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Irreversible prey diapause as an optimal strategy of a physiologically extended Lotka-Volterra model

Abstract We propose an optimal control framework to describe intra-seasonal predator-prey interactions, which are characterized by a continuous-time dynamical model comprising predator and prey density, as well as the energy budget of the prey over the season length. The model includes a time-dependent decision variable for the prey, representing the portion of the prey population in time that is active, as opposed to diapausing (a state of physiological rest). The predator follows autonomous dynamics and accordingly it remains active during the season.

The proposed model is a generalization of the classical Lotka-Volterra predator-prey model towards non-autonomous dynamics that furthermore include the effect of an energy variable. The model has been inspired by a specific biological system of predatory mites (*Acari: Phytoseiidae*) and prey mites (so-called fruit-tree red spider mites) (*Acari: Tetranychidae*) that feed on leaves of apple trees – its parameters have been instantiated based on field knowledge. The goal of the work is to understand the decisions of the prey mites to enter diapause (a state of physiological rest) given the dynamics of the predatory mites: this is achieved by solving an optimization problem hinging on the maximization of the prey population contribution to the next season.

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The main features of the optimal strategy for the prey are shown to be that (1) once in diapause, the prey does not become active again within the same season and hence diapause is an irreversible process; (2) for the vast majority of parameter space, the portion of prey individuals entering the diapause within the season does not decrease in time; (3) with an increased number of predators, the optimal population strategy for the prey is to start diapause earlier and to enter the diapause more gradually. This optimal population strategy will be studied for its ESS properties in our future research.

Keywords Predator-prey problems · fruit-tree red spider mites · game theory · optimal control · singular characteristics

Mathematics Subject Classification (2000) 49L20 · 92B05 · 93C15

1 Introduction

Predator-prey interactions have traditionally been modeled either as continuous time differential equations (Lotka-Volterra type models) or as difference equations (Nicholson-Bailey type models) (14; 21; 35; 36). The latter type of models are of biological interest because they highlight that such interactions proceed over a fixed time horizon, namely with one or more discrete generations within a season that is favorable for growth (e.g. summer in temperate regions), whereas they are interrupted during seasons that are critical for growth (e.g. winter). Although this feature adds to the biological realism of such models, they ignore the continuous character of the interactions during the season. Therefore, it is of interest to develop general models that can account both for continuous interactions and overlapping generations in summer seasons and discrete periods without interactions during winter seasons (28). Such general models become even more essential when the 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 (5; 33).

The motivation to consider model with these features comes in this work from studies on the use of predatory mites (*Acari: Phytoseiidae*) for biological pest control of fruit-tree red spider mites (*Acari: Tetranychidae*), as well as of the herbivores that feed on and damage leaves of apple trees (12; 13). In this environment, winters (covering 6-7 months) are usually harsh and as such endanger the survival of prey (12) and (even more so) that of predators (8; 12). Predator and prey densities in the following summer season depend on their numbers entering a state of physiological rest (the so-called diapause state) during the previous year. The decision to enter diapause promotes the survival of the individual during winter and emerges from induction by a combination of sufficiently long night lengths and low temperatures (34). However, using another similar spider mite species (more amenable to experimental treatment), it was shown that the decision to enter diapause also depends on predator density during summer (16; 18; 19). 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 too many prey mites would make the same decision, this could create a negative feedback on the predatory mite population, so that at some point in time the prey mites would profit from the decreased predation risk by terminating their diapause and returning to the leaves. This leads us to conclude that the prey's decision to enter diapause is part of a game where the predator is the leader and the prey needs to find a best response to the predator. Another complicating factor is that an early diapause raises the demands on the energy store of the individual prey 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 (17). Thus, the decision to enter diapause within a year will depend on the current internal energy store of the prey mite, as this will have far-reaching consequences for winter survival and reproduction in the summer season of the next year. Given the negative feedback between predator and prey and the complexity of the decisions that prey mites are faced with making, it is virtually impossible to intuitively pinpoint the most likely strategies that will emerge from natural selection. In this article, we will use an optimal control approach to find the strategies that are best for the prey population as a whole. If there is an optimal solution, then this may not necessarily be the best solution for any given prey individual, because selection acts on individuals being the vehicles of genes. This is why the optimal solution found in this article needs to be tested for its evolutionary stability by studying its resistance to invasions of mutant individuals with alternative strategies, once the problem is extended to multiple seasons.

Historical background of our model: The optimal control model that we propose has been developed as an extension of classical predator-prey model defined by Lotka-Volterra dynamics (21; 35; 36). The new model allows for a control structure, in order to analyze behavioral strategies of the prey mites. The parametrization of the model has been based on (12; 13). In the literature, the classical Lotka-Volterra model has been extended to a framework allowing for n different interacting populations (10), as well as to an input-dependent setup (15), following the first study of controlled predator-prey models in (9). Reachability properties of controlled Lotka-Volterra systems were studied in (6). The n -dimensional Lotka-Volterra system was extended in (11), where a stabilization issue was studied. A simplification of the controlled Lotka-Volterra model and its subsequent extension was recently investigated in (1).

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

n - season number

T_n - length of the n -th summer season

$R_n(t)$ - red spider mite population at time $t \in [0, T_n]$, within the n -th season

$r_n(t)$ - rescaled red spider mite population at time $t \in [0, T_n]$, within the n -th summer season

$P_n(t)$ - predatory mite population at time $t \in [0, T_n]$, within the n -th summer season

$p_n(t)$ - rescaled predatory mite population at $t \in [0, T_n]$, within the n -th summer season

- $E_n(t)$ - internal energy of the prey at time $t \in [0, T_n]$, within the n -th summer season
- $u_n(t)$ - decision variable (control) of the red fruit-tree spider mites (prey), within the n -th summer season
- $a(\tau), b(\tau), c(\tau)$ - additional variables for the characteristic system in reverse time
- \mathcal{S} - singular surface (as used in the analysis of the optimal control problem)
- \mathcal{C} - singular surface for the simplified case with full energy
- τ_1 - time of the first event (optimal strategy of the prey becoming non-zero in reverse time τ)
- τ_2 - time of the second event (optimal strategy of the prey becoming 1 after being lower than 1 in reverse time τ)
- τ_3 - time of the third event (optimal strategy of the prey becoming lower than 1 after being equal to 1 in reverse time τ)
- J_n - intra-seasonal fitness function for the prey, within the n -th season
- J^K - inter-seasonal fitness function for the prey over K years
- V - cost function in reverse time

The subscript n is dropped whenever the study focuses on a single season.

The article is structured as follows. Section 2 introduces an inter-seasonal (multiple seasons) model, discusses and motivates the structure of its intra-seasonal (single season) part, and hints at extensions toward a game. With focus on a single season, Section 3 formally studies the optimal strategies of the prey. Section 4 elaborates on the biological interpretation of the obtained results and Section 5 discusses possible extensions and sketches future work.

2 Model of the interaction between predatory and fruit-tree red spider mites

The model describes the interactions between predatory mites (predator) and fruit-tree red spider mites (prey). We begin by formulating a control-dependent model for the intra-seasonal (single season) dynamics (Section 2.1) and then extending it to the inter-seasonal (multiple seasons) dynamics (Section 2.2). Section 2.3 discusses the biological relevance of the modeling choices.

The model allows characterizing the seasonal strategy of the prey as a solution of an optimal control problem. Each yearly season is divided into two parts: the *summer* and *winter* season. The predator is assumed to be active during the entire summer season. With regard to the interaction between predatory and fruit-tree red spider mites, during the summer season both species can feed, respectively by predation and by feeding on leaves of apple trees, which leads to reproduction. Furthermore, prey can enter diapause, a quiescent state that protects from the environment and from predation – this in particular entails the decoupling between the species (whereas predation involves the interaction between them). During the winter season the species do not interact, and their populations independently decline at a constant rate. The dynamics during winter are thus trivial and will be simply modeled by a reset of the energy and population levels. Over an entire year, we model the summer season with continuous dynamics, while the winter season is described by discrete dynamics.

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 Summer interactions

In this section we focus on the dynamics of the prey (fruit-tree red spider mites) in the summer season, assuming the predator (predatory mites) continues to forage actively over the entire summer.

The (summer) fitness function for the prey J_n models its survival capability, and is related to the number of the individuals which enter diapause during the summer. The shape of the fitness is as follows:

$$J_n(u_n) = \int_0^{T_n} (1 - u_n(t')) E_n(t') R_n(t') dt'. \quad (2.1)$$

In (2.1) the constant T_n denotes the length of the n -th summer. With the function u_n (no explicit time dependence) we denote the strategy for the prey, namely $u_n(t), t \in [0, T_n]$. The decision variable $u_n(t)$ indicates the portion of the prey population being active at time t : $u_n(t) \in [0, 1]$, for $t \in [0, T_n]$. $R_n(t)$ represents the prey population at time t . Accordingly, the quantity $(1 - u_n(t))R_n(t)$ represents the number of the prey individuals in diapause at time t . Furthermore, the variable $E_n(t) \in [0, 1]$ represents the (normalized) energy that is available to an average individual within the prey population: if $E_n(t) = 0$, then the average individual is dead, whereas $E_n(t) = 1$ represents maximal fitness.

