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Introduction strategies for biological control agents subject to Allee effects

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Abstract— **The efficiency of biological control as crop protection methodology is deeply impacted by inter- and intra-specific interactions. As such, Allee effects among biocontrol agents such as pest predators should be taken into account to design biological control schemes. We investigate this problem through two models of increasing complexity: the first one concentrates on the predator dynamics whose establishment is hampered by a strong Allee effect and the second one models both predator and prey dynamics. In the latter case, pest eradication is targeted despite diminished predation efficiency when predator density is low. Considering augmentative biological control through periodic impulsive predator releases we show that, when it succeeds, pest control is accelerated in both models by taking rare and large releases over frequent and smaller ones.**

Index Terms— **Predator-prey models, positive density dependence, impulsive differential equations, semi-discrete models, stabilization.**

I. INTRODUCTION

Biological control is the use of natural enemies such as predators, parasites and parasitoids in order to contain another organism population density at a lower level than in their absence [1]. Despite some resounding successes such as the use of a trichogramma to control corn-borers [2], biological control has seen unexpected failures in the past two decades [3], [4].

To improve these processes, it is important to better understand the different forms of interactions between pests and their enemies. For instance, different works have studied the influence of competition or interference between biological control agents [5], [6]. Other complex forms of interactions are brought about by positive, rather than negative, influence of natural enemies on their conspecifics.

Allee effects or positive density dependence is characterized by such a positive relationship between individual fitness or per capita growth and the size or density of a population. This phenomenom has been described by W.C. Allee who showed that intraspecific cooperation could lead to positive density dependence [7], [8]. At the population scale, Allee effects translate into a waning of population growth (weak Allee effect) or its decline (strong Allee effect) when the population is small. The main biological mechanism producing Allee effects is associated to sexual reproduction and the difficulty to find mates at low densities. For example, a mate-finding Allee effect has been proved for Glanville fritillary butterfly [9]. Biocontrol agents also undergo Allee effects [10]: for instance, the introduction of the parasitoid *Aphelinus asychis* (Walker) to control the pest *Diuraphis noxia* (Mordvilko) [11] has been shown to be negatively impacted by Allee effects.

Our study concerns augmentative biological control, that is the repeated introduction of natural enemies, which will here be predators, to control a pest. We will try to identify how many and how frequently natural enemies should be released to achieve pest eradication. The presence of repeated releases sets us in a context where continuous dynamics are disrupted by jumps in biocontrol agents density.

We can formalize this kind of processes by using ordinary differential equations to describe continuous dynamics most of the time and a predator release is taken as a brutal change in their density. That way, we can treat these changes as instantaneous and model them by discrete equations at given instants noted t_k with $k \in \mathbb{N}$. Such dynamics are usually modelled as [12]:

$$\begin{cases} \dot{x} = f(x(t),t), \; t \neq t_k, \\ x(t_k^+) = F(x(t_k),t_k), \end{cases} \tag{1}$$

with x the vector of population densities and f their dynamics. The notation t_k^+ is used to describe the instant right after t_k and $F(x(t_k),t_k) - x(t_k)$ represents the impulses of densities at the instant t_k. Here we consider the sequence $(t_k)_{k\in\mathbb{N}}$ defining the predator releases as T-periodic, *i.e.* $t_{k+1} = t_k + T$, moreover the impulse sizes will not depend on the state variable $x(t_k)$ since no accurate state estimate is usually available in agronomic applications.

This paper aims to study augmentative biological control schemes in which biocontrol agents are subject to Allee effects and to determine what release strategies could be more efficient to control pest populations. The introduction strategies will be studied with models of increasing complexity: in Section II, we will consider predator dynamics only while both prey and predators will be invastigated in Section III. Section IV deals with some numerical illustrations and is followed by general discussions on release strategies in Section V.

II. SINGLE SPECIES DYNAMICS

For now, pest and crop are kept implicit and only the introduced biocontrol agents population is modelled. The success of the biological control scheme will be evaluated through introduction success; predator establishment is supposed to translate into efficient pest control.

