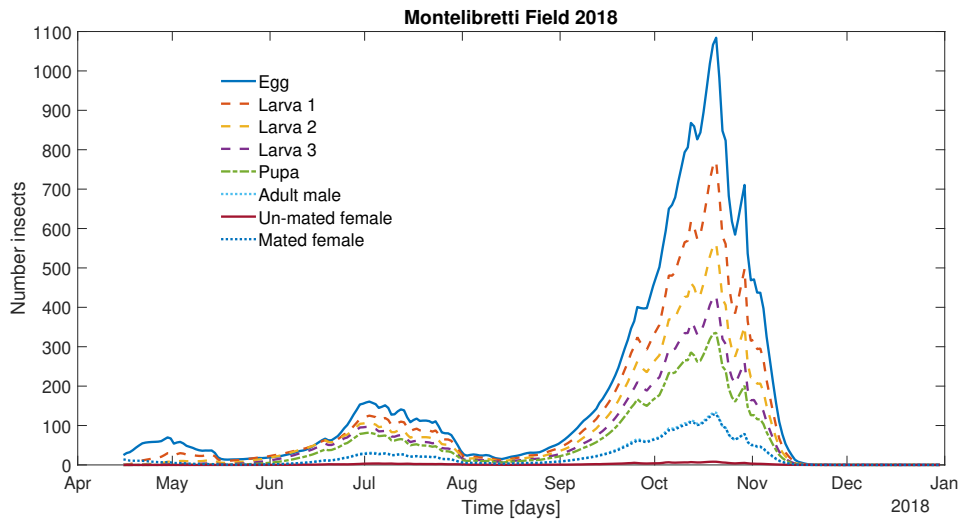Figure 5: Development of the individuals within the different life stages.

Figure 6: Development of the individuals within the different life stages.

Due to the length of the survey, this season highlights the model behavior better than the other ones. For this reason, two additional plots (one for each field) were reported in Fig. 6 and Fig. 5 with all the *D. suzukii* life stages of

the model.
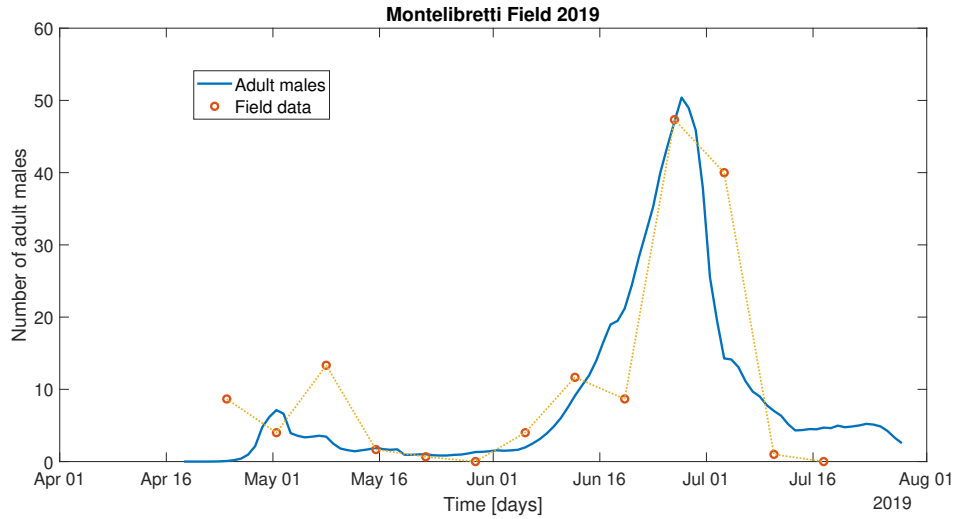

Figure 7: Development of adult males: comparison between simulations and field data.

In the growing season 2019, the last year of survey, the day zero for the simulation was fixed to the 18 April. In the Montelibretti field four population peaks were assessed at the field trials occurring on 25 April, 11 May, 11 and 28 June, respectively, while simulations reported only two peaks centered on 1 May and 27 June (Fig. 7). Moreover, the 2019 Montelibretti field reported a population density overall higher with respect to Monterotondo field.