The system dynamics within the n -th summer season is modeled as follows (here $P_n(t)$ denotes the predator population in time t):

$$\frac{dE_n(t)}{dt} = -m(1 - u_n(t))E_n(t) + d u_n(t) - d u_n(t) E_n(t), \quad (2.2)$$

$$\frac{dP_n(t)}{dt} = -\alpha P_n(t) + \beta \gamma u_n(t) P_n(t) R_n(t), \quad (2.3)$$

$$\frac{dR_n(t)}{dt} = -\alpha R_n(t) + \gamma u_n(t) E_n(t) R_n(t) - \beta u_n(t) P_n(t) R_n(t). \quad (2.4)$$

The quantities $\alpha, \beta, \gamma > 0$ and $m, d > 0$ are given parameters. Both the number of predators $P_n(t)$ and that of prey $R_n(t)$ decrease at a rate α . In equation (2.3) the number of predators $P_n(t)$ increases at a rate that is proportional to the predation, represented by the product of the number of actual active prey $u_n(t)R_n(t)$ and the number of predators $P_n(t)$ with feeding rate $\beta\gamma$. Whenever active, the prey population rate change in (2.4) decreases – due to predation – proportionally to the number of active prey and number of predators (at rate β), whereas it increases – due to feeding and reproduction – proportionally to the number of prey and the average internal energy (with rate γ). The energy of the prey in (2.2) varies as follows: whenever active (feeding), it increases proportionally to the distance to its maximum $(1 - E_n(t))$ with rate d ; on the other hand, whenever in diapause it decreases proportionally to the actual average energy of the prey (with rate m), as individuals in diapause slowly utilize their energy.

Remark 1 Let us analyze the equilibrium dynamics obtained for extreme values of the input. The points $P_n^* = R_n^* = 0$ are always equilibria. Whenever $u_n \equiv 0$, they represent with $E_n^* = 0$ the only asymptotically stable equilibrium point. Conversely, whenever $u_n \equiv 1$, the model admits two equilibria for (E_n^*, P_n^*, R_n^*) :

$(1, 0, 0)$, and $\left(1, \frac{\gamma - \alpha}{\beta}, \frac{\alpha}{\beta\gamma}\right)$. To ensure nonnegativity of equilibria, γ has to be higher than α (we will see below that a further requirement on β to obtain quantities larger than one will not be necessary). Moreover, equilibrium $(1, 0, 0)$ is unstable, whereas $\left(1, \frac{\gamma - \alpha}{\beta}, \frac{\alpha}{\beta\gamma}\right)$ is marginally stable (namely, related to periodic trajectories over the two populations). Selecting a $u_n \in (0, 1)$ leads to the requirement $d \geq m$, which allows for values of $\frac{dE_n}{dt} \geq 0$. \square

Remark 2 The dynamical model in (2.2)-(2.3)-(2.4) is a straightforward generalization of the known Lotka-Volterra, predator-prey model (21; 35; 36), which is obtained when $E_n(t) = 1, u_n(t) = 1, \forall t \in [0, T_n]$. Notice that the energy value $E_n = 1$ is an equilibrium for the dynamics whenever the control is kept constant and equal to one. In other words, Lotka-Volterra dynamics represent a special configuration of the model, where the energy is at its maximum, and where the prey is always active (namely, feeding and breeding). \square

The optimal behavior of the prey maximizes its fitness in (2.1). We will denote this optimal ratio by $u_n^*(t), t \in [0, T_n]$, which can be found by solving the following optimal control problem:

$$\begin{cases} u_n^* = \arg \sup_{u_n} \int_0^{T_n} (1 - u_n(t')) E_n(t') R_n(t') dt', \\ \text{subject to: (2.2) - (2.3) - (2.4).} \end{cases} \quad (2.5)$$

2.2 Winter dynamics

As mentioned at the beginning of Section 2, the winter dynamics is modeled by discrete resets in the predator and prey population levels, as well as in the internal energy of the prey. It is observed that only a portion of the predators entering winter survives. On the other hand, the prey has a chance to survive winter only if it enters it in diapause, therefore a portion of the prey entering the diapause during the summer will survive the winter that follows. However, it is observed that the survival rate of the diapaused prey is higher than the survival rate of the (active) predator. Moreover, due to the winter, the energy level of the prey is supposed to drop remarkably.

If we consider the dynamics over K seasons, for $n \in \{1, \dots, K-1\}$ the resets of the state variables can be defined as follows:

$$\begin{aligned} P_{n+1}(0) &= l_n P_n(T_n), \\ R_{n+1}(0) &= \iota_n \int_0^{T_n} (1 - u_n(t')) R_n(t') dt', \\ E_{n+1}(0) &= o_n E_n(T_n), \end{aligned}$$

where $1 > \iota_n > l_n > o_n > 0$. The reset constants can be functions of the (winter) season length. The fitness function of the prey over K years can be written as

$$J^K(u) = \sum_{n=1}^K J_n(u_n),$$

and it is a function of the strategy $u = (u_1, \dots, u_n)$.

Investigating the optimal strategy for the prey over multiple seasons (years) is an interesting goal, which is related to the evolutionary stability of the optimal strategy found. Bifurcation analysis can be used in order to determine parameter domains for which the proposed optimal strategy is evolutionary stable (7). Comparison of the outcome of our research with the research defining under which conditions evolution indeed leads to the optimal strategy found by maximizing certain criteria (26; 27) can then be made.

As a first step for the study of the optimal behavior over multiple seasons, this work focuses on the solution of the optimal control problem within a single (n -th) summer season.

2.3 Discussion on the model

In the proposed model, prey have to trade-off between the number of active and diapaused individuals, since diapaused individuals increase their number of descendants in the next generation (season). The optimal pattern of such a decision depends on both the environment and the physiological state of an individual (22). To determine the optimal life history of an individual it is useful to incorporate physiological variables in the model (22; 31) – in this work we have embedded a dynamical energy variable. The prey individuals are thus described by two variables: their energy (physiological variable) and their population. Therefore, the problem of maximizing the number of descendants can be translated into a “dynamic model of energy allocation and investment” (29).

While the internal energy of the prey $E(t) \in [0, 1]$ is important for the system behavior, the internal energy of the predator is not essential to characterize the optimal behavior of the prey, and one can assume that this internal energy is proportional to the number of active prey, because these are being predated once all of its individuals are active.

Most existing energy allocation models appear to be focused on a single individual, not taking into account potential population-dependent environmental feedback (see the review (29) and (20; 30)). The model considered in this paper describes growth of a population size in interaction with the growth of another population, and thus accounts for the influence of the individual population size as well as for active-diapause strategy of individuals. As discussed, in our model the population-dependent environmental feedback in the shape of an energy variable is explicit. This also allows embedding season-dependent environmental variability into the model. We also provide a more formal argument (see Appendix A) on the necessity to include energy in the model in order to effectively study the diapause process.

We focus on the optimal strategy of the prey within one summer, while the predator is present and active. The main goal is to see what type of strategy the prey employ in presence of the predator and whether their entering diapause is reversible or not (i.e. whether once they enter the diapause, they never become active again). The study of the multi-seasonal dynamics of the system (such as the evolutionary stability, optimal behavior of the prey for multiple seasons) is a future step of this research.

While our objective is to find the optimal behavior of the prey in the summer season, one can also focus on the situation in which the predatory mites decide their active/diapause ratio during the summer season in response to external conditions or food shortage. In such a case the problem formulated in (2.5) can be extended into a Stackelberg game (2; 32), with the predator acting as a leader and the prey as the follower. Games of Stackelberg kind are needed, since the fitness function of the predator would differ from that of the prey (the predatory mites have chance to survive the winter even if they are in the diapause at the end of the season). This fact, together with the asymmetry of the roles between the predator and prey is a motivation for defining the problem as a Stackelberg game. As the Stackelberg game is more general than a Nash game, the solution of the Stackelberg game would coincide with the solution of the Nash game if the hierarchy between the predatory and prey mites would not play a role (2). A Stackelberg game formulation between the predator and prey represents a natural extension of our model.

3 Study of the structure of the optimal strategy of the prey within a summer season

In this section we discuss the solution of the optimal control problem in (2.5), focusing on the optimal strategy of the prey within a single summer season. Recall that the control structure of the predator is fixed, which leads to focusing on the strategy of the prey. Following Bellman's approach (3), we apply the method of singular characteristics (24; 25) to formalize the solution of the problem.

Let us start with parameterizing the model. Using information from (12; 13) regarding the average number the fruit-tree red spider mites eaten by an adult predatory mite per day and the average reproduction and death rates of both predatory and fruit-tree red spider mites, we set the parameters α , γ , and m in (2.5) to the following values: $\alpha = \frac{1}{20}$, $\gamma = \frac{1}{5}$, $m = \frac{1}{250}$. Moreover, note that the following substitution can be used in (2.5): $P_n = \frac{1}{\beta} p_n$, $R_n = \frac{1}{\beta} r_n$. Consequently, the parameter β does not play a role in (2.5) and can thus be disregarded: notice that the new population variables p_n and r_n have now arbitrary units, which will simplify the dynamical analysis of the model.

In the remainder of the text we will focus on the optimal strategy of the prey within one (n -th) summer season, therefore we will drop the subscript n in p_n , r_n , E_n^R , u_n^R , and T_n , defining the variables p , r , E , u , and T instead.

