

Intra-seasonal Strategies Based on Energy Budgets in a Dynamic Predator-Prey Game

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Abstract

We propose a game-theoretical model to describe intra-seasonal predator-prey interactions between predatory mites (*Acari: Phytoseiidae*) and prey mites (also called fruit-tree red spider mites) (*Acari: Tetranychidae*) that feed on leaves of apple trees. Its parameters have been instantiated based on laboratory and field studies.

The continuous-time dynamical model comprises predator and prey densities, along with corresponding energy levels, over the length of a season. It also includes time-dependent decision variables for the predator and the prey, representing the current portions of the predator and prey populations that are active, as opposed to diapausing (a state of physiological rest).

Our aim is to find the optimal active/diapausing ratio during a season of interaction between predatory mites and prey mites: this is achieved by solving a dynamic game between predator and prey. We hereby extend our previous work that focused solely on the optimal strategy for the prey. Firstly, we analyze optimal behavior of the prey. Secondly, we show that the optimal strategy for the predator is to stay active the entire season. This result corresponds to biological observations.

Keywords: Mathematical models, predator-prey interactions, dynamic noncooperative game theory, diapause, mites, fruit orchard

1 Introduction and motivations

The work presented in this article is inspired by studies on the use of predatory mites (*Acari: Phytoseiidae*) for biological pest control of fruit-tree red spider mites (*Acari: Tetranychidae*) that feed on and thereby damage leaves of apple trees [5, 6].

This system involves continuous interactions and overlapping generations in summer seasons, as well as discrete periods without interactions, and is therefore an example of a hybrid system, in the biological literature referred to as a semi-discrete system [10, 14]. Winters (covering 6-7 months) are usually harsh and as such endanger the survival of fruit-tree red spider (prey) mites [5] and (even more so) that of predatory mites [4, 5].

Predatory mites and prey mites densities in the following summer season depend on the number of individuals in the previous year that have a chance to survive the winter. For the prey, this number equals to the number of prey individuals that are in a

state of physiological rest (the so-called diapause state) at the end of the season, as prey that is active at the end of the summer season does not have a chance to survive. The decision to enter diapause promotes the survival of the prey individual during winter and it emerges from induction by a combination of sufficiently long night lengths and low temperatures [20]. Focusing on a single season, in [17] we have shown that if the predator stays active the entire season the optimal strategy of the prey can be described as follows (see Figure 1):

1. In the beginning of the summer season the prey can be in any state (all active, all in diapause, or anything inbetween), whereas at the end of the summer season all prey individuals are in diapause.
2. If all prey individuals are active in early summer, the prey will start entering diapause at a certain point in time and the proportion of diapausing individuals increases monotonically. Similarly, if only part of the prey population is active in early summer, then all prey end up being in diapause at one point in time and stay in diapause until the next year. Yet, if all prey individuals are in diapause in early summer, then they continue to stay in diapause until the next year.
3. The time (expressed in real time) of diapause onset depends on the energy of the prey, on predator population size, and on the rate of energy utilization, but it is independent of prey population size (i.e. timing of diapause does not require quorum sensing).
4. If predators are absent in the environment, all prey individuals are in diapause later than if the predators are present (see Figure 2). Empirical observations on diapause of fruit-tree red spider mites on apple trees in the field (Sabelis and Overmeer, unpublished data) reveal that virtually all individuals become active in early summer and starting from a certain point in time the population enters diapause, gradually. Moreover, experimental manipulation of the predator population in the field showed that the fruit-tree red spider mites enter diapause earlier in the presence of predatory mites and once in diapause they stay in diapause. However, apart from an effect of predator presence also the density of fruit-tree red spider mites had an effect on the time at which diapause was initiated, suggesting that some form of quorum sensing (possibly via spider-mite induced plant volatiles) takes place.

Using another similar spider mite species (more amenable to experimental treatment), it was experimentally shown that the decision to enter diapause also depends on predator density during summer [7–9]. From the point of view of the prey mite this behavior makes intuitive sense as it faces a grim future with increasing predator densities and thus an increased risk of death: it may then do better by giving up reproduction, moving away from leaves to twigs and branches (a refuge from predation, but without food) and by entering diapause earlier than indicated by the predictors of season length (night length and temperature). However, if many prey mites would make the same decision, this could create a negative feedback on the predatory mite population, which could lead them to enter diapause. Consequently, at some point in time the prey mites

