

A predator–prey population dynamics simulation for biological control of *Frankliniella occidentalis* (Western Flower Thrips) by *Orius laevigatus* in strawberry plants

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HIGHLIGHTS

- Simulates thrips population dynamics in the presence of *Orius* predators.
- Identifies suitable *Orius* release rates to control thrips under a target threshold.
- Thrips oviposition rate and *Orius* egg survival rate are highly influential parameters.
- Thrips handling time by *Orius* had little impact on both species populations' dynamics.

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ABSTRACT

The use of predatory insect species to control agricultural pests is a key aspect of Integrated Pest Management (IPM) that can help to reduce the use of chemical pesticides. A simulation model that captures the population dynamics and interactions of this predator–prey system can serve as a valuable IPM decision-support tool. However, such a simulation is challenging to construct due to the interactions between life stages of insect predators, prey and the crop plants. *Frankliniella occidentalis* (Western Flower Thrips, WFT) is an economically devastating global pest that damages diverse crops. *Orius laevigatus* is an effective and commercially available predator that controls WFT. We, therefore, developed a population dynamics simulation that models their interactions to better understand these insects' predator–prey dynamics in a strawberry crop. The model considers critical multi-stage predator–prey interaction, prey consumption reduction due to intraspecific competition, and the relationship between predation and oviposition rates of *Orius*. The simulation was structured using the boxcar train method, a stage-structured approach allowing insect populations to flow from one stage to the next over time. It was parameterised using data from existing literature. The results indicate the potential of the model to forecast the predator and prey species' population dynamics for different initial populations. A global sensitivity analysis identified that the daily oviposition rate of WFT and egg survival rate of *Orius* were the most significant parameters. The prey handling time of *Orius* on WFT did not significantly impact population variation. This model provides a useful tool for scenario exploration and assessment of the effects of *Orius* on WFT that can aid decision-making in IPM prior to implementation.

1. Introduction

Thrips (Thysanoptera), of which there are approximately 100 pest

species, include some that are among the most significant agricultural insect pests globally (Kumar et al., 2013). These cause harm to plants via oviposition, feeding, and by transmitting plant viruses (Morse and

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Hoddle, 2006; Stuart et al., 2011). To control thrips populations, Integrated Pest Management (IPM) often includes application of biological control agents, such as predatory insect species, as an effective alternative to chemicals. For example, *Orius* spp (Hemiptera: Anthocoridae) is a well-known, commercially available predator of thrips (Stuart et al., 2011; Mouden et al., 2017). Development of an IPM program for thrips control on a particular crop requires a thorough understanding of the complexity of the population dynamics and interactions of thrips, *Orius* and the crop plants. A simulation of such a system that quantifies insect population dynamics and interactions can potentially act as a predictive and decision-support tool for IPM. Here, we describe the development and results of a novel simulation to address this need.

The life history (biological) parameters of an insect species, such as juvenile development rates, survival, adult longevity and reproduction, encapsulate essential knowledge for understanding their population dynamics. Many published studies have estimated and reported thrips life history parameters on different host plants derived from lab or field experiments (Gaum et al., 1994; Nondillo et al., 2009; Sampson et al., 2014). Additionally, several studies have evaluated the effectiveness of *Orius* species as biological control agents for thrips and other prey by assessing their life history parameters, behavioral interactions and predation capacity (Sanchez and Lacasa, 2002; Zhang et al., 2021; Kordestani et al., 2021; Mouratidis et al., 2022). Despite this, few studies have used these published life-history parameters to develop population dynamic models for thrips and *Orius*, either individually or in the presence of both species (Wang and Shipp, 2001; Sanchez and Lacasa, 2002; Burgio et al., 2004; Nothnagl et al., 2008). Among these studies, only Sanchez and Lacasa (2002) and Burgio et al. (2004) investigated the population dynamics of thrips in the presence of *Orius*. However, that model did not consider crucial factors such as the multi-stage predator-prey relationship between *Orius* and thrips where adult and nymph *Orius* prey on both larval and adult stages of thrips. It also overlooked the reduction of predation rate due to intraspecific competition among *Orius*, the impact of predation rate on reproductive capacity of *Orius*, or the influence of the host plant on insect life history parameters and predator-prey interactions. These factors are significant in a predator-prey system, and neglecting them may lead to an unrealistic exponential increase or decrease in simulated insect populations. According to a recent review by Alexandridis et al. (2021), predictive models of natural pest control have been inadequately explored. Consequently, this study presents a comprehensive, novel predator-prey population dynamics simulation of thrips and *Orius* that accounts for the above-mentioned factors.

The life history and behaviours of insects are highly species- and host plant-dependent. Therefore, it is crucial to define the parameters of a model based on a target insect species and the environment in which it is being modelled. Among the approximately 100 thrips species worldwide, *Frankliniella occidentalis* (Western Flower Thrips) (WFT) are one of the most damaging for many greenhouse crops (Reitz, 2009; Stuart et al., 2011; Mouden et al., 2017; Reitz et al., 2020). WFT are resistant to many insecticides, thus, biological control agents are crucial management tools (Mouden et al., 2017; Reitz et al., 2020). *Orius laevigatus* is one of the most effective commercially available *Orius* species to control WFT (Mouden et al., 2017; Kordestani et al., 2021; Mouratidis et al., 2022). Thus, in this study, we model the population dynamics of prey WFT and predatory *O. laevigatus*. We selected strawberries as the host plant to model since they are a common berry crop that is highly vulnerable to WFT attacks (Shakya et al., 2010; Sampson et al., 2014; Atakan et al., 2016).

Our objective here is to build a comprehensive model to simulate the population dynamics of WFT and their predator *O. laevigatus* in strawberry, incorporating their complex predator-prey interactions. This will fill existing gaps in the literature and can inform the timing and release numbers of *Orius* to achieve effective IPM control. Model parameters were derived using data from the literature. For simplicity, and due to the lack of empirical data to parameterise a phenological model at

multiple temperatures, the temperature in our model is kept constant at 25 °C. However, we designed our simulation for easy adaptation to other thrips and *Orius* species, host plants and temperatures. We conducted a thorough sensitivity analysis of our model to identify the most influential parameters of the predator-prey system. In the remainder of the paper, we refer to *F. occidentalis* as WFT and *O. laevigatus* as *Orius*.

2. Method

2.1. Boxcar model

The population dynamic simulation of WFT and *Orius* is structured using the escalator boxcar train method (Goudriaan and Van Roermund, 1993; Lefelaar, 2012). In this model, a boxcar train represents an insect's life stage. A boxcar train can be further broken into classes, or individual boxcars, of identical widths (γ) along a developmental axis. Boxcars represent an insect population's development distribution within a single life stage. Each boxcar represents a cohort of insects sharing state variables. Where necessary, boxcar trains can be chained together to represent an insect's entire life cycle (Fig. 1). For instance, three separate boxcar trains can be chained together to model the entire life cycle of an insect population by describing the development of insect cohorts from the egg stage, to the juvenile stage and then the adult stage.

The population shift from one boxcar to the next within a train describes the temporal development of insects within a life stage. When the development process of an insect cohort has covered a boxcar width (γ), the entire population of that boxcar is shifted to the next boxcar. In addition, inflow and outflow for each boxcar are defined in each simulation time step (Δt) explicitly. Inflow into the first boxcar of the egg stage occurs due to adult oviposition. Inflow into the first boxcar of the other stages represents recruitment from a previous life stage and corresponds to the outflow from the final boxcar of the previous life stage (i.e., completions of a life stage). Lateral outflows from each boxcar represent insect deaths due to natural causes and predation. See Goudriaan and Van Roermund (1993) for more detail on the boxcar model.

In our implementation, separate boxcar trains were used to describe egg (f^e), larva (f^l), pupa (f^p) and adult (f^a) stages of WFT. The adult stage boxcar train was divided into 40 boxcars, and other stages were divided into 10. For *Orius*, the main life stages - egg (o^e), nymph (o^n) and adult (o^a) - were represented using separate boxcar trains containing 10, 25, and 70 boxcars respectively. The number of boxcars for each life stage was determined to enable our simulation time step to be fine enough to resolve any value less than 0.5 days across all stages.

In general, temperature affects the biological parameters of insects (Cocuzza et al., 1997; Gaum et al., 1994). Studies have shown that the most suitable range for both WFT and *Orius* is between 25 °C and 28 °C (Cocuzza et al., 1997; Nondillo et al., 2008; Nondillo et al., 2009; Rahman et al., 2010). For simplicity, we kept the temperature in our model constant at 25 °C. However, we designed our simulation to be easily adapted to other thrips and *Orius* species, host plants and temperatures. We specifically modeled the insect population per strawberry flower as there is a strong correlation between the numbers of WFT per flower and fruit damage (Sampson et al., 2014). All the symbols used in this study, along with their definitions, are listed in Appendix A for easy reference.

2.2. Model parameter estimation

Population abundance of WFT and *Orius* in each boxcar train depends on the biological parameters for the rates of development, reproduction and mortality. Values of these parameters are sourced from the literature (Table 1 and 2). Based on these, we compute the other important simulation parameters using the formulae below.

The development rate of egg and immature stages of both species can be derived as follows (Eq. 1):

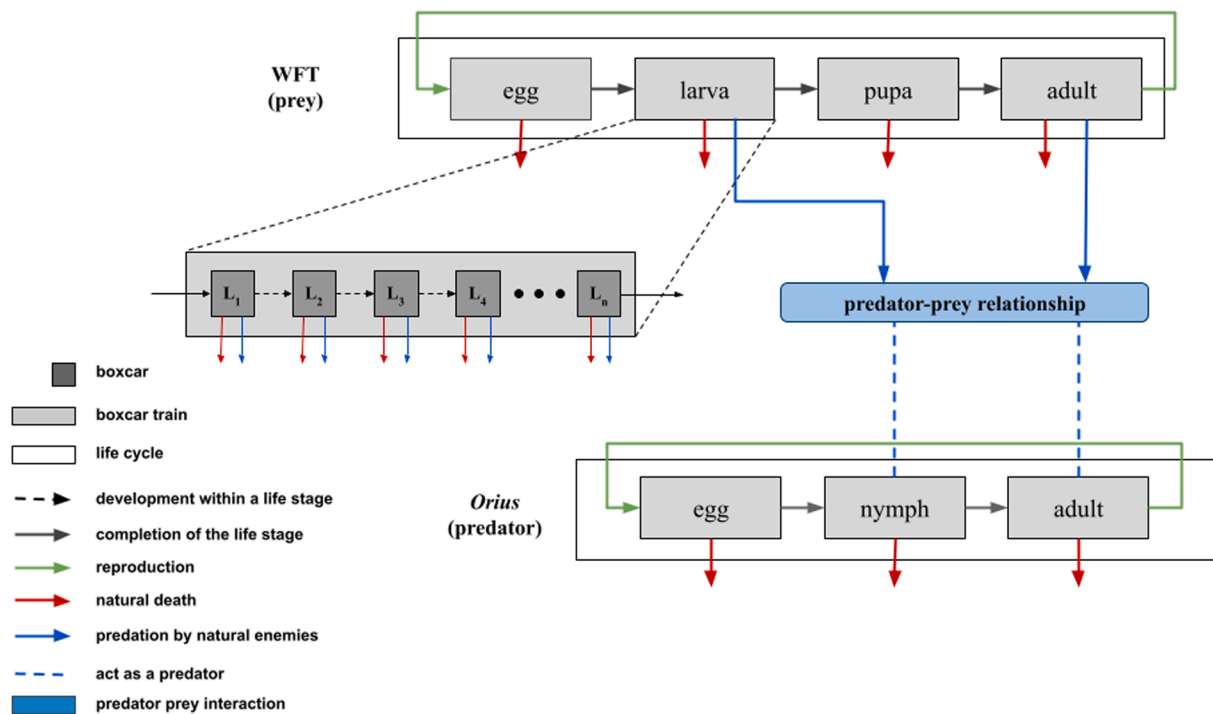


Fig. 1. Boxcar model.

