

# Internship Report

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## **Mathematical model of *Ceratitis capitata* population dynamics in Corsica in a context of control with the Sterile Insect Technique (SIT)**

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## Abstract

In this internship report, we investigate a three-dimensional semi-discrete model to represent the population dynamics of *Ceratitis capitata* in the Corsican context and in a sterile insect technique design perspective. The model is calibrated compiling data from literature. We demonstrate that the model can be simplified into equations that approximate very well the original model dynamics for realistic parameter values. The simplified model dynamics are shown to be invariant, up to re-scaling, of a model parameter linked to intra-specific competition. This parameter actually determines the spatial scale at which population dynamics are considered. The simplified model admits one or two equilibria depending on the basic reproduction number  $R$ . If  $R < 1$ , the population goes to extinction, while when  $R > 1$ , there exists a positive equilibrium which is locally asymptotically stable. With the reference parameter set, the reproduction number  $R \approx 111$ . Hence, there exists a positive asymptotically stable equilibrium point to which population dynamics converge with time. In our simulations, the dynamics gets very close to the equilibrium within a season. A sensitivity analysis performed on larval density at the end of the simulation shows it is most influenced by the *per capita* oviposition rate and the larval mortality rate. These two biological processes are thus important to leverage control *C. capitata* population. Finally, we explore a first approach on the original model to control *C. capitata* imposing a constant density of sterile males in the system. A ratio of 0.51 to 1 between sterile males and wild males are required to drive the population close to extinction.

**Keywords :** **population dynamics, semi-discrete model, Ordinary differential equations, *Ceratitis capitata*, Sterile Insect Technique**

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## Résumé

Dans ce rapport de stage, nous étudions un modèle semi-discret en trois dimensions représentant la dynamique de population de *Ceratitis capitata* dans le contexte corse et adapté à une perspective de TIS. Le modèle est paramétré à partir des données issues de la littérature. Nous démontrons que le modèle peut être simplifié tout en restant très proche de la dynamique du modèle original pour des valeurs de paramètres réalistes. La dynamique du modèle simplifié est totalement indépendante du paramètre de compétition, celui-ci déterminant l'échelle spatiale à laquelle nous considérons le système. Le modèle simplifié admet un ou deux équilibres en fonction du taux de reproduction de la population  $R$ . Si  $R < 1$ , la population est vouée à l'extinction, alors que lorsque  $R > 1$ , il existe un équilibre positif qui est localement asymptotiquement stable. Avec les paramètres de référence, le taux de reproduction du modèle est de  $R \approx 111$ . Par conséquent, il existe un point d'équilibre positif asymptotiquement stable vers lequel la dynamique de la population converge avec le temps. En simulant le modèle, les dynamiques de population convergent près de l'état d'équilibre en une seule saison. Ensuite, l'analyse de sensibilité effectuée sur la densité larvaire à la fin de la simulation montre qu'elle est majoritairement influencée par le taux de ponte des femelles *per capita* et le taux de mortalité larvaire. Ces deux processus biologiques représentent deux leviers majeurs pour contrôler la population de *C. capitata*. Enfin, nous explorons une première approche sur le modèle original pour contrôler *C. capitata* en imposant une densité constante de mâles stériles dans le système. Un ratio de 0,51 à 1 entre les mâles stériles et les mâles sauvages est nécessaire pour mener la population à l'extinction.

**Mots-clés :** **dynamique des populations, modèle semi-discret, Équations différentielles ordinaires, *Ceratitis capitata*, Technique de l'Insecte Stérile**

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# 1 Introduction

Agricultural pests may cause dramatic damages to crops and have major economic impacts (Cavalloro, 1986; Siebert & Cooper, 1995; Stonehouse *et al.*, 1998; Oliveira *et al.*, 2014; Kamaraj *et al.*, 2018). In particular, insect pests are among the main drivers of productivity losses in agricultural cropping systems worldwide (DeBach *et al.*, 1991; Metcalf & Luckmann, 1994), provoking hundred million euros of crop losses each year (Siebert & Cooper, 1995; Stonehouse *et al.*, 1998).

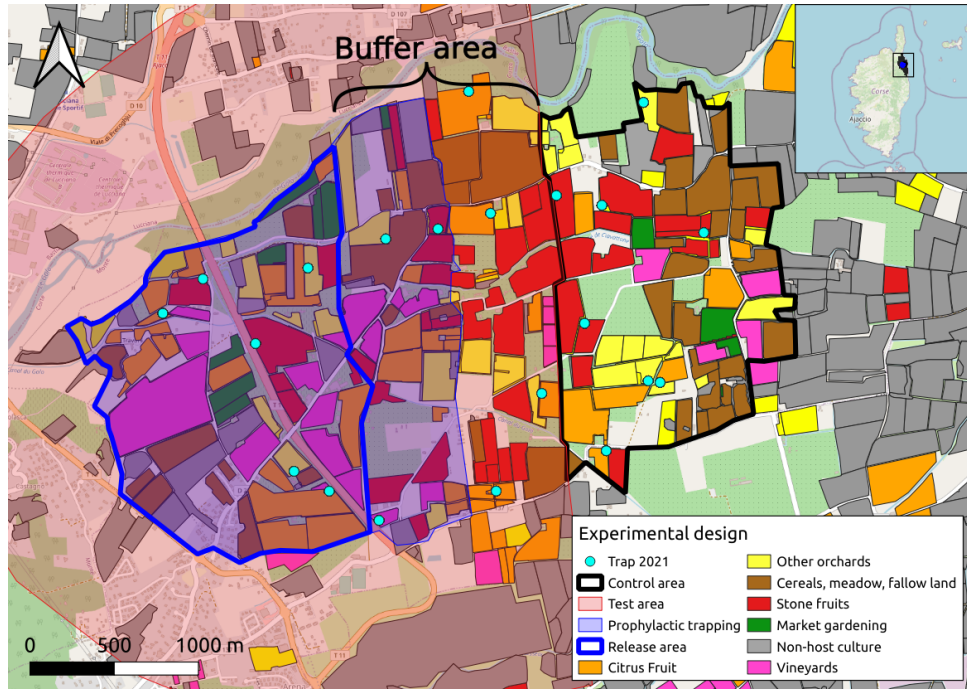
To manage pest outbreaks, farmers can rely on cultural, mechanical, chemical and biological methods (DeBach *et al.*, 1991). The first lever are formed by physical and cultural practices. Trapping, field sanitation and crop rotation can be implemented to control pest outbreak (Liquido, 1993; El-Sayed *et al.*, 2006). The second lever is based on pesticides. Even If multiple control methods have been described in the literature, pest control has long relied mostly on chemical pesticides use (DeBach *et al.*, 1991; Metcalf & Luckmann, 1994). Nowadays, phytosanitary and phytopharmaceutical products are extensively used to control a wide range of crop pests. In 2020, for instance, 3.5 million tons of pesticides were sprayed worldwide in pest control operations (Sharma *et al.*, 2019). Although these products are primarily designed to target pests, they actually also pollute the environment, cause high damages to biodiversity (Harpaz & Rosen, 1971; Robinson *et al.*, 2021), and endanger human health (Agee *et al.*, 1982; Blair *et al.*, 2015; Kim *et al.*, 2017). In addition, the efficiency of pesticides tends to decrease through time by selecting for pest resistance (Carson, 2002; Georghiou, 2012). Regarding the environmental problems sired by pesticides, it is necessary to develop and adopt environmentally friendly solutions to control pests (Lewis *et al.*, 1997). Since the 20th century, sustainable solutions based on the exploitation of natural regulations applied to pest management have gained renewed interests (Kiss, 2019). The third lever entails nature-based solutions such as biocontrol. Biological control or biocontrol is defined as the use of living agents as natural enemies in controlling pest (Stenberg *et al.*, 2021). One of the first remarkable success was recorded in late 1880 in California, in controlling the cotton cushion scale (*Icerya purchasi*) by introducing the coccinellid (*Rodolia cardinali*) and the vedalia beetle (*Rodolia cardinalis*) from Australia (Caltagirone, 1981). Recently, biocontrol has rapidly grown in pest management. Nowadays, in Europe, biocontrol is widely employed and appears over time as a strong alternative to pesticides use (Barratt *et al.*, 2018).