3.1 Formal statement of the optimal control problem

Problem (2.5) can be rewritten as

$$u^* = \arg \sup_u \int_0^T (1 - u(t')) E(t') r(t') dt', \quad (3.1)$$

subject to the following dynamics:

$$\frac{dE}{dt} = -\frac{1}{250}(1-u)E + du - duE, \quad (3.2)$$

$$\frac{dp}{dt} = -\frac{1}{20}p + \frac{1}{5}upr, \quad (3.3)$$

$$\frac{dr}{dt} = -\frac{1}{20}r + \frac{1}{5}uEr - upr, \quad (3.4)$$

with the control input $u(t) \in [0, 1]$, the energy of the prey $E(t) \in [0, 1]$, whereas $p(t)$ represents the (rescaled) concentration of the predator and $r(t)$ that of the prey, for $t \in [0, T]$, with summer length T , expressed in days. The only parameter left within the dynamical relations is $d \in (\frac{1}{250}, 1]$, which affects the rate of change of the energy level.

The two classical approaches to the solution of problem (3.1), subject to (3.2)-(3.3)-(3.4), are Pontryagin's maximum principle and Bellman's dynamical programming approach (3; 4). Here, we choose the latter approach, since Pontryagin's principle leads to candidate solutions only, and the validation of which of these candidate solutions is optimal can be a difficult task.

As standard in Bellman's approach, let us introduce a reverse time $\tau = T - t$ and a corresponding value function

$$V(p, r, E, t, u) = \int_{T-t}^T (1-u(t'))r(t')E(t')dt'. \quad (3.5)$$

The value function (3.5) is to be maximized for any $\tau \in [0, T]$ as the prey selects an optimal strategy denoted by $u^*(\tau)$ over $[0, T]$. Notice that, whenever dealing with the new time variable τ , we shall refer to the dynamics of the corresponding variables along this "reverse time". In order to find the optimal control, the following Hamilton-Jacobi-Bellman (HJB) equation has to be satisfied (3):

$$\begin{aligned} -\frac{\partial V}{\partial \tau} + \sup_u \left(\frac{\partial V}{\partial E} \left(-\frac{1}{250}(1-u)E + du - duE \right) + \frac{\partial V}{\partial p} \left(-\frac{1}{20}p + \frac{1}{5}upr \right) \right. \\ \left. + \frac{\partial V}{\partial r} \left(-\frac{1}{20}r + \frac{1}{5}uEr - upr \right) + (1-u)Er \right) = 0. \end{aligned} \quad (3.6)$$

Let us introduce the additional variables $a \stackrel{\text{def}}{=} \frac{\partial V}{\partial E}$, $b \stackrel{\text{def}}{=} \frac{\partial V}{\partial p}$, $c \stackrel{\text{def}}{=} \frac{\partial V}{\partial r}$, obtaining the following characteristic system (24) (here $E' = \frac{dE}{d\tau}$, and similarly for the remaining variables):

$$\begin{cases} E' = \frac{1}{250}(1-u)E - du + duE, \\ p' = \frac{1}{20}p - \frac{1}{5}upr, \\ r' = \frac{1}{20}r + upr - \frac{1}{5}uEr, \\ a' = -\frac{1}{250}(1-u)a - dua + \frac{1}{5}urc + (1-u)r, \\ b' = -\frac{1}{20}b + \frac{1}{5}urb - urc, \\ c' = \frac{1}{5}upb - \frac{1}{20}c - upc + \frac{1}{5}uEc + (1-u)E. \end{cases} \quad (3.7)$$

3.2 Solution of the optimal control problem

As shown in (23), from equation (3.6) it can be seen that the optimal control u^* maximizes the quantity $u\mathcal{S}$, where

$$\mathcal{S} = \frac{1}{250}Ea + da - dEa + \frac{1}{5}prb - prc + \frac{1}{5}Erc - Er, \quad (3.8)$$

and where the quantity \mathcal{S} is defined as $\mathcal{S} = \partial h / \partial u$, with h representing the argument of the supremization in the HJB equation (3.6). Notice that the quantity \mathcal{S} is a function of the variables in (3.7) and of time – unless stated otherwise, we shall not explicitly write out these dependencies.

The optimal control takes the following form (23):

$$u^* = \text{Heav } \mathcal{S} = \begin{cases} 1, & \text{if } \mathcal{S} > 0, \\ 0, & \text{if } \mathcal{S} < 0. \end{cases} \quad (3.9)$$

Furthermore, whenever $\mathcal{S}(\tau) = 0$, then $u^*(\tau) \in (0, 1)$, which denotes a mixed¹ strategy. On the other hand, if $u^*(\tau) \in (0, 1)$ is optimal, then $\mathcal{S}(\tau) = 0$ is invariant with respect to τ for $u^*(\tau)$, which implies that $\mathcal{S}(\tau) = 0$, as well as $\mathcal{S}'(\tau) = 0$, $\mathcal{S}''(\tau) = 0$ (and similarly for higher-order derivatives), which can be shown by application of the Jacobi brackets (23).

The transversal conditions (23; 24) follow from the equations:

$$a(T) = b(T) = c(T) = 0,$$

and from the assumption that the number of the players and the energy level has to be nonzero at the end of the summer season (if the energy level is equal to zero, then the prey population did not survive; furthermore, if either population level is at zero, both have gone extinct):

$$E(T) \stackrel{\text{def}}{=} E^f > 0, \quad p(T) \stackrel{\text{def}}{=} p^f > 0, \quad r(T) \stackrel{\text{def}}{=} r^f > 0.$$

Let us denote the value of \mathcal{S} for state variables evaluated at time T by $\mathcal{S}(T)$. It follows that $\mathcal{S}(T) = -E(T)r(T) < 0$, and, therefore,

$$u(T) = \text{Heav}(\mathcal{S}(T)) = 0.$$

Remark 3 Let us emphasize the result above as a first conclusion on the shape of the strategy of the prey: the strategy ends up in a diapause state at the end of the summer season. This conclusion can also be directly inferred from the shape of the cost function in (3.1). \square

It is possible to emit the characteristic field (24) in reverse time, starting from the terminal surface at time T , with $u^*(\tau) = 0$. This yields, for $\tau \geq 0$:

$$\begin{cases} E(\tau) = E^f e^{\frac{\tau}{250}}, \\ p(\tau) = p^f e^{\frac{\tau}{20}}, \\ r(\tau) = r^f e^{\frac{\tau}{20}}; \end{cases} \quad (3.10)$$

$$\begin{cases} a(\tau) = \frac{500}{27} r^f (e^{\frac{\tau}{20}} - e^{-\frac{\tau}{250}}), \\ b(\tau) = 0, \\ c(\tau) = \frac{500}{27} E^f (e^{\frac{\tau}{250}} - e^{-\frac{\tau}{20}}). \end{cases} \quad (3.11)$$

¹ Mixed strategies are often referred to as singular or intermediate strategies.

Note that the expressions in (3.11) contain constants from the quantities in (3.10), as expected from (3.7). The presence of explicit solutions of the characteristic system allows a precise study of events related to the behavior of the optimal strategies – this is further elaborated in the next section.

3.2.1 Study of the time of the event when $u^*(\tau) = 0$ changes to $u^*(\tau) \in (0, 1)$

We investigate the time τ_1 related to the verification of the condition $\mathcal{S}(\tau_1) = 0$, which leads to the situation when $u^*(\tau_1)$ becomes positive (see pictorial representation in Fig. 1).

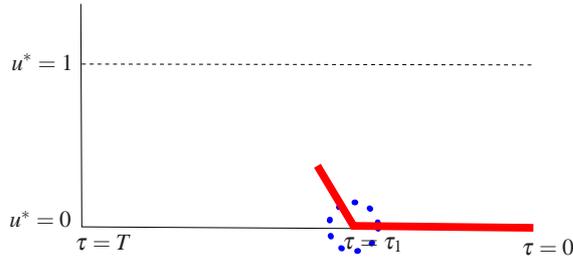


Fig. 1 Event time τ_1 , corresponding to the optimal control $u^*(\tau_1)$ becoming positive. Recall that the formulation is in reverse time.

The continuity of the characteristic trajectories (24) in (3.10)-(3.11) implies that equation $\mathcal{S}(\tau_1) = 0$ can be rewritten as follows:

$$\begin{aligned} r^f & \left(-\frac{2}{27} E^1 (e^{-\frac{\tau_1}{250}} - e^{\frac{\tau_1}{20}}) - \frac{500}{27} d (e^{-\frac{\tau_1}{250}} - e^{\frac{\tau_1}{20}}) \right. \\ & + \frac{500}{27} d E^1 (e^{-\frac{\tau_1}{250}} - e^{\frac{\tau_1}{20}}) + \frac{500}{27} p^f (e^{\frac{\tau_1}{20}})^2 E^f (e^{-\frac{\tau_1}{20}} - e^{\frac{\tau_1}{250}}) \\ & \left. - \frac{100}{27} E^1 e^{\frac{\tau_1}{20}} E^f (e^{-\frac{\tau_1}{20}} - e^{\frac{\tau_1}{250}}) - E^1 e^{\frac{\tau_1}{20}} \right) = 0, \end{aligned}$$

where we have introduced the new quantity $E^1 \stackrel{\text{def}}{=} E(\tau_1)$.