Monterotondo field reported three peaks for the experimental populations, occurred on 27 April, 12 June and 4 July, respectively, while simulations indicated two peaks centered on 30 April and 25 June (Fig. 8). The higher inhomogeneity of the experimental populations in this season is underlined by the χ^2-values listed in Table 4: the highest and the lowest χ^2-values assessed in the three-year survey were, in fact, assessed on 2019. The R^2
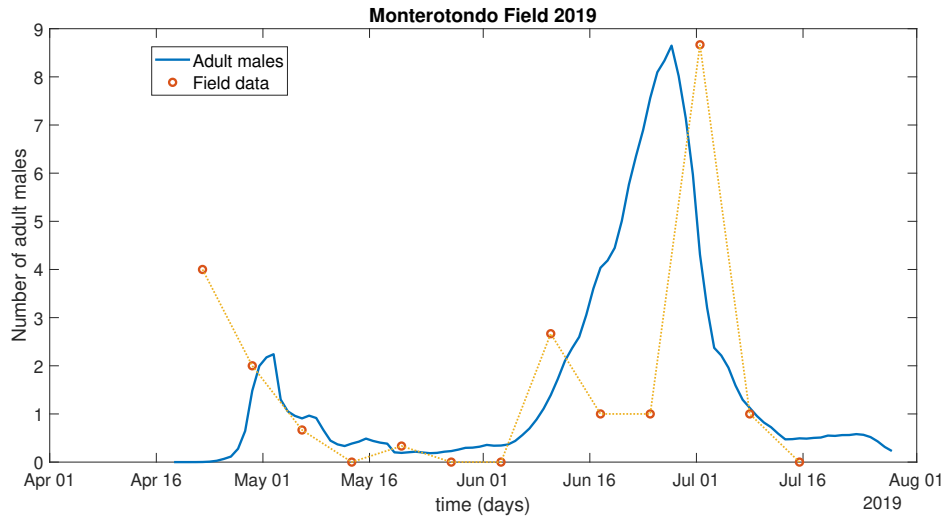
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Figure 8: Development of adult males: comparison between simulations and field data.

values, instead, confirm the reliability of the model in representing the field data also in 2019.

4. Discussions and conclusion

The case study of *D. suzukii* confirms the reliability of the novel model (6) introduced in this work in representing ectotherms' life cycle. It is worth to remark that, despite the approximations and simplifications due to the lack of more accurate data about the biology of the spotted wing drosophila. Most notably, despite the fact that simulations were performed in open loop, the model faithfully describes the trend of all the experimental populations.

The most interesting results are provided by the growing season 2018, when the field trials provided the longer availability of monitoring data to

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compare with simulations. With a single simulation, the model was capable to describe the spring and early-middle autumn generations, as well as the apparent absence of *D. suzukii* in the late summer. The only anomaly that the model was not able to predict was the apparent increase of the experimental population in the late autumn of 2018.

This last fact deserves some discussion and represents an interesting starting point for future investigations. We believe that a major cause of this apparent increase of the counted number of males might be actually induced by a distortion introduced by the traps. In fact, the scarcity of food in these fields due to the dormancy of the great part of the wild and cultivated plants occurring in late-autumn/winter may elicit the adults towards the traps (which are food-based) to look for food. Accordingly it is reasonable to assume that the high number of captured insects in the late 2018 in both fields may be mostly provoked by an increase of efficiency of the traps due to food scarcity in the fields. Unfortunately, to the best of our knowledge, there is no evidence in the current literature to confirm this supposition, even though it is suggested by our empirical observations.

These data, however, also raise the point that clearly in winter the field population does not go so close to the zero as predicted by the model. We believe this is due to the mortality rate function used, that overestimates the mortality as the temperature decreases too much. It is implicitly supposed that outside the temperature thresholds provided by the Briére function the development rate is zero, while the mortality rate goes to very high values (typically around 1 $days^{-1}$ or above). This is not completely true, as showed also by Dalton et al. [58] and it is well known that a certain portion of

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the population is able to survive the entire winter and restart reproduction as temperature raise again. We believe that further studies are needed to understand better the winter ecology of the *D. suzukii* from a quantitative point of view. The hope is that this would allow to predict numerically the spring generations on the basis of what happens in the previous autumn and on the meteorological features of the winter.