Table 1
Biological parameters of WFT used in our model.

Parameter	Symbol	Default Value	±sd
<i>Development time (days)</i>			
Egg stage ^a	d_{fe}	4.1	0.398
Larva stage ^b	d_{fl}	4.9	1.198
Pupa stage ^b	d_{fp}	3.5	0.7801
<i>Survival rate (%)</i>			
Egg stage ^a	sr_{fe}	65.5	4.27
Larva stage ^b	sr_{fl}	83.3	-
Pupa stage ^b	sr_{fp}	82.3	-
Female adult longevity (days) ^b	d_{fa}	14.8	-
Sex ratio (female: male) ^b	x_f	0.78:0.22	-
<i>Reproduction parameters</i>			
Pre-oviposition period (days) ^b	po_f	2.5	0.16
Oviposition period (days) ^b	op_f	11	-
Daily oviposition rate (eggs/female) ^b	or_f	7.4	3.52

^a Based on the parameter values reported in Nondillo et al. (2008)

^b Based on the parameter values reported in Nondillo et al. (2009)

Table 2
Biological parameters of Orius used in our model.

Parameter	Symbol	Default Value	±sd
<i>Development time (days)</i>			
Egg stage ^a	d_{oe}	4.55	0.569
Nymph stage ^b	d_{on}	12.07	0.001
<i>Survival rate (%)</i>			
Egg stage ^a	sr_{oe}	88	32.5
Nymph stage ^b	sr_{on}	58	-
Female adult longevity (days) ^b	d_{oa}	34.00	3.436
Sex ratio (female: male) ^a	x_o	1:1	-
<i>Reproduction parameters</i>			
Pre-oviposition period (days) ^b	po_o	3.11	0.002
Oviposition period (days) ^b	op_o	11.88	3.097
Daily oviposition rate (eggs/female) ^b	or_o	5.73	-

^a Based on the parameter values reported in Mouratidis et al. (2022)

^b Based on the parameter values reported in Kordestani et al. (2021)

$$r_i^s = \frac{1}{d_i^s} \tag{1}$$

where r_i^s ($days^{-1}$) is the development rate of particular stage s of an insect species i , and d_i^s is the development time of that stage.

The instantaneous mortality rate of the egg and immature stages of both insect species can be computed as the natural logarithm of the finite survival rate of these stages (Eq. 2):

$$m_i^s = \ln(sr_i^s) \tag{2}$$

where m_i^s is the instantaneous mortality rate for stage s of an insect species i , and sr_i^s is the survival rate for the stage. The calculations of the development rate and the instantaneous mortality rate for different stages of WFT and Orius using the aforementioned formulae are shown in Table 3. For the adult stages of WFT and Orius, we assume that the insects live for periods of d_{fa} and d_{oa} respectively, and that they die at the end of the period.

2.2.1. Predator-prey relationship between Orius and WFT (Functional Response)

Adult and nymph Orius feed on both adult and larval stage WFT (Funderburk et al., 2000; Coll and Guershon, 2002). It is uncommon for Orius to prey on thrips in the egg and larval stages. This is because thrips lay their eggs in plant tissues, which provides protection to the eggs

Table 3
Development rate and instantaneous mortality rate of different stages of WFT and Orius.

Species/Stage	Development rate		Mortality rate	
	Symbol	Value	Symbol	Value
WFT				
Egg stage	r_{fe}	0.2439	m_{fe}	-0.4231
Larva stage	r_{fl}	0.204	m_{fl}	-0.1827
Pupa stage	r_{fp}	0.2857	m_{fp}	-0.1964
Orius				
Egg stage	r_{oe}	0.2198	m_{oe}	-0.1278
Nymph stage	r_{on}	0.0922	m_{on}	-0.5447

under the surface of the plant (Kumar and Omkar, 2021). After completing the larval stages, thrips eventually descend to the soil, entering the pupal stage. They remain in the soil until completing development and emerging as adults (Kumar and Omkar, 2021).

The nymphal stage of *Orius* has five phases. Based on observations by Cocuzza et al. (1997), the 1st and 2nd stage nymphs of *Orius* spend most of their time resting on flowers or leaves; their diet mainly consists of pollen and occasionally WFT larvae. Thus, in our model we assume that only nymphs of *Orius* beyond the 2nd stage – nymphs that have lived for 40% of the duration of the nymph stage – have the potential to attack WFT.

We adopt a type II functional response (Holling, 1959; DeLong, 2021) for our model, as used in previous studies (Montserrat et al., 2000; Arnó et al., 2008; Liu et al., 2018; Rehman et al., 2020; Zhang et al., 2021; Rahman et al., 2022), to describe the density-dependent feeding rate of *Orius* spp. on prey. Formally, the density-dependent prey consumption rate y_{fj}^i of an i^{th} stage *Orius* individual on the j^{th} stage of WFT can be modelled as follows:

$$y_{fj}^i = \frac{a_{fj}^i N_{fj}}{1 + a_{fj}^i h_{fj}^i N_{fj}} \quad (3)$$

where a_{fj}^i and h_{fj}^i are the space clearance rates (search rates or attack efficiency) and the handling time of the i^{th} stage of *Orius* on the j^{th} stage of WFT respectively. N_{fj} is the number of j^{th} stage WFT on a strawberry flower.

Since the nymph and adult *Orius* forage on both adult and larva WFT, the standard type II functional response can be extended to represent the predation rates of *Orius* individuals of a certain stage (o^a or o^n) with respect to two prey size groups (f^a or f^l) (i.e., a multi-stage functional response) (DeLong, 2021; Xia et al., 2003; Xia et al., 2018) as follows:

$$y_{fj}^i = \frac{a_{fj}^i N_{fj}}{1 + a_{fj}^i h_{fj}^i N_{fj} + a_{fj}^i h_{fj}^i N_{fj}'} \quad (4)$$

where y_{fj}^i is the predation rate (*prey eaten/day*) of i^{th} stage *Orius* prey on the j^{th} stage of WFT. N_{fj} and N_{fj}' are the larva and adult WFT populations per flower (Table 4).

The space clearance rate (a) corresponds to the space that the predator effectively clears of prey per unit of time, while handling time (h) is the time required for the predator to kill, consume, and digest prey before resuming the search for food (DeLong, 2021). The parameter values for the space clearance rate and the handling times for each predator-prey stage are derived using data from the literature (see Table 4) as described next. Please see Appendix B for a detailed explanation of parameter estimation.

Table 4
Parameter values for multi-stage functional response.

Predator - <i>Orius</i>	Prey - WFT	Space clearance rate		Handling time	
		Symbol	Value	Symbol	Value
Adult (o^a)	Adult (f^a)	a_{fa}^a	1.05	h_{fa}^a	0.045
Nymph (o^n)	Adult (f^a)	a_{fa}^n	0.90	h_{fa}^n	0.08
Adult (o^a)	Larva (f^l)	a_{fl}^a	1.05	h_{fl}^a	0.01
Nymph (o^n)	Larva (f^l)	a_{fl}^n	0.90	h_{fl}^n	0.02
Other parameters		Symbol	Value		
Interference coefficient		w	1.095		

Finding a_{fa}^a and h_{fa}^a . To estimate these parameters, we consulted a study by Shakya et al. (2010), that reports the functional response of adult *Orius* prey on different densities of adult WFT in strawberries at $25 \pm 1^\circ\text{C}$. These data are used to find parameter values for a_{fa}^a and h_{fa}^a using Eq. 3².

Finding h_{fa}^n and a_{fa}^n . To the best of our knowledge, no previous studies have reported the data required to directly derive h_{fa}^n and a_{fa}^n . Thus, we adopt the following approach to estimate them using the data on *Orius sauteri* and *Dendrothrips minowai* Priesner (tea thrip) (Thysanoptera: Thripidae) reported in (Zhang et al., 2021). That study reports the functional response curves for 4th nymph and adult *O. sauteri* preying on adult *Dendrothrips minowai* Priesner (tea thrip) (Thysanoptera: Thripidae) at a temperature of $25 \pm 1^\circ\text{C}$. Assuming that the fitness (foraging capacity) ratio between the nymph and adult stages of different *Orius* species is similar, we first calculate the ratios for the handling time and the clearance rate between adult and nymph *O. sauteri*. We then used these ratios to estimate the values for h_{fa}^n and a_{fa}^n based on the a_{fa}^a and h_{fa}^a values calculated above².

Finding a_{fl}^a and a_{fl}^n . Experimental results by Xia et al. (2003) have shown that for predators within a single life stage, there is little variation in the space clearance rate between different prey size groups. In particular, this difference is insignificant within the temperature range $20 - 35^\circ\text{C}$. Thus, we assume that $a_{fa}^a = a_{fl}^a$ and $a_{fa}^n = a_{fl}^n$.

Finding h_{fl}^a and h_{fl}^n . Adult *Orius* consume 22.5 WFT larva per day at a population density of 25 larvae per strawberry flower at $25 \pm 1^\circ\text{C}$ (Shakya et al., 2010). Using this data for Eq. 3, the value for h_{fl}^a is estimated. To estimate h_{fl}^n , we adopt the same approach that we used to estimate h_{fa}^n based on the data reported by Zhang et al. (2021)².

Per capita foraging rates usually decrease with the density of a predator due to their intra-specific interference response. The type II multi-stage functional response (Eq. 4) can be modified to incorporate this interference competition by including the amount of time that a predator spends on interference competition with other predators (DeLong, 2021) as follows:

$$y_{fj}^i = \frac{a_{fj}^i N_{fj}}{1 + w(N_{0^{n+a}} - 1) + a_{fj}^i h_{fj}^i N_{fj} + a_{fj}^i h_{fj}^i N_{fj}'} \quad (5)$$

where $N_{0^{n+a}}$ is the number of *Orius* (both adults and nymphs) per flower, and w is the interference coefficient (the time wasted per predator) (DeLong, 2021).

To estimate w in Eq. 5, we used data from Zhang et al. (2021) that corresponds to the intra-specific interference response of predators for *O. sauteri* on *Dendrothrips minowai* Priesne. We assume that the reduction in the consumption of WFT by *Orius* due to interference competition follows the same pattern. Thus, we estimate w by fitting the modified predation rate for the different densities of *Orius* on WFT to Eq. 5².