An example of such biocontrol alternative is the Sterile Insect Technique (SIT) (Knipling, 1979; Vreysen *et al.*, 2021). The Sterile Insect Technique consist in the massive release of sterile males of a given pest species in order to reduce the reproductive potential of the population (Knipling, 1955). Matings between wild females and sterile males produce unviable offspring. SIT aims to break population growth and reached control of the focal population. Knipling is the first author to mathematically theorise SIT applied to pest control in late 1930 (Van der Vloedt & Klassen, 1991). Notably, he introduced the crucial notion of overflooded

ratio largely taken in future SIT publication. This term corresponds to the ratio between sterile males and fertile males ensuring control or population extinction (Barclay, 2016). Since its work, Knippling hypothesis were proved several times by laboratory and field studies (Bushland & Hopkins, 1953). One of the first field experiment was conducted in Curaçao (Lesser Antilles) to successfully eradicate the new world screw-worm in 7 weeks (Baumhover *et al.*, 1955; Lindquist, 1955). At a larger scale, in 1970, *Anopheles quadrimaculatus* malaria vectors were eradicated from El Salvador with SIT program (Weidhaas *et al.*, 1974). More recently, in 1990, screw-worm (*Cochliomyia hominivorax*) was eradicated in 6 months of massive sterile male releases (Cunningham *et al.*, 1992). Nowadays, SIT has been applied to at least 20 species as coleopteran, lepidopteran and especially dipteran with for example the fruits flies (Krafsur, 1998; Oliva *et al.*, 2021; Vreysen *et al.*, 2021).

In France, CeraTIS (Gestion Territoriale de la Ceratite en Corse par la Technique de l’Insecte Stérile, 2020-2024) is the first project involving the Sterile Insect Technique (SIT) in an agricultural context, aiming at controlling the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) (Diptera : Tephridae) in Corsican orchards. Traditionally considered as a monogamous species, *C. capitata* has long been considered as a good target for SIT programs (Enkerlin, 2005; Reddy & Rashmi, 2016), though, a growing body of evidence suggests now that medfly females can copulate more than once (Mossinson & Yuval, 2003; Bonizzoni *et al.*, 2006; Bertin *et al.*, 2010). The 800-ha study area is composed of citrus fruits (orange, clementine), stone fruits (plum, nectarine) and vineyards (Figure 1). *C. capitata* is known to be a major pest of citrus fruits (Back & Pemberton, 1918; Carey, 1984; Krainacker *et al.*, 1987). In Corsica, citrus production represents 1.800 ha (Marí *et al.*, 2006), with clementine representing 80% of this production (Millet *et al.*, 2020). Fruit farming is the second economic source on the island. CeraTIS is divided into three components. The first component consists in improving sterile male release strategies by characterising biological and ecological parameters on the study area (Figure 1). For this task, predictive tools will be proposed to model the population dynamics of *C. capitata* in the Corsican framework. The second component will focus on the technical implementation, involving stakeholders. Sterile males will be imported from Spain and released from April to December. Finally, in a later component, sociological investigation will be conducted to assess the project perception by participants and in order to raise stakeholders’ awareness. Deployment strategies will be adapted accordingly to ensure SIT long-term viability at the Corsican scale. In the CeraTIS project, I will contribute to the first component by modelling *C. capitata* population dynamics in a Sterile Insect Technique control design perspective, with special attention to the Corsican context.

Few models of *C. capitata* dynamics have yet been published. Carey (1982) proposed a Leslie matrix to represent *C. capitata* dynamics. The population is structured in 40 stages, with a two-day time step. All survival and fecundity rates are stage-dependent. Although this type of model is widely used in population studies, it represents fairly simple dynamics and the linearity of the formalism does not account for complex non-linear interactions. In



**Figure 1:** CeraTIS Corse experimental design on Corsican Eastern plain. We realized the map with QGIS 3.10. Based on the former CeraTIS Corse map, we updated parcel register and detailed the experimental design

another approach, [El Messoussi \*et al.\* \(2007\)](#) and [Manoukis & Hoffman \(2014\)](#) used a multi-agent model to represent *C. capitata* dynamics. In this model, each fly is an agent. The model represents the individual interactions with a high degree of complexity. Although this formalism allows precise modelling, individual-based models are not tractable for general understanding and control of the system, beyond extensive simulations. These models are not adapted or difficult to transfer to the Corsican context. Therefore, we need to elaborate a model describing *C. capitata* population dynamics in the Corsican context and suited to the design and study SIT control strategies.

To achieve this, we need to consider a major feature in *C. capitata* population dynamics not taken into account in the models found in the literature. Indeed, a strong seasonality has been demonstrated in *C. capitata* dynamics. Several authors recorded repetition patterns in *C. capitata* occurrence every year, first in summer and then in fall ([Carey, 1991](#); [Israely \*et al.\*, 2004](#); [Bjeliš \*et al.\*, 2007](#); [Escudero-Colomar \*et al.\*, 2008](#); [Radonjić \*et al.\*, 2013](#)). In Corsican eastern plain, *C. capitata* demonstrates a strong seasonality occurrence in fall every year (CeraTIS data unpublished). We thus aim to develop a system of non-linear differential equations taking into account the seasonality aspect of the *C. capitata* growth relevant to the Corsican context. This preliminary step is essential to the project development, because it will help to guide the sterile male field releases.

To reach this objective, we described *C. capitata* population dynamics with a system of non-linear differential equations. We demonstrated that this original system can be approximated by a simplified system, that we analyzed mathematically in order to characterize the following

properties: the equilibria and their stability, and the respective effect of each parameter on the output dynamics. Lastly, we explored the effect of an introduction of sterile males on the population dynamics.

## 2 Materials and Methods

### 2.1 The biology of *Ceratitis capitata*

#### 2.1.1 Origin & Impact

The Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) (Diptera : Tephridae) is native from tropical East Africa in the Kenyan sub-Saharan east region (Gasperi *et al.*, 1991; Baruffi *et al.*, 1995; Malacrida *et al.*, 1998). According to Malacrida *et al.* (1998), medflies have colonized France in 1885. Nowadays, the presence of *C. capitata* has been documented worldwide (Sciarretta *et al.*, 2018). The medfly is described as one of the major threats against crops as grape, stone fruits or citrus fruits (Messenger, 1959; Liquido *et al.*, 1990; Sciarretta *et al.*, 2018). For instance, in 1991, the medfly cost about 493 millions to 875 millions dollars annually in California (Siebert & Pradhan, 1991; Siebert & Cooper, 1995). In Pakistan, *C. capitata* recent damages have been estimated at 200 millions annually (Stonehouse *et al.*, 1998).