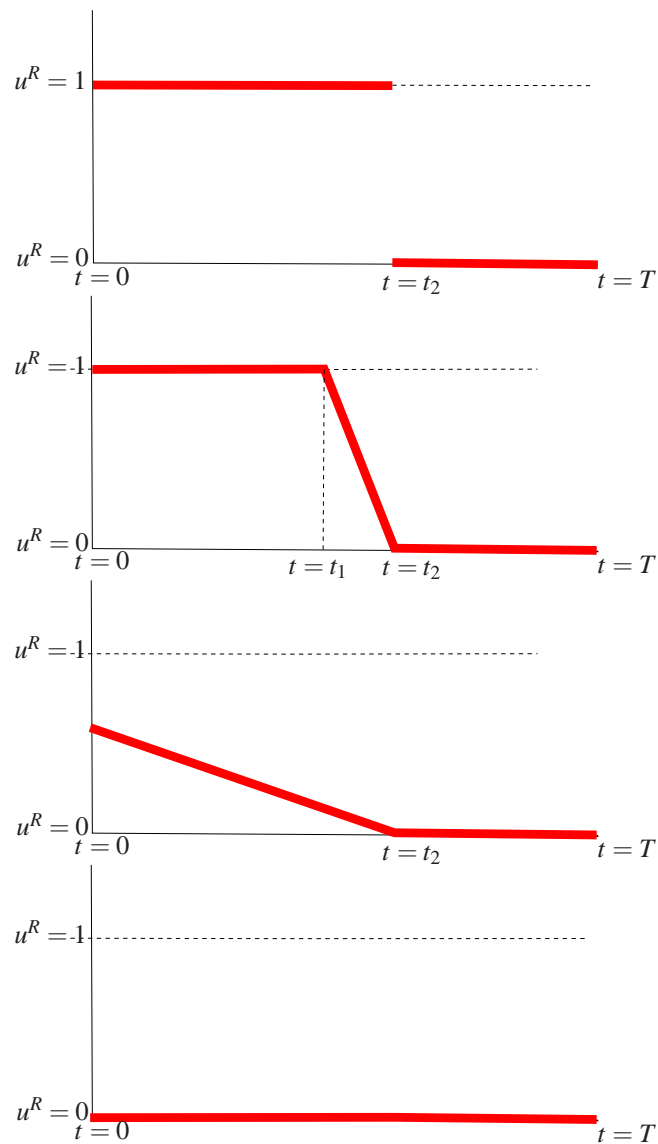


Figure 1: Scheme of possible optimal strategies u^R for the prey. Based on the proposed dynamics and optimization problem, we have shown irreversibility and (largely) monotonicity of the strategy profile. Notice that the optimal strategies do not need to be continuous corresponding to the singular events in the outcome of the optimization problem.

would profit from the decreased predation risk by terminating their diapause and returning to the leaves, which in turn could trigger the predatory mites to become active

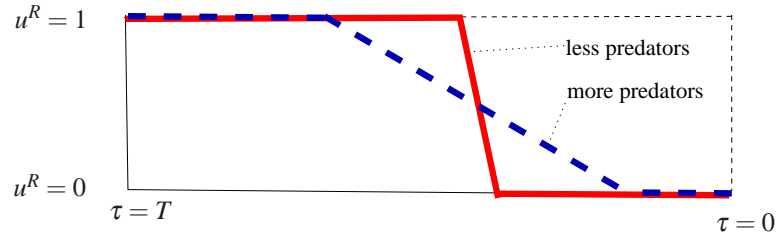


Figure 2: If the number of predators increases, the prey individuals begin to enter diapause earlier but more gradually.

again. Another complicating factor is that an early prey diapause raises the demands on the energy level of the individual mite, which needs to cover a longer period before terminating diapause at the beginning of the next summer season – the energy level at diapause termination will determine the reproductive capacity of the prey mite [9]. Thus, the decision to enter diapause within a year will depend on the current internal energy level of the mite, as this will have far-reaching consequences for winter survival and reproduction in the summer season of the next year.

There is less information on the diapause behavior of the predatory mites. However, the predatory mites are much more flexible in entering diapause/active state and can switch multiple times during the season. Physiological decision variables depend on the predator and prey densities reached during summer, rather than only on reliable season indicators, such as night/day length and temperature [3, 19].

This leads us to conclude that the predator’s and prey’s decision to enter diapause is part of a game between the two species. While we think that this game is a Stackelberg game with the population of predatory mites acting as a leader and population of the prey mites acting as a follower [1, 18], we will elaborate on this claim when analyzing the optimal behavior of both parties involved.

Notation: In the rest of this document, unless stated otherwise, the following notation will be used:

T - length of the summer season

$R(t)$ - fruit-tree red spider (prey) mite population at time $t \in [0, T]$, within the summer season

$P(t)$ - predatory mite population at time $t \in [0, T]$, within the summer season

$E^R(t)$ - internal energy of the prey at time $t \in [0, T]$, within the summer season

$E^P(t)$ - internal energy of the predator at time $t \in [0, T]$, within the summer season

$u^R(t)$ - decision variable (control) of the fruit-tree red spider mites (prey), within the summer season

$u^P(t)$ - decision variable (control) of the predatory mites (predator), within the summer season

$\alpha_R(\tau), \alpha_{ER}(\tau), \alpha_{EP}(\tau), \alpha_P(\tau), \beta_R(\tau), \beta_{ER}(\tau), \beta_{EP}(\tau), \beta_P(\tau)$ - additional variables for the characteristic system in reverse time

$\mathcal{A}_P, \mathcal{A}_R$ - singular surfaces (as used in the analysis of the game)

J^P - fitness function for the fruit-tree red spider mites, within the summer season

J^R - fitness function for the predatory mites, within the summer season

The article is structured as follows. Section 2 introduces the dynamic game between the predatory mites and the prey mites. Section 3 formally studies the optimal strategies of the predator and prey in this game. Section 4 elaborates on the biological interpretation of the results and proposes a new model to describe interactions in different predator-prey systems. Section 5 concludes the article, discusses possible extensions, and sketches future work.

