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

Kateřina Staňková · Alessandro Abate · Maurice W. Sabelis

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 length of a season. 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 includes 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 laboratory and field studies. 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. 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

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irreversible process; (2) for the vast majority of parameter space, the portion of prey individuals entering 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 diapause more gradually. This optimal population strategy will be studied for its ESS properties in a sequel to the work presented in this article.

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) (Lotka 1920; Volterra 1926, 1978; Hopper 1987). 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 (Pachepsky et al. 2008). 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 (Danks 1987; Tauber et al. 1986).

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 (Helle and Sabelis 1985a,b). In this environment, winters (covering 6–7 months) are usually harsh and as such endanger the survival of prey (Helle and Sabelis 1985a) and (even more so) that of predators (Fitzgerald and Solomon 1991; Helle and Sabelis 1985a). Predator and prey densities in the following summer season depend on their numbers entering a state of physiological rest (the so-called diapause state) near the end of 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 (Veerman 1992). 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 (Kroon et al. 2004, 2005, 2008). 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 (Kroon and Veenendaal 2005). 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 employ an optimal control approach to find the best strategies for the prey population as a whole. If there is an optimal solution, then this may not necessarily be the evolutionarily best solution for any given prey individual, since selection acts on individuals being the vehicles of genes. Moreover, adaptive landscapes (sensu Wright (1932)) may shift in the course of invasion by mutants. Therefore, it remains to be seen whether the intra-seasonal optimal solutions obtained in this work are robust against invasions of mutants with alternative strategies (Gyllenberg and Service 2011; Metz 2008).

Historical background of our model: The optimal control model that we propose has been developed as an extension of the classical Lotka–Volterra predator–prey model (Lotka 1920; Volterra 1926). Our model includes a control mechanism that allows the prey individuals being active or in diapause.

In the literature, the classical Lotka–Volterra model has been extended to a framework allowing for n different interacting populations (Gouzé 1993), as well as to an input-dependent setup (Kolmanovskii and Koroleva 1991), following the first study of controlled predator–prey models in Goh et al. (1974). Reachability properties of controlled Lotka–Volterra systems were studied in DeLeenheer and Aeyels (2000). The n-dimensional Lotka–Volterra system was extended in Gouzé (1994), where a stabilization issue was studied.

Two models have been published on questions related to the problem at hand in this article (Akhmetzhanov et al. 2011; Gyllenberg et al. 1996). In Akhmetzhanov et al. (2011) a controlled predator–prey model based on the simplified Lotka–Volterra dynamics is introduced and optimal reproduction behavior of the prey is studied. This model includes internal energy of the prey similarly to the model introduced in this article. In Gyllenberg et al. (1996) a hybrid model including continuous mortality and discrete reproduction at the end of the season is introduced. This model is based on the assumption that the life span of the predator is much longer than that of the prey and focuses mainly on inter-seasonal behavior of the system in question.

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

n	Season number
T_n	Length of the nth 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
$\mathscr{S}$	Singular surface (as used in the analysis of the optimal control problem)
$\mathscr{C}$	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 hits at extensions toward a game. With focus on a single season, Sect. 3 formally studies the optimal strategies of the prey. Section 4 elaborates on the biological interpretation of the obtained results. 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 (Sect. 2.1) and then extending it to the inter-seasonal (multiple seasons) dynamics (Sect. 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 year is divided into two parts: the *summer* and *winter* season. The predator is assumed to be active during the entire summer season. With regards to the interaction between predatory and fruit-tree red spider mites, during the summer season both species can feed (which leads to reproduction), respectively by predation and by feeding on leaves of apple trees. Furthermore, prey can enter diapause, a quiescent state that protects it from the environment and from predation—this in particular entails the decoupling between the species. 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:

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

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):

$$\frac{\mathrm{d}E_n(t)}{\mathrm{d}t} = -m\,(1 - u_n(t))E_n(t) + d\,u_n(t) - d\,u_n(t)\,E_n(t), \tag{2.2}$$

$$\frac{\mathrm{d}P_n(t)}{\mathrm{d}t} = -\alpha\,P_n(t) + \beta\,\gamma\,u_n(t)\,P_n(t)\,R_n(t), \tag{2.3}$$

$$\frac{\mathrm{d}R_n(t)}{\mathrm{d}t} = -\alpha\,R_n(t) + \gamma\,u_n(t)\,E_n(t)\,R_n(t) - \beta\,u_n(t)\,P_n(t)\,R_n(t). \tag{2.4}$$

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 Eq. (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 $(1, \frac{\gamma-\alpha}{\beta}, \frac{\alpha}{\beta\gamma})$. 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 $(1, \frac{\gamma-\alpha}{\beta}, \frac{\alpha}{\beta\gamma})$ 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 $\frac{\mathrm{d}E_n}{\mathrm{d}t} \geq 0$.

Remark 2 The dynamical model in Eqs. (2.2)–(2.4) is a straightforward generalization of the known Lotka–Voltera, predator–prey model (Lotka 1920; Volterra 1926), 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).

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 (here arg sup reads as "arguments of the supremum" and indicate the points at which the supremum occurs):

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

2.2 Winter dynamics

As mentioned at the beginning of Sect. 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 (diapaused) prey is supposed to drop.

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

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

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 $u = (u_1, \ldots, u_n)$.

Investigating the optimal strategy for the prey over multiple seasons (years) is an interesting goal, which is related to the evolutionarily stability of the optimal strategy found. Bifurcation analysis can be used in order to determine parameter domains for which the proposed optimal strategy is evolutionarily stable (Diekmann et al. 2007). 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 (Metz 2008; Metz et al. 2008) 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 (McNamara and Houston 1996). To determine the optimal life history of an individual it is useful to incorporate physiological variables in the model (McNamara and Houston 1996; Persson and Roos 2003). In our model 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" (Perrin and Sibly 1993).