#### 2.1.2 Abiotic conditions

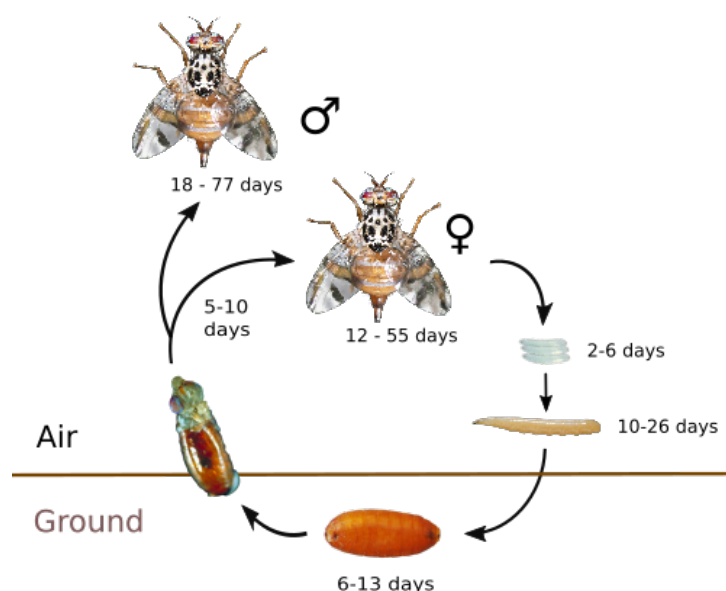
*C. capitata* is able to persist in a wide variety of climates (Messenger, 1959). The medfly is a multivoltine species that does not undergo diapause and that is little resistant to cold conditions (Christenson & Foote, 1960; Joachim-Bravo *et al.*, 2001). Winter has been demonstrated as the major limiting climatic factor for this species (Bodenheimer, 1925; Messenger & Flitters, 1954; Messenger, 1959; Israely *et al.*, 2004). Multiple authors have sought to determine how medfly survive through winter (Israely *et al.*, 2004; Peñarrubia-María *et al.*, 2012). It seems that adults fail overwintering, while a few larvae survive through winter and restart the population next season (Michelakis, 1992; Papadopoulos *et al.*, 1996; Peñarrubia-María *et al.*, 2012).

#### 2.1.3 Life cycle

The biological cycle of *C. capitata* is presented below in Figure 2. Life cycle is completed through four stages : egg, larva, pupa and adult. Stage lengths are extracted from Thomas *et al.* (2019). The length of stages are highly variable because they are strongly dependent on abiotic factors and hosts. Eggs are deposited by females under fruit peels (Back & Pemberton, 1918; Gjullin, 1931). Egg stage length is about 2 to 6 days. After hatching, larvae grow in the fruits during about 10 to 26 days. Once larvae are mature, they sink into the ground where pupation occurs. Pupae live in the soil for about 6 to 13 days, after which, adult emerges from the soil. The life cycle is completed in about 20 days in optimum conditions to about 100 days in cooler



conditions (Thomas *et al.*, 2019). Females develop during 5 to 10 day, after which, mating is physiologically possible (Christenson & Foote, 1960; Duyck *et al.*, 2002). Females have in average a shorter lifespan than males (33.5 vs. 47.5 days) (extracted from publication review, see Table 6 in Appendix).



**Figure 2:** *Ceratitidis capitata* life cycle (from right to left : egg, larva, pupa and adult)

#### 2.1.4 Host preference

*C. capitata* is an opportunistic polyphagous species infesting more than 350 plants including fruit trees, vegetables and nuts (Liquido *et al.*, 1990; White & Elson-Harris, 1992; Thomas *et al.*, 2019). Medfly reproductive success varies depending on hosts (Hafsi *et al.*, 2016). Some fruits are known to be particularly damaged by medfly infestation as for example, apple, peach, plum and citrus fruits (Liquido *et al.*, 1990; Katsoyannos *et al.*, 1997; Papadopoulos *et al.*, 2002). Survival, larval development and adult fecundity are maximized on these types of fruits (Krainer *et al.*, 1987; Duyck, 2010). The medfly female seems to be able to discriminate suitable hosts and thus increase its reproductive success (Cooley *et al.*, 1986; Joachim-Bravo *et al.*, 2001). Before the beginning of oviposition, females gauge host suitability by visual (color), physical (shape and size) and tactile senses (hard vs. bumpy) (Nakagawa *et al.*, 1978; Cytrynowicz *et al.*, 1982). Female medflies preference turns on ripe fruits (Agee *et al.*, 1982; Liquido *et al.*, 1990; Joachim-Bravo *et al.*, 2001).

#### 2.1.5 Reproductive Behaviour & Oviposition

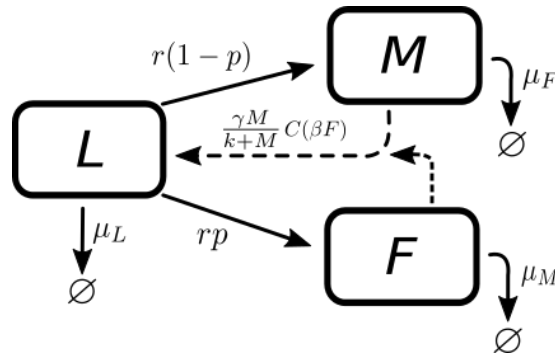
*Ceratitidis capitata* is a lekking species (Leftwich, 2012). Prior to mating, several males form lek (males aggregate) in late morning or early afternoon in the canopy on leaves undersurface or fruits (Prokopy & Hendrichs, 1979). Once male are perched, pheromone-calling starts by emitting sex pheromones to attract females (Arita & Kaneshiro, 1986). Time spent calling,

pheromones quality and male size seem to be determinant in females choice (Field *et al.*, 1999; Shelly, 2001; Shelly *et al.*, 2007). Once sufficient males are gathered, females are able to select from the lek the most suitable mating partner. Such a reproductive behavior entails unequal reproductive success among males (Shelly, 2001; Whittier *et al.*, 1994; Whittier & Kaneshiro, 1995). Once copulation is finished, females lay in average 7 to 42 eggs per day beneath the peel or in pre-existing cracks and wounds (data extracted from literature review, see Table 2). Broods are adjusted depending on hosts (McDonald & McInnis, 1985). Deterrent pheromones named Host Marking Pheromones (HMP) are left on the opposition site to insure even distribution in available hosts and to prevent larval competition (Prokopy *et al.*, 1978; McDonald & McInnis, 1985; Roitberg & Prokopy, 1987). In the case where females encounter on a fruit, competition seems to result in a decrease in oviposition level *per capita* (McDonald & McInnis, 1985).