2 Game-theoretical model of the interaction between predatory mites and fruit-tree red spider mites

Each year is divided into two parts: the *summer* and the *winter* season. The predatory mites and the fruit-tree red spider mites can consume food (prey and apple leaves, respectively) only during the summer season (which is essential for their reproduction). Furthermore, both predator and prey can enter diapause, a quiescent state that protects from the environment, from predation, or possibly lack of food. Hence, this implies a decoupling of predator and prey depending on the population fraction in diapause. During the winter season the species do not interact, and their populations independently decline at a constant rate, therefore we focus on the summer interaction only. The dynamics during winter are trivial and can be simply modeled by a reset (i.e., a decrease) of the energy and population levels.

The model that we propose describes the interactions between predatory mites (predator) and fruit-tree red spider mites (prey) within a single summer season¹ and allows characterizing the seasonal strategy of both predator and prey as a solution of a dynamic game between them.

In the remainder of the text the terms “summer season” and “winter season” are used interchangeably with the terms “summer” and “winter”, respectively.

2.1 Model formulation

The summer interactions between the predatory mites and the prey mites can be formulated as a game played with a finite horizon $[0, T]$ in which the predatory mites select a $u^{P,*}(t) \in [0, 1]$ for $t \in [0, T]$, where

$$u^{P,*} = \arg \sup_{u^P(\cdot)} \int_0^T (-\alpha P(t) + \beta \delta u^P(t) E^P(t) P(t)) dt, \quad (2.1)$$

¹Extension of our work into multiple seasons is a subject of our future research.

whereas the prey mites choose a $u^{R,*}(t) \in [0, 1]$ for $t \in [0, T]$, where

$$u^{R,*} = \arg \sup_{u^R(\cdot)} \int_0^T (1 - u^R(t)) E^R(t) R(t) dt, \quad (2.2)$$

subject to the following system dynamics:

$$\frac{dE^P}{dt} = -ac(1 - u^P)E^P + eu^P u^R R - au^P E^P, \quad (2.3)$$

$$\frac{dE^R}{dt} = -dh(1 - u^R)E^R + f(t)g(R)u^R - du^R E^R, \quad (2.4)$$

$$\frac{dP_n}{dt} = -\alpha P + \beta \delta u^P E^P P, \quad (2.5)$$

$$\frac{dR_n}{dt} = -\varepsilon R + \delta u^R E^R R - \gamma u^P u^R P R. \quad (2.6)$$

In (2.3) $a > 0$ is the energy decrease rate for the predator when active, ac (with $c \in [0, 1)$) is the energy decrease rate for the predator when in diapause, e is the energy increase rate for the predator when feeding (here the energy increase is proportional to the number of active fruit-tree red spider mites that are preyed upon and to the number of active predatory mites).

In (2.4), $d > \frac{1}{250}$ is the energy decrease rate for the prey when active, dh (with $h \in [0, 1)$) is the energy decrease rate for the prey when in diapause, $f(t)$ is a time-dependent function characterizing the presence of nutrients for the fruit-tree red spider mites in the environment ($0 < f(\cdot) \ll 1$), $g(R_n) \in [0, 1]$ is a non-increasing function of its variable, which represents competition among individuals fruit-tree red spider mites – hence $f(t)g(R_n)u^R$ is a term representing the increase of energy on the prey due to its active state.

The number of predatory mites slowly decreases with rate $\alpha > 0$ and increases proportionally to their energy and number of active individuals with rate $\beta \delta$, where $\beta > 0$, $\delta > 0$.

The number of fruit-tree red spider mites decreases with death rate $\varepsilon > 0$, increases proportionally to their energy and number of active individuals with rate $\delta > 0$, and decreases proportionally to the number of active predatory mites and number of active fruit-tree red spider mites with rate $\gamma > 0$.

E^P and E^R refer to the energy levels of the predator and prey, respectively. Since the energy of an organism is not a quantity that can be directly measured, we normalize these variables as $E^P, E^R \in [0, 1]$, so that they become ratios.

Based on [15] we set parameter h to $h = \frac{1}{250d}$. We assume that the increase of the energy of the prey from feeding (composition of the effects of the environment and competition among the prey ($f(t)g(R)$)) equals to the decrease rate of energy of the prey when active (d), i.e., $d = f(t)g(R)$. Based on field data and [15, 16], we set $\delta = \frac{1}{5}$, $\alpha = \frac{1}{20}$. Additionally, observing that predator and prey are of the same size and their death rates are approximately equal [15, 16], the dynamics in (2.3)–(2.6) can be

rewritten as follows (with β replaced by b in notation):

$$\frac{dE^P}{dt} = -\frac{1}{250}(1-u^P)E^P + du^P u^R R - du^P E^P, \quad (2.7)$$

$$\frac{dE^R}{dt} = -\frac{1}{250}(1-u^R)E^R + du^R - du^R E^R, \quad (2.8)$$

$$\frac{dP}{dt} = -\frac{1}{20}P + \frac{1}{5}bu^P E^P P, \quad (2.9)$$

$$\frac{dR}{dt} = -\frac{1}{20}R + \frac{1}{5}u^R E^R R - \frac{1}{5}u^P u^R P R, \quad (2.10)$$

where $E^R(t) \in [0, 1]$, $E^P(t) \in [0, 1]$, $P(t) > 0$, $R(t) > 0$ for each $t \in [0, T]$ with T known.