2.2.2. The relationship between predator oviposition rate and the number of prey consumed - numerical response

The numerical response of insect predators is modelled by assuming that the daily oviposition rate of adult females increases with their daily predation rate (Crawley, 1975). This is approximated using a linear relationship – every prey eaten results in a constant increase in the predator’s daily oviposition rate up to a maximum value (prey required for satiation) (Crawley, 1975; Rahman et al., 2012; Madahi et al., 2015; Nasreen et al., 2021; Loko et al., 2022). Hence, the daily oviposition rate (eggs/female/day) of an adult *Orius* female (e^{o^a}) is formulated as

¹ See Table 4 for the definition of these parameters.

² We present detailed steps of these calculations in Appendix B

follows:

$$e^{\sigma^a} = m \times y^{\sigma^a} + c \quad (6)$$

$$y^{\sigma^a} = y_{f^{\sigma^a}}^{\sigma^a} + \frac{y_{f^{\sigma^a}}^{\sigma^a}}{2} \quad (7)$$

where y^{σ^a} is the predation rate of *Orius*. Here, we assume that the nutrients gained by *Orius* from consuming a WFT larva are equivalent to half of the nutrients gained from an adult WFT (see Eq. 7) for two reasons: (1) the size of an adult WFT is approximately twice that of a larva; and (2) *Orius* consumes around twice as many larval thrips as adult thrips (Shakya et al., 2010).

To find the parameters for Eq. 6 (Table 5), we adopt the following strategies.

Finding m and c . *Orius* spp. can supplement its diet with pollen and plant tissues (Zuma et al., 2022; Lorenzo et al., 2019). Other strawberry plant pest species, such as aphids and mites, can also act as alternative prey for *Orius* spp. when thrip density is low (Venzon et al., 2002; Wang et al., 2014; Zuma et al., 2022). Hence, with no thrips present, *Orius* can survive and reproduce in strawberry crops. But some of these alternative food sources, such as pollen, may not be as nutritionally rich as thrips for *Orius* reproduction, as evidenced by a reduction in their daily oviposition rate (Bernardo et al., 2017). Here, we define c as the constant oviposition rate of *Orius* when WFT density is zero. The efficacy of *Orius* for biological control of *M. euphorbiae*, mediated by the presence of companion plants and externally supplied alternative prey in strawberry plants, has been evaluated by Zuma et al. (2022). We adopt these experimental results for our *Orius* population in conditions where only *M. euphorbiae* is present in the strawberry to calculate c ($= 0.5$) for our model (Appendix C). The daily oviposition rate of *Orius* is ~ 5.73 when the predation rate is 12 adult WFT per day (Shakya et al., 2010; Kordostani et al., 2021). By using this value in Eq. 6, we calculate the value for m as 0.436^3 .

2.3. Simulation Process

In this subsection, we discuss the larval stage of WFT as an example of how the population dynamics are modelled inside each life stage using the boxcar model. The same approach was followed for all of the other life stages. For a detailed description of the boxcar train model, see (Goudriaan and Van Roermund, 1993).

Our model adopts the following procedure to compute the population changes inside a larval stage for a single simulation time step Δt .

Initially, we modelled the γ_{f^l} cyclic development width of a boxcar in the larval stage as:

$$\gamma_{f^l} = \gamma_{f^l} + r_{f^l} \times \Delta t \quad (8)$$

where r_{f^l} is the development rate of the larval stage at temperature 25°C . Here, γ_{f^l} measures the level of completion inside a boxcar, which is incremented by $r_{f^l} \times \Delta t$ in every simulation step Δt .

Then, the change in the population $\Delta N_{f^l,0}$ in the first boxcar of the

Table 5
Model parameters related to daily fecundity of *Orius* that depend on their consumption rate of WFT.

Parameter	Symbol	Value
The oviposition rate of <i>Orius</i> when WFT density is zero (I.e., supplement their diet from alternative food sources)	c	0.5
The incremental increase of the oviposition rate of <i>Orius</i> per prey consumed	m	0.436

larval stage during a simulation time step Δt is formulated as:

$$\begin{aligned} \Delta N_{f^l,0} = & \frac{N_{f^e,last}}{(\Gamma_{f^e} - \gamma_{f^e})} \times r_{f^l} \times \Delta t - N_{f^l,0} \times m_{f^l} \times \Delta t - \frac{y_{\sigma^a}^{f^l} \times N_{\sigma^a}}{b_{f^l}} \\ & \times \Delta t - \frac{y_{\sigma^a}^{f^l} \times N_{\sigma^a}}{b_{f^l}} \times \Delta t \end{aligned} \quad (9)$$

where $\frac{N_{f^e,last}}{(\Gamma_{f^e} - \gamma_{f^e})} \times r_{f^l} \times \Delta t$ denotes the recruitments from the last boxcar of the egg stage to the first boxcar of the larval stage. Here, $N_{f^e,last}$ is the population size contained within the last boxcar of the egg stage. Γ_{f^e} and γ_{f^e} denote the boxcar width and cyclic development width of the egg stage respectively. Population reduction due to natural death can be measured as $N_{f^l,0} \times m_{f^l} \times \Delta t$, where $N_{f^l,0}$ is the population of the first boxcar of the larval stage and m_{f^l} is the instantaneous mortality rate of the larval stage. The population reductions due to predation by nymph and adult stages of *Orius* can be described using $\frac{y_{\sigma^a}^{f^l} \times N_{\sigma^a}}{b_{f^l}} \times \Delta t$ and $\frac{y_{\sigma^a}^{f^l} \times N_{\sigma^a}}{b_{f^l}} \times \Delta t$ respectively. Here, N_{σ^a} and N_{σ^a} are the total numbers of nymph and adult *Orius* in the simulation at time t . b_{f^l} is the total number of boxcars in the larval stage.

For the i^{th} middle boxcar (i.e., all boxcars except the first and last), the change in the population $\Delta N_{f^l,i}$ is computed as:

$$\Delta N_{f^l,i} = -N_{f^l,i} \times m_{f^l} \times \Delta t - \frac{y_{\sigma^a}^{f^l} \times N_{\sigma^a}}{b_{f^l}} \times \Delta t - \frac{y_{\sigma^a}^{f^l} \times N_{\sigma^a}}{b_{f^l}} \times \Delta t \quad (10)$$

where $N_{f^l,i}$ is the population of the i^{th} middle boxcar.

For the last boxcar, we measure the population change $\Delta N_{f^l,last}$ as:

$$\begin{aligned} \Delta N_{f^l,last} = & -\frac{N_{f^l,last}}{(\Gamma_{f^l} - \gamma_{f^l})} \times r_{f^l} \times \Delta t - N_{f^l,last} \times m_{f^l} \times \Delta t - \frac{y_{\sigma^a}^{f^l} \times N_{\sigma^a}}{b_{f^l}} \\ & \times \Delta t - \frac{y_{\sigma^a}^{f^l} \times N_{\sigma^a}}{b_{f^l}} \times \Delta t \end{aligned} \quad (11)$$

where $\frac{N_{f^l,last}}{(\Gamma_{f^l} - \gamma_{f^l})} \times r_{f^l} \times \Delta t$ is the number of individuals from the population recruited to the next stage (i.e. the inflow to the first boxcar of the pupal stage), and $m_{f^l} \times \Delta t$ denotes the population reduction due to death. Γ_{f^l} is the boxcar width of the larval stage, and $N_{f^l,last}$ is the number of larva in the last boxcar.

The population shifts from one boxcar to the next within the larval stage when the following condition is satisfied:

$$\gamma_{f^l} \geq \Gamma_{f^l} \quad (12)$$

When the condition given in Eq. 12 is satisfied, the population is shifted to the next boxcar:

$$N_{f^l,i} = \begin{cases} 0 & \text{if } i = 0 \\ N_{f^l,i-1} & \text{otherwise} \end{cases} \quad (13)$$

Also, with the satisfaction of the condition in Eq. 12, the cyclic development time γ_{f^l} is reinitialized:

$$\gamma_{f^l} = \gamma_{f^l} - \Gamma_{f^l} \quad (14)$$

The operation of the simulation for the other thrips and *Orius* life stages are similar to that just described. It is important to note that the inflows to the first boxcar of the egg stage occur as a result of female adult egg-laying. Death due to predation by *Orius* affects only the larval and adult stages of thrips. The instantaneous mortality rate is applied only to the immature stages of both species, while adults live until their average lifespan and die at the end of that stage.

³ We present these calculations in Appendix C.

2.4. Sensitivity Analysis

We used global sensitivity analysis techniques to evaluate the relative contributions of each individual parameter to model behaviour and to explore the interactions between parameters and model output variance. Global sensitivity analysis involves varying all parameters simultaneously over the entire parameter space to capture the relationships between input and output in complex models (Zhang et al., 2015). To conduct our sensitivity analysis, we selected Sobol' indices with the Sobol sampling technique; this is suitable for capturing monotonic and non-monotonic interactions between variables (Zhang et al., 2015; Tosin et al., 2020).

Sobol' indices are variance-based indices that can identify the fraction of the variance in the output that can be attributed to an individual variable alone or with interaction effects (Zhang et al., 2015; Tosin et al., 2020). Sobol' indices are typically divided into two categories: first-order indices and total-order indices. First-order indices represent the contribution of a single input variable to the total output variance, while total-order indices represent the contribution of a single input variable and all its interactions with other input variables to the total output variance. Sobol' indices range between 0 and 1, where 0 indicates no contribution, and 1 indicates a full contribution to the total output variance. The higher the Sobol' indices values, the more influential the respective model parameters. While there is no clear threshold established, a commonly accepted cutoff value for this is 0.05, which serves to distinguish significant parameters from insignificant ones (Zhang et al., 2015). Sobol sensitivity analysis requires a relatively large number of samples – it requires evaluating the model at $s(k+2)$ points, where k is the number of input parameters and s is the sample size. To generate uniform samples of parameter space for this, we utilised Sobol's sequence, which is a quasi-random, low-discrepancy sequence.

The model used in our study consists of 31 parameters, all of which are assumed to follow normal distributions for sampling. If the standard deviation of experimental data was not reported along with the mean value in a study from which we extracted a parameter value, or if it could not be calculated, we used 10% of the mean value as the standard deviation. Due to the complexity of our model, we conducted a sensitivity analysis based on four scenarios (Table 6). We calculated Sobol's indices of the parameters against the populations of WFT adults and larvae, and *Orius* adult and nymph populations, every 5 days over a simulation period of 90 days. For each simulation, we set the initial population sizes to be two WFT adults and two larvae per flower. The value for *Orius* adults and nymphs was 0.2 per flower. Sensitivity analysis was conducted, with a sample size of 4096, using the open-source Python library, SALib (Herman and Usher, 2017; Iwanaga et al., 2022).

Table 6
Scenarios for sensitivity analysis.