## 2.2 Modelling

### 2.2.1 Model description

We developed two-models of *C. capitata* population dynamics based on the life cycle and biology of *C. capitata* (Figure 2). These models are structured by stages. The four-compartment model is composed of four stages: larva (L), male (M), virgin females (V) and mated females (F). Due to a lack of space, only three-compartment model will be detailed below. Three-compartment model is composed of 3 stages : larval (L), male (M), and female (F). Our larval stage corresponds to egg, larval and pupa stages in the biological life cycle (Figure 2). A schematic representation of three-compartment model is presented in Figure 3. This model was developed and run using Python 3.8.5.



**Figure 3:** Flow diagram of *Ceratitis capitata* population dynamics

The model is composed of three-nonlinear equations, describing variations of larvae (L), females (F) and males (M) through time (System (1)).

$$\begin{cases} \dot{L} = \frac{\gamma M}{k+M} C(\beta F) F - rL - \mu_L L, \\ \dot{F} = r(1-p)L - \mu_F F, \\ \dot{M} = rpL - \mu_M M. \end{cases} \quad (1)$$

Within a compartment, individuals have the same characteristics. There is no individual heterogeneity. At each time step, three biological processes occur : emergence ( $r$ ), oviposition ( $\gamma$ ) and death ( $\mu$ ). Oviposition rate term ( $\gamma$ ) represents the number of eggs laid per female per day, it includes the maturation rate, fecundity rate and oviposition rate. We assume that matings occur instantaneously after maturity, so we overlook fecundity rate. Then, as maturation rate represents a small period compared to oviposition rate, we overlook maturation rate. In this model, oviposition occurs until death, and this is the case for *C. capitata* (Vargas *et al.*, 1984). *C. capitata* is a lekking species, so male density are determinant in the reproduction (Prokopy & Hendrichs, 1979). We assume that female oviposition was affected by male density according to an rectangular hyperbola term  $\frac{M}{k+M}$  depicting the probability of mating: the higher male density is, the higher the probability for a female to mate. When parameter  $k$  increases but the density of males  $M$  remains constant, the probability for a female to mate decreases. When  $k$  is small compared to  $M$ , then :  $\frac{M}{k+M} \rightarrow 1$ . That means, regardless of  $k$ , if  $M$  is large, enough males are present to fertilize females, who mate thus with a probability closed to 1.

Secondly, oviposition is limited by competition between females (McDonald & McInnis, 1985). To model the competition  $C(\beta F)$ , we decided to consider two functions:  $\frac{1}{1+\beta F}$  and  $e^{-\beta F}$ , where competition increases when  $\beta$  increases. This two functions represent the reduction of the *per capita* oviposition rate ( $\gamma$ ) when the number of females increases. They behave similarly, i.e.,  $\lim_{F \rightarrow +\infty} C(\beta F) = 0$ . Nevertheless, the difference can be found in the global oviposition, when  $\lim_{F \rightarrow +\infty} e^{-\beta F} = 0$ , it can be seen as a strong competition. While  $\lim_{F \rightarrow +\infty} \frac{F}{1+\beta F} = \frac{1}{\beta} > 0$ , would rather be a weak competition. Simulations were run using the weak competition function.

Larvae develop in adults at rate  $r$ , with a proportion  $p$  of males and a proportion  $(1 - p)$  of females. The sex-ratio is assumed to be constant. Finally, all stages undergo specific mortalities:  $\mu_L$ ,  $\mu_F$  and  $\mu_M$ .

The previous system represents medfly growth during suitable season for a period  $\tau$  :  $\forall t \in [nT, nT + \tau]$ . The  $\tau$  period represents the medfly growth suitable season from end-June to end-October (CeraTIS data unpublished). During the cold season, adult stages of the medfly are assumed to die out, and only a proportion  $\phi$  of the larvae present at the end of the previous season survives (with  $0 < \phi < 1$ ). Assuming that time is initiated at the beginning of a growing season, and that a year last  $T$ , we have:

$$L((n+1)T) = \phi L(nT + \tau), F((n+1)T) = 0, \text{ and } M((n+1)T) = 0. \quad (2)$$

### 2.2.2 Parameter calibration

Parameters used to simulate the model are summarized in Table 1. Values were extracted from literature review, combining thirteen studies, or refitted if required (see details in Appendix 2). The  $\beta$  parameter was calibrated using CeraTIS project trapping data in order to adjust the system at a trap scale (to reach about 300 adults ).

**Table 1:** Review of model parameters from literature and refitting

Parameter	Description	Value	Unit
$r$	larval emergence rate	<b>0.047</b>	day <sup>-1</sup>
$p$	male proportion in offspring	<b>0.50</b>	-
$k$	mating half-saturation constant	1	♂ density
$\gamma$	oviposition rate	<b>25.52</b>	eggs / (♀.day)
$\beta$	oviposition competition between females	<b>0.85</b>	(♀ density) <sup>-1</sup>
$\mu_L$	larval mortality rate	<b>0.061</b>	day <sup>-1</sup>
$\mu_M$	male mortality rate	<b>0.036</b>	day <sup>-1</sup>
$\mu_F$	female mortality rate	<b>0.050</b>	day <sup>-1</sup>

## 2.3 Model analysis

The three-compartment model presented in equation (1) was studied using classical dynamical system tools. In a first step, we show how the system can be approximated and scaled to a simpler system that does not depend on the competition parameter  $\beta$  provided  $M \gg k$ . Consequently, we study the dependence of the model in regards to  $\beta$  parameters. Then, we studied the equilibria of this approximated system and characterize their stability. To facilitate the analytic resolution, number of males  $M$  are supposed in excess. Insofar, as  $k$  is small compared to  $M$ :  $\frac{M}{K+M} \approx 1$ . Hence,  $\dot{L}$  and  $\dot{F}$  are independent of  $M$ , and it allows us to consider a simplified two-dimensional system. To explore model dynamics, simulations were conducted using reference parameter set presented in Table 1. We chose the following initial conditions: 10 larvae and no adults. We compared the original model (1) and the same but simplified model, assuming that males are not limiting.

### 2.3.1 Sensitivity analysis

We conducted a global sensitivity analysis on the simplified model (3). We analysed the sensitivity of a model output of agronomic interest, the density of larvae at the end of the season (from simulations), to the parameter ranges identified from the literature. We retained all parameters involved, except the sex-ratio  $p$  set to its reference value ( $p = 0.5$ ) and the male mortality rate  $\mu_M$ , as the male dynamics does not impact the larvae in the simplified model. For each of the four parameters retained ( $r$ ,  $\gamma$ ,  $\mu_L$  and  $\mu_F$ ), three values were tested [min – reference – max] (see Table 2 in Appendix). We chose a variance-based method (Sobol, 1990; Wu *et al.*, 2013). A full factorial design was used to explore the parameter space. An ANOVA was then conducted to obtain the variance decomposition: we considered each parameter as a factor with three levels and we set a linear model with two-way interactions between the output and the parameters. Finally, Sobol Sensitivity Indices (SI) and Total Sensitivity Indices (TSI) were calculated for each parameter as follows: the SI is the ratio between the sum of squares of the parameter main effect and the total sum of squares. The TSI is the ratio between the sum of squares of the parameter main effect plus its interactions and the total sum of squares.