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A. A classical model

The most commonly used model of strong Allee effects corresponds to [13], [14], [15]:

$$\dot{y} = r_y y \left(1 - \frac{y}{K_y}\right)\left(\frac{y}{A} - 1\right). \tag{2}$$

Biocontrol agents density is represented by y and $\dot{y}$ is its temporal derivative. $K_y > 0$ is the carrying capacity of the environment and $0 < A < K_y$ a threshold under which the population decreases; A is termed the Allee threshold. r_y is some positive constant. The growth function is represented in Figure 1.

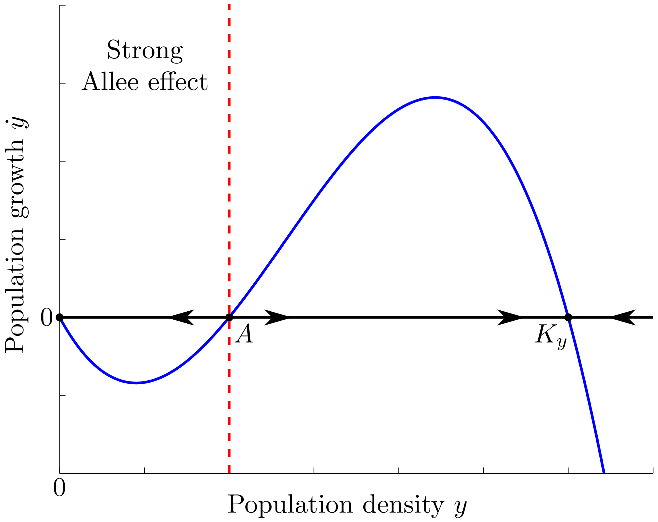

Fig. 1. Growth function $r_y y\left(1 - \frac{y}{K_y}\right)\left(\frac{y}{A} - 1\right)$. A is an unstable equilibrium and 0 and K_y are stable equilibria, when y drops below A, the population goes extinct. Above A, the population converges to the carrying capacity K_y.

A strong Allee effect occurs due to the negativity of the growth function for small densities of population. Equation (2) represents an Allee effect since the growth rate is increasing up to $y = \frac{A+K_y}{2} > A$. Establishment success is then achieved if the population is brought above $y = A$.

B. Generalization

We note that the main feature of the previous model that keeps population introduction success from being trivial is that the growth function is negative for $y < A$. We now propose a generalization of the aforementioned model, that presents these features:

Hypotheses 2.1: g is a $\mathscr{C}^1$-function such that $g(0) = 0$, $g(y) < 0$ on $(0, A)$, $g(A) = 0$ and $g'(A) > 0$.
The challenge is to bring y from 0 to some value above A so that the population settles. We define a discrete equation modelling repeated releases of individuals [16]:

$$y(t_k^+) = y(t_k) + \mu T. \tag{3}$$

Thereby at each instant t_k, we introduce a quantity μT of individuals noting μ the introduction rate and T the period at which we release them. With such a definition, the release strategy is decoupled: the introduction rate μ (*i.e.* the number of introduced biocontrol agents per unit time) and the period at which they are introduced. Thanks to this notation, this model makes it possible to identify how to best deploy over time similar quantities of biocontrol agents. The model then becomes

$$\begin{cases} \dot{y} = g(y),\ t \neq t_k, \\ y(t_k^+) = y(t_k) + \mu T. \end{cases} \tag{4}$$

This is a generalization of problems that have been previously studied [12], [17]. We want to identify μ and T values that allow population establishment, *i.e.* $y(t) > A$ for some t. Since the dynamics are in one dimension, this requires that a release can at least compensate any population decrease taking place through the continuous dynamics during a period T.

In what follows, we denote $y(0^+)$ and $F_T(y(0^+)) = y(T)$ the densities at the beginning and the end of a period $(0^+, T]$. We get the following result:

Theorem 2.1: For any $T > 0$, there exists a threshold release rate $\mu_s(T)$ such that if $\mu > \mu_s(T)$ the population settles above A. $\mu_s(T)$ is the largest solution of

$$\begin{cases} g(F_T(y(0^+))) = g(y(0^+)), \\ \mu_s(T) = \dfrac{y(0^+) - F_T(y(0^+))}{T}, \end{cases} \tag{5}$$

with $y(0^+) \in [0, A]$.