Within a summer, the goal of both predator and prey (the *players*) is to maximize their chances of survival [2, 21], which translates to the optimization problems defined by (2.1) and (2.2), subject to the dynamical constraints (2.7)–(2.10).

3 Solution of the game

Firstly, we formulate the problem of the predator and the problem of the prey via Hamilton-Jacobi-Bellman equations. Subsequently, we study the optimal strategies for both the predator and for the prey, and we discuss their biological relevance.

3.1 Hamilton-Jacobi-Bellman formulation for the predator

Let us introduce a reverse time $\tau = T - t$ and value functions for both the predator and the prey. The value function for the predator in reverse time reads as

$$V^P = \int_{T-t}^T \left(\frac{1}{5}bu^P E^P P - \frac{1}{20}P \right) d\tau, \quad (3.1)$$

and the related Hamilton-Jacobi-Bellman (HJB) equation can be written as follows:

$$\begin{aligned} \mathcal{H}^P = & \frac{\partial V^P}{\partial t} + \max_{u^P} \left(\alpha_{E^P} \left(-\frac{1}{250}(1-u^P)E^P + du^P u^R R - du^P E^P \right) \right. \\ & + \alpha_{E^R} \left(-\frac{1}{250}(1-u^R)E^R + du^R - du^R E^R \right) \\ & + \alpha_P \left(-\frac{1}{20}P + \frac{1}{5}bu^P E^P P \right) \\ & \left. + \alpha_R \left(-\frac{1}{20}R + \frac{1}{5}u^R E^R R - \frac{1}{5}u^P u^R P R \right) + \frac{1}{5}bu^P E^P P - \frac{1}{20}P \right), \quad (3.2) \end{aligned}$$

with $\alpha_{E^P} = \frac{\partial V^P}{\partial E^P}$, $\alpha_P = \frac{\partial V^P}{\partial P}$, $\alpha_{E^R} = \frac{\partial V^P}{\partial E^R}$, and $\alpha_R = \frac{\partial V^P}{\partial R}$.

The corresponding system of characteristics in reverse time τ is then (with x' de-

noting $\frac{dx}{d\tau} = -\frac{dx}{dt}$ for a general state variable x)

$$(E^P)' = \frac{1}{250}(1-u^P)E^P - d u^P u^R R + d u^P E^P, \quad (3.3)$$

$$(E^R)' = \frac{1}{250}(1-u^R)E^R - d u^R - d u^R E^R, \quad (3.4)$$

$$P' = \frac{1}{20}P - \frac{1}{5}b u^P E^P P, \quad (3.5)$$

$$R' = \frac{1}{20}R - \frac{1}{5}u^R E^R R + \frac{1}{5}u^P u^R P R, \quad (3.6)$$

$$\alpha'_{EP} = -\alpha_{EP} \left(\frac{1}{250}(1-u^P) + d u^P \right) + \frac{1}{5}b u^P \alpha_{PP} + \frac{1}{5}b u^P P, \quad (3.7)$$

$$\alpha'_{ER} = -\alpha_{ER} \left(\frac{1}{250}(1-u^R) + d u^R \right) + \frac{1}{5}\alpha_R u^R R, \quad (3.8)$$

$$\alpha'_P = \alpha_P \left(-\frac{1}{20} + \frac{1}{5}b u^P E^P \right) - \frac{1}{5}\alpha_R u^P u^R R + \frac{1}{5}b u^P E^P - \frac{1}{20}, \quad (3.9)$$

$$\alpha'_R = d \alpha_{EP} u^P u^R + \alpha_R \left(-\frac{1}{20} + \frac{1}{5}u^R E^R - \frac{1}{5}u^P u^R P \right), \quad (3.10)$$

with transversality conditions $\alpha_{EP}(0) = \alpha_{ER}(0) = \alpha_P(0) = \alpha_R(0) = 0$ and with $E^P(0) \in (0, 1)$, $E^R(0) \in (0, 1)$, $P(0) > 0$, $R(0) > 0$. The singular surface corresponding to the HJB equation (3.2) is

$$\mathcal{A}_P = \alpha_{EP} \left(\frac{1}{250}E^P + d u^R R - d E^P \right) + \frac{1}{5}b \alpha_P E^P P - \frac{1}{5}u^R \alpha_R P R + \frac{1}{5}b E^P P. \quad (3.11)$$

Then the optimal strategy for the predator is obtained as $u^P = \text{Heav } \mathcal{A}_P$, i.e.,

$$u^P = \begin{cases} 1, & \text{if } \mathcal{A}_P > 0, \\ 0, & \text{if } \mathcal{A}_P < 0. \end{cases}$$

Moreover, $u^P \in (0, 1)$ if $\mathcal{A}_P = 0$ [11–13].