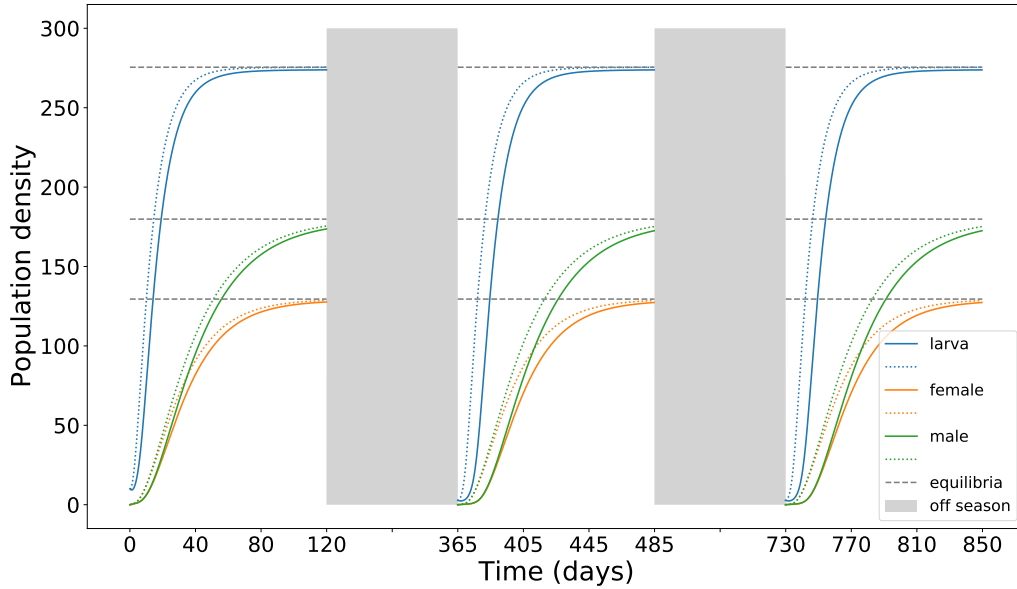
### 2.3.2 Adaptation to SIT context/ A step towards sterile males introduction

Following my internship, this population dynamics model will be used in the CeraTIS project to study and optimize sterile male releases. A first step to study the impact of sterile males consists in introducing a fixed number of sterile males ( $M_S$ ) in the male density dependent term:  $\frac{M}{k+M+M_S}$ . We tested an input of 0 to 100 sterile males  $M_S$ , ran simulations on a whole season, and graphically compared population densities at the end of the season to estimate the  $M_S$  impact.

## 3 Results

### 3.1 Simulation

Three-season simulations of both model (1) and a simplified model assuming  $M \gg k$  (non limiting males) are presented in Figure 4. We notice that the dynamics resulting from both models looks similar, so the assumption that males are not limiting is reasonable. Simulations show that the population increases drastically (Figure 4). Concerning larvae, they reach an equilibrium or saturation at the end of a season, and it is almost the case for adult stages. At the end of a season, we observe 300 adults among which about 175 males and 125 females. Larval densities are much more important than adults densities, despite an higher mortality rate ( $\mu_L = 0.061$  vs.  $\mu_F = 0.050$  and  $\mu_M = 0.036$ ).



**Figure 4:** Model simulations during three seasons. Solid curves represent the model in equation (1), while dotted curves the simplified model with non limiting males ( $\frac{M}{k+M} \approx 1$ ). A season lasts 120 days, which corresponds to *C. capitata* suitable season in Corsica (end-June to end-October). Light gray represents winter season. Dashed horizontal lines represent the asymptotically stable equilibrium calculated in section 3.2.2

## 3.2 Model analysis

### 3.2.1 Model simplification

The assumption that males are in excess ( $M \gg k$ ) is a good approximation (Figure 4), that we can use to simplify the model. We studied the model by analyzing the dynamics of  $(l, f, m) = (\beta L, \beta F, \beta M)$ . Considering equation (1) with strong  $C(\beta F) = e^{-\beta F}$  or weak  $C(\beta F) = \frac{1}{1+\beta F}$  competition and the  $k$  approximation described above, we have:

$$\begin{aligned} l = \beta L &\Rightarrow \dot{l} = \beta \dot{L} = \gamma C(\beta F) \beta F - (\mu_L + r) \beta L = \gamma C(f) f - (\mu_L + r) l \\ f = \beta F &\Rightarrow \dot{f} = \beta \dot{F} = r(1-p) \beta L - \mu_F \beta F = r(1-p) l - \mu_F f \\ m = \beta M &\Rightarrow \dot{m} = \beta \dot{M} = r p l - \mu_M m \end{aligned}$$

Hence, under the assumption that  $k$  is small compared to  $M$ , *i.e.*, when  $m$  remain high compared to  $\beta k$ , then  $\dot{l}, \dot{f}, \dot{m}$  are represented by the following system :

$$\begin{cases} \dot{l} = \gamma C(f) f - (\mu_L + r) l \\ \dot{f} = r(1-p) l - \mu_F f \\ \dot{m} = r p l - \mu_M m \end{cases} \quad (3)$$

For a given solution  $l(t), f(t)$  and  $m(t)$  of (3), we then obtain original variables as  $L = l/\beta, F = f/\beta$  and  $M = m/\beta$ . This shows that the model dynamics is independent of the  $\beta$  parameter, provided that the assumption on non limiting males holds. Parameter  $\beta$  is hence a scaling parameter.

### 3.2.2 Equilibrium point

We notice on Figure 4 that equilibrium is almost reached in one season. It thus makes sense to study the model behavior at equilibrium. Equations involving  $\dot{l}$  and  $\dot{f}$  in (3) only depend on  $l$  and  $f$ , and are independent of  $m$ . As a result we considered the following system in two-dimensions:

$$\begin{cases} \dot{l} = \gamma C(f) f - (\mu_L + r) l, \\ \dot{f} = r(1-p) l - \mu_F f. \end{cases} \quad (4)$$

At equilibrium,  $\dot{f} = 0 \Rightarrow r(1-p)l - \mu_F f = 0 \Rightarrow l = \frac{\mu_F}{(1-p)r} f$ . Thus :

$$\dot{l} = 0 \Rightarrow \gamma C(f) f - (\mu_L + r) l = 0 \Rightarrow f \left( \gamma C(f) - \frac{\mu_F(\mu_L + r)}{(1-p)r} \right) = 0.$$

At this point,  $\dot{l} = 0$  when either  $f = 0$  or  $\gamma C(f) - \frac{\mu_F(\mu_L + r)}{(1-p)r} = 0$ . When  $f = 0$ , then the first equilibrium point is  $(0,0)$ , which always exists. The other equilibrium must verify:

$$C(f) = \frac{\mu_F(\mu_L + r)}{\gamma(1-p)r} \quad (5)$$

Since  $C(0) = 1$  and  $C'(f) < 0$ , (5) has a (unique) positive solution  $f^*$  if and only if the right hand side is lower than one, *i.e.*, if:

$$R = \frac{\gamma(1-p)r}{\mu_F(\mu_L + r)} > 1, \quad (6)$$

otherwise, the only equilibrium is  $(0,0)$ . Finally, the second equilibrium when it exists is:

$$(l^*, f^*) = \left( \frac{\mu_F f^*}{r(1-p)}, f^* \right) \text{ with } f^* = C^{-1}(1/R)$$