Proof: We first compute the maximum with respect to $y(0^+)$ of function $y(0^+) - F_T(y(0^+))$ which represents, on a fixed period $(0^+, T]$, the maximum decrease of the population. The threshold release rate $\mu_s(T)$ is then the minimum introduction rate allowing to compensate this maximum decrease, *i.e.* $\mu_s(T)T = \max\limits_{y(0^+)} (y(0^+) - F_T(y(0^+)))$. Then, for all $\mu > \mu_s(T)$, the release ensures that $y(T^+) > y(0^+)$ for all $y(0^+) \in [0, A]$ so that the population eventually settles above A.

Differentiating $y(0^+) - F_T(y(0^+))$ with respect to $y(0^+)$, we find that it has extrema when $F_T'(y(0^+)) = 1$. Using separation of variables, we have that

$$\int_{y(0^+)}^{F_T(y(0^+))} \frac{1}{g(y)} dy = \int_{0^+}^{T} dt, \tag{6}$$

which, differentiated with respect to $y(0^+)$, yields

$$F_T'(y(0^+)) = \frac{g(F_T(y(0^+)))}{g(y(0^+))}.$$

A necessary condition to get the maximum decrease of the population is that

$$g(F_T(y(0^+))) = g(y(0^+)),$$

which is the first equation of (5).

The threshold $\mu_s(T)$ is defined as compensating the maximum decrease of the population during a period T so that

$$y(T^+) = F_T(y(0^+)) + \mu_s(T)T = y(0^+)$$

which is the second equation of (5).

Equation (5) could be satisfied for different $y(0^+)$ values so that it is necessary to take the largest $\mu_s(T)$ satisfying (5) since it maximises population decrease over a period T. ■

We can note that the maximum decrease is obtained for initial densities $y(0^+)$ giving the same value of growth function at the beginning and the end of the fixed period $g(F_T(y(0^+))) = g(y(0^+))$ as it is represented in Figure 2. The corresponding solution avoids the regions close to the extinction $y = 0$ and the Allee threshold $y = A$ where the population decrease is slow.

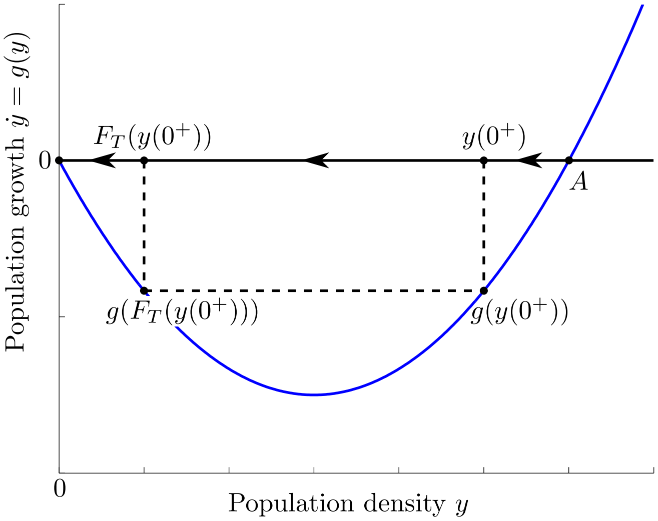

Fig. 2. For a fixed period T, the maximum decrease on the period will be to take the initial density $y(0^+)$ such that at the end of the period, $g(F_T(y(0^+))) = g(y(0^+))$.

III. PREDATOR-PREY DYNAMICS

To account for a more detailed description of the biological control process, we now turn to a model explicitly encompassing pest dynamics: a predator-prey model in which predators suffer from an Allee effect. Up to now, such models remain fairly rare [18], [19], [20]. The measure of success of the biological program is then the eradication of the prey