From the transversality conditions we can derive that $u^P(\tau = 0) = \text{Heav } \mathcal{A}_P(\tau = 0) = \text{Heav } \left(\frac{1}{5}b E^P(0) P(0) \right) = 1$. Note that \mathcal{A}_P is independent of E^R and of α_{ER} . Further, note that regardless of the strategy of the prey the predator is active at the end of the season.

3.2 Hamilton-Jacobi-Bellman formulation for the prey

Similarly as in Section 3.1, we can introduce the reverse time $\tau = T - t$ so that the value function for the prey becomes:

$$V^R = \int_{T-t}^T (1-u^R) E^R R d\tau, \quad (3.12)$$

and the corresponding Hamilton-Jacobi-Bellman equation is:

$$\begin{aligned} \mathcal{H}^R = & \frac{\partial V^R}{\partial t} + \max_{u^R} \left(\beta_{E^P} \left(-\frac{1}{250}(1-u^P)E^P + d u^P u^R R - d u^P E^P \right) \right. \\ & + \beta_{E^R} \left(-\frac{1}{250}(1-u^R)E^R + d u^R - d u^R E^R \right) \\ & + \beta_P \left(-\frac{1}{20}P + \frac{1}{5}b u^P E^P P \right) \\ & \left. + \beta_R \left(-\frac{1}{20}R + \frac{1}{5}u^R E^R R - \frac{1}{5}u^P u^R P R \right) + (1-u^R) E^R R \right), \end{aligned} \quad (3.13)$$

with $\beta_{E^P} = \frac{\partial V^R}{\partial E^P}$, $\beta_P = \frac{\partial V^R}{\partial P}$, $\beta_{E^R} = \frac{\partial V^R}{\partial E^R}$, and $\beta_R = \frac{\partial V^R}{\partial R}$.

The corresponding system of characteristics is then (again introducing derivative in reverse time for any state variable x as $x' = \frac{dx}{d\tau} = -\frac{dx}{dt}$)

$$(E^P)' = \frac{1}{250}(1-u^P)E^P - d u^P u^R R + d u^P E^P, \quad (3.14)$$

$$(E^R)' = \frac{1}{250}(1-u^R)E^R - d u^R + d u^R E^R, \quad (3.15)$$

$$P' = \frac{1}{20}P - \frac{1}{5}b u^P E^P P, \quad (3.16)$$

$$R' = \frac{1}{20}R - \frac{1}{5}u^R E^R R + \frac{1}{5}u^P u^R P R, \quad (3.17)$$

$$\beta'_{E^P} = -\beta_{E^P} \left(\frac{1}{250}(1-u^P) + d u^P \right) + \frac{1}{5}b u^P \beta_P P, \quad (3.18)$$

$$\beta'_{E^R} = \beta_{E^R} \left(-\frac{1}{250}(1-u^R) - d u^R \right) + \frac{1}{5}\beta_R u^R R + (1-u^R) R, \quad (3.19)$$

$$\beta'_P = \beta_P \left(-\frac{1}{20} + \frac{1}{5}\beta u^P E^P \right) - \frac{1}{5}u^P u^R \beta_R R, \quad (3.20)$$

$$\beta'_R = \beta_R \left(-\frac{1}{20} + \frac{1}{5}u^R E^R - \frac{1}{5}u^P u^R P \right) + d u^P u^R \beta_{E^P} + (1-u^R) E^R, \quad (3.21)$$

with transversality conditions $\beta_{E^P}(0) = 0$, $\beta_{E^R}(0) = 0$, $\beta_P(0) = 0$, $\beta_R(0) = 0$, and assuming $E^R, E^P \in [0, 1]$, $E^P(0) > 0$, $E^R(0) > 0$, $P(0) > 0$, $R(0) > 0$.

The singular surface corresponding to the HJB equation (3.13) is

$$\mathcal{A}_R = d u^P R + \beta_{E^R} \left(\frac{1}{250}E^R + d - d E^R \right) + \beta_R \left(\frac{1}{5}E^R R - \frac{1}{5}u^P P R \right) - E^R R. \quad (3.22)$$

Similarly as before, the optimal $u^R = \text{Heav } \mathcal{A}_R$, i.e.,

$$u^R = \begin{cases} 0, & \text{if } \mathcal{A}_R < 0, \\ 1, & \text{if } \mathcal{A}_R > 0, \end{cases}$$

and $u^R \in (0, 1)$ if $\mathcal{A}_R = 0$. The value of u^R for $\tau = 0$ is equal to 0 as $\mathcal{A}_R(0) = -E^R(0)R(0) < 0$, i.e., regardless of the strategy of the predator the prey is in diapause at the end of the season. Moreover, note that (3.22) is independent of E^P and of β_{E^P} .