Scenario	Description	Parameters being changed	No. of parameters
I	Only WFT present in the environment	Biological parameters of WFT	11 (Table 1)
II	Only <i>Orius</i> present in the environment	Biological parameters of <i>Orius</i>	9 (Table 2)
III	Both WFT and <i>Orius</i> present in the environment	Parameters related to the interaction between WFT and <i>Orius</i> (i.e, parameters in multi-stage functional response and the predation rate-dependent daily oviposition rate of <i>Orius</i>)	11 (Table 4, 5)
IV	Both WFT and <i>Orius</i> present in the environment	All parameters	31

3. Results

3.1. Simulation results

Fig. 2a shows that the WFT population exponentially increases over time in the absence of *Orius*. For the first 20 days, both the larva and adult WFT populations remain below 20 individuals per flower. After that, the population increases rapidly. However, the WFT population is controlled in the presence of different *Orius* densities (see Figs. 2b and 2c). When the initial densities of WFT: *Orius* are increased from 1:0.1 to 1:0.2, the peak WFT population is reduced. Additionally, even when WFT are absent from the environment, *Orius* reproduced and built its population (Fig. 2d). However, the population's rate of increase is much lower than when WFT are present as prey. Fig. 2 demonstrates how our simulation facilitates the analysis of the population dynamics of WFT in the presence of different *Orius* densities. Additionally, Appendix D offers a preliminary analysis of how the population dynamics of the WFT and *Orius* predator-prey system vary with temperature.

3.2. Comparison with field-collected data

To assess the suitability of our model in identifying insect population dynamics in real crop conditions, we utilised pest monitoring data provided by a strawberry farm in Victoria, Australia. The farm comprises multiple polytunnel planting blocks, creating a semi-protected environment. Trained pest monitoring staff regularly observe and document the presence of pests and their biological control agents on strawberry flowers in each block every two weeks. They report thrips population levels per flower, categorised as low (0–5), medium (5–10), or high (> 10), as well as the percentage of flowers where they observe *Orius*. To validate our simulation results, we specifically analysed the reported *Orius* population from two blocks (referred to as Block I and Block II) which are located ~1km apart, over a six-month period during the 2019–2020 strawberry season in Victoria. Please note that the daily average temperature during the reported data period varied between 11°C and 29°C (Appendix F).

At the beginning of the monitoring period, Block I had a high WFT population, while Block II had a low to medium population. To accurately represent these different initial thrips levels, our simulation was initialised with 6.25 larva and 6.25 adult thrips per flower for Block I, and 2.5 larva and 2.5 adult thrips per flower for Block II. Our system was initialised with 1 *Orius* per flower, consisting of 0.5 adults and 0.5 nymphs per flower. We considered a system of 100 flowers and simulated the populations of *Orius* and thrips using the aforementioned initial conditions. To perform this simulation, we set C (the oviposition rate of *Orius* when no thrips are present) in Eq. 6 to zero and adjusted the value of m (increase of the oviposition rate of *Orius* per prey consumed) accordingly. This adjustment was made under the assumption that the daily egg-laying rate of *Orius* is solely dependent on the nutrients obtained from consuming thrips. This approach is adopted because the number of flowers varies throughout the season, particularly towards the end when the number of flowers per unit area tends to decrease compared to the middle of the season. In Fig. 3, we present the reported values from the farm (i.e., observed % flowers that have *Orius* on them) for Blocks I and II, and the corresponding simulation results for the *Orius* population per flower.

Typically, as the abundance of *Orius* per flower increases on a strawberry farm, there is a corresponding increase in the percentage of flowers with *Orius*. Therefore, our aim was to evaluate whether we could observe similar patterns between the reported values and our simulation output for *Orius* populations. According to the reported values for Block I, the percentage of flowers with *Orius* gradually increases during the early stages of the season, reaches its peak between days 42 and 84, and then starts to decrease. A similar pattern can be observed in the simulated results for Block I (Fig. 3).

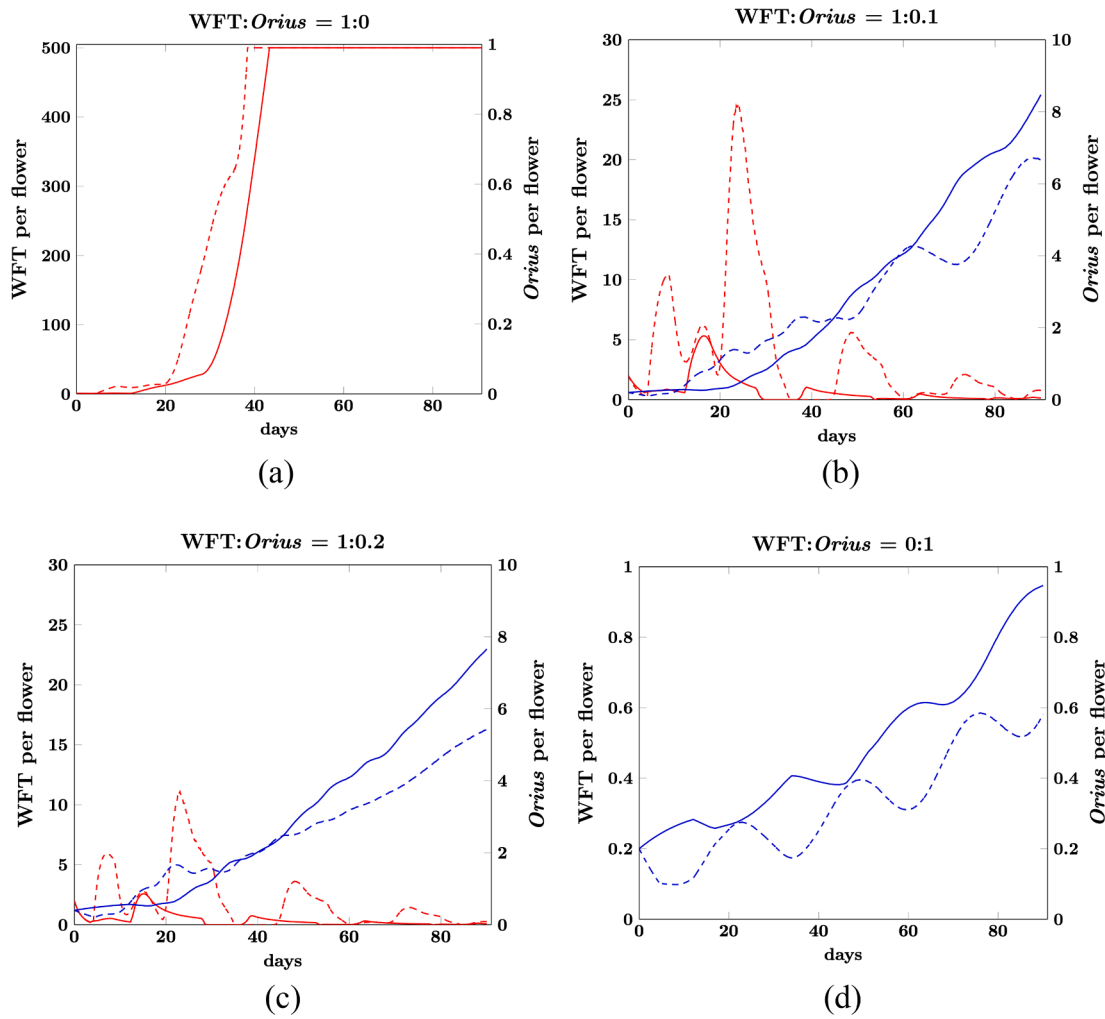


Fig. 2. Population variation of WFT and *Orius* over 90 days with different initial prey-to-predator densities at 25 °C. Each line denotes population variation of adult WFT (—), WFT larvae (---), adult *Orius* (—) and nymph *Orius* (---). The initial population densities per flower in each figure in the order of adult WFT, larva WFT, adult *Orius*, and larva *Orius* are: (a) 2, 2, 0, 0; (b) 2, 2, 0.2, 0.2; (c) 2, 2, 0.4, 0.4; and (d) 0, 0, 0.2, 0.2. The total number of flowers is 100.

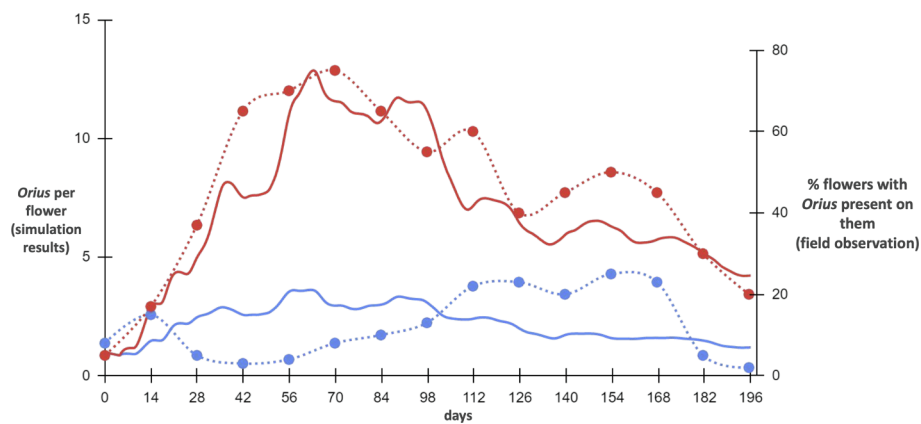


Fig. 3. This figure compares the monitored farm *Orius* population dynamics to simulation results. Dotted lines represent the percentage of flowers with *Orius* recorded by the pest monitoring staff for strawberry Blocks I and II. Continuous lines indicate the simulated *Orius* population (combining adults and nymphs) per flower. Legend: Simulated *Orius*/flower Block I (—); simulated *Orius*/flower Block II (—); reported percentage of flowers with *Orius* Block I (---); reported percentage of flowers with *Orius* Block II (---).

It is evident that the percentage of flowers with *Orius* in Block II is consistently lower than in Block I throughout the reporting period (Fig. 3). These two blocks have different initial thrips infestation levels per flower. Our simulation demonstrates similar dynamics, with the

Orius population per flower in Block II consistently lower than in Block I throughout the simulation period (Fig. 3). In Block II, the reported percentage of flowers with *Orius* reaches its peak during the second half of the period. However, in our simulation model, the *Orius* population

starts to gradually decrease during this period. The strawberry farmers at our field site released additional *Orius* on multiple occasions until day 70 due to the low initial *Orius* population. This difference in dynamics between the reported values and the simulated values for Block II may be attributed to these interventions.

The studied strawberry crops grow in a semi-protected environment where various unmodeled factors may influence insect populations. Temperature fluctuations, the presence of alternative prey for *Orius*, other predators that consume thrips, and the use of chemicals on the farm can all impact *Orius* and thrips populations. Within the state of Victoria, Australia, plague thrips also coexist with WFT on strawberry crops during the early flowering season (Amarathunga et al., 2022) and *Cucumeris* species are used alongside *Orius* to control thrips. Therefore, to accurately predict the numbers of *Orius* and thrips per flower throughout the strawberry season, our model needs adjustment to account for these extremely complex factors. This is discussed later in Section 4.

3.3. Results of sensitivity analysis

The parameter sensitivity analysis based on the first-order Sobol' indices are presented in Fig. 4. The main findings of the sensitivity analysis based on the scenarios of Table 6 over the 90-day simulation period are below.

Scenario I. In this scenario, we investigated the effect of the biological parameters of WFT on their population dynamics by isolating the thrips boxcar model from the rest of the model (or by setting the initial *Orius* population to zero). The sensitivity analysis indicates that, among the 12 biological parameters considered here, the oviposition rate (or_f) is the most important parameter contributing to the variance of both adult and larval WFT populations (Fig. 4a and 4d), followed by the development time of larval (d_{f1}) and pupal (d_{f2}) stages.