### 3.2.3 Equilibrium point stability

To evaluate the Jacobian matrix of model (4), we compute the partial derivatives:

$$\frac{\partial \dot{l}}{\partial l} = -(\mu_L + r); \quad \frac{\partial \dot{l}}{\partial f} = \gamma(C'(f)f + C(f)); \quad \frac{\partial \dot{f}}{\partial l} = (1-p)r; \quad \frac{\partial \dot{f}}{\partial f} = -\mu_F$$

$$\text{So that: } \Gamma(l, f) = \begin{pmatrix} -(\mu_L + r) & \gamma(C'(f)f + C(f)) \\ (1-p)r & -\mu_F \end{pmatrix}$$

We evaluate the Jacobian at equilibrium. At  $(0,0)$ , we get:

$$\Gamma(0,0) = \begin{pmatrix} -(\mu_L + r) & \gamma \\ (1-p)r & -\mu_F \end{pmatrix} \Rightarrow \begin{aligned} \text{Tr}(\Gamma(0,0)) &= -\mu_L - r - \mu_F < 0, \\ \text{Det}(\Gamma(0,0)) &= (\mu_L + r)\mu_F - \gamma(1-p)r \end{aligned}$$

Thus,  $\text{Det}(0,0) \& \text{Tr}(0,0) < 0$  when (6) holds true and positive, otherwise, if  $R < 1$ ,  $(0,0)$  is locally asymptotically stable (LAS), and if  $R > 1$ ,  $(0,0)$  is unstable.

Suppose now that (6) holds, then  $(l^*, f^*)$  is in the positive orthant, and:

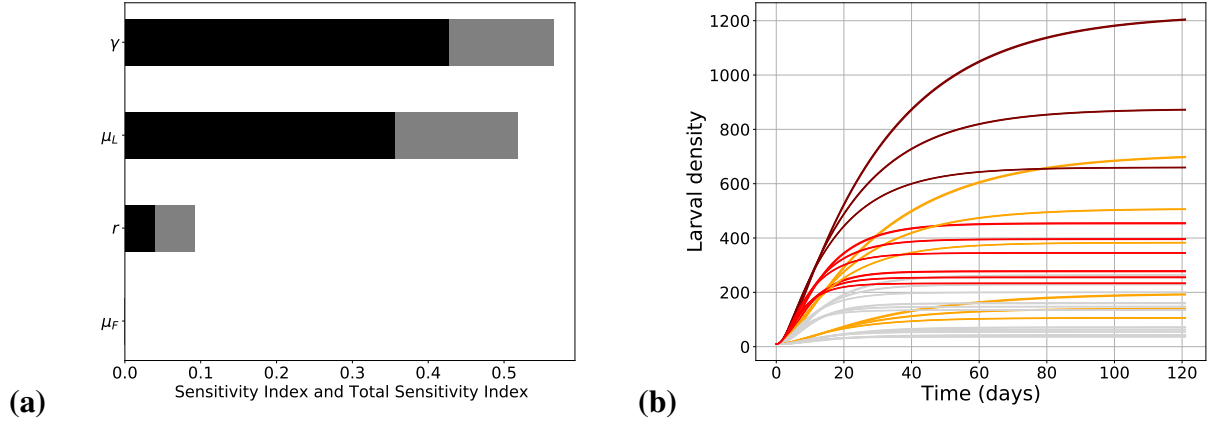
$$\Gamma(l^*, f^*) = \begin{pmatrix} -(\mu_L + r) & \gamma(C'(f^*)f^* + C(f^*)) \\ (1-p)r & -\mu_F \end{pmatrix}$$

which implies that:  $\begin{cases} \text{tr}(\Gamma(l^*, f^*)) < 0, \\ \text{Det}(\Gamma(l^*, f^*)) = (\mu_L + r)\mu_F - \gamma(1-p)r(C'(f^*)f^* + C(f^*)). \end{cases}$

At equilibrium,  $(\mu_L + r)\mu_F = \gamma(1-p)r C(f^*)$ , so  $\text{Det}(\Gamma(l^*, f^*)) = -\gamma(1-p)r C'(f^*)f^* > 0$ , and  $(l^*, f^*)$  is LAS since  $C'(f^*) < 0$ .

### 3.3 Sensitivity analysis

Sensitivity analysis results are presented in Figure 5. Three values were used per parameter: the reference value of Table 1 (and Table 2) and the extreme values of the range presented in Table 2.

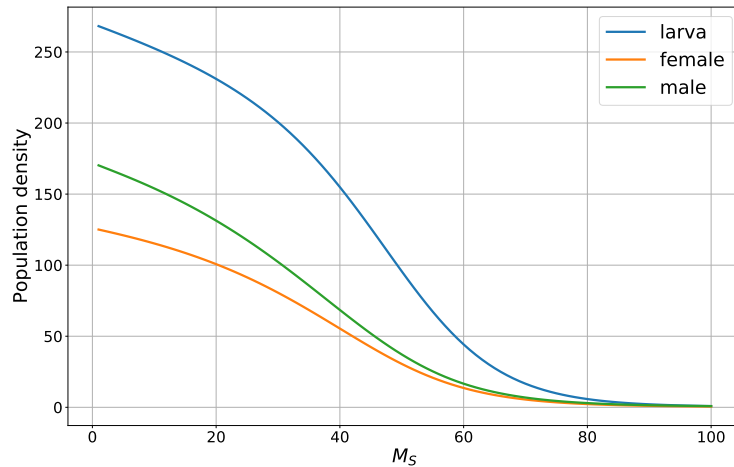


**Figure 5:** Sensitivity analysis conducted on model (3). **(a)** Total sensitivity index per parameter, broken out in main effect (black bar, SI) and interactions (grey bar). **(b)** Simulations for all parameter combinations, highlighted for high  $\gamma$  values (red) and low  $\mu_L$  values (orange), both high  $\gamma$  and low  $\mu_L$  (maroon) and all other combination (light gray).

The *per capita* oviposition rate  $\gamma$  and the larva mortality rate  $\mu_L$  are the parameters that most influence the larval density at the end of the simulation, with TSI higher than 50 %, as shown in Figure 5(a). There are moderate interactions between parameters. Higher  $\gamma$  and lower  $\mu_L$  values favour high final larva densities, as shown in Figure 5(b).

### 3.4 A step towards sterile males introduction

We simulated a constant input of 0 to 100 sterile males in the system (Figure 6).



**Figure 6:** Evolution of population density at the end of the season per stage when  $M_S$  increased



These simulations show that population density values at the end of the simulation decrease and tend to zero when  $M_S$  increases. Without SIT, the number of males ( $M$ ) is about 175. From  $M_S = 90$ , the total population is close to extinction. So a sterile to fertile male ratio of  $\frac{90}{175} = 0.51$ , should allow to reach population extinction.

## 4 Discussion

### 4.1 A model of *C. capitata* dynamics relevant to the CeraTIS project

A three-dimensional semi-discrete model of *C. capitata* population dynamics was proposed, taking into account the strong seasonality of the medfly (Israely *et al.*, 2004; Bjeliš *et al.*, 2007; Escudero-Colomar *et al.*, 2008; Radonjić *et al.*, 2013). Medfly growth is represented during a growing season interrupted by winters. At the onset of winter, adult populations die out and only a few proportion of larva survives and initiates the next season (Michelakis, 1992; Papadopoulos *et al.*, 1996; Peñarrubia-María *et al.*, 2012).