Remark 4 Note that the above equation is satisfied independently of the value of r^f , the final prey density. This leads to claim that the time τ_1 of the first event depends exclusively on the number of predators at the end of the summer (p^f), on the final energy of the prey (E^f), and is furthermore parameterized by the constant d . This observation is interesting from a biological viewpoint, since it seems to indicate that the event related to having the whole prey population in diapause is independent of the concentration of the same population (which can be associated to the absence of a form of quorum sensing). \square

From (3.10), let us substitute $E^1 = E^f e^{\frac{\tau_1}{250}}$. Assuming as essential a nonzero value for r^f , it is possible to express the time of the first event τ_1 as follows:

$$\tau_1 = 500 \ln w,$$

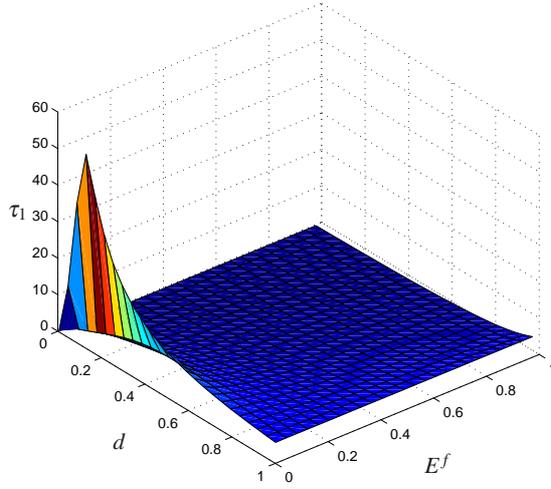


Fig. 2 Graph of the dependence of τ_1 with respect to d and E^f , for the case where $p^f = 0$.

with w being the smallest real-valued root of the following high-order polynomial:

$$\begin{aligned}
& 625 \cdot 10^8 ((w^{29} - w^2)E^f - w^{27} + 1)d + 625 \cdot 10^8 (w^{54} - w^{27})E^f p^f \\
& + ((1 - 125 \cdot 10^8)w^{31} + (125 \cdot 10^8 + 1)w^4)(E^f)^2 \\
& + (3125 \cdot 10^6 w^{29} + 25 \cdot 10^7 w^2)E^f.
\end{aligned} \tag{3.12}$$

As discussed above, note that τ_1 depends on the energy of the prey at the end of the summer E^f , the number of individuals of the predator at the end of the summer p^f , and on parameter d . However, it is independent of the number of individuals of the prey at the end of the summer r^f .

The dependence of the time of the first switch τ_1 on the parameters E^f and d , for the case when $p^f = 0$, is illustrated in Figure 2. It can be shown that values of τ_1 decrease with increasing p^f (see Section 3.4 for more details).

3.2.2 Investigation of the existence of a second event: if $\exists \tau_2 > \tau_1 : u^(\tau_2) = 1$, does there $\exists \tau_3 > \tau_2$ and a $\delta > 0 : \forall \tau \in (\tau_3, \tau_3 + \delta], u^*(\tau) \in [0, 1)$?*

We have so far investigated the existence of $\tau \geq \tau_1$ (in reverse time), which are such that $\mathcal{S}(\tau) = 0$ and $u^*(\tau) \in (0, 1)$. We will study of the properties of $u^*(\tau)$ over $\mathcal{S}(\tau) = 0$ in the next section. Assume that there is a time $\tau_2 > \tau_1$ which is associated to the condition $\mathcal{S}(\tau) > 0$: we investigate whether the condition $\mathcal{S}(\tau) = 0, \tau > \tau_2$, can be met again (see Fig. 3 for a pictorial representation). More precisely, we look for a time $\tau_3 > \tau_2$ and a $\delta > 0$ such that, for any $\tau \in (\tau_3, \tau_3 + \delta], u^*(\tau) \in [0, 1)$.

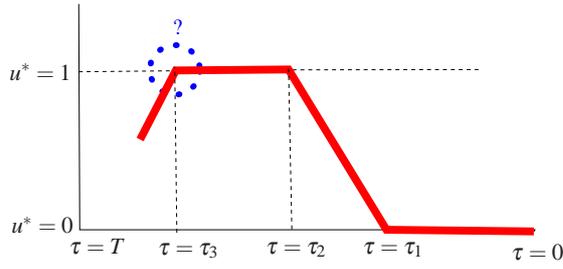


Fig. 3 Study of the existence of a second event in reverse time: can the optimal strategy u^* again admit values within the interval $[0, 1)$, after being equal to 1?

Whenever $u^*(\tau) = 1$ the characteristic system takes the following form (again in reverse time):

$$\begin{cases} E' = -d + dE, \\ p' = \frac{1}{20}p - \frac{1}{5}pr, \\ r' = \frac{1}{20}r + pr - \frac{1}{5}Er, \\ a' = -da + \frac{1}{5}rc, \\ b' = -\frac{1}{20}b + \frac{1}{5}rb - rc, \\ c' = \frac{1}{5}pb - \frac{1}{20}c - pc + \frac{1}{5}Ec. \end{cases} \quad (3.13)$$

System (3.13) is not explicitly integrable. However, from (3.13) (top equation) with an initial condition $E^2 \in (0, 1)$, we can get an explicit expression for E if $u^* = 1$ and $\tau \geq \tau_1$:

$$E(\tau) = 1 + (E^2 - 1)e^{d(\tau - \tau_1)}, \quad (3.14)$$

which is monotonically decreasing with τ and lead to the following non-negativity condition:

$$\tau \leq \tau_1 - \frac{1}{d} \ln(1 - E^2) \stackrel{\text{def}}{=} \tau_2^{\max},$$

where $E^2 = E(\tau_2) \in (0, 1)$. The value τ_2^{\max} represents an (possibly infinite) upper bound on the length of time during which the prey is physiologically active.

Proposition 31 (*Nonexistence of a second event*) *The optimal control problem in the reverse time τ , defined by the system of characteristics in (3.7), admits at most one event in u , namely if $u(\tau)$ takes the value 1, then $u(\tau')$, $\tau' \geq \tau$ never enters again the interval $[0, 1)$.*

Proof. See Appendix B. □

3.3 Properties of the optimal control over the singular curve: optimal mixed strategies

So far it has been shown that the optimal control $u^*(\tau)$ starts (at the end of the summer, in reverse time) at a value equal to 0, that may enter a singular state at time τ_1 (possibly switching discontinuously to the value 1), and that whenever

it takes the value 1, it remains equal to that value thereafter, until $\tau = T$ (which corresponds to the start of the summer season in real time). Alternatively, it may happen that either $u^*(\tau)$ remains equal to 0 for all τ (i.e., $\mathcal{S}(\tau) < 0$ for all $\tau \in [0, T]$), or that $u^*(\tau)$ will move away from the value 0, while remaining bounded within $(0, 1)$ (namely, within the surface $\mathcal{S}(\tau) = 0$), thus never reaching the value 1 (this would be related to the condition $\mathcal{S}(\tau) \leq 0$ for all $\tau \in [0, T]$).

In the following we study the behavior of the optimal control u^* on the singular surface $\mathcal{S} = 0$. We are especially interested in “regularity” properties for u^* , and particularly in possible ranges of the parameter value d for which $u^*(\tau)$ is a nondecreasing function (in reverse time) whenever $\mathcal{S}(\tau) = 0$: this would allow ruling out the biologically inconsistent behavior depicted in Figure 4.

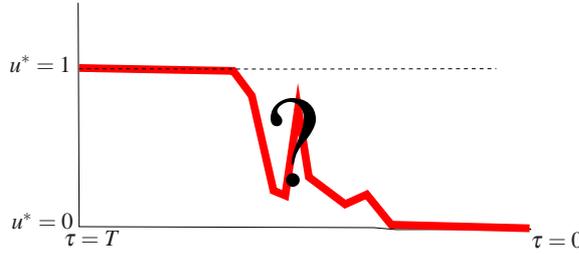


Fig. 4 We investigate the properties mixed strategies in time: is a non-monotonic profile of u^* possible, or is $\frac{du^*}{d\tau}$ nondecreasing (in reverse time) within $\mathcal{S} = 0$?

The optimal control u^* on the singular surface is denoted by u^s , and recall that we focus on the case $u^s < 1$. The characteristics on the singular surface are obtained by solving the following system of equations:

$$\begin{cases} E' = \frac{1}{250}(1 - u^s)E - du^s + du^s E, \\ p' = \frac{1}{20}p - \frac{1}{5}u^s pr, \\ r' = \frac{1}{20}r + u^s pr - \frac{1}{5}u^s Er, \\ a' = -\frac{1}{250}(1 - u^s)a - du^s a + \frac{1}{5}u^s rc + (1 - u^s)r, \\ b' = -\frac{1}{20}b + \frac{1}{5}u^s rb - u^s rc, \\ c' = \frac{1}{5}u^s pb - \frac{1}{20}c - u^s pc + \frac{1}{5}u^s Ec + (1 - u^s)E. \end{cases} \quad (3.15)$$

The initial conditions for the dynamics above can be derived from (3.11) by setting $\tau = \tau_1$ (recall again that the characteristics are continuous (24)):

$$\begin{cases} E(\tau_1) \stackrel{\text{def}}{=} E^1 = E^f e^{\frac{\tau_1}{250}}, \\ p(\tau_1) \stackrel{\text{def}}{=} p^1 = p^f e^{\frac{\tau_1}{20}}, \\ r(\tau_1) \stackrel{\text{def}}{=} r^1 = r^f e^{\frac{\tau_1}{20}}; \end{cases} \quad (3.16)$$

$$\begin{cases} a(\tau_1) \stackrel{\text{def}}{=} a_1 = \frac{500}{27} r^f (e^{\frac{\tau_1}{20}} - e^{-\frac{\tau_1}{250}}), \\ b(\tau_1) \stackrel{\text{def}}{=} b_1 = 0, \\ c(\tau_1) \stackrel{\text{def}}{=} c_1 = \frac{500}{27} E^f (e^{\frac{\tau_1}{250}} - e^{-\frac{\tau_1}{20}}). \end{cases} \quad (3.17)$$

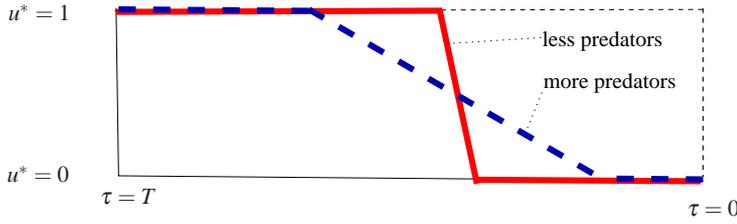


Fig. 5 Numerical simulations suggest that if the number of predators increases, then the prey individuals begin to enter diapause earlier but more gradually.