3.3 Optimal strategy for the prey

In the following analysis, we confine ourselves to a specific structure for the strategy of the prey, which turned out to be optimal if the predatory mites are active the entire season [17]. More precisely, we assume that the optimal action of the prey is as shown in Figure 3:

$$u = \begin{cases} 1 & \text{if } t \in [0, t_1), \\ \frac{t-t_2}{t_1-t_2} & \text{if } t \in [t_1, t_2), \\ 0 & \text{if } t \in [t_2, T]. \end{cases} \quad (3.23)$$

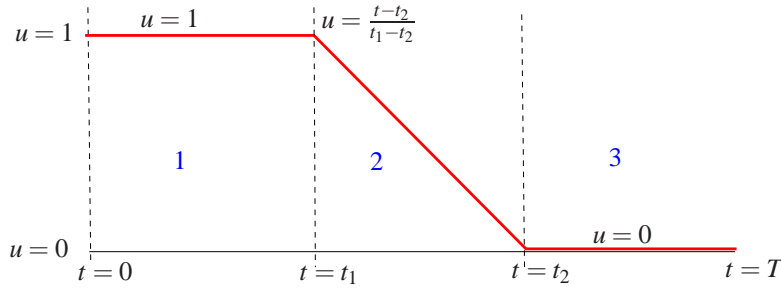


Figure 3: Assumed shape for the optimal strategy of the prey mites.

Then the optimization problem of the prey can be written as the solution of

$$(t_1^*, t_2^*) = \arg \sup_{t_1, t_2} \int_0^T (1 - u^R(t)) E^R(t) R(t) dt. \quad (3.24)$$

subject to (2.3)–(2.6). The dynamics of the model can then be distinguished as that for $t \in [0, t_1)$ (Phase 1), for $t \in [t_1, t_2)$ (Phase 2), and for $t \in [t_2, T]$ (Phase 3), as described in the following.

Phase 1 Notice that for $t \in [0, t_1]$ we can see that $J^R = 0$ and (2.3)–(2.6) can be rewritten as:

$$\frac{dE^P}{dt} = -\frac{1}{250}(1 - u^P)E^P + d u^P R - d u^P E^P, \quad (3.25)$$

$$\frac{dE^R}{dt} = d - dE^R, \quad (3.26)$$

$$\frac{dP}{dt} = -\frac{1}{20}P + \frac{1}{5}\beta u^P E^P P, \quad (3.27)$$

$$\frac{dR}{dt} = -\frac{1}{20}R + \frac{1}{5}E^R R - \frac{1}{5}u^P P R. \quad (3.28)$$

Phase 2 Notice that for $t \in [t_1, t_2]$ we can see that $J^R = \int_{t_1}^{t_2} \frac{t_1-t}{t_1-t_2} E^R(t) r(t) dt$ and

(2.3)–(2.6) can be rewritten as:

$$\frac{dE^P}{dt} = -\frac{1}{250}(1-u^P)E^P + du^P \frac{t-t_2}{t_1-t_2}R - du^P E^P, \quad (3.29)$$

$$\frac{dE^R}{dt} = -\frac{1}{250} \frac{t_1-t}{t_1-t_2}E^R + d \frac{t-t_2}{t_1-t_2} - d \frac{t-t_2}{t_1-t_2} E^R, \quad (3.30)$$

$$\frac{dP}{dt} = -\frac{1}{20}P + \frac{1}{5}bu^P E^P P, \quad (3.31)$$

$$\frac{dR}{dt} = -\frac{1}{20}R + \frac{t-t_2}{5(t_1-t_2)}E^R R - \frac{1}{5}u^P \frac{t-t_2}{t_1-t_2}PR. \quad (3.32)$$

Phase 3 Notice that for $t \in [t_2, T]$ we can see that $J^R = \int_{t_2}^T E^R(t)r(t)dt$ and (2.3)–(2.6) can be rewritten as:

$$\frac{dE^P}{dt} = -\frac{1}{250}(1-u^P)E^P - du^P E^P, \quad (3.33)$$

$$\frac{dE^R}{dt} = -\frac{1}{250}E^R, \quad (3.34)$$

$$\frac{dP}{dt} = -\frac{1}{20}P + \frac{1}{5}bu^P E^P P, \quad (3.35)$$

$$\frac{dR}{dt} = -\frac{1}{20}R. \quad (3.36)$$

With reasoning in reverse time, $\tau_1 = T - t_2$ and $\tau_2 = T - t_1$.