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. In fact, 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 (Perrin and Sibly 1993) and (Perrin et al. 1993; Lika and Kooijman 2003)). 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 is made explicit through an energy variable. 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 in diapause—they ever become active again). The study of the multi-seasonal dynamics of the system (such as the evolutionarily 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 (Başar and Olsder 1999; Staňková 2009), with the predator acting as the leader and the prey as the follower. Games of the Stackelberg type 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 (Başar and Olsder 1999). 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 (1957), we apply the method of singular characteristics (Melikyan 1998; Melikyan and Olsder 2010) to formalize the solution of the problem.

Let us start with parameterizing the model. Using information from Helle and Sabelis (1985a,b) 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

$$u^* = \arg\sup_u \int_0^T (1 - u(t'))E(t')\, r(t')\mathrm{d}t', \tag{3.1}$$

subject to the following dynamics:

$$\frac{\mathrm{d}E}{\mathrm{d}t} = -\frac{1}{250}(1-u)\, E + d\, u - d\, u\, E, \tag{3.2}$$

$$\frac{\mathrm{d}p}{\mathrm{d}t} = -\frac{1}{20}\, p + \frac{1}{5}\, u\, p\, r, \tag{3.3}$$

$$\frac{\mathrm{d}r}{\mathrm{d}t} = -\frac{1}{20}\, r + \frac{1}{5}\, u\, E\, r - u\, p\, r, \tag{3.4}$$

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)–(3.4), are Pontryagin's maximum principle and Bellman's dynamical programming approach (Bellman 1957; Bertsekas 2003; Başar and Olsder 1999; Kirk 1970; Dreyfus 2002). Here, we choose the latter approach, since Pontryagin's maximum principle provides only necessary conditions that the optimal solution must satisfy, and the validation of which of these candidate solutions is optimal can be a difficult task.

Bellman's dynamical programming approach provides, on the other hand, sufficient conditions that the solution must satisfy.

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

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

The value function (3.5) is to be maximized for any $\tau \in [0, T]$ as the 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 (Bellman 1957):

$$\begin{aligned} -\frac{\partial V}{\partial \tau} + \sup_u \left(\frac{\partial V}{\partial E} \left(-\frac{1}{250}(1-u)\, E + d\, u - d\, u\, E \right) + \frac{\partial V}{\partial p} \left(-\frac{1}{20} p + \frac{1}{5}\, u\, p\, r \right) \right. \\ \left. + \frac{\partial V}{\partial r} \left(-\frac{1}{20} r + \frac{1}{5} u\, E\, r - u\, p\, r \right) + (1-u)\, E\, r \right) = 0. \end{aligned} \tag{3.6}$$

Let us introduce the additional variables $a \overset{\text{def}}{=} \frac{\partial V}{\partial E}$, $b \overset{\text{def}}{=} \frac{\partial V}{\partial p}$, $c \overset{\text{def}}{=} \frac{\partial V}{\partial r}$, obtaining the following characteristic system (Melikyan 1998) (here $E' = \frac{\mathrm{d}E}{\mathrm{d}\tau}$, and similarly for the remaining variables):

$$\begin{cases} E' = \frac{1}{250}(1-u)E - d\, u + d\, u\, E, \\ p' = \frac{1}{20} p - \frac{1}{5} u\, p\, r, \\ r' = \frac{1}{20} r + u\, p\, r - \frac{1}{5} u\, E\, r, \\ a' = -\frac{1}{250}(1-u)a - dua + \frac{1}{5} u\, r\, c + (1-u)r, \\ b' = -\frac{1}{20} b + \frac{1}{5} u\, r\, b - u\, r\, c, \\ c' = \frac{1}{5} u\, p\, b - \frac{1}{20} c - u\, p\, c + \frac{1}{5} u\, E\, c + (1-u)E. \end{cases} \tag{3.7}$$

3.2 Solution of the optimal control problem

As shown in Melikyan (1994), from Eq. (3.6) it can be seen that the optimal control u^* maximizes the quantity $u\,\mathscr{S}$, where

$$\mathscr{S} = \frac{1}{250} Ea + da - dEa + \frac{1}{5} p\, r b - p\, r\, c + \frac{1}{5} E\, r\, c - E\, r, \tag{3.8}$$

and where the quantity $\mathscr{S}$ is defined as $\mathscr{S} = \partial h / \partial u$, with h representing the argument of the supremization in the HJB Eq. (3.6). Notice that the quantity $\mathscr{S}$ 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 Melikyan (1994):

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

Furthermore, whenever $\mathscr{S}(\tau) = 0$, then $u^*(\tau) \in (0, 1)$, which denotes a mixed[1] strategy.

On the other hand, if $u^*(\tau) \in (0, 1)$ is optimal, then $\mathscr{S}(\tau) = 0$ is invariant with respect to τ for $u^*(\tau)$, which implies that $\mathscr{S}(\tau) = 0$, as well as $\mathscr{S}'(\tau) = 0$, $\mathscr{S}''(\tau) = 0$ (and similarly for higher-order derivatives), which can be shown by application of the Jacobi brackets (Melikyan 1994).

The transversal conditions (Melikyan 1998, 1994) 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 $\mathscr{S}$ for state variables evaluated at time T by $\mathscr{S}(T)$. It follows that $\mathscr{S}(T) = -E(T)\,r(T) < 0$, and, therefore,

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

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).

It is possible to emit the characteristic field (Melikyan 1998) in reverse time, starting from the terminal surface at time T, with $u^*(\tau) = 0$. This yields, for $\tau \geq 0$:

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

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

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

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

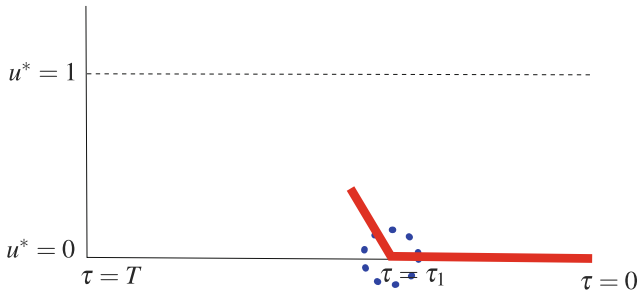

Fig. 1 Event time τ_1, corresponding to the optimal control $u^*(\tau_1)$ becoming positive. Recall that the formulation is in reverse time

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 $\mathscr{S}(\tau_1) = 0$, which leads to the situation when $u^*(\tau_1)$ becomes positive (see pictorial representation in Fig. 1).