From the relations $\mathcal{S} = 0$, $\mathcal{S}' = 0$, $\mathcal{S}'' = 0$, and from the set of equations (3.15), a , b , and $\frac{du^s}{d\tau}$ can be expressed in terms of u^s , c , E , p , and r . While the expression of $\frac{du^s}{d\tau}$ can be expressed as a function of the system variables, its form does not allow for an easy analysis. We are particularly interested in the values of d for which $\frac{du^s}{d\tau}$ is non-negative: this would relate to an optimal strategy for the prey that is non-increasing in real time. We have observed this time-dependent profile for the mixed strategies consistently in simulations.

As a partial result, we try to find explicit values for d , for which $\frac{du^s}{d\tau} \geq 0$ for all possible r , E , and c , in the special instance of the absence of predators.

Proposition 32 (*Non-negativity of $\frac{du^s}{d\tau}$ in the absence of predators*) *In the absence of predators, there exists d^{\min} such that for any $E \in (0, 1)$, $u^s \in (0, 1)$, and r , the inequality $\frac{du^s}{d\tau} \geq 0$ holds for all $d > d^{\min}$.*

Proof. See Appendix C. □

3.4 Dependence of the optimal strategy on the predator density

Biological evidence suggests that a higher predator density in the environment induces an earlier diapause (Sabelis and Overmeer, unpublished data). Results of our analysis are aligned with this observation, although we could not prove this claim for the entire domain of initial parameters. Based on our reverse-time study, numerical analysis of the roots of equation (3.12) have shown τ_1 decreases if p^f (predator population level at the end of the summer season) increases. This leads us to claim that once the predator concentration level increases, the prey mites should enter diapause earlier but more gradually than if less predatory individuals were present, which would lead to a later complete diapause state than if less predatory mites were present. Recall that we have shown in the model that once prey individuals start entering diapause, they never become active again. The overall behavior is depicted in Figure 5.

Model simulations suggest the following:

- In the real time prey individuals start entering diapause earlier if the number of predatory individuals increases.
- The moment when all prey individuals enter diapause occurs later in the season if there are more predators at the end of the summer season.

- It is observed that in the case $p \neq 0$, $\frac{du}{dt} \leq 0$, and that the number of predators decreases as the prey start entering diapause.

4 Biological interpretation and recapitulation of the outcomes of the study

The inspiration for the development of the model has come from empirical observations on the interaction between predatory mites and fruit-tree red spider mites on apple trees. The spider mites feed on leaves during summer and may move away from leaves to lay winter eggs (the diapausing stage) on twigs, branches, and trunks of the tree where they cannot feed but are free of predatory mites. Setting model parameters to realistic values for this system and studying the model either analytically or numerically has led to conclude that the following behavior of the fruit-tree red spider mites is optimal:

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 diapaused 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 next year. Yet, if all prey individuals are in diapause in early summer, then they continue to stay in diapause until next year.
3. The time (in real time) of diapause onset state depends on the energy of the prey, on predator population size and on the rate of energy utilization (parameter d), 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 present. 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 gradually enters diapause, definitely not instantly. 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, 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 volatile) takes place.

Figure 6 summarizes possible optimal strategy profiles $u^*(\tau)$, $\tau \in [0, T]$, for the prey. Note that while we could not prove yet that the optimal strategy of the prey is non-increasing with t for all possible d , but could show that it is indeed non-increasing in the special case that $p = 0$ for all but a small range of the parameter d . This expected behavior has however been always observed in simulation.

5 Conclusion and research outlook

A dynamical model of the summer and winter predator-prey interactions between mites has been put forward. This model is an extension of the classic Lotka-Volterra

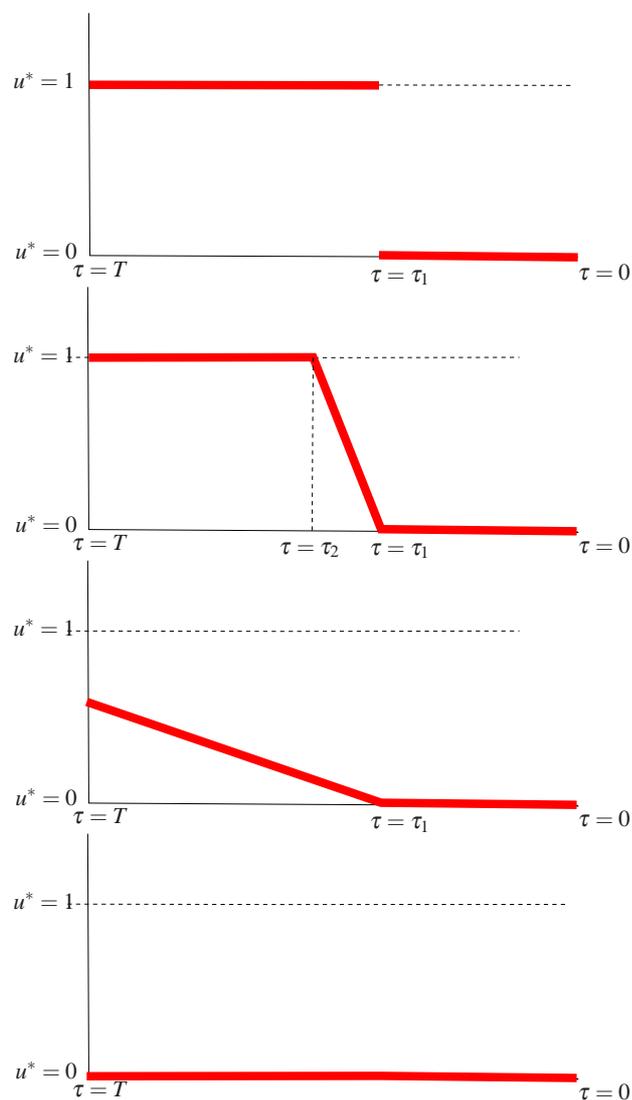


Fig. 6 Scheme of possible optimal strategies u^* for the prey. Based on the proposed dynamics and optimization problem, we have shown irreversibility and (largely) the monotonicity of the strategy profile. Notice that the optimal strategies do not need to be continuous corresponding to the singular events in the outcome of the optimization problem.

models in that it includes not only the dynamics of predator and prey populations, but also the dynamics of their energy level and an input for the prey. We have considered the case where predators do not enter diapause until after the summer season, but prey have the option to give up reproduction during summer and enter a refuge from predation where they also stay during winter. An optimal control problem formulation based on a population fitness function defined by the number

of diapausing individuals has allowed the study of the optimal behavior for the prey in the summer 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 prey population, 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 evolutionary stable.

An extension of the optimal control problem to a game-theoretical problem is not out of reach as long as the predator is either active or in diapause, without having an option to choose a mixed strategy. The more general solution is topic of further research.

References

1. Akhmetzhanov, A., Groganard, F., Mailleret, L.: Optimal life-history strategies in seasonal consumer-resource dynamics. *Evolution* **65**(11), 3113–3125 (2011)
2. Başar, T., Olsder, G.J.: *Dynamic Noncooperative Game Theory*. SIAM, Philadelphia, Pennsylvania (1999)
3. Bellman, R.: *Dynamic Programming*. Princeton University Press, Princeton, New Jersey (1957)
4. Bertsekas, D.P.: *Nonlinear Programming*. Athena Scientific, Belmont, Massachusetts (2003)
5. Danks, H.: *Insect Dormancy: An Ecological Perspective*. Biological Survey of Canada, Ottawa, Canada (1987)
6. DeLeenheer, P., Aeyels, D.: Accessibility properties of controlled Lotka-Volterra systems. In: *Proceedings of the 39th IEEE Conf. on Decision and Control*, pp. 3977–3981. Sydney, USA (2000)
7. Diekmann, O., Gyllenberg, M., Metz, J.A.J.: Physiologically structured population models: towards a general mathematical theory. In: Takeuchi, Y., Iwasa, Y., Sato, K. (eds.) *Biological and Medical Physics, Biomedical Engineering*, pp. 5–20. Springer, Berlin (2007)
8. Fitzgerald, J., Solomon, M.: Diapause induction and duration in the phyto-seiid mite *Typhlodromus pyri*. *Experimental & Applied Acarology* **12**, 135–145 (1991)
9. Goh, B., Leitmann, G., Vincent, T.: Optimal control of a prey-predator system. *Mathematical Biosciences* **19**, 263–286 (1974)
10. Gouzé, J.: Global behavior of n-dimensional Lotka-Volterra systems. *Mathematical Biosciences* **113**, 231–242 (1993)
11. Gouzé, J.: Global stabilization of n-dimensional population models by a positive control. In: *Proceedings of the 33rd IEEE Conf. on Decision and Control*, pp. 1335–1336. Orlando, USA (1994)