Although additional future validations are necessary, and the link between the late autumn generations and the next spring ones have still to be numerically established, the existence of such link is well known and documented in the literature [74, 75, 76]. In view of this fact, the fact that both simulations and data show a relevant peak of insects in middle October is a highly relevant evidence that is worth to mention. It is documented in the current literature [49] that this autumn population develops on fruits fallen on the ground before the harvest or on secondary host plants.

Currently, in most orchards these insect generations are not controlled by farmers as they occur after the harvest. However, the high peak reached by this population, combined with the fact that this population is likely linked with the amount of successful overwintering insects, suggest that it would be convenient to perform autumn/winter control actions in order to reduce potential infestations on ripening fruits in the subsequent spring. Controlling the last generation of *D. suzukii* occurring in the year, moreover, has the advantage to allow the use of active ingredients in a season where the cherries are not present in the field. Accordingly, a preventive control action can help to reduce the number of treatments during the fruit growing season, resulting in a healthier product for consumers.

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Overall, the model showed the most efficient response in the fields with the higher population densities, where the fluctuations in the experimental population were lower. Note that even though it was assumed that the population peaks correspond to single generations, it may happened that in the case of low population densities the peaks correspond to fluctuations of the catches corresponding to the same generation. Given this fact, the model described faithfully the increase and decrease of the populations even in the cases where the peaks of simulated and field populations were not completely overlapped.

The results presented in this work are in line with the results of Rossini et al. [34] where a generalized version of the Von Foerster equation (a first order PDE) was applied to simulate the same field dataset of the present study. Contrary to this work, however, different fertility and mortality rate functions were used. Moreover the use of the generalised Von Foerster equation made necessary to run a single simulation for each generation of the year. The advantage of a model based on a system of ODEs is both conceptual and practical, as stated in the introduction, and the application in the case study of the spotted wing drosophila preliminary confirms this claim.

Among the models used to represent the spotted wing drosophila, also the Distributed Delay Model (9) was applied, in 2016, [77] to predict potential invasions in America, Europe and Mediterranean basin. However, one of the main issues in applying the DDM, is the determination of the number of age classes, since there is not a direct connection between the number of equations of the model and the number of identifiable life stages [72, 78]. In addition, the DDM expresses difficulties in representing a two-sexed populations, since

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there is not a specific equation for males and females. The physiologically-based model that we have introduced hereby, instead, not only includes the DDM as special case, but has the great advantage to avoid the calibration necessary to determine the number of its age classes.

The distinction between the mated and non-mated females or, more in general, between the female stage 1 and female stage 2 makes the representation of the life cycle of most of the ectotherms more realistic. At first sight, in the case of the spotted wing drosophila, one can think to eliminate directly the non-mated female stage, with a consequent elimination of an equation by the system. Even if practically this choice can be reasonable (with a suitable re-tuning of the parameters), it is not from a conceptual point of view. The transition towards the stage of non-mated females, in fact, is necessary from a biological point of view, since the individuals continue to develop before becoming mated. It is known from the literature [79] that after the emergence the adult females become mated in a time range of 1-3 days. Avoiding the non-mated stage in the model, hence, means to anticipate the reproduction of the aforementioned time range, introducing a distortion in the description of the population dynamics.

The same mechanism of reproduction described by our model was presented by Nance et al. [18] in the case of the *Aedes albopictus* and by Otero et al. [20] in the case of *Aedes aegypti*, as showed in Section 2.3: the adult females also in this case were distinguished in mated and non mated ([18]) or in two gonotrophic cycles ([20]), even though no reference to the modelling of males is made. Also in those cases the differentiation of the adult female stage in two substages provided a more reliable description of the life cycle,

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as confirmed by their results. The difference of our model with respect to the model of Nance et al. [18] and Otero et al. [20] is the generalization of the system of ODEs in order to consider both the sexes and the birth rate. In addition, we have extended the concept of life stage to all the stages that are entomologically "identifiable", without considering the preimmaginal stages as a single stage. This make the model suitable for most species of agricultural interest, given a clear description of the life cycle.