The continuity of the characteristic trajectories (Melikyan 1998) in (3.10), (3.11) implies that equation $\mathscr{S}(\tau_1) = 0$ can be rewritten as follows:

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

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).

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

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

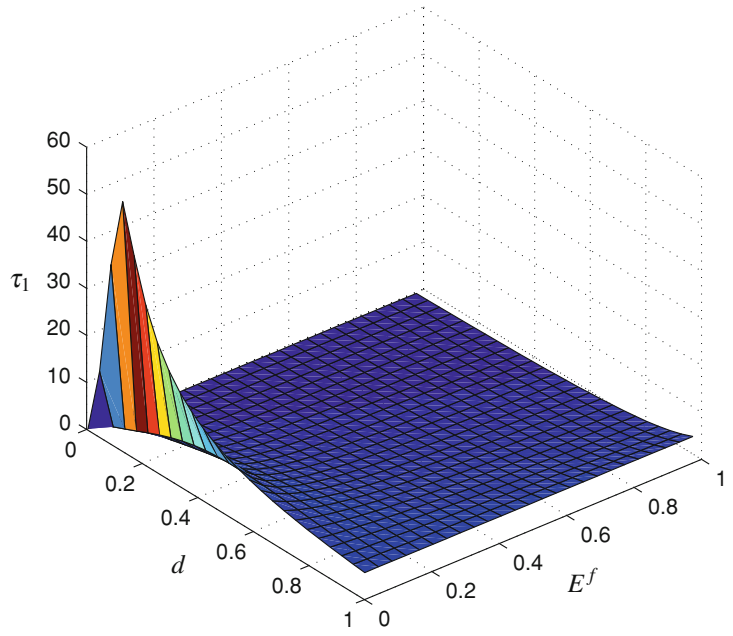

Fig. 2 Graph of the dependence of τ_1 with respect to d and E^f, for the case where $p^f = 0$

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

$$\begin{aligned} &625 \cdot 10^8((w^{29} - w^2)E^f - w^{27} + 1)d + 625 \cdot 10^8(w^{54} - w^{27})E^f p^f \\ &+((1 - 125 \cdot 10^8)w^{31} + (125 \cdot 10^8 + 1)w^4)(E^f)^2 \\ &+(3{,}125 \cdot 10^6 w^{29} + 25 \cdot 10^7 w^2)E^f. \end{aligned} \tag{3.12}$$

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 Fig. 2. It can be shown that values of τ_1 decrease with increasing p^f (see Sect. 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 $\mathscr{S}(\tau) = 0$ and $u^*(\tau) \in (0, 1)$. We will study of the properties of $u^*(\tau)$ over $\mathscr{S}(\tau) = 0$ in the next section. Assume that there is a time $\tau_2 > \tau_1$ which is associated to the condition $\mathscr{S}(\tau) > 0$: we investigate whether the condition $\mathscr{S}(\tau) = 0, \tau > \tau_2$, 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 $\tau \in (\tau_3, \tau_3 + \delta]$, $u^*(\tau) \in [0, 1)$.

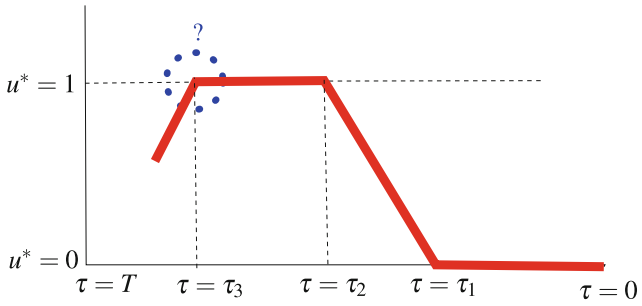

Fig. 3 Study of the existence of a second event in reverse time: can the optimal strategy u^* again admit values within the interval [0, 1), after being equal to 1?

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

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

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 $\tau \geq \tau_1$:

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

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 $\tau_2^{\max}$ represents an (possibly infinite) upper bound on the length of time during which the prey is physiologically active.

Proposition 3.1 (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

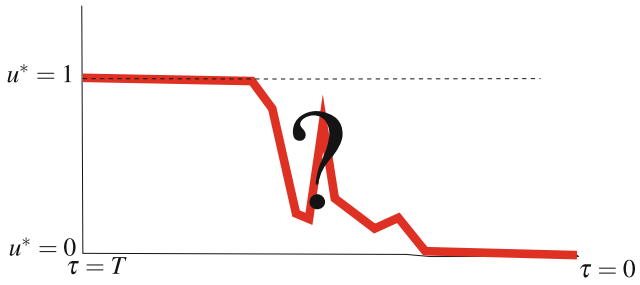

Fig. 4 We investigate the properties mixed strategies in time: is a non-monotonic profile of u^* possible, or is $\frac{\mathrm{d}u^*}{\mathrm{d}\tau}$ nondecreasing (in reverse time) within $\mathscr{S} = 0$?

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., $\mathscr{S}(\tau) < 0$ 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 $\mathscr{S}(\tau) = 0$), thus never reaching the value 1 (this would be related to the condition $\mathscr{S}(\tau) \leq 0$ for all $\tau \in [0, T]$).

In the following we study the behavior of the optimal control u^* on the singular surface $\mathscr{S} = 0$. 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 $\mathscr{S}(\tau) = 0$: this would allow ruling out the biologically inconsistent behavior depicted in Fig. 4.