Model simulations are presented in Figure 4. One of the main result is that population dynamics almost converge to an equilibrium within a season (Figure 4). We observed that there were more males than females at the end of a season, which is due to a higher mortality of females. This observation is consistent with the literature, where males live in average longer than females (Vargas *et al.*, 2000; Pieterse *et al.*, 2020). We observed a much higher larval density than adult densities (Figure 4). This is due to an important *per capita* oviposition rate, which counterbalances a high larval mortality rate. In our model, the larval stage is key since the majority of crop damages is caused by larvae developing and feeding on fruit pulp (Prokopy & Economopoulos, 1976). Such a property contrasts with classical SIT modelling studies, *e.g.*, to fight mosquitoes) which are more concerned with adult females, which are the damaging stage (Gentile *et al.*, 2015).

### 4.2 Model simplification and scaling

We demonstrated that model equation (1) can be simplified into equations that approximate very well the original model dynamics for realistic parameter values (Figure 4). Indeed, when males are sufficiently numerous so that they do not limit matings ( $M \gg k$ ), the male density dependent term in the larvae dynamics approaches 1. The corresponding simplified model is then essentially linear, with a single nonlinear term linked to female competition :  $\gamma C(\beta F)F$ . This characteristic entails that the simplified model dynamics are fully independent of the competition parameter, so that, when  $\beta$  varies, population dynamics are invariant up to a simple rescaling of larval, female and male densities.

A first consequence of this  $\beta$ -invariance property is that the competition parameter actually determines the spatial scale at which population dynamics are considered. In this work,  $\beta$  was

calibrated as to represent *C. capitata* dynamics at the scale of an area covered by a typical field trap in the CeraTIS project test zone (Figure 1), as illustrated in Figure 4. A second consequence of  $\beta$ -invariance is that we can perform an extensive study of the mathematical properties of the simplified rescaled model (3) to characterize with a good degree of confidence the dynamics of the original model (1).

### 4.3 Mathematical analysis

Model (3) admits one or two equilibria depending on whether the basic reproduction number  $R$  is below or above 1 (equation (6)). If  $R < 1$ , the population ultimately goes to extinction, while when  $R > 1$ , there exists a positive equilibrium which is locally asymptotically stable, so that the reproduction number value determines the asymptotic behavior of the system. If the *per capita* oviposition rate  $\gamma$ , the emergence rate  $r$  or the proportion of females  $(1 - p)$  are high, the system would tend to an equilibrium. On the contrary, if the mortality rates  $\mu_F$  and  $\mu_L$  are high, then the population would be more prone to go to extinction. In the reference parameter set we gathered from literature (Table 1), we can compute the reproduction number as  $R \approx 111$ . Hence, as observed in Figure 4, there exists a positive asymptotically stable equilibrium point to which population dynamics converge with time.

The main assumption leading to the simplified model is that male density is large compared to the mating parameter  $k$ . This assumption is reasonable most of the time during a season (Figure 4) but falls short at the beginning of a season, when males are limiting. Indeed, the original model (1) suppose that matings condition offspring production by females, what produces Allee effect dynamics when population densities are close to 0 (Courchamp *et al.*, 2008). Nevertheless, because of the high reproduction capacities of *C. capitata*, population densities at which Allee effects impact the dynamics are actually very small (extinction for densities below  $10^{-2}$ , personal observations on simulations). Therefore the simplified model only slightly overestimates population increase, with a short delay of  $\approx 6$  days, but otherwise equivalent dynamics (Figure 4). Accordingly, since the reproduction number  $R$  is a good metric of the simplified model dynamics, we are confident that it should also be a good indicator for the original model (1) dynamics early in the season, at least for parameter values relevant to *C. capitata* biology and field conditions.

### 4.4 Sensitivity analysis

A sensitivity analysis performed on larval density at the end of the simulation showed it was most influenced by the *per capita* oviposition rate  $\gamma$  and the larval mortality rate  $\mu_L$ . Parameters  $\gamma$  and  $\mu_L$  are highly variable depending on abiotic factors and hosts (Hafsi *et al.*, 2016). The Mediterranean climate of Corsica and the diversity of host crops in the study area are thus expected to bring about an important level of variability in *C. capitata* population dynamics. Furthermore, the combination of  $\gamma$  and  $\mu_L$  drives essential characteristics of the model dynam-

ics: a low  $\gamma$  and a large  $\mu_L$  (*resp.* large  $\gamma$  and low  $\mu_L$ ) will give rise to low (*resp.* large) larvae densities at the end of a season. For that reason, modifying oviposition ( $\gamma$ ) or larval mortality ( $\mu_L$ ) rates can represent two major levers in order to control *C. capitata* population.

## 4.5 A step towards sterile males introduction

For several reasons, *C. capitata* has long been considered as a good target for SIT ([Enkerlin, 2005](#); [Reddy & Rashmi, 2016](#)). The goal of CeraTIS project is to control the *C. capitata* population by inundative releases of sterile males (SIT) which directly decreases female fecundity. We explored a first approach on model (1) to control *C. capitata* imposing a constant density of sterile males  $M_S$  in the system. We observed that for a population composed of 300 equivalent adults per trap, an intake of 90 equivalent sterile males per trap during the season led the population close to extinction. In Figure 6, a ratio of 0.51 to 1 between sterile males and wild males are required to reach population extinction. Such ratio entails an important effort and cost from managers. In order to reduce the number of sterile flies deployed, SIT is often employed in combination with other methods ([Fauvergue \*et al.\*, 2020](#)). For instance, field sanitation brings out to remove ripe fruits from infestation sites, and thus increase larval mortality rate  $\mu_L$ . SIT combined with this types of strategies can be a powerful tool in order to control *C. capitata*.

## 4.6 Perspectives

Based on my internship results, future work will focus on further adapting the model in integrating a male sterile compartment. From this model adaptation, the objective will be to study different release strategies and SIT scenarios. In parallel, to further study the properties of the current models, a study involving comparison between three and four compartments model will be conducted.

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## Annexe

Parameter values implemented in equation 1 are summarized below in Table 2. Parameters includes experimental data from literature and data obtained from calculation.

**Table 2:** Review of model parameters: reference values (in bold) and ranges (minimal and maximal values) identified in the literature.