3.4 Optimal strategy for the predator

Since $u^P(0) = 1$ and $u^R(0) = 0$, (3.3)–(3.10) translates into

$$(E^P)' = dE^P, \quad (3.37)$$

$$(E^R)' = \frac{1}{250}E^R, \quad (3.38)$$

$$P' = \frac{1}{20}P - \frac{1}{5}bE^P P, \quad (3.39)$$

$$R' = \frac{1}{20}R, \quad (3.40)$$

$$\alpha'_{E^P} = -d\alpha_{E^P} + \frac{1}{5}b\alpha_P P + \frac{1}{5}bP, \quad (3.41)$$

$$\alpha'_{E^R} = -\frac{1}{250}\alpha_{E^R}, \quad (3.42)$$

$$\alpha'_P = \alpha_P \left(-\frac{1}{20} + \frac{1}{5}bE^P \right) + \frac{1}{5}bE^P - \frac{1}{20}, \quad (3.43)$$

$$\alpha'_R = -\frac{1}{20}\alpha_R. \quad (3.44)$$

The solution of (3.37)–(3.44) can be computed explicitly as follows:

$$E^P(\tau) = E^P(0)e^{d\tau}, \quad (3.45)$$

$$E^R(\tau) = E^R(0)e^{\frac{\tau}{250}}, \quad (3.46)$$

$$P(\tau) = P(0)e^{\frac{bE^P(0)bE^P(0)e^{d\tau}}{5d} + \frac{\tau}{20}}, \quad (3.47)$$

$$R(\tau) = R(0)e^{\frac{\tau}{20}}, \quad (3.48)$$

$$\alpha_{EP}(\tau) = \left(\frac{bP(0)e^{d\tau}}{5d} - \frac{bP(0)}{5d} \right) e^{-d\tau}, \quad (3.49)$$

$$\alpha_{ER}(\tau) = 0, \quad (3.50)$$

$$\alpha_P(\tau) = \left(-e^{\frac{\tau}{20} - \frac{bE^P(0)e^{d\tau}}{5d}} + e^{-\frac{bE^P(0)}{5d}} \right) e^{-\frac{\tau}{20} + \frac{bE^P(0)e^{d\tau}}{5d}}, \quad (3.51)$$

$$\alpha_R(\tau) = 0. \quad (3.52)$$

Substituting (3.45)–(3.52), $u^P = 1$, and $u^R = 0$ into (3.11) yields

$$\mathcal{A}_P = \frac{bP(0)(E^P(0)e^{d\tau} - E^P(0) + 250dE^P(0))}{1250d} \quad (3.53)$$

Note that this expression is **always positive** (note that $d > 1/250$). In other words, in reverse time, the predator is initially active and remains active until all prey are in diapause.

If u^R changes from 0 to different values, the expression for the singular surface (3.11) changes. While the system of characteristics (3.3)–(3.10) with $u^P = 1$ and $u^R \in (0, 1]$ cannot be solved explicitly, we can observe (Section 3.3) that if $u^R \in (0, 1)$, then $(u^R)' = -\frac{1}{\tau_1 - \tau_2} = \frac{1}{\tau_2 - \tau_1} = \Delta$ and $(u^R)'' = 0$. If $u^P \in (0, 1)$, conditions $\mathcal{A}_P = 0$, $\mathcal{A}'_P = \{\mathcal{A}_P, h\} = 0$, $\mathcal{A}''_P = \{\mathcal{A}'_P, h\} = 0$, where $\{\cdot, \cdot\}$ denotes Jacobi brackets [13] and h is the expression supremized in (3.2), have to be satisfied. Solving this system of three equations, with $(u^R)' = \Delta$, $(u^R)'' = 0$, and subject to (3.3)–(3.10), leads to only degenerate solution $\alpha_{EP} = 0$, $\alpha_P = -1$, $\alpha_R = 0$. This degenerate solution, which can be easily derived directly from (3.11), cannot be achieved when emitting characteristics (3.3)–(3.10) from their initial values. Moreover, the same degenerate solution will be found if we replace u^R in the equations $\mathcal{A}_P = 0$, $\mathcal{A}'_P = \{\mathcal{A}_P, h\} = 0$, $\mathcal{A}''_P = \{\mathcal{A}'_P, h\} = 0$ by 1. Therefore, we can conclude that the predator will not change strategy from $u^P = 1$ and will stay active the entire season.

Remark 3.1 In [17] a three-dimensional model, in which the energy of the predator was not included, was used to show that the optimal behavior of the prey is the one shown in Section 3.3. The underlying assumption was that the predator stays active the entire season. As this strategy turned out to be the optimal strategy of the predator in the model proposed in this paper, we could use the argumentation from [17] to confirm our hypothesis regarding the structure of $u^{R,*}$. Technically, the proofs will be the same if we assume that $d \gg 0$, while for d close to $\frac{1}{250}$ the underlying analysis becomes much more complex.

One can see that as the optimal strategy of the predator can be decoupled from the optimal strategy of the prey, it does not matter whether the problem is defined as

a Stackelberg game or as a Nash game because the result of these two games will coincide.

4 Discussion

In this paper we have searched optimal active/diapause ratios for the predatory mites and the fruit-tree red spider mites when there are no extra energetic costs to go in or out of diapause and when their decisions depends on both densities and energy levels of either species. The optimal strategy for the prey mites coincides with the results of our previous work [17]: Even if the prey mites do not encounter costs to enter the diapause, their optimal strategy is to go into diapause only once per season. This implies that, once decided, the diapause is irreversible. In this article we have shown that the best response of the predatory mites to this strategy of the prey mites should be to stay active for the entire season, again assuming no energetic costs for entering or leaving the diapause state.