Scenario II. This scenario investigates the influence of biological parameters of *Orius* on their population dynamics. We isolated the *Orius* component from the rest of the model (or set the initial WFT population to zero) and ran the simulation (Fig. 4g and 4j). Our analysis reveals that the survival rate of eggs (sr_{oe}) has the greatest contribution to the output variance on both adult and nymph populations, followed by the oviposition period (op_o). In addition, we observed that the development time of the egg stage (d_{oe}), the survival rate of the nymph stage (sr_{on}), the sex ratio (x_o), and the oviposition rate (or_o) have weak but still significant influences on both nymph and adult *Orius* populations.

Scenario III. This scenario investigates the effect of parameters related to the interaction between *Orius* and WFT on their population dynamics while keeping their biological parameters at default values. We studied 11 parameters, 9 from the multistage functional response (Eq. 5) and 2 from the prey consumption-dependent oviposition rate of *Orius* (Table 4). The results indicate that during the first 30 days of the simulation period, none of the 11 parameters showed a significant influence on WFT population (Fig. 4b and 4e). However, after 30 days, the space clearance rates and the intra-specific interference completion coefficient (w) significantly affect the thrips population. Moreover, after 55 days, the oviposition rate of *Orius* when feeding on secondary food sources (c) displayed a significant but weak impact on the WFT population.

The results also indicate that parameters m , the oviposition rate of *Orius* per thrips consumed, and c , the oviposition rate of *Orius* when feeding on secondary food sources, contribute the most to the variation in the *Orius* population. The Sobol' indices value for m on both nymph and adult *Orius* initially increases up to ~ 0.85 until the first 35 days. It then decreases over the remaining simulation period. In contrast, the Sobol' indices value for c is initially very low and starts to increase after ~ 40 days. This value reaches ~ 0.8 at the end of the simulation period. Besides these two parameters, the space clearance rates of *Orius* also show a significant influence on both nymph and adult *Orius* populations,

and their Sobol' indices vary between 0.2 – 0.3 during the simulation period.

Scenario IV. In this scenario all 31 model parameters were changed simultaneously to identify which had the most impact on the populations of *Orius* and WFT. Our analysis revealed that the egg survival rate (sr_{oe}) and oviposition period (op_o) of *Orius*, and the oviposition rate of WFT (or_f), significantly affect both populations. Additionally, we found that the development time of the larval stage (d_{f1}) impacted the WFT population. The survival rate of the nymph stage (sr_{on}) showed a weak but significant influence on the adult *Orius* population (Sobol' indices < 0.2).

It was observed that in all four test scenarios, four parameters representing the handling time of the multistage functional response did not show a significant impact on either the WFT or *Orius* populations.

4. Discussion

Population dynamic simulations of insect predator–prey systems can benefit crop growers by informing their IPM practices. In IPM, the lowest population density of a pest that will cause economic damage to a particular crop is called the “Economic Injury Level” (EILs) (Shakya et al., 2010; Sampson et al., 2014). The EIL for WFT in strawberry crops is typically based on the assessment of thrips density in flowers as there is a strong correlation between the number of WFT per flower and fruit damage (Amarathunga et al., 2022; Sampson et al., 2014). An “action threshold” (AT) is the pest density at which a control strategy should be executed to prevent the EIL from being reached (Sampson et al., 2014). Growers need to know the ATs of their crop pests to take timely actions to prevent crop damage and avoid unnecessary pesticide spraying. The AT of a particular crop pest depends on the control strategy, and it can be relaxed in the presence of its predatory species (Shakya et al., 2010; Sampson et al., 2014).

For strawberries in Australia and the UK, the EIL is ~ 5 adult WFT per flower (Sampson et al., 2014; Steiner and Goodwin, 2005). The general practice of IPM in strawberry is to release *Orius* during the early flowering season, and to monitor thrips and *Orius* levels on flowers weekly or fortnightly throughout the flowering season. Based on the pre-defined threshold levels of thrips and *Orius*, growers decide whether to release more *Orius* into the field or apply other compatible spray treatments. Having a population dynamics simulation model of thrips and *Orius* on strawberries can help to forecast thrips population variation with different densities of *Orius*. This facilitates a superior *Orius* release strategy than one solely dependent on pre-defined thresholds. For example, our simulation results show that initial ratios of 1:0.1 and 1:0.2 of WFT to *Orius* will help prevent WFT populations from reaching the EIL level (Fig. 2b and 2c). Therefore, our model might be used to suggest the optimal number of *Orius* for release to maintain the WFT population below a predefined threshold. Additionally, simulations like ours allow researchers to investigate different management strategies that may be too costly or time-consuming to test in experimental trials. Simulations could also help to inform the design of proper field experiments.

Understanding how pest or predator populations vary over time can provide insights that aid pest control decision-making. For example, with the settings we used for our model the WFT population's rate of increase climbs steeply after 20 days, indicating that it would have been preferable to take control measures before then. A similar population dynamic was observed in simulation results conducted on WFT in greenhouse cucumber (Iwanaga et al., 2022). With the predator–prey ratios given in Figs. 2b and 2c, the WFT larva population will peak during the 20–30 day period. Growers can therefore take control measures during this time to avoid further escalation of their pest population. For instance, they might introduce secondary predatory species, such as predatory mites, that prey on the larval stage of WFT. *Orius* populations can increase, even in the absence of WFT, by feeding on alternative food sources found on strawberry farms (e.g., strawberry

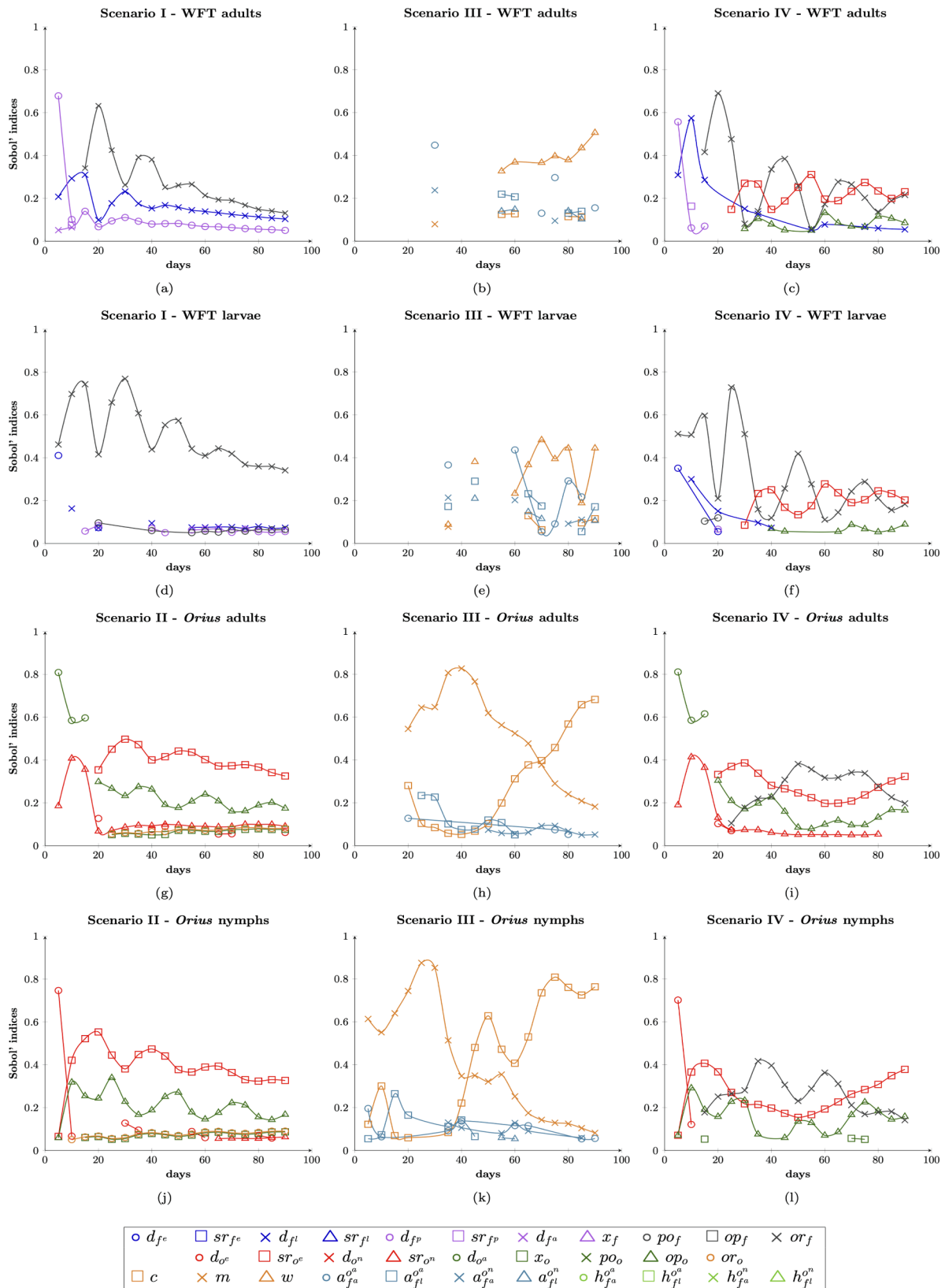


Fig. 4. The first order Sobol' indices for model parameters at 5-day intervals over a 90-day period, under the four scenarios of Table 6. Only statistically significant results are plotted, i.e. parameters with Sobol's indices > 0.05 and p-values > 0.05. (Please refer to Appendix A for the definitions of symbols).

pollen and plant parts). But their growth rate will be very slow compared to the case where WFT are present (Fig. 2d). Hence, farmers can provide supplementary pollen and *Ephestia kuehniella* eggs as food for *Orius*, or they can plant companion plants (e.g., *Lobularia maritima*) that provide quality food for *Orius* to support an increase in these insects' abundance when the thrips population is low (Zuma et al., 2022).

4.1. Discussion of sensitivity analysis results

Our sensitivity analysis revealed that the daily oviposition rate of WFT was one of the most influential parameters on both thrips and *Orius* populations. This could have been due to the oviposition rate contributing directly to the increase of the thrips population. A similar finding was reported by Wang and Shipp (2001) in a local sensitivity analysis of their model of the population dynamics of WFT on greenhouse cucumber. The reported daily oviposition rate of WFT in strawberries varies widely around its mean value (6.67 ± 3.52) (Nondillo et al., 2009) and depends highly on the host plant. For instance, at 25°C, eggs laid per female can be as high as 79.65 on bean pods or as low as 9.65 on cucumber (Gaum et al., 1994; Zhi et al., 2005). When thrips feed on strawberry flowers, the average number of eggs per female is around 70 (the value used in our study), but it is around 8.5 when they feed on strawberry leaves (Nondillo et al., 2009). Given that the daily oviposition rate greatly influences both WFT and *Orius* populations, and that it can take on a range of values, it is crucial to fine-tune this parameter when using the model for decision-making. Another example concerns the egg survival rate and oviposition period of *Orius*. These parameters strongly contribute to the dynamics of the *Orius* population when it is alone, and also impact the thrips population when the two insect species coexist on the strawberry farm. Therefore researchers ought to focus on tuning such parameters identified during sensitivity analysis to improve a model's performance, or when adapting the model to a specific site or circumstance.