12. Helle, W., Sabelis, M.W.: Spider Mites: Their Biology, Natural Enemies and Control, *World Crop Pests*, vol. 1A. Elsevier (1985)
13. Helle, W., Sabelis, M.W.: Spider Mites: Their Biology, Natural Enemies and Control, *World Crop Pests*, vol. 1B. Elsevier (1985)
14. Hopper, J.L.: Opportunities and handicaps of antipodean scientists: A. J. Nicholson and V. A. Bailey on the balance of animal populations. *Historical Records of Australian Science* **7**(2), 179–188 (1987)
15. Kolmanovskii, V., Koroleva, N.: Control of a predator-prey system with intraspecies competition. *Journal of Applied Mathematics and Mechanics* **55**, 588–595 (1991)
16. Kroon, A., Veenendaal, R., Bruin, J., Egas, M., Sabelis, M.W.: Predation risk affects diapause induction in the spider mite *Tetranychus urticae*. *Experimental and Applied Acarology* **34**, 307–314 (2004)
17. Kroon, A., Veenendaal, R.L.: Trade-off between diapause and other life-history traits in the spider mite *Tetranychus urticae*. *Ecological Entomology* **23**(3), 298–304 (2005)
18. Kroon, A., Veenendaal, R.L., Bruin, J., Egas, M., Sabelis, M.W.: “Sleeping with the enemy” – predator-induced diapause in mite. *Naturwissenschaften* **95**, 1195–1198 (2008)
19. Kroon, A., Veenendaal, R.L., Egas, M., Bruin, J., Sabelis, M.W.: Diapause incidence in the two-spotted spider mite increases due to predator presence, not due to selective predation. *Experimental and Applied Acarology* **35**(1-2), 73–81 (2005)
20. Lika, K., Kooijman, S.A.L.M.: Life history implications of allocation to growth versus reproduction in dynamic energy budgets. *Bulletin Of Mathematical Biology* **65**, 809–834 (2003)
21. Lotka, A.J.: Undamped oscillations derived from the law of mass action. *Journal of the American Chemical Society* **42**, 1595–1599 (1920)
22. McNamara, J., Houston, A.I.: State-dependent life histories. *Nature* **380**(6571), 215–221 (1996)
23. Melikyan, A.: Necessary optimality conditions for a singular surface in the form of synthesis. *Journal of Optimization Theory and Applications* **82**(2), 203–217 (1994)
24. Melikyan, A.: *Generalized Characteristics of First Order PDEs: Applications in Optimal Control and Differential Games*. Birkhäuser, Boston (1998)
25. Melikyan, A., Olsder, G.: Boundary singularities and characteristics of Hamilton-Jacobi equation. *Journal of Dynamical and Control Systems* **16**(1), 77 – 99 (2010)
26. Metz, J.A.J., Mylius, S., Diekmann, O.: Even in the odd cases when evolution optimizes, unrelated population dynamical details may shine through in the ess. *Evolutionary Ecology Research* **10**, 655–666 (2008)
27. Metz, J.A.J., Mylius, S., Diekmann, O.: When does evolution optimize? *Evolutionary Ecology Research* **10**, 629–654 (2008)
28. Patchepsky, E., Nisbet, R., Murdoch, W.: Between discrete and continuous: Consumer-resource dynamics with synchronized reproduction. *Ecology* **89**(1), 280–288 (2008)
29. Perrin, N., Sibly, R.: Dynamic-models of energy allocation and investment. *Annual Review Of Ecology And Systematics* **24**, 379–410 (1993)

30. Perrin, N., Sibly, R., Nichols, N.: Optimal-growth strategies when mortality and production-rates are size-dependent. *Evolutionary Ecology* **7**(6), 576–592 (1993)
31. Persson, L., Roos, A.D.: Adaptive habitat use in size structured populations: Linking individual behavior to population processes. *Ecology* **84**(5), 1129–1139 (2003)
32. Staňková, K.: On Stackelberg and Inverse Stackelberg Games & Their Applications in the Optimal Toll Design Problem, the Energy Market Liberalization Problem, and in the Theory of Incentives. Ph.D. thesis, Delft University of Technology, Delft, The Netherlands (2009)
33. Tauber, M., Tauber, C., Masaki, S.: Seasonal adaptations of insects. Oxford University Press, New York, USA (1986)
34. Veerman, A.: Diapause in phytoseiid mites: a review. *Experimental and Applied Acarology* **14**, 1–60 (1992)
35. Volterra, V.: Variations and fluctuations of the number of the individuals in animal species living together. In: Chapman, R. (ed.) *Animal Ecology*. Mc. GrawHill, New York (1926)
36. Volterra, V.: Variations and fluctuations in the number of coexisting animal species (1927). In: Scudo, F., Ziegler, J. (eds.) *The golden age of theoretical ecology: 1923- 1940*, pp. 65–234. Springer-Verlag, Berlin, Germany (1978)

Appendix A: Why energy has to be included in the model (quantitative argument from Section 2.3)

Let us consider the instantiated model in (3.2)–(3.4), and assume that the population-dependent environmental feedback is not explicit, namely $E(t) = 1$, $t \in [0, T]$. Then the optimization problem (3.1)–(3.4) simplifies to

$$\begin{aligned} u^* &= \arg \sup_u \int_0^T (1-u)r dt'; \\ \frac{dp}{dt} &= \left(\frac{1}{5}ur - \frac{1}{20} \right) p, \\ \frac{dr}{dt} &= \left(\frac{1}{5}u - \frac{1}{20} - up \right) r. \end{aligned}$$

Introducing a value function $W(p, r, t, u) = \int_{T-t}^T (1-u)r dt'$ and the new variables $b \stackrel{\text{def}}{=} \frac{\partial W}{\partial p}$ and $c \stackrel{\text{def}}{=} \frac{\partial W}{\partial r}$, it is possible to show that the optimal control takes the form $u^* = \text{Heav } \mathcal{C}$, where

$$\mathcal{C} = \left(\frac{1}{5}pb - pc + \frac{1}{5}c - 1 \right) r,$$

which, as in the more general case, implies that the optimal behavior of the prey is again fully independent of the prey population level, and that $u^* = 0$ at the end of the season. The characteristic system can be expressed as follows:

$$\begin{cases} p' = \frac{1}{20}p - \frac{1}{5}upr, \\ r' = \frac{1}{20}r + upr - \frac{1}{5}ur, \\ b' = -\frac{1}{20}b + \frac{1}{5}urb - urc, \\ c' = \frac{1}{5}upb - \frac{1}{20}c - upc + \frac{1}{5}uc + 1 - u. \end{cases}$$

With reference to the reverse time τ , selecting a $u = 0$ and transversal conditions $b(0) = c(0) = 0$ yields:

$$\begin{aligned} p' &= \frac{1}{20}p \Rightarrow p(\tau) = p(0) e^{\frac{\tau}{20}}, \\ r' &= \frac{1}{20}r \Rightarrow r(\tau) = r(0) e^{\frac{\tau}{20}}, \\ b' &= -\frac{1}{20}b \Rightarrow b(\tau) = b(0) e^{-\frac{\tau}{20}} = 0, \\ c' &= 1 - \frac{1}{20}c \Rightarrow c(\tau) = 20 + e^{-\frac{\tau}{20}}(c(0) - 20) = 20 - 20e^{-\frac{\tau}{20}}. \end{aligned}$$

Hence, the condition $\mathcal{C} = 0$, related to mixed optimal strategies and $u^s \in (0, 1)$, can take place at time τ_1 if the following condition holds:

$$\begin{aligned} -p(0) \left(e^{\frac{\tau_1}{20}} \right)^2 r(0) \left(20 - 20e^{-\frac{\tau_1}{20}} \right) + \frac{1}{5} r(0) e^{\frac{\tau_1}{20}} \left(20 - 20e^{-\frac{\tau_1}{20}} \right) - r(0) e^{\frac{\tau_1}{20}} = \\ r(0) \left(-20p(0) e^{\frac{\tau_1}{10}} + 20p(0) e^{\frac{\tau_1}{20}} + 3e^{\frac{\tau_1}{20}} - 4 \right) = 0 \end{aligned} \quad (5.1)$$

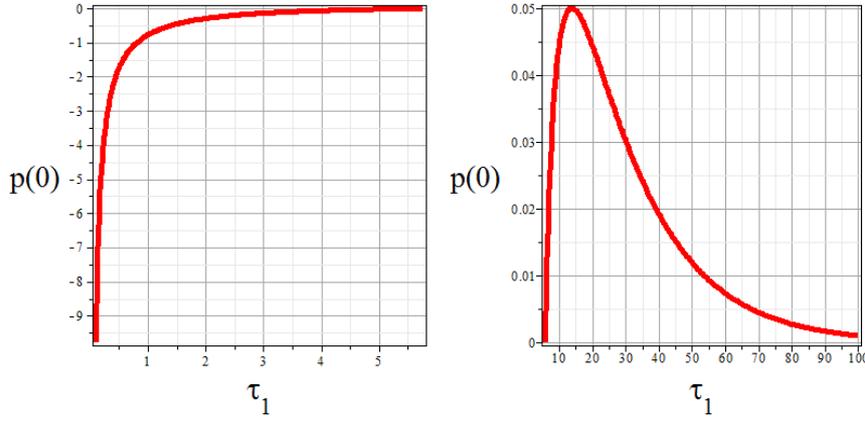


Fig. 7 If $p(0)$ and τ_1 are situated above the red curve, then $u^* = 0$ for the entire summer. (The variable τ_1 has to be higher than $-20 \ln \frac{3}{4} \approx 5.75$ as displayed in the left plot.)