The outcome of our analysis regarding the prey mites is remarkably close to the empirical observations: in reality the fruit-tree red spider mites have an irreversible diapause. Additionally, the prey mites also enter a so-called “deep diapause”. Once the prey mites are in the ‘deep’ diapause, it is not easy to bring them to a non-diapause state (e.g. they require a cold period of a certain length before they can come out of diapause). It is possible that this deep diapause evolved after the selection for an irreversible diapause predicted by our model (assuming at least potentially a very flexible decision without costs for entering or leaving the diapause state). Once this choice was made, there were probably other reasons why it was selectively advantageous to evolve a deep diapause (such reasons may be to invest more in anti-freeze chemistry at the expense of energy for other purposes such as reproduction). The deep diapause allows the spider mites to survive the winter better than for example predatory mites that exhibit a very flexible diapause state (crude estimates of winter survival for the prey mites are in the order of 50% whereas for predatory mites they are in the order of 5%).

The outcome of our analysis regarding the predatory mites is rather close to real observations: while in our model the predatory mites stay active the entire season, in reality the predatory mites might enter diapause at the very end of the summer season (actually in autumn, which is part of the winter season in our model), i.e., when there is no prey. Moreover, the predatory mites have a very flexible diapause. Collecting predatory mites in the winter and bringing them to the lab to offer them prey virtually always results in the predatory mites resuming feeding within two days and reproducing within four days. This represents a great flexibility when compared to the fruit-tree red spider mites (it may take one or two months for the prey mites to become active again depending on the cold period they already experienced). This “light diapause” of the predatory mites may have as a consequence that they survive the winter less well (less than 5% of them survives) than the spider mites.

Under natural conditions the predatory mites usually keep the spider mites at very low levels, meaning that they may experience prey shortage in some periods (and possibly a motivation to enter diapause in summer). Under those conditions it is not easy

to find the predatory mites on leaves as well as elsewhere on the plant. Hence, any predatory mite entering diapause will be difficult to find too. It is expected that the predatory mites respond to low prey density by entering diapause, but become active again as soon as there is prey available.

Under agricultural conditions, however, predatory mites may suffer from pesticide use (against spider mites or against pests other than spider mites) and there is much evidence that this allows the spider mites to increase in numbers and reach the status of a pest. Under those conditions, spider mites may suffer severe food competition and then they may also respond to plant food shortage by going into diapause.

Predatory mites rarely enter diapause before the end of the season under agricultural conditions and if they do they have a flexible diapause that allows them to enter and leave the diapause state, e.g. depending on temperature prey availability. Such flexible strategies do not emerge as a solution from the model above, but they may arise as optimal strategies in different models.

Let us consider another game, in which predator and prey choose $u^{P,*}$ and $u^{R,*}$, respectively, such that

$$u^{P,*}(\cdot) = \arg \sup_{u^P(\cdot) \in [0,1]} \int_0^T (u^P(-P + \gamma u^R P R)) dt, \quad (4.1)$$

$$u^{R,*}(\cdot) = \arg \sup_{u^R(\cdot) \in [0,1]} \int_0^T (1 - u^R(t)) E^R(t) R(t) dt, \quad (4.2)$$

while

$$\frac{dE^R}{dt} = -(1 - u^R) E^R + d(1 - E^R) u^R, \quad (4.3)$$

$$\frac{dP}{dt} = u^P(-P + \gamma u^R P R), \quad (4.4)$$

$$\frac{dR}{dt} = E^R R - b u^P P R, \quad (4.5)$$

with $\gamma \in (0, 1)$. Adopting the HJB approach again, we can show that while the optimal strategy of the prey does not change, the predator will end up in diapause unlike what was predicted by the model discussed in this paper. Moreover, this new model is much simpler to solve as it is only three-dimensional and the characteristic system for both predator and prey can be solved explicitly if they adopt bang-bang actions. The comparison of different models, those including energy levels and those excluding them, is a subject of our ongoing research.

5 Conclusions and future work

In this article, a dynamical model of the predator-prey interactions between predatory mites and fruit-tree red spider mites during summer has been described and analyzed. This model is an extension of the classic Lotka-Volterra models in that it includes not only the dynamics of predator and prey populations, but also the dynamics of their

energy levels and energy decision controls for both predator and prey. We have considered the case where both predator and prey can enter diapause. We have shown that it is optimal for the predator to stay active the entire season, while the prey stays active in the beginning of the season, later enters the diapause and stay in diapause until the end of the season.

While the correspondence between theoretical predictions and empirical observations on mites is encouraging, there are also limitations (mostly analytical) that should spawn new work. Moreover, it is still to be shown that optimal summer behavior of the predator and prey populations, as derived in this study, is resistant against invasion by mutant strategies and robust against structural modifications, such as the inclusion of predator decisions to enter diapause or not. Ultimately, we hope to explain winter dynamics of predatory mites and fruit-tree red spider mites based on optimal timing of diapause induction in summer. The use of bifurcation analysis can help determining for which parameter domains the proposed optimal strategies are evolutionarily stable.

Different models of the predator-prey interactions will lead to different optimal strategies of the predator and prey. Analysis and comparison of such different models is a subject of our future research.

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