An implicit assumption of our study, and of the great part of the models presented in literature, is that the population is closed, namely there are no immigration/emigration terms. Future works will extend to the case of open populations. Migration terms can be introduced in the specific stage equations with slight modifications, considering that the incoming/outcoming individuals are proportional to specific "migration rate" functions. Also here the advantage to have equations specific for each identifiable stage allows to include the biological notions into the model. It is known that not all the stages are allowed to move or migrate. To be more concrete, let us refer to the case of the spotted wing drosophila, where the egg and larval instars represent the great part of the life cycle. The motion in this part of the life cycle is limited to the plant scale. Accordingly it is reasonable to say that these are "static stages". On the other hand, adults fly and spread within the field and towards other fields, looking for oviposition sites or individuals of the other sex for mating. Even though the aforementioned example is referred to the case study considered hereby, once the biological traits of the species are, known the same specific considerations can be done accordingly. This aspect leaves to suppose that migration terms can be considered for the

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model spatialization: if the field is subdivided in a lattice, it is possible to consider a matrix of "local populations" able to migrate from neighbouring parcels.

Spatial patterns of insects (and animal in general) is usually represented with second order PDEs, where a reaction and a diffusion term is considered [26, 80, 81, 82]. However, this representation does not consider the subdivision of the life cycle in physiological age classes (age is usually considered as a time), nor the dependence of the development on environmental parameters. On the other hand, other authors [77] proposed the insertion of physiologically based models (the DDM, more specifically) in GIS systems, without considering, nevertheless, the interaction between neighbouring parcels of the grid. The model presented in this work, once provided with migration terms, can potentially solve the problem of modelling the spatial diffusion of insect pests and ectotherms in general. In addition, the mathematical representation of males and females provides an advantage in the introduction of migration terms for all the species where the motion is allowed only for one of the two sexes. This is, for instance, the case of the *Opheroptera brumata* where the males can migrate actively and the females can only move passively (because of underdeveloped wings) [83]. Also considering the aforementioned example, *O. brumata* has a different behavior for males and females, since males emerge a week earlier on average with respect to females, and can mate multiple times. Our model, with the specific assumptions, can describe a behavior of this type, also and it is our main purpose of future developments and studies.

Always remaining in the context of potential applications and future de-

velopments, it is worth to remind that the results presented in this study were obtained in open loop, without using the data collected to improve the estimation at each data collection time. The advantage of working with systems of ODEs, and more specifically with linear systems, is the possibility to use the theory of the Kalman filtering to correct the predictions on the basis of the present and past monitoring data. Future works will study how the use of Kalman filtering can improve the estimation and the prediction of a population behaviour.

Acknowledgements

Conflict of interest

The authors declare that they have no conflict of interest.

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Function	Description
$x_e(t)$	Number of individuals in the egg stage at time t.
$x_{L_i}(t)$	Number of individuals in the ith larval stage at time t.
$x_{A_m}(t)$	Number of individuals in the adult male stage at time t.
$x_{A_{f_1}}(t)$	Number of individuals in the female adult substage 1 at time t.
$x_{A_{f_2}}(t)$	Number of individuals in the female adult substage 2 at time t.
$M_e(t)$	Mortality rate of the eggs at time t.
$M_{L_i}(t)$	Mortality rate of the ith larval instar at time t.
$M_{A_m}(t)$	Mortality rate of adult males at time t.
$M_{A_{f_1}}(t)$	Mortality rate of adult females substage 1 at time t.
$M_{A_{f_2}}(t)$	Mortality rate of adult females substage 2 at time t.
$\beta_1(t)$	Fertility rate of the adult females substage 1 at time t.
$\beta_2(t)$	Fertility rate of the adult females substage 2 at time t.
$G_e(t)$	Development rate function of the egg stage.
$G_{L_i}(t)$	Development rate function of the ith larval stage at time t.
$G_{A_{f_1}}(t)$	Development rate function of the adult females substage 1 at time t.
$G_{A_{f_2}}(t)$	Development rate function of the adult females substage 2 at time t.
$S_R(t)$	Sex ratio of the species: $S_R(t)$ for females, $1 - S_R(t)$ for males.
$G_{1 \to 2}(t)$	Transition rate of adult females to substage 2 from the substage 1 at time t.
$G_{1 \leftarrow 2}(t)$	Transition rate of adult females to return in the substage 1 from the substage 2 at time t.