Parameter	Description	Value & [Range]	Unit
$r$	larval emergence rate <sup>1</sup>	<b>0.047</b> [0.033 - 0.061]	day <sup>-1</sup>
$p$	males proportion in offspring <sup>2</sup>	<b>0.50</b> [0.45 - 0.55]	-
$k$	mating half-saturation constant	[1 - 100]	♂ density
$\gamma$	oviposition rate <sup>3</sup>	<b>25.52</b> [6.8 - 41.5]	eggs / (♀.day)
$\beta$	oviposition competition	0.85	(♀ density) <sup>-1</sup>
$\mu_L$	larval mortality rate <sup>4</sup>	<b>0.061</b> [0.002 - 0.120]	day <sup>-1</sup>
$\mu_M$	male mortality rate <sup>5</sup>	<b>0.036</b> [0.014 - 0.057]	day <sup>-1</sup>
$\mu_F$	female mortality rate <sup>5</sup>	<b>0.050</b> [0.018 - 0.083]	day <sup>-1</sup>

<sup>1</sup> Larval emergence rate<sup>†</sup> are calculated from : (Shoukry & Hafez, 1979; Carey, 1982, 1984; Vargas *et al.*, 1984; Krainacker *et al.*, 1987; Vargas *et al.*, 2000; Duyck *et al.*, 2002; Papadopoulos *et al.*, 2002; Diamantidis *et al.*, 2011)

<sup>2</sup> Males proportion<sup>\*</sup> is extracted from : Pieterse *et al.* (2020)

<sup>3</sup> Oviposition rate<sup>\*</sup> is extracted from : Shoukry & Hafez (1979); Carey (1984); Krainacker *et al.* (1987); Vargas *et al.* (2000); Papadopoulos *et al.* (2002); Duyck (2010); Pieterse *et al.* (2020)

<sup>4</sup> Larval mortality<sup>†</sup> is calculated from : (Vargas *et al.*, 2000; Pieterse *et al.*, 2020)

<sup>5</sup> Adult mortality<sup>†</sup> is extracted from (Vargas *et al.*, 2000; Pieterse *et al.*, 2020)

#### 4.7 Emergence rate estimation : $r$

Developmental time from egg to adult are summarized in Table 3. When information is missing, developmental time is calculated in summing egg, larval and pupa developmental time. As a result, larval developmental time varies between : **16.33** days in lychee and **30.4** days in apple. At the end of the development time, larvae become adult, then emergence rate is calculated using :  $r = \text{development time}^{-1}$ .

**Table 3:** Emergence rate based on developmental time (days) from experiment. Developmental times are extracted from experimental data from literature.

Literature	Dev. time* days	$r$ day <sup>-1</sup>	Medium	T °C
Shoukry & Hafez (1979)	22.9	0.044	artificial	25
Carey (1982)	24	0.042	artificial	25
Carey (1984)	[18.7 - 26.1]	[0.053 - 0.038]	fruits	25
Vargas <i>et al.</i> (1984)	19	0.053	artificial	-
Krainacker <i>et al.</i> (1987)	[16.33 - 22.05]	[0.061 - 0.045]	fruits	30±5
Vargas <i>et al.</i> (2000)	20.2	0.050	fruits	24
Duyck <i>et al.</i> (2002)	18	0.056	artificial	25
Papadopoulos <i>et al.</i> (2002)	30.4	0.033	apple	25
Diamantidis <i>et al.</i> (2011)	[16.87 - 19.68]	[0.060 - 0.050]	artificial	25

#### 4.8 Larval mortality estimation : $\mu_L$

Developmental time are extracted from Table 3. Survival from egg to adult are summarized in Table 4. Survival is defining by the proportion of eggs hatched, proportion of pupation and proportion of emergence. In the case where survival from egg to adult are missing, survival is calculated in multiplying egg, larva and pupa survival , otherwise survival is extracted as it is. Starting from exponential growth resolution formula :  $N_t = N_0 e^{-\mu t}$ . Larval instantaneous mortality can be estimated as :

$$L_t = L_0 e^{-\mu t} \Leftrightarrow \frac{L_t}{L_0} = e^{-\mu t} \left( \frac{L_t}{L_0} = survival \right)$$

$$survival = e^{-\mu t} \Leftrightarrow \ln(survival) = -\mu t$$

$$\mu_L = -\frac{\ln(survival)}{t}$$

**Table 4:** Larval mortality based on developmental time (days) and survival

Literature	Dev. time days	Survival proportion	$\mu_L$ -	T °C
Shoukry & Hafez (1979)	22.9	0.32 <sup>†</sup>	0.05	25
Carey (1984)	[18.7 - 26.1]	[0.96 - 0.54]	[0.0021 - 0.024]	25
Vargas <i>et al.</i> (1984)	19	0.49 <sup>†</sup>	0.038	-
Krainacker <i>et al.</i> (1987)	[16.33 - 22.05]	[0.21 - 0.07]	[0.096 - 0.12]	30±5
Vargas <i>et al.</i> (2000)	20.2	0.63 <sup>†</sup>	0.023	24
Duyck <i>et al.</i> (2002)	18	0.73 <sup>†</sup>	0.017	25
Papadopoulos <i>et al.</i> (2002)	30.4	0.33	0.036	25
Diamantidis <i>et al.</i> (2011)	[16.87 - 19.68]	[0.70 - 0.81]	[0.021 - 0.011]	25

<sup>†</sup> calculation data obtained by multiplying survival

#### 4.9 Oviposition rate estimation : $\gamma$

Oviposition rate are summarised in Table 5. Minimum oviposition rates are reported in apple with **6.8** eggs/female/day (Vargas *et al.*, 1984). Maximum oviposition rates are reported in papaya, with **41.45** eggs/female/day (Pieterse *et al.*, 2020).

**Table 5:** Review of *per capita* oviposition rate per day based on literature. Oviposition rates are extracted from experimental data from literature.

Literature	Oviposition rate* eggs/female/day	Medium	T °C
Shoukry & Hafez (1979)	[9.1 - 12.7]	artificial	30 & 25
Carey (1984)	14.2	fruits	25
Vargas <i>et al.</i> (1984)	19	artificial	-
Krainacker <i>et al.</i> (1987)	[8.5 – 19.7]	raspberry - orange	30±5
	8.5	raspberry	30±5
	19.7	orange	30±5
Vargas <i>et al.</i> (2000)	[6.8 - 11.2]	papaya	24° & 35
Duyck <i>et al.</i> (2002)	20.9	artificial	25
Papadopoulos <i>et al.</i> (2002)	8.5	apple	25
Pieterse <i>et al.</i> (2020)	[8.9 - 41.45]	fruits	-

#### 4.10 Male and female mortality rate estimation : $\mu_M$ and $\mu_F$

Male and females lifespan and mortality are summarized in Table 6. At the end of the adult lifespan, adults are expected to die, thus mortality are calculated as :  $\mu = \text{lifespan}^{-1}$ . When life span information was unavailable. For publication whose allow it, male and female lifespan are calculated as : lifespan total - immature stage life span. Mortality values are rounded to the nearest one-thousandth.

**Table 6:** Male and female lifespan (days) based on literature. Adult lifespans are extracted from experimental data from literature.

Literature	Lifespan* days	$\mu_M$ & $\mu_F$ $\text{day}^{-1}$	Medium	T °C
Shoukry & Hafez (1979)	♀ [25.5 - 31]	[0.039 - 0.032]	fruits	30° - 25°
	♂ [25 - 36.5]	[0.040 - 0.027]	”	30° - 25°
Carey (1984)	♀ [39 - 46.4]	[0.026 - 0.022]	fruits	”
	♂ [40.5 - 47.9]	[0.025 - 0.021]	”	”
Vargas <i>et al.</i> (1984)	♀ 31.9	0.031	artificial	-
Vargas <i>et al.</i> (2000)	♀ 54.8	0.018	fruits	24 & 35
	♂ 71.6	0.014	”	24 & 35
Papadopoulos <i>et al.</i> (2002)	♀ 21.1	0.047	artificial	-
	♂ 29.5	0.034	”	”
Pieterse <i>et al.</i> (2020)	♀ [12 - 17.5]	[0.083 - 0.057]	nectarine - plum	-
	♂ [17.6 - 35.5]	[0.057 - 0.036]	apple - plum	-