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:

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

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 (Melikyan 1998):

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

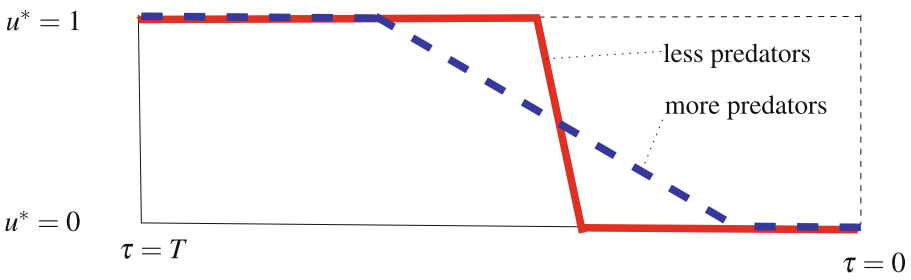

Fig. 5 Numerical simulations suggest that if the number of predators increases, then the prey individuals begin to enter diapause earlier but more gradually

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

From the relations $\mathscr{S} = 0$, $\mathscr{S}' = 0$, $\mathscr{S}'' = 0$, and from the set of Eq. (3.15), a, b, and $\frac{\mathrm{d}u^s}{\mathrm{d}\tau}$ can be expressed in terms of u^s, c, E, p, and r. While the expression of $\frac{\mathrm{d}u^s}{\mathrm{d}\tau}$ 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 $\frac{\mathrm{d}u^s}{\mathrm{d}\tau}$ 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 $\frac{\mathrm{d}u^s}{\mathrm{d}\tau} \geq 0$ for all possible r, E, and c, in the special instance of the absence of predators.

Proposition 3.2 (Non-negativity of $\frac{\mathrm{d}u^s}{\mathrm{d}\tau}$ 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* $\frac{\mathrm{d}u^s}{\mathrm{d}\tau} \geq 0$ *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 Eq. (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 Fig. 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 $p \neq 0$, $\frac{\mathrm{d}u}{\mathrm{d}t} \leq 0$, 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 lead 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 volatiles) 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

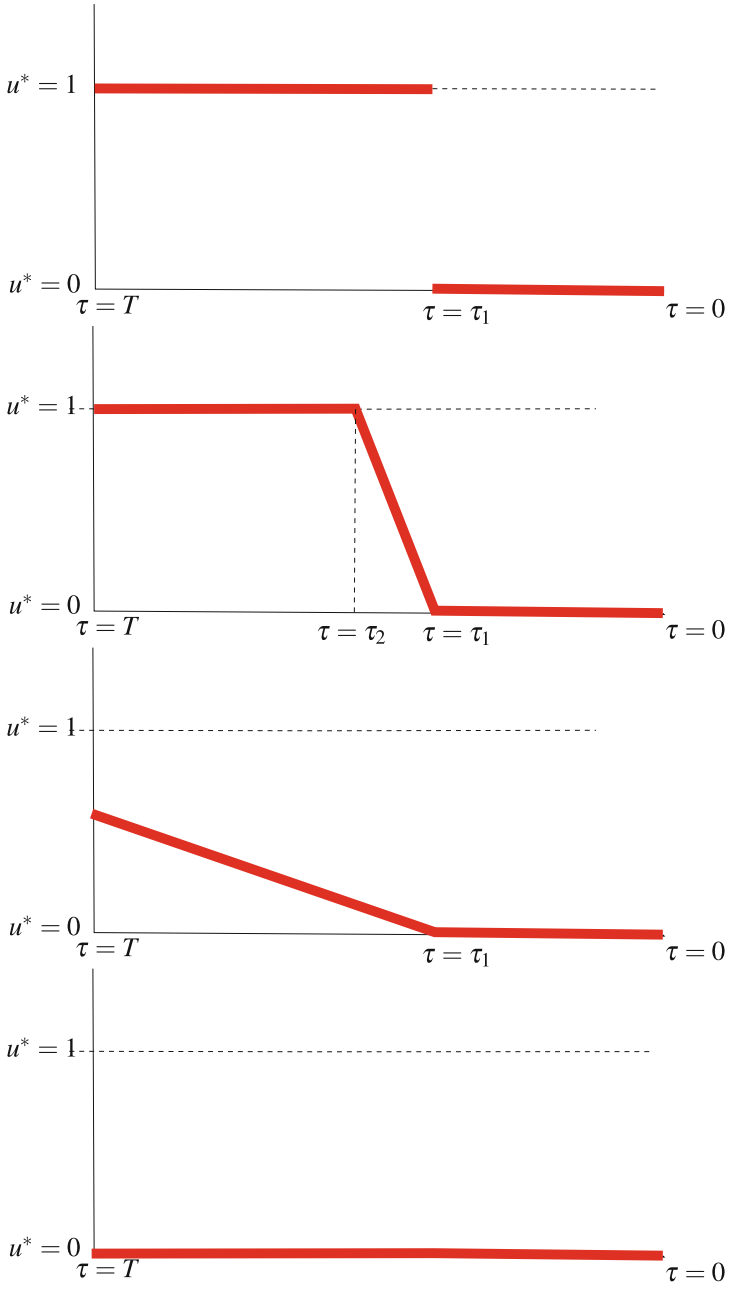

Fig. 6 Scheme of possible optimal strategies u^* for the prey. Based on the proposed dynamics and optimization problem, we have shown irreversibility and (largely) the monotonicity of the strategy profile. Notice that the optimal strategies do not need to be continuous corresponding to the singular events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

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 simulations.

5 Conclusion and research outlook

A dynamical model of the summer and winter predator–prey interactions between mites has been described and analyzed in this article. This model is an extension of

the classic Lotka–Voltera 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. Based on a population fitness function defined by the the number of diapausing individuals we developed an optimal control model to assess optimal behavior of the prey during summer.

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 evolutionarily stable.

The optimal control problem considered in this article can be readily extended to a game-theoretical problem, provided that the predator is either active or in diapause, without having an option to choose a mixed strategy. The more general solution is a topic of further research.