The number of thrips consumed by an *Orius* depends on space clearance rates, prey handling times, and the interference coefficient. The sensitivity analysis reveals that the space clearance rate significantly influences both populations, whereas handling time does not. The number of prey consumed by an *Orius* adult directly affects its daily oviposition rate. Thus, it is important to accurately estimate space clearance rates for different predator-prey stages. Handling time mainly limits the maximum number of prey consumed by a predator per day. *Orius* can consume up to around 12 adult WFT per day. Hence, if the WFT population density is low or moderate, handling time does not greatly affect the number of WFT consumed by an *Orius* per unit time. However, it can influence the output populations when WFT density is high. The interference coefficient w reduces the predation rate of *Orius* when their population increases. When the *Orius* per flower is ≤ 1 , w does not affect the predation rate, explaining why w does not affect the WFT population during the initial period of simulations (day < 35).

The daily oviposition rate of *Orius* depends on three parameters: m , representing the increment in daily oviposition rate per thrips consumed, c , the oviposition rate of *Orius* when feeding on secondary food sources, and the number of WFT consumed which is determined by the functional response curve. When the number of WFT per flower is high, the daily oviposition rate of *Orius* is mainly dominated by m . It is dominated by c when the WFT population is low. This explains the opposite trend in the Sobol' indices of these two variables during the sensitivity analysis conducted for scenario III.

4.2. Extending the model for field conditions: model limitations and future work

The analysis of Section 3.2 comparing field observations and simulation results demonstrates the potential of our model to simulate insect population variation in real strawberry crops. However, to accurately predict the exact number of insect populations per flower throughout

the strawberry season, the model would need to account for specific field conditions.

The model parameters in this study were established from data in the literature that were primarily derived from laboratory experiments. Some of the data were used as the basis for calculations to derive new values that, with appropriate assumptions, match our simulation conditions while maintaining their biological relevance. To reduce uncertainty in the model predictions, tuning the parameters using population data collected from actual strawberry fields (controlled, semi-protected or open-field) should be addressed in future work. The current model consists of 31 parameters, so tuning them using field-collected data may be complex. However, the process can be simplified by prioritising tuning of parameters that, according to the sensitivity analysis, have the greatest impact on model output.

In this study, we set the temperature parameter to a constant 25 °C, which is within the optimal growth range for WFT and *Orius*. However, temperature variations throughout a season, particularly in semi-protected or open-field environments, can significantly impact the biological parameters of insects (Cocuzza et al., 1997; Sanchez and Lacasa, 2002; Nondillo et al., 2008). For example, the mean longevity of *Orius* adults, feeding on *E. kuehniella* eggs and honeybee pollen, was observed to be 34.6 days at 20 °C and decreased to 15.2 days at 35 °C (Sanchez and Lacasa, 2002). The mean number of eggs laid by a female WFT on cucumber increased from 2.76 to 10.65 as the temperature rose from 15 °C to 30 °C (Gaum et al., 1994). The experiment conducted by Park and Lee (2020) also showed fluctuating temperature can negatively affect the biological parameters of the WFT. Thus, integrating temperature effects into the model is important for effectively applying it in varying temperature conditions. Please refer to our analysis in Appendix D, which offers insights into the predator-prey population dynamics of *Orius* and WFT at various temperatures. To accommodate these temperature variations, each parameter needs to be formulated as a function of temperature. Furthermore, some biological parameters may vary with humidity, precipitation, and other climate conditions; this requires further investigation to adapt our model to a semi-protected or open-field environment (Groves et al., 2001; Steiner et al., 2011; Park and Lee, 2020). Additionally, the oviposition and mortality rates of adult insects may vary with age, hence formulating them as a function of age can enhance population dynamic predictions (Gaum et al., 1994; Wang and Shipp, 2001).

WFT typically move very short distances (< 0.3m/day) per day, with random dispersal (Rhainds and Shipp, 2004; Sampson et al., 2014), a reliance on the wind for long-distance travel (Nyasani et al., 2017; Reitz et al., 2020), and they sometimes aggregate patchily in strawberry fields (Amarathunga et al., 2021b). Incorporating such dispersal patterns into our model could enhance its accuracy. By contrast, adult *Orius* species are typically good fliers and active foragers (Malais et al., 2004). Understanding their movement patterns is especially important when the population of WFT is low, as *Orius* can emigrate from the field and the model may then overestimate the *Orius* population. Also, the establishment of *Orius* in a strawberry field heavily depends on various other factors, including the availability of resources within the field. Banker plants play a crucial role by providing pollen for *Orius* to feed on and creating an ideal breeding environment (Zuma et al., 2022). Additionally, the presence of alternative prey species and the field's condition, whether protected, semi-protected, or open, influence *Orius* establishment (Zuma et al., 2023). Despite being highly effective predators, *Orius* is sensitive to many pesticides. Some pesticides used for controlling other pests in strawberries can have direct toxicity or sublethal effects on them, hindering *Orius* establishment and reducing their efficacy (Moscardini et al., 2013). Therefore, studying and incorporating these additional factors may enhance simulation accuracy.

It takes around 42 days for strawberry flowers to complete their life cycle from a white bud to a red strawberry fruit in a flowering season that lasts up to about 5 months (Sampson et al., 2014). The number of flowers per unit area varies during the season (Sampson et al., 2014) and

therefore thrip density in flowers increases towards the end of flower flushes when the insects are concentrated into fewer flowers. Additionally, the abundance of WFT at different development stages can vary greatly between flower stages (Sampson et al., 2014). Although it does not have a significant impact on short-term population predictions, integrating strawberry phenology across a season into our boxcar model would improve its long-term predictions.

Our study focused on the pest thrips - WFT (*F. occidentalis*), the predatory *Orius-O. laevigatus*, and the host plant, strawberry. However, *Orius insidiosus* and *Orius majusculus* are also used for controlling thrips, including WFT, in crops worldwide (Funderburk et al., 2000; Lorenzo et al., 2019; Mouratidis et al., 2022; Zhang et al., 2021). It would be possible to adopt our model for other *Orius* and thrips species to in the future. The biological parameters of thrips species vary depending on the host plant, and those of *Orius* can depend on both their prey species and host plant (Lorenzo et al., 2019; Mouratidis et al., 2022). Consequently, model parameters must be adjusted to match a specific prey-predator system. In some cases, growers may use multiple predatory species to manage pests. Therefore, understanding pest population dynamics in the presence of multiple predators is a key research problem. For example, predatory mites *Neoseiulus cucumeris* and *Amblyseius swirskii* are released with *Orius* to control WFT populations in strawberries. However, the predator-prey relationship in such a system is complex and subject to intraguild predation. Our boxcar model is extensible and, in the future, could be adapted to simulate the dynamics of multiple predator species.

The recent review by Alexandridis et al. (2021) emphasizes the difficulty of creating models that accurately predict the performance of biological pest control on farms. This challenge arises because there is always a trade-off – models can either be too general and lack realism, or very realistic but only work in a narrow range of situations. Thus, our proposed model is a good starting point for predicting the population dynamics of WFT in the presence of *Orius* that can serve as a useful tool to aid IPM decision-making. Also, evaluating the model against observational data or integrating it with such data is also crucial. With the help of AI, collecting species population data for that may become easier and more efficient in the future (Amarathunga et al., 2021a).

5. Conclusion

In this study, we propose a comprehensive predator-prey population

Appendix A. List of symbols

The list below shows the symbols that appear in the study along with their definitions. We have arranged the symbols in the order of their appearance in the paper and based on how easy they are to understand. We have also grouped together related symbols. Please note that the list is not in alphabetical order.

Symbol	Explanation
f	<i>Frankliniella occidentalis</i> (Western Flower Thrips) (WFT)
o	<i>Orius laevigatus</i> (<i>Orius</i>)
e	egg stage
l	larval stage
p	pupal stage
n	nymph stage
a	adult stage
f^e	egg stage of WFT
f^l	larval stage of WFT
f^p	pupal stage of WFT
f^a	adult stage of WFT
o^e	egg stage of <i>Orius</i>
o^n	nymphal stage of <i>Orius</i>
o^a	adult stage of <i>Orius</i>
d_{fs}	development time of WFT egg

(continued on next page)

dynamic simulation model of the insect pest WFT and its predator *Orius* in strawberries. Our model demonstrates the potential to forecast WFT population variations from different initial populations of *Orius* on strawberry flowers. Thus, it can assist to determine *Orius* release rates that maintain WFT populations below economic thresholds. The global sensitivity analysis on the model parameters reveals that the daily oviposition rate of WFT and the egg survival rate of *Orius* are the parameters that contribute the most to population variation. The nymphal survival rate and length of the oviposition period of *Orius*, and the duration of the larval stage of WFT, also significantly influence the model output. From the parameters related to the interaction, thrips prey handling time by *Orius* does not show a significant impact on the population variations of either insect species. To reduce uncertainty in the model predictions and to use it for pest management decision-making, tuning model parameters using data collected from the target environment would be required. Our proposed model provides a comprehensive starting point for predicting the population dynamics of WFT in the presence of *Orius* that is sufficiently detailed that it can potentially aid IPM decision-making.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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(continued)

Symbol	Explanation
d_{f1}	development time of WFT larva
d_{fp}	development time of WFT pupa
d_{fa}	life duration of WFT adult
d_{of}	development time of <i>Orius</i> egg
d_{on}	development time of <i>Orius</i> nymph
d_{oa}	life duration of <i>Orius</i> adult
sr_{fe}	survival rate of WFT egg
sr_{f1}	survival rate of WFT larva
sr_{fp}	survival rate of WFT pupa
sr_{of}	survival rate of <i>Orius</i> egg
sr_{on}	survival rate of <i>Orius</i> nymph
x_f	sex ratio (female: male) of WFT adults
x_o	sex ratio (female: male) of <i>Orius</i> adults
po_f	pre-oviposition period of WFT female adult
po_o	pre-oviposition period of <i>Orius</i> female adult
op_f	oviposition period of WFT female adult
op_o	oviposition period of <i>Orius</i> female adult
or_f	daily oviposition rate (eggs/female) of WFT
or_o	daily oviposition rate (eggs/female) of <i>Orius</i>
r_{fe}	development rate of WFT egg
r_{f1}	development rate of WFT larva
r_{fp}	development rate of WFT pupa
r_{of}	development rate of <i>orius</i> egg
r_{on}	development rate of <i>orius</i> nymph
m_{fe}	mortality rate of WFT egg
m_{f1}	mortality rate of WFT larva
m_{fp}	mortality rate of WFT pupa
m_{of}	mortality rate of <i>Orius</i> egg
m_{on}	mortality rate of <i>Orius</i> nymph
a_{fa}^{oa}	space clearance rate (predator - <i>Orius</i> adult, prey - WFT adult)
a_{fa}^{on}	space clearance rate (predator - <i>Orius</i> nymph, prey - WFT adult)
a_{f1}^{oa}	space clearance rate (predator - <i>Orius</i> adult, prey - WFT larva)
a_{f1}^{on}	space clearance rate (predator - <i>Orius</i> nymph, prey - WFT larva)
h_{fa}^{oa}	handling time (predator - <i>Orius</i> adult, prey - WFT adult)
h_{fa}^{on}	handling time (predator - <i>Orius</i> nymph, prey - WFT adult)
h_{f1}^{oa}	handling time (predator - <i>Orius</i> adult, prey - WFT larva)
h_{f1}^{on}	handling time rate (predator - <i>Orius</i> nymph, prey - WFT larva)
w	interference coefficient
c	the oviposition rate of <i>Orius</i> when WFT density is zero
m	the incremental increase of the oviposition rate of <i>Orius</i> per prey consumed
Δt	simulation time step
γ	cyclic development width of a boxcar
ΔN	the change in the population
Γ	boxcar width

Appendix B. Parameter estimation: predator–prey relationship between *Orius* and WFT

Finding a_{fa}^{oa} and h_{fa}^{oa} .⁴ To estimate these parameters, we consulted a study (Shakya et al., 2010), that reports the functional response of adult *Orius* prey on different densities of adult WFT in strawberries at $25 \pm 1^\circ\text{C}$. These data are used to find parameter values for a_{fa}^{oa} and h_{fa}^{oa} using Eq. 3.