Table 2: Comparison between the model (6) and the models (7)-(10)

Model (6)	Banks et al.[9]	Nance et al.[18]	Manetsch [17] Vansickle [19]	Otero et al. [20]
n	1	1	h	2
$x_e(t)$	x_e	E	Q_0	E
$x_{L_i}(t)$	x_N	I	Q_i	L,P
$x_{A_m}(t)$	Omitted	Omitted	Omitted	Omitted
$x_{A_{f_1}}(t)$	x_A	A_h	Omitted	A_1
$x_{A_{f_2}}(t)$	Omitted	A_g	Omitted	A_2
$M_e(t)$	d_e	μ_E	0	m_e
$M_{L_i}(t)$	d_N	m_I	$AR(t)$	$m_L - \alpha L, m_P$
$M_{A_m}(t)$	0	0	0	0
$M_{A_{f_1}}(t)$	$d_A(T_{t-270})$	$m_A(t) + \mu_r$	0	m_a
$M_{A_{f_2}}(t)$	0	$m_A(t) + \mu_r$	0	m_a
$\beta_1(t)$	$b(T_{t-270})$	0	0	egn
$\beta_2(t)$	0	$(1 - \frac{E}{k_E(1+\alpha P)})\beta$	0	egn
$G_e(t)$	$r_e(T_{t-270})$	$f_E(t)$	$hG(t)$	$elr(1 - \gamma(L))$
$G_{L_i}(t)$	$r_N(T_{t-270})$	$f_I(t)$	$hG(t)$	lpr, par
$G_{A_{f_1}}(t)$	1	0	0	ovr_1
$G_{A_{f_2}}(t)$	0	γ_{A_g}	0	ovr_2
$G_{1 \to 2}(t)$	0	$f_{A_h}(t)$	0	ovr_1
$G_{1 \leftarrow 2}(t)$	0	γ_{A_g}	0	0
$S_R(t)$	1	1	0	$\frac{1}{2}ef$

Table 3: List of the parameters (± standard error) used to simulate *Drosophila suzukii* populations. χ^2, R^2 and number of degrees of freedom are also reported in the table. The column reference indicates the literature from which data or parameters were retrieved, while if some information is missing a * above the name of the function is indicated.

Rate function	Parameter $\pm SE$	χ^2-value	R^2-value	NDF (n)	Reference
Briére (11)	$a = (1.20 \pm 0.15) \cdot 10^{-4}$ $T_L = 3 \pm 2$ $T_M = 30 \pm 1$ $m = 6 \pm 3$	0.0014	0.99	3	[34, 55] Parameters and data
Mortality (12)	$a_1 = (-5 \pm 1) \cdot 10^{-5}$ $b_1 = (5 \pm 8) \cdot 10^{-4}$ $c_1 = 0.1 \pm 0.2$ $d_1 = (2.2 \pm 0.3) \cdot 10^{-5}$ $e_1 = 1.3 \pm 0.9$	0.2174	0.84	10	[53] Data
Fertility* (14)	$\alpha = 659.06$ $\gamma = 88.53$ $\lambda = 52.32$ $\delta = 6.06$ $\tau = 22.87$ $T_{min} = 5$ $T_{max} = 30$	–	–	–	[53] Parameters

Table 4: Numerical evaluation of the goodness of the simulation in representing adult male populations.

Growing season	Experimental field	χ^2-value	R^2-value
2017	Montelibretti	9.11	0.73
	Monterotondo	–	–
2018	Montelibretti	73.93	0.74
	Monterotondo	56.61	0.67
2019	Montelibretti	971.37	0.80
	Monterotondo	2.98	0.72