Appendix A: Why energy has to be included in the model (quantitative argument from Sect. 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

$$
\begin{aligned}
u^* &= \arg\sup_u \int_0^T (1-u) r \, \mathrm{d}t'; \\
\frac{\mathrm{d}p}{\mathrm{d}t} &= \left(\frac{1}{5} u r - \frac{1}{20}\right) p, \\
\frac{\mathrm{d}r}{\mathrm{d}t} &= \left(\frac{1}{5} u - \frac{1}{20} - u\, p\right) r.
\end{aligned}
$$

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

$$
\mathscr{C} = \left(\frac{1}{5} p b - p c + \frac{1}{5} c - 1\right) r,
$$

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:

$$\begin{cases} p' = \frac{1}{20}p - \frac{1}{5}u\,p\,r, \\ r' = \frac{1}{20}r + u\,p\,r - \frac{1}{5}u\,r, \\ b' = -\frac{1}{20}b + \frac{1}{5}u\,rb - u\,rc, \\ c' = \frac{1}{5}u\,pb - \frac{1}{20}c - u\,pc + \frac{1}{5}u\,c + 1 - u. \end{cases}$$

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

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

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

$$\begin{aligned} &-p(0)(\mathrm{e}^{\frac{\tau_1}{20}})^2 r(0)\,(20 - 20\,\mathrm{e}^{-\frac{\tau_1}{20}}) + \frac{1}{5}\,r(0)\mathrm{e}^{\frac{\tau_1}{20}}(20 - 20\,\mathrm{e}^{-\frac{\tau_1}{20}}) - r(0)\,\mathrm{e}^{\frac{\tau_1}{20}} \\ &= r(0)(-20p(0)\mathrm{e}^{\frac{\tau_1}{10}} + 20\,p(0)\mathrm{e}^{\frac{\tau_1}{20}} + 3\,\mathrm{e}^{\frac{\tau_1}{20}} - 4) = 0 \end{aligned} \tag{6.1}$$

Assuming that $r(0) > 0$, the equality in (6.1) is satisfied if $p(0) = \frac{-3+4\,\mathrm{e}^{-\frac{\tau_1}{20}}}{20\,\mathrm{e}^{\frac{\tau_1}{20}}(-1+\mathrm{e}^{-\frac{\tau}{20}})}$. 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 Fig. 7. For all the values of $(\tau_1, p(0))$, such that $p(0) < \frac{-3+4\,\mathrm{e}^{-\frac{\tau_1}{20}}}{20\,\mathrm{e}^{\frac{\tau_1}{20}}(-1+\mathrm{e}^{-\frac{\tau}{20}})}$ (below the curve in Fig. 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 he curve $p(0)$ is upper bounded

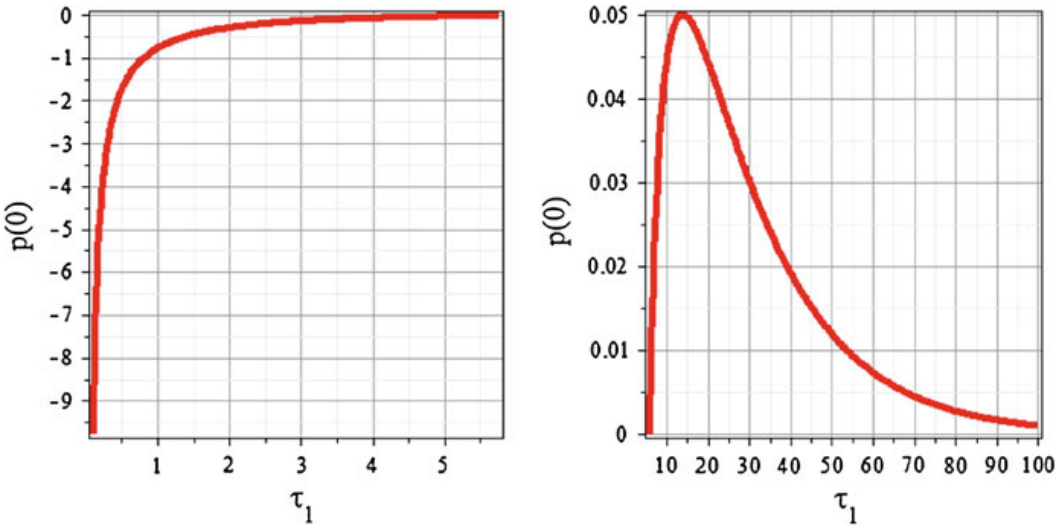

Fig. 7 If $p(0)$ and τ_1 are situated *above the red curve*, then $u^* = 0$ for the entire summer. (The variable τ_1 has to be higher than $-20 \ln \frac{3}{4} \approx 5.75$ as displayed in the *left plot*) (color figure online)

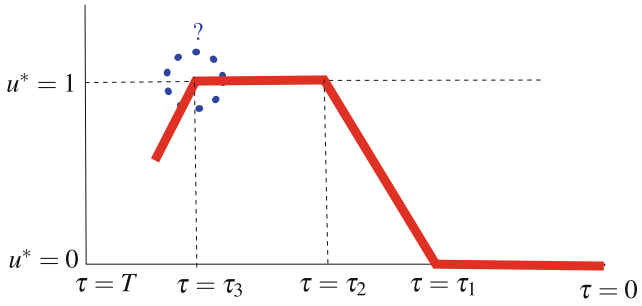

Fig. 8 Study of the existence of a second event in reverse time: can the optimal strategy u^* again admit values within the interval [0, 1), after being equal to 1?

by the quantity $(\gamma - \alpha)$ which, given the ranges of interest, is again a very small quantity.