In their experiment, individual *Orius* adults were provided with 5, 10, 15, or 20 adult WFT on 4 cm-diameter strawberry leaf discs, and the number of consumed WFT by each *Orius* individual after 24 h was recorded. The nonlinear least-squares method was employed to obtain the best fit for Type II functional response using the reported data, ensuring that the predicted daily consumption rate by the fitted curve remained lower than the reported values. The estimated values for a_{fa}^{oa} and h_{fa}^{oa} were 1.05 and 0.045, respectively. This fitted curve provides a lower bound for the daily consumption rate of *Orius* on WFT when the thrips density is below approximately 25 (Fig. B.1). However, it tends to overestimate the daily consumption rate when the density exceeds approximately 30 thrips per flower. Nevertheless, growers typically prevent thrips densities from reaching such high levels (> 30) due to the potential for excessive damage to the strawberry flowers and fruits (for strawberries, the Economic Injury Level (EIL) is ~ 5 adults WFT per flower and this will be discussed in detail in Section 4). To incorporate the published data into our model, we assumed that the area of the leaf disc used in the original experiment equaled the area of a strawberry flower. Additionally, it should be noted that *Orius* individuals were isolated and starved for 24 h at the beginning of the experiment, which might have influenced the daily predation rate.

⁴ See Table 4 for the definition of these parameters.

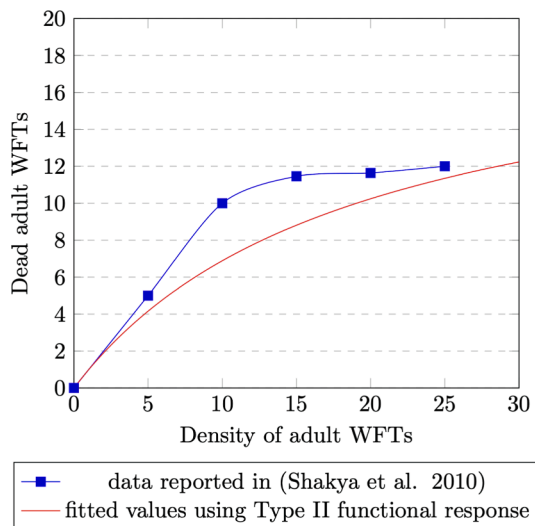


Fig. B.1. Type II functional response curve for density dependent daily predation rate of adult *Orius* on adult WFT.

Finding h_{fa}^{oa} and a_{fa}^{oa} . To the best of our knowledge, no previous studies have reported the data required to directly derive h_{fa}^{oa} and a_{fa}^{oa} . Thus, we adopt the following approach to estimate them using the data on *O. sauteri* and *Dendrothrips minowai* Priesner (tea thrip) (Thysanoptera: Thripidae) reported in (Zhang et al., 2021). That study reports the functional response curves for 4th nymph and adult *O. sauteri* preying on adult *Dendrothrips minowai* Priesner (tea thrip) (Thysanoptera: Thripidae) at a temperature of $25 \pm 1^\circ\text{C}$. Assuming that the fitness (foraging capacity) ratio between the nymph and adult stages of different *Orius* species is similar, we first calculate the ratios for the handling time and the clearance rate between adult and nymph *O. sauteri*. We then used these ratios to estimate the values for h_{fa}^{oa} and a_{fa}^{oa} based on the a_{fa}^{oa} and h_{fa}^{oa} values calculated above.

Table B.1

Space clearance rate and handling time of *O.sauteri* 4th nymph and adult preying on *Dendrothrips minowai* Priesner adults based on the reported values in the study (Zhang et al., 2021).

	4 th nymph	Adult	ratio ($\frac{\text{nymph}}{\text{adult}}$)
Space clearance rate	0.7373	0.8573	0.8600
Handling time	0.05882	0.03270	1.7988

Finding a_{fa}^{oa} and h_{fa}^{oa} . Experimental results in Xia et al. (2003) have shown that for predators within a single stage, there is little variation in the space clearance rate between different prey size groups. In particular, this difference is insignificant within the temperature range $20 - 35^\circ\text{C}$. Thus, we assume that $a_{fa}^{oa} = a_{fa}^{oa}$ and $a_{fa}^{oa} = a_{fa}^{oa}$.

Finding h_{fa}^{oa} . Adult *Orius* consume approximately 22.5 WFT larva per day at a population density of 25 larvae per strawberry flower at $25 \pm 1^\circ\text{C}$ (Shakya et al., 2010). Using this data for Eq. 3, the value for h_{fa}^{oa} is estimated. Estimating the value of h_{fa}^{oa} accurately by simply adjusting the functional response curve (Eq. 3) to pass through the coordinate $x = 25$ and $y = 22.5$ is challenging due to the nonlinearity of the function, even when the value for a_{fa}^{oa} is known. To overcome this challenge, we assume a linear relationship between the predation rate and prey density, represented by a straight line passing through the origin with a gradient m ($y = mx$), where $m = 0.9$. Although the actual gradient should be higher than m for lower values of x and lower than m for higher values of x , this linear relationship can be used to generate approximate coordinates for the system within the range of $x = 0$ and $x = 25$. Using these approximated coordinates and the value for a_{fa}^{oa} calculated above, we fit a type II functional response curve to estimate a more logical value for h_{fa}^{oa} (Fig. B.2).

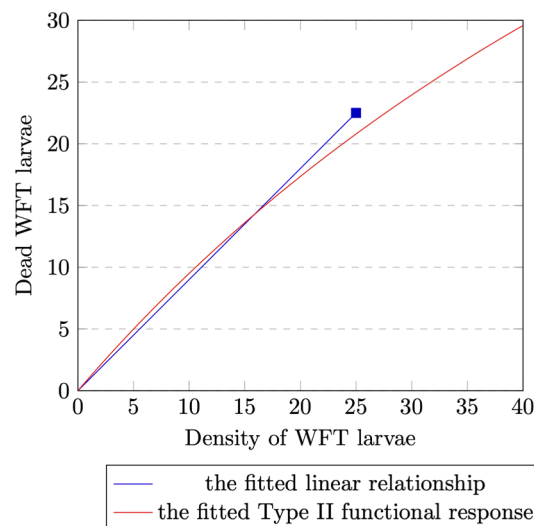


Fig. B.2. Type II functional response curve for density dependent daily predation rate of adult *Orius* on WFT larvae.

Finding $h_{fi}^{o^a}$. To estimate $h_{fi}^{o^a}$, we adopt the same approach that we used to estimate $h_{fa}^{o^a}$ based on the data reported by Zhang et al. (2021).

Finding the interference coefficient w . To estimate w in Eq. 5, we used data reported in (Zhang et al., 2021) that corresponds to the intra-specific interference response of predators for *O. sauteri* on *Dendrothrips minowai* Priesne. We assume that the reduction in the consumption of WFT by *Orius* due to interference competition follows the same pattern. Thus, we estimate w by fitting the modified predation rate for the different densities of *Orius* on WFT to Eq. 5. (see Table B.1).

Their experiment involved investigating changes in the daily predation rates of adult and 4th instar nymph *O. sauteri* by varying their densities (1, 2, 3, or 4 insects), while keeping the prey population constant at 30 *Dendrothrips minowai* (Table B.2). Based on the reported values, we calculated the percentage reduction in predation rates for different predator densities. Using Eq. 3, we computed the daily predation rates of nymph and adult *Orius* for different densities of adult WFT (5, 10, 15, 20, 25, and 30) in the absence of intra-specific competition between *Orius*. Subsequently, the calculated percentage reduction in predation rates was applied to adjust these values for adult and nymph *Orius* densities of 1, 2, 3, and 4. This generated a dataset representing the predation rate of *Orius* on WFT with varying densities of predators and prey. To estimate the value of w for nymph and adult *Orius*, this dataset was fitted to Eq. 5. Finally, the w values obtained for nymph and adult were averaged, resulting in a final value of 1.095.

Table B.2

Intra-specific interference response of *O.sauteri* reported in the study (Zhang et al., 2021).

stage	no of <i>O.sauteri</i>	Daily predation rate	calculated % reduction of predation rate
4th nymph	1	15.3	0
	2	11.2	26.79%
	3	8	47.71%
	4	6.25	58.16%
adult	1	18.7	0
	2	12.5	33.16%
	3	8.6	54.01%
	4	6.9	63.10%

Appendix C. Parameter estimation: The relationship between predator oviposition rate and the number of prey consumed

Finding c . *Orius* spp. can supplement its diet with pollen and plant tissues (Zuma et al., 2022; Lorenzo et al., 2019). Other strawberry plant pest species, such as aphids and mites, can also act as alternative prey for *Orius* when WFT density is low (Venzone et al., 2002; Zuma et al., 2022). Hence, with zero WFT density, *Orius* can survive and reproduce in strawberry crops. But these supplementary foods provide limited nutrition to support *Orius* reproduction, as evidenced by a reduction in their daily oviposition rate (Bonte and De Clercq, 2010; Bernardo et al., 2017; Lorenzo et al., 2019; Zuma et al., 2022). Here, we define c as the constant oviposition rate of *Orius* when WFT density is zero. The efficacy of *Orius* for biological control of *M. euphorbiae* (aphid), mediated by the presence of companion plants and externally supplied alternative prey in strawberry plants, has been evaluated by Zuma et al. (2022). We adopt these experimental results for our *Orius* population in conditions where only *M. euphorbiae* is present in the strawberry, to calculate c for our model. Zuma et al. (2022) conducted weekly counts of *Orius* per strawberry plant for 8 weeks in a controlled greenhouse (with a temperature of 25 °C). We fitted their reported weekly counts of *Orius* per strawberry plant using our population model, adjusting the oviposition rate of *Orius* from 0 to 1 in increments of 0.1, and selected the best-fit value as c , which is equal to 0.5 (Fig. C.1). We kept the biological parameters of *Orius* the same as stated in Table 2 and only changed the daily oviposition rate. In this scenario, we only need to consider the *Orius* component of the model.