Assuming that $r(0) > 0$, the equality in (5.1) is satisfied if $p(0) = \frac{-3+4e^{-\frac{\tau_1}{20}}}{20e^{\frac{\tau_1}{20}}(-1+e^{-\frac{\tau_1}{20}})}$.

Assuming that $p(0) \geq 0$, a time τ_1 such that $u(\tau_1) \neq 0$ exists if $\tau_1 \geq -20 \ln \frac{3}{4} \approx 5.75$. Furthermore, pairs $(\tau_1, p(0))$ related to possible non-zero optimal strategies for the prey are those corresponding to the curve depicted in Figure 7. For all the values of $(\tau_1, p(0))$, such that $p(0) < \frac{-3+4e^{-\frac{\tau_1}{20}}}{20e^{\frac{\tau_1}{20}}(-1+e^{-\frac{\tau_1}{20}})}$ (below the curve in

Figure 7) the optimal strategy of the prey is to switch to an active state, namely $u^*(\tau) = 1 \forall \tau \geq \tau_1$. For all the remaining values of $(\tau_1, p(0))$, which in practice means for $p(0) > 0.05$ and any τ_1 , the optimal strategy of the prey is to remain in diapause for the entire summer season: this in practice would deplete the energy of the prey and therefore would lead to its death. This leads to the conclusion that modeling the interactions of the considered system without including the energy variable leads to inconsistent outcomes.

The argument can be generalized to models that are parameterized as in (3.3)-(3.4), that is where α and γ have not been fixed to the values $1/20$ and $1/5$, respectively. It can be algebraically shown that the maximal value of the curve $p(0)$ is upper bounded by the quantity $(\gamma - \alpha)$ which, given the ranges of interest, is again a very small quantity.

Appendix B: Proof of Proposition 31

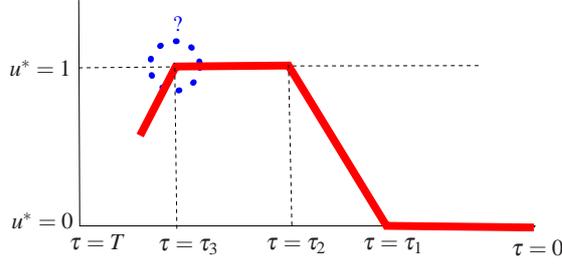


Fig. 8 Study of the existence of a second event in reverse time: can the optimal strategy u^* again admit values within the interval $[0, 1)$, after being equal to 1?

As portrayed in Figure 8, let us assume that there exists a time $\tau_3 : u^*(\tau_3) = 1$ and there exists a $\delta > 0 : \forall \tau \in (\tau_3, \tau_3 + \delta] : u^*(\tau) \in [0, 1)$. Let variable $E_2 \stackrel{\text{def}}{=} E(\tau_2)$. Setting $u^* = 1$ for $\tau > \tau_2$, the energy $E(\tau)$ satisfies

$$E(\tau) = 1 + (E_2 - 1)e^{d(\tau - \tau_2)},$$

therefore $E_3 \stackrel{\text{def}}{=} E(\tau_3) = 1 + (E_2 - 1)e^{d(\tau_3 - \tau_2)}$. Moreover, let us introduce the following variables: $a_3 \stackrel{\text{def}}{=} a(\tau_3)$, $c_3 \stackrel{\text{def}}{=} c(\tau_3)$, $p_3 \stackrel{\text{def}}{=} p(\tau_3)$, and $r_3 \stackrel{\text{def}}{=} r(\tau_3)$.

At time $\tau = \tau_3$, the condition $\mathcal{S} = 0$ has to be satisfied. Substituting expression for E_3 into equation $\mathcal{S} = 0$ leads to

$$\begin{aligned} & \frac{1}{250} (1 + e^{d(\tau_3 - \tau_2)} (E_2 - 1)) a_3 + d a_3 - d (1 + e^{d(\tau_3 - \tau_2)} (E_2 - 1)) a_3 + \frac{1}{5} p_3 r_3 b_3 \\ & - p_3 r_3 c_3 + \frac{1}{5} (1 + e^{d(\tau_3 - \tau_2)} (E_2 - 1)) r_3 c_3 - (1 + e^{d(\tau_3 - \tau_2)} (E_2 - 1)) r_3 = 0. \end{aligned}$$

From this equation we can express E_2 as:

$$E_2 = 1 + \frac{a_3 + 50 p_3 r_3 b_3 - 250 p_3 r_3 c_3 + 50 r_3 c_3 - 250 r_3}{e^{d\Delta} (250 d a_3 - a_3 - 50 r_3 c_3 + 250 r_3)}, \quad (5.2)$$

where we have set $\Delta = \tau_3 - \tau_2 > 0$. Since $E_2 \in (0, 1]$, the inequality (5.2) is satisfied only if

$$1 > \frac{250 p_3 r_3 c_3 - a_3 - 50 p_3 r_3 b_3 - 50 r_3 c_3 + 250 r_3}{e^{d\Delta} (250 d a_3 - a_3 - 50 r_3 c_3 + 250 r_3)} \geq 0. \quad (5.3)$$

Recall that if there is a second event at time τ_3 , then $\mathcal{S}(\tau_3) = 0$, but also $\mathcal{S}'(\tau_3) = \mathcal{S}''(\tau_3) = \dots = 0$. From the equation $\mathcal{S}' = 0$ the parameter a_3 can be

expressed in terms of the other variables:

$$\begin{aligned}
a_3 = & \frac{r_3}{10d} (2c_3 - 2c_3e^{d\Delta} + 875e^{d\Delta}E_2 - 2500p_3 + 375 - 125p_3c_3 \\
& + 2500e^{d\Delta}p_3 + 25p_3b_3 + 500e^{2d\Delta}(E_2)^2 - 1000e^{2d\Delta}E_2 + 2c_3e^{d\Delta}E_2 \\
& - 2500e^{d\Delta}E_2p_3a_3 + 2500de^{d\Delta} - 2500de^{d\Delta}E_2 \\
& + 500e^{2d\Delta} - 875e^{d\Delta}). \tag{5.4}
\end{aligned}$$

Furthermore, b_3 can be expressed from the equation $\mathcal{S}'' = 0$ (after substituting (5.4) into this same equation), and likewise c_3 can be expressed from the condition $\mathcal{S}''' = 0$ (after substituting expressions for a_3 and b_3 into this equation) – we omit reporting the expressions for b_3 and c_3 , as their computation is straightforward.

Denoting the nominator and denominator of the fraction in Equation (5.3) as “Nom” and “Den”, respectively, there are two cases characterizing the necessary conditions in (5.3), for the existence of a $\tau_3 > \tau_2$ such that $u(\tau) = 1$ for $\tau \in [\tau_2, \tau_3]$ and of a $\delta > 0 : \forall \tau \in (\tau_3, \tau_3 + \delta], u(\tau) \in (0, 1)$:

Case 1

$$0 \leq \text{Nom}, \tag{5.5}$$

$$0 < \text{Den}, \tag{5.6}$$

$$0 < \text{Den} - \text{Nom}. \tag{5.7}$$

Case 2

$$0 \geq \text{Nom}, \tag{5.8}$$

$$0 > \text{Den}, \tag{5.9}$$

$$0 > \text{Den} - \text{Nom}. \tag{5.10}$$

The quantities Den and Nom can be then written with E_2 expressed by (5.2). In the following, the two cases are considered in detail.

Case 1: Condition (5.5) implies

$$250r_3 - 50p_3r_3b_3 + 250p_3r_3c_3 - 50r_3c_3 \leq a_3, \tag{5.11}$$

whereas condition (5.6) implies

$$a_3 < \frac{50r_3(c_3 - 5)}{250d - 1} \tag{5.12}$$

and condition (5.7) implies

$$a_3 < \frac{50r_3(e^{d\Delta}c_3 - 5e^{d\Delta} - b_3p_3 + 5p_3c_3 - c_3 + 5)}{-e^{d\Delta} + 250e^{d\Delta}d + 1}. \tag{5.13}$$

Note that inequalities (5.11) and (5.12) imply either

$$0 < -50r_3b_3 + 250r_3c_3 \tag{5.14}$$

and

$$p_3 < -\frac{250d(c_3 - 5)}{(250d - 1)(b_3 - 5c_3)}, \quad (5.15)$$

or

$$-50r_3b_3 + 250r_3c_3 < 0 \quad (5.16)$$

and

$$\frac{-250d(c_3 - 5)}{(250d - 1)(b_3 - 5c_3)} < p_3. \quad (5.17)$$

We have substituted the expressions for a_3 , b_3 , and c_3 into inequalities (5.14), (5.15), and (5.16), (5.17), respectively. Assuming that $p_3 > 0$, $r_3 > 0$, $E^f \in (0, 1]$, and $d > \frac{1}{250}$, in both cases it can be shown that

$$a_3 > \frac{50r_3(e^{d\Delta}c_3 - 5e^{d\Delta} - b_3p_3 + 5p_3c_3 - c_3 + 5)}{-e^{d\Delta} + 250e^{d\Delta}d + 1},$$

which contradicts equation (5.13) and therefore also equation (5.7).