Appendix B: Proof of Proposition 3.1

As portrayed in Fig. 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

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

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

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

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

From this equation we can express E_2 as:

$$E_2 = 1 + \frac{a_3 + 50\,p_3 r_3\,b_3 - 250\,p_3 r_3 c_3 + 50\,r_3\,c_3 - 250\,r_3}{\mathrm{e}^{d\,\Delta}(250\,d\,a_3 - \,a_3 - 50\,r_3\,c_3 + 250\,r_3)}, \tag{7.1}$$

where we have set $\Delta = \tau_3 - \tau_2 > 0$.

Since $E_2 \in (0, 1]$, the inequality (7.1) is satisfied only if

$$1 > \frac{250\,p_3 r_3 c_3 - a_3 - 50\,p_3 r_3\,b_3 - 50\,r_3\,c_3 + 250\,r_3}{\mathrm{e}^{d\,\Delta}(250\,d\,a_3 - \,a_3 - 50\,r_3\,c_3 + 250\,r_3)} \geq 0. \tag{7.2}$$

Recall that if there is a second event at time τ_3, then $\mathscr{S}(\tau_3) = 0$, but also $\mathscr{S}'(\tau_3) = \mathscr{S}''(\tau_3) = \cdots = 0$. From the equation $\mathscr{S}' = 0$ the parameter a_3 can be expressed in terms of the other variables:

$$\begin{aligned} a_3 = \frac{r_3}{10\,d}(&2\,c_3 - 2\,c_3\mathrm{e}^{d\,\Delta} + 875\,\mathrm{e}^{d\Delta}E_2 - 2{,}500\,p_3 + 375 - 125\,p_3\,c_3 \\ &+2{,}500\,\mathrm{e}^{d\Delta}p_3 + 25\,p_3\,b_3 + 500\,\mathrm{e}^{2\,d\,\Delta}(E_2)^2 - 1{,}000\,\mathrm{e}^{2\,d\,\Delta}E_2 + 2\,c_3\mathrm{e}^{d\,\Delta}E_2 \\ &-2{,}500\,\mathrm{e}^{d\,\Delta}E_2\,p_3\,a_3 + 2{,}500\,d\mathrm{e}^{d\,\Delta_3} - 2{,}500\,d\mathrm{e}^{d\Delta}E_2 \\ &+500\,\mathrm{e}^{2\,d\Delta} - 875\,\mathrm{e}^{d\Delta}). \end{aligned} \tag{7.3}$$

Furthermore, b_3 can be expressed from the equation $\mathscr{S}'' = 0$ (after substituting (7.3) into this same equation), and likewise c_3 can be expressed from the condition $\mathscr{S}''' = 0$ (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 Eq. (7.2) as "Nom" and "Den", respectively, there are two cases characterizing the necessary conditions in (7.2), 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

$$0 \leq \text{Nom}, \tag{7.4}$$
$$0 < \text{Den}, \tag{7.5}$$
$$0 < \text{Den} - \text{Nom}. \tag{7.6}$$

Case 2

$$0 \geq \text{Nom}, \tag{7.7}$$

$$0 > \text{Den}, \tag{7.8}$$

$$0 > \text{Den} - \text{Nom}. \tag{7.9}$$

The quantities Den and Nom can be then written with E_2 expressed by (7.1).

In the following, the two cases are considered in detail.

Case 1: Condition (7.4) implies

$$250\, r_3 - 50\, p_3\, r_3\, b_3 + 250\, p_3\, r_3\, c_3 - 50\, r_3\, c_3 \leq a_3, \tag{7.10}$$

whereas condition (7.5) implies

$$a_3 < \frac{50\, r_3 (c_3 - 5)}{250\, d - 1} \tag{7.11}$$

and condition (7.6) implies

$$a_3 < \frac{50\, r_3 (\mathrm{e}^{d\,\Delta}\, c_3 - 5\, \mathrm{e}^{d\Delta} - b_3\, p_3 + 5\, p_3\, c_3 - c_3 + 5)}{-\mathrm{e}^{d\Delta} + 250\, \mathrm{e}^{d\,\Delta} d + 1}. \tag{7.12}$$

Note that inequalities (7.10) and (7.11) imply either

$$0 < -50\, r_3\, b_3 + 250\, r_3\, c_3 \tag{7.13}$$

and

$$p_3 < -\frac{250\, d (c_3 - 5)}{(250\, d - 1)(b_3 - 5\, c_3)}, \tag{7.14}$$

or

$$-50\, r_3\, b_3 + 250\, r_3\, c_3 < 0 \tag{7.15}$$

and

$$\frac{-250\, d (c_3 - 5)}{(250\, d - 1)(b_3 - 5\, c_3)} < p_3. \tag{7.16}$$

We have substituted the expressions for a_3, b_3, and c_3 into inequalities (7.13), (7.14), (7.15) and (7.16), 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

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

which contradicts Eq. (7.12) and therefore also Eq. (7.6).

Case 2: Condition (7.7) implies

$$250\,r_3 - 50\,p_3\,r_3 b_3 + 250\,p_3\,r_3\,c_3 - 50\,r_3\,c_3 \geq a_3, \tag{7.17}$$

whereas condition (7.8) implies

$$a_3 > \frac{50\,r_3(c_3 - 5)}{250\,d - 1} \tag{7.18}$$

and condition (7.9) implies

$$a_3 > \frac{50\,r_3(\mathrm{e}^{d\Delta}c_3 - 5\,\mathrm{e}^{d\Delta} - b_3\,p_3 + 5\,p_3\,c_3 - c_3 + 5)}{-\mathrm{e}^{d\Delta} + 250\,\mathrm{e}^{d\Delta}\,d + 1}. \tag{7.19}$$

Note that the inequalities in (7.17) and (7.18) imply either

$$0 < -50\,r_3 b_3 + 250\,r_3 c_3 \tag{7.20}$$

and

$$p_3 > \frac{-250\,d(c_3 - 5)}{(-1 + 250\,d)(b_3 - 5\,c_3)}, \tag{7.21}$$

or

$$-\,50\,r_3 b_3 + 250\,r_3 c_3 < 0 \tag{7.22}$$

and

$$\frac{-250\,d(c_3 - 5)}{(-1 + 250\,d)(b_3 - 5\,c_3)} > p_3. \tag{7.23}$$

We have substituted expressions for a_3, b_3, and c_3 into inequalities (7.20), (7.21), (7.22) and (7.23), 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

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

which contradicts Eq. (7.19) and therefore also Eq. (7.9). □

Appendix C: Proof of Proposition 3.2

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

$$\begin{cases} E' = \frac{1}{250}(1-u)E - d\,u + d\,u\,E, \\ r' = \frac{1}{20}r - \frac{1}{5}u\,E\,r, \\ a' = -\frac{1}{250}(1-u)a - dua + \frac{1}{5}u\,r\,c + (1-u)r, \\ c' = -\frac{1}{20}c + \frac{1}{5}u\,E\,c + (1-u)E. \end{cases} \tag{8.1}$$

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

$$\mathscr{S} = \frac{1}{250}Ea + da - dEa + \frac{1}{5}E\,r\,c - E\,r, \tag{8.2}$$

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

$$\begin{gathered} 100\,(E^f)^2 w^{31} + (-25\,E^f - 500\,d\,E^f)w^{29} + 500\,d\,w^{27} \\ -100\,(E^f)^2 w^4 + (-2\,E^f + 500\,dEf)w^2 - 500\,d. \end{gathered}$$

From (8.1), 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 $\mathscr{S} = 0$, $\mathscr{S}' = 0$, and $\mathscr{S}'' = 0$ 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:

$(E(-25\,E^2 - 29 \cdot 10^3\,dE^3 + 125 \cdot 10^3\,d^2E^2 + 116\,E^3 - 13 \cdot 10^3\,d\,E + 230 \cdot 10^3\,d^2 + 67{,}750\,dE^2 - 375 \cdot 10^3\,d^2E))/(4\,(-125\,d\,E^2 - 5 \cdot 10^3\,d^2E - 21\,E^4 - 1{,}250 \cdot 10^3\,d^3 + 100\,E^5 - 9 \cdot 10^3\,dE^3 + 54{,}250\,dE^4 + 531{,}250\,d^2E^2 - 875 \cdot 10^3\,d^2E^3 + 1{,}250 \cdot 10^3\,d^3E + 250 \cdot 10^3\,d^2E^4 - 25 \cdot 10^3\,E^5 d))$.

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 $u^s \neq [0, 1]$ "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 $\mathscr{S}''' = 0$ we can derive the expression of $\frac{\mathrm{d}u^s}{\mathrm{d}\tau}$. 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:

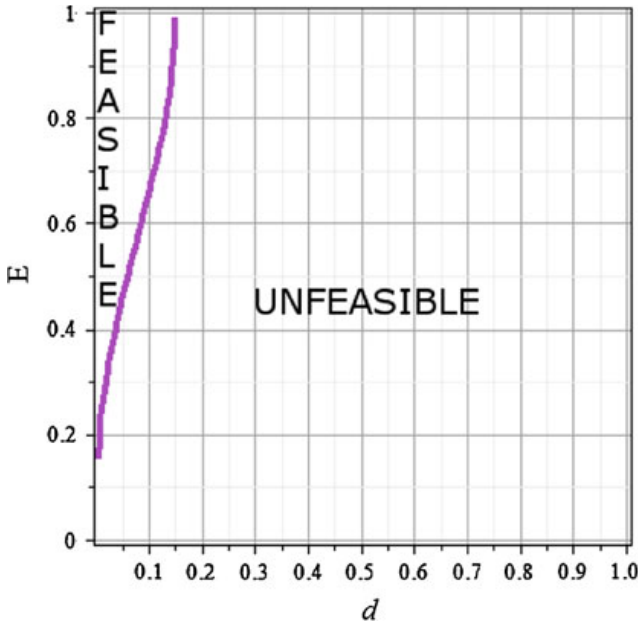

Fig. 9 Regions of d and E for which $u^s \in (0, 1]$. The *purple bold line* corresponds to d and E for which $u^s = 1$ and coincides with the boundary of the feasibility region (color figure online)

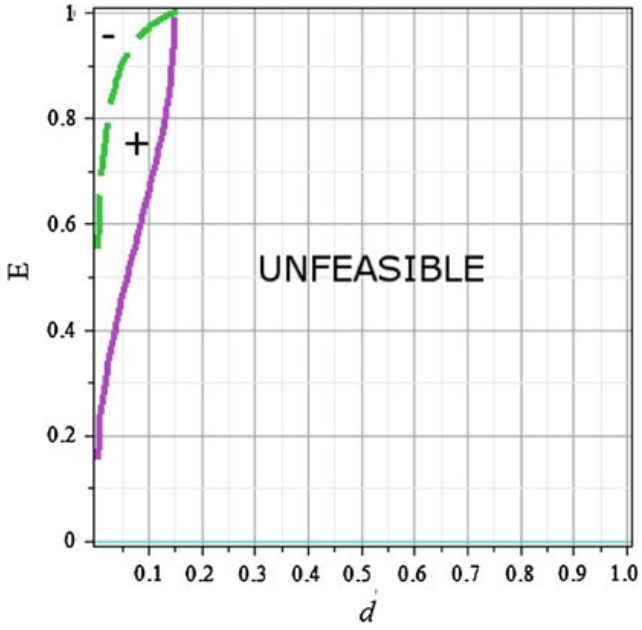

Fig. 10 Regions of d and E for which $\frac{\mathrm{d}u^s}{\mathrm{d}\tau} > 0$ (denoted with a $+$) and for which $\frac{\mathrm{d}u^s}{\mathrm{d}\tau} < 0$ (denoted by a $-$). The *green dashed line* corresponds to the (d, E) values for which $\frac{\mathrm{d}u^s}{\mathrm{d}\tau} = 0$ (color figure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

- 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.

Let us further elaborate on the latter case (presence of mixed strategies) with the help of Fig. 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. □

References

Akhmetzhanov A, Grognard F, Mailleret L (2011) Optimal life-history strategies in seasonal consumer-resource dynamics. Evolution 65(11):3113–3125

Başar T, Olsder GJ (1999) Dynamic noncooperative game theory. SIAM, Philadelphia

Bellman R (1957) Dynamic programming. Princeton University Press, Princeton

Bertsekas DP (2003) Nonlinear programming. Athena Scientific, Belmont

Danks H (1987) Insect dormancy: an ecological perspective. Biological Survey of Canada, Ottawa

DeLeenheer P, Aeyels D (2000) Accessibility properties of controlled Lotka–Volterra systems. In: Proceedings of the 39th IEEE conference on decision and control, Sydney, USA, pp 3977–3981

Diekmann O, Gyllenberg M, Metz JAJ (2007) Physiologically structured population models: towards a general mathematical theory. In: Takeuchi Y, Iwasa Y, Sato K (eds) Biological and medical physics, biomedical engineering. Springer, Berlin, pp 5–20

Dreyfus S (2002) Richard Bellman on the birth of dynamic programming. Oper Res 50(1):48–51

Fitzgerald J, Solomon M (1991) Diapause induction and duration in the phytoseiid mite *Typhlodromus pyri*. Exp Appl Acarol 12:135–145

Goh B, Leitmann G, Vincent T (1974) Optimal control of a prey-predator system. Math Biosci 19:263–286

Gouzé J (1993) Global behavior of n-dimensional Lotka–Volterra systems. Math Biosci 113:231–242

Gouzé J (1994) Global stabilization of n-dimensional population models by a positive control. In: Proceedings of the 33rd IEEE conference on decision and control, Orlando, USA, pp 1335–1336

Gyllenberg M, Hanski I, Lindström T (1996) A predator–prey model with optimal suppression of reproduction in the prey. Math Biosci 134(2):119–152

Gyllenberg M, Service R (2011) Necessary and sufficient conditions for the existence of an optimisation principle in evolution. J Math Biol 62(3):359–369

Helle W, Sabelis MW (eds) (1985a) Spider mites: their biology, natural enemies and control. World crop pests, vol 1A. Elsevier, Amsterdam, p 403

Helle W, Sabelis MW (eds) (1985b) Spider mites: their biology, natural enemies and control. World crop pests, vol 1B. Elsevier, Amsterdam, p 458

Hopper JL (1987) Opportunities and handicaps of antipodean scientists: A. J. Nicholson and V. A. Bailey on the balance of animal populations. Hist Rec Aust Sci 7(2):179–188

Kirk DE (1970) Optimal control theory, an introduction. Prentice Hall, Englewood Cliffs

Kolmanovskii V, Koroleva N (1991) Control of a predator–prey system with intraspecies competition. J Appl Math Mech 55:588–595

Kroon A, Veenendaal R, Bruin J, Egas M, Sabelis MW (2004) Predation risk affects diapause induction in the spider mite *Tetranychus urticae*. Exp Appl Acarol 34:307–314

Kroon A, Veenendaal RL (2005) Trade-off between diapause and other life-history traits in the spider mite *Tetranychus urticae*. Ecol Entomol 23(3):298–304

Kroon A, Veenendaal RL, Bruin J, Egas M, Sabelis MW (2008) Sleeping with the enemy—predator-induced diapause in mite. Naturwissenschaften 95:1195–1198

Kroon A, Veenendaal RL, Egas M, Bruin J, Sabelis MW (2005) Diapause incidence in the two-spotted spider mite increases due to predator presence, not due to selective predation. Exp Appl Acarol 35(1–2):73–81
Lika K, Kooijman SALM (2003) Life history implications of allocation to growth versus reproduction in dynamic energy budgets. Bull Math Biol 65:809–834
Lotka AJ (1920) Undamped oscillations derived from the law of mass action. J Am Chem Soc 42:1595–1599
McNamara J, Houston AI (1996) State-dependent life histories. Nature 380(6571):215–221
Melikyan A (1994) Necessary optimality conditions for a singular surface in the form of synthesis. J Optim Theory Appl 82(2):203–217
Melikyan A (1998) Generalized characteristics of first order PDEs: applications in optimal control and differential games. Birkhäuser, Boston
Melikyan A, Olsder G (2010) Boundary singularities and characteristics of Hamilton–Jacobi equation. J Dyn Control Syst 16(1):77–99
Metz JAJ, Mylius S, Diekmann O (2008) Even in the odd cases when evolution optimizes, unrelated population dynamical details may shine through in the ESS. Evol Ecol Res 10:655–666
Metz JAJ, Mylius S, Diekmann O (2008) When does evolution optimize? Evol Ecol Res 10:629–654
Pachepsky E, Nisbet R, Murdoch W (2008) Between discrete and continuous: consumer-resource dynamics with synchronized reproduction. Ecology 89(1):280–288
Perrin N, Sibly R (1993) Dynamic-models of energy allocation and investment. Ann Rev Ecol Syst 24:379–410
Perrin N, Sibly R, Nichols N (1993) Optimal-growth strategies when mortality and production-rates are size-dependent. Evol Ecol 7(6):576–592
Persson L, Roos AD (2003) Adaptive habitat use in size structured populations: linking individual behavior to population processes. Ecology 84(5):1129–1139
Stanková K (2009) 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
Tauber M, Tauber C, Masaki S (1986) Seasonal adaptations of insects. Oxford University Press, New York
Veerman A (1992) Diapause in phytoseiid mites: a review. Exp Appl Acarol 14:1–60
Volterra V (1926) Variations and fluctuations of the number of the individuals in animal species living together. In: Chapman R (ed) Animal Ecology. McGrawHill, New York
Volterra V (1927) 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. Springer, Berlin, pp 65–234
Wright S (1932) The roles of mutation, inbreeding, crossbreeding, and selection in evolution. In: Proceedings of the sixth international congress on genetics, pp 355–366