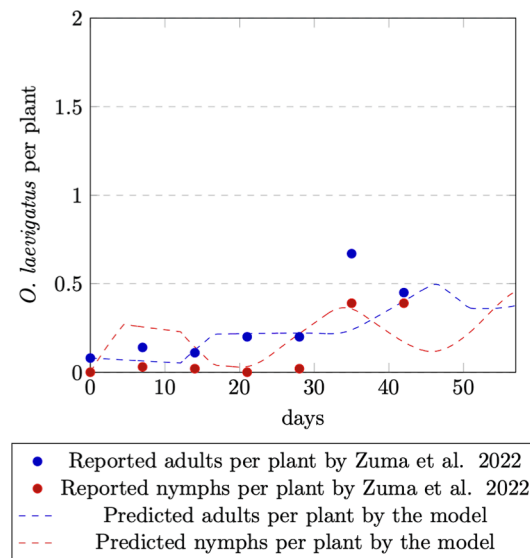


Fig. C.1. The population dynamics of *Orius* when WFT density is zero ($c = 0.5$).

Finding c. The daily oviposition rate of *Orius* is ~ 5.73 when the predation rate is 12 adult WFT per day (Shakya et al., 2010; Kordestani et al., 2021). By using this value in Eq. 6, we calculate the value for m as 0.436.

Appendix D. Potential impacts of temperature on population dynamics of predator–prey system

In this study, we selected a consistent temperature of 25 °C as the base for modeling the predator–prey system. However, an insect’s biological parameters are inherently influenced by temperature, significantly impacting the dynamics of predator–prey interactions (Deligeorgidis et al., 2006; Sanchez and Lacasa, 2002). Therefore, incorporating temperature effects into the model is important for predictive application of the model outside this baseline. Here, we conduct an initial assessment of how the dynamics of a predator–prey system involving *Orius* and WFT in strawberry fields vary across different temperature settings.

Due to the lack of specific data in the literature for our modeled scenario, we relied on reported values from studies that examined the biological parameters *Orius* and WFT under various experimental conditions. Deligeorgidis et al. (2006) investigated the biological parameters of WFT in cucumber across four different temperature values ranging from 15 °C to 30 °C. Similarly, Sanchez and Lacasa (2002) determined the biological parameters of *Orius* across four different temperature values ranging from 20 °C to 35 °C. In their study, *Orius* were fed *Ephestia kuehniella* eggs and honeybee pollen and were provided with *Pelargonium* leaves as the oviposition substance. Reported values in these studies indicate that the development time of immature stages, adult longevity, female pre-oviposition period, and oviposition periods are longer at 20 °C compared to 25 °C, while these values are shorter at 30 °C than at 25 °C. Conversely, the number of eggs laid by a female adult is highest at 20 °C and decreases with rising temperatures.

Considering data availability, we chose two temperature values around 25 °C, specifically 20 °C and 30 °C for this analysis. We initially calculated the proportional increase or decrease of each parameter of each species at 20 °C and 30 °C relative to 25 °C using published data from Deligeorgidis et al. (2006) and Sanchez and Lacasa (2002). Under the assumption that the variation in an insect species’ biological parameters across different temperature values follows a consistent pattern irrespective of the host plant or food source (i.e., the ratio of biological parameters at different temperature values for a species remains consistent), we derived the biological parameter values for WFT and *Orius* based on our available data for 25 °C, documented in Table 1 and Table 2. The calculated biological parameter values for WFT and *Orius* at 20 °C and 30 °C are presented in Table D.1 and Table D.2, respectively. Due to the lack of available data, we made the assumption that sex ratio and the survival rates of the immature stages of WFT and *Orius* are similar to their values at 25 °C, and that the parameter values of functional response mirror those at 25 °C. The resulting predator–prey population dynamics at 20 °C and 30 °C are illustrated in Fig. D.1.

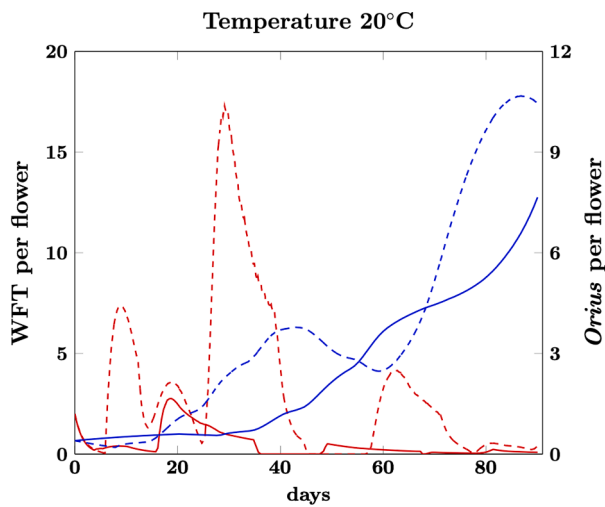
The simulation results demonstrate clear differences in the predator–prey population dynamics of WFT and *Orius* at different temperature values (Fig. D.1). The simulations indicate that an initial ratio of 1:0.2 of WFT to *Orius* at all three temperatures can effectively prevent WFT populations from reaching the Economic Injury Level (EIL), which is estimated to be around 5 adult WFT per flower (Sampson et al., 2014). Notably, the simulation revealed a peak in WFT larvae, reaching approximately 17 per flower at a temperature of 20 °C within 30–40 days, highlighting the need for close monitoring. To address the variability in field temperature conditions and to achieve more precise predictions regarding the population dynamics of WFT and *Orius* in strawberries, each parameter within the model needs to be expressed as a function of temperature. This necessitates future laboratory and field experiments.

Table D.1
Biological parameters of WFT derived for 25 °C and 30 °C.

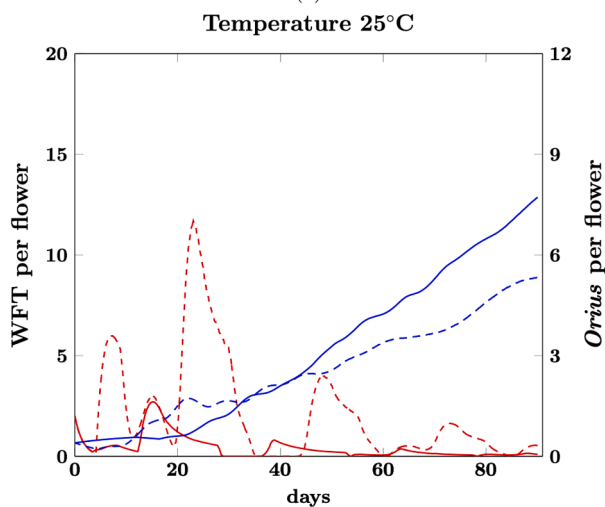
Parameter	Symbol	25 °C	20 °C	30 °C
<i>Development time (days)</i>				
Egg stage	d_{fe}	4.1	5.88	4.06
Larva stage	d_{fl}	4.9	6.47	4.12
Pupa stage	d_{fp}	3.5	3.75	1.86
<i>Survival rate (%)</i>				
Egg stage	sr_{fe}	65.5	-	-
Larva stage	sr_{fl}	83.3	-	-
Pupa stage	sr_{fp}	82.3	-	-
Female adult longevity (days)	d_{fa}	14.8	18.65	11.1
Sex ratio (female: male)	x_f	0.78:0.22	-	-
<i>Reproduction parameters</i>				
Pre-oviposition period (days)	po_f	2.5	2.8	2.42
Oviposition period (days)	op_f	11	13.53	8.36
Daily oviposition rate (eggs/female)	or_f	7.4	8.20	6.88

Table D.2
Biological parameters of *Orius* derived for 20 °C and 30 °C.

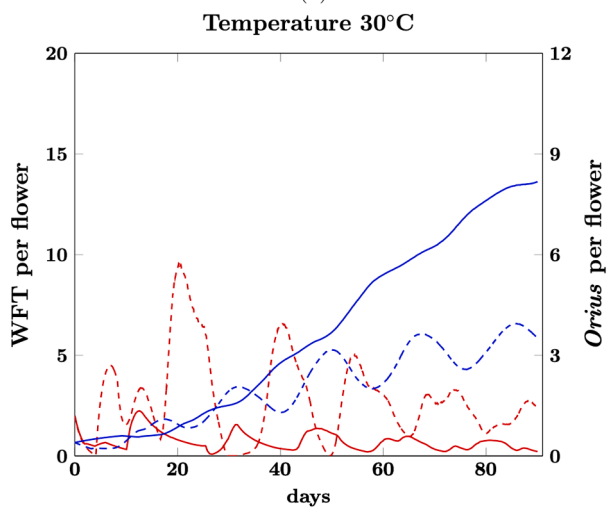
Parameter	Symbol	25 °C	20 °C	30 °C
<i>Development time (days)</i>				
Egg stage	d_{oe}	4.55	7.83	3.19
Nymph stage	d_{on}	12.07	20.28	9.17
<i>Survival rate (%)</i>				
Egg stage	sr_{oe}	88	-	-
Nymph stage	sr_{on}	58	-	-
Female adult longevity (days)	d_{oa}	34.00	72.76	22.1
Sex ratio (female: male)	x_o	1:1	-	-
<i>Reproduction parameters</i>				
Pre-oviposition period (days)	po_o	3.11	5.44	1.71
Oviposition period (days)	op_o	11.88	23.28	8.09
Daily oviposition rate (eggs/female)	or_o	5.73	3.30	5.23



(a)



(b)



(c)

Fig. D.1. Population variation of WFT and *Orius* over 90 days at three different temperature values - (a) 20 °C; (b) 25 °C; and (c) 30 °C. Each line denotes population variation of adult WFT (—), WFT larvae (- - -), adult *Orius* (—) and nymph *Orius* (- - -). The initial population densities per flower were: 2 adult WFT; 2 larva WFT; 0.4 adult *Orius*; and 0.4 larva *Orius*. The total number of flowers was 100.

Appendix E. Summary of biological parameters of WFT and *Orius* under various environmental conditions

A summary of biological parameters of Western Flower thrip (WFT) and *Orius laevigatus*, along with their predator–prey relationship under various experimental setups can be found at <https://doi.org/10.26180/24635697>. The data was extracted from studies published in the literature, only to provide insights into how these parameters vary based on different factors (e.g., temperature, host plant, and prey type or alternative food sources).

Appendix F. Temperature data from the field

The average daily temperature during the reported data period in Section 3.2 can be found in Fig. F.1. The maximum and minimum daily temperature records were obtained from the nearest weather station to the strawberry farm, on the Bureau of Meteorology, Australian Government website⁵.

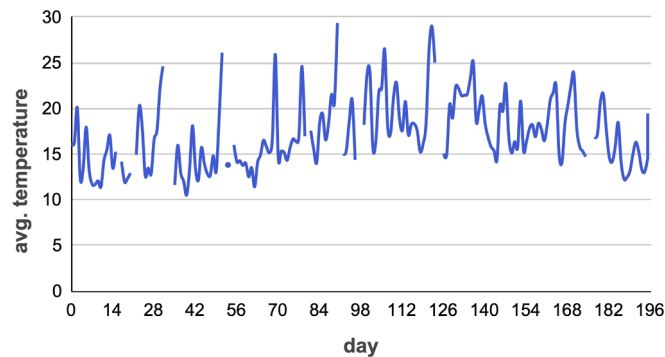


Fig. F.1. The average daily temperature during the reported data period in Section 3.2.

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⁵ <http://www.bom.gov.au/climate/data/>

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