Case 2: Condition (5.8) implies

$$250r_3 - 50p_3r_3b_3 + 250p_3r_3c_3 - 50r_3c_3 \geq a_3, \quad (5.18)$$

whereas condition (5.9) implies

$$a_3 > \frac{50r_3(c_3 - 5)}{250d - 1} \quad (5.19)$$

and condition (5.10) implies

$$a_3 > \frac{50r_3(e^{d\Delta}c_3 - 5e^{d\Delta} - b_3p_3 + 5p_3c_3 - c_3 + 5)}{-e^{d\Delta} + 250e^{d\Delta}d + 1}. \quad (5.20)$$

Note that the inequalities in (5.18) and (5.19) imply either

$$0 < -50r_3b_3 + 250r_3c_3 \quad (5.21)$$

and

$$p_3 > \frac{-250d(c_3 - 5)}{(-1 + 250d)(b_3 - 5c_3)}, \quad (5.22)$$

or

$$-50r_3b_3 + 250r_3c_3 < 0 \quad (5.23)$$

and

$$\frac{-250d(c_3 - 5)}{(-1 + 250d)(b_3 - 5c_3)} > p_3. \quad (5.24)$$

We have substituted expressions for a_3 , b_3 , and c_3 into inequalities (5.21), (5.22), and (5.23), (5.24), respectively. Assuming that $p_3 > 0$, $r_3 > 0$, $E^f \in (0, 1]$, and $d > \frac{1}{250}$, in both cases it can be shown that

$$a_3 < \frac{50 r_3 (e^{d\Delta} c_3 - 5 e^{d\Delta} - b_3 p_3 + 5 p_3 c_3 - c_3 + 5)}{-e^{d\Delta} + 250 e^{d\Delta} d + 1},$$

which contradicts equation (5.20) and therefore also equation (5.10). \square

Appendix C: Proof of Proposition 32

If $p = 0$, the characteristic system takes the following form in reverse time:

$$\begin{cases} E' = \frac{1}{250}(1-u)E - du + duE, \\ r' = \frac{1}{20}r - \frac{1}{5}uEr, \\ a' = -\frac{1}{250}(1-u)a - dua + \frac{1}{5}urc + (1-u)r, \\ c' = -\frac{1}{20}c + \frac{1}{5}uEc + (1-u)E. \end{cases} \quad (5.25)$$

Furthermore, the surface \mathcal{S} can be expressed as

$$\mathcal{S} = \frac{1}{250}Ea + da - dEa + \frac{1}{5}Er c - Er, \quad (5.26)$$

It is again easy to check that $u^s(0) = 0$ in reverse time, and that $\tau_1 = 500 \ln w$, with w being the smallest root of the following polynomial

$$100(E^f)^2 w^{31} + (-25E^f - 500dE^f)w^{29} + 500dw^{27} - 100(E^f)^2 w^4 + (-2E^f + 500dEf)w^2 - 500d.$$

From (5.25), the energy level E^1 of the prey entering diapause is $E(\tau_1) = E^f e^{\frac{\tau_1}{250}}$. Figure 2 represents the values of τ_1 as functions of d and E^f . Notice that $E^1 \geq 1$ for $E^f \geq 0.9775$, therefore in the following we will assume that $E^f \in (0, 0.9775)$. (Moreover, recall that $d > 1/250$.)

Equations $\mathcal{S} = 0$, $\mathcal{S}' = 0$, and $\mathcal{S}'' = 0$ allow expressing $a(\tau)$, $c(\tau)$, and $u^s(\tau)$ in terms of $r(\tau)$ and $E(\tau)$, respectively. Of interest to this proof, the expression for the mixed strategy $u^s(\tau)$ reads as the ratio of two polynomials: $(E(-25E^2 - 29 \cdot 10^3 dE^3 + 125 \cdot 10^3 d^2 E^2 + 116E^3 - 13 \cdot 10^3 dE + 230 \cdot 10^3 d^2 + 67750dE^2 - 375 \cdot 10^3 d^2 E)) / (4(-125dE^2 - 5 \cdot 10^3 d^2 E - 21E^4 - 1250 \cdot 10^3 d^3 + 100E^5 - 9 \cdot 10^3 dE^3 + 54250dE^4 + 531250d^2 E^2 - 875 \cdot 10^3 d^2 E^3 + 1250 \cdot 10^3 d^3 E + 250 \cdot 10^3 d^2 E^4 - 25 \cdot 10^3 E^5 d))$.

Remarkably, the expression is independent of r , which aligns to earlier outcomes on the independence of the prey population density.

Since u^s cannot by definition take values that are lower than 0 or greater than 1, we denote the values for (d, E) for which $u^s \in [0, 1]$ as “feasible” and we will call those for which $u^s \notin [0, 1]$ “unfeasible.” Figure 9 represents the feasibility regions for (d, E) , assuming $d \in (\frac{1}{250}, 1]$ and $E \in (0, 0.9775]$. The feasible region for the given parameters corresponds to possible trajectories that have mixed strategies, whereas the unfeasible region relates to trajectories that stay always in diapause mode ($u^s = 0$), or discontinuously switch to $u^s = 1$. In either case, trajectories for the optimal strategy will be non-decreasing in reverse time.

From $\mathcal{S}''' = 0$ we can derive the expression of $\frac{du^s}{d\tau}$. Figure 10 plots the parts of the feasibility region for which u^s is increasing and decreasing, respectively.

With focus on the feasible region, the following observations can be made:

- For $d > 0.15$, no mixed strategy takes place, since the parameter space corresponds to the unfeasible region.
- For $\frac{1}{250} < d < 0.15$, either
 - no mixed strategy takes place if E is small, else
 - a mixed strategy u^s takes place.

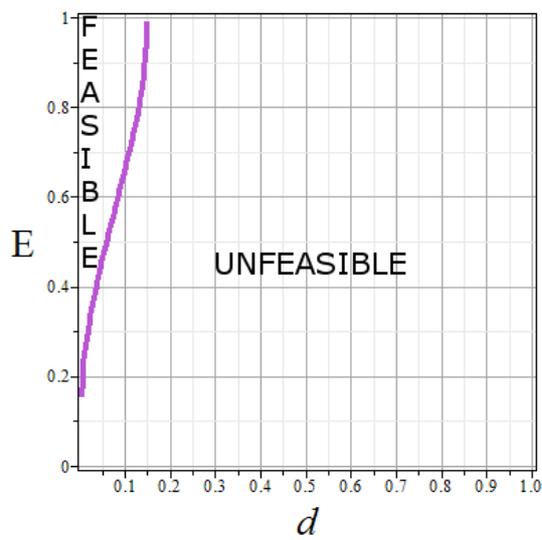


Fig. 9 Regions of d and E for which $u^s \in (0, 1]$. The purple bold line corresponds to d and E for which $u^s = 1$ and coincides with the boundary of the feasibility region.

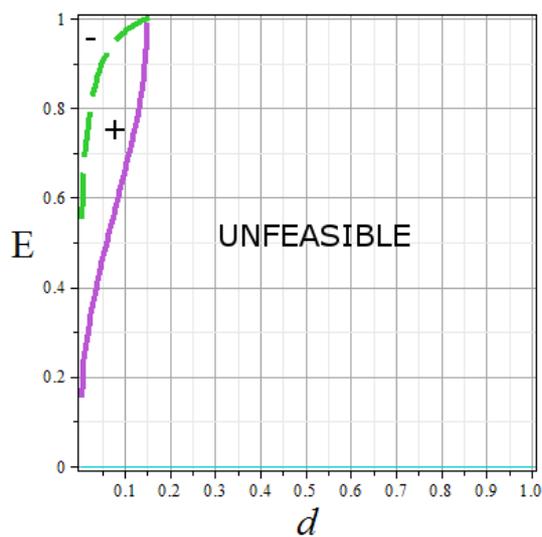


Fig. 10 Regions of d and E for which $\frac{du^s}{d\tau} > 0$ (denoted with a +) and for which $\frac{du^s}{d\tau} < 0$ (denoted by a -). The green dashed line corresponds to the (d, E) values for which $\frac{du^s}{d\tau} = 0$.

Let us further elaborate on the latter case (presence of mixed strategies) with the help of Figure 10. Recall that

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

and assume the dynamics at time τ_1 land in a region where u^s has negative derivative. It can be numerically shown that the values of u^s are quite small in this region. Because of the values of $E > 0.5$ and $1/250 < d < 0.15$, $E' > 0$ persistently, given that $du^s/dt < 0$. This regime will be sustained until $E = 1$, which will force u^s to switch to $u^* = 1$. Given the values of the quantities of interest, this will happen for a short interval – if $d = \frac{1}{250}$, the interval will be approximately less than 0.5, whereas if $d \sim 0.15$, the interval will be even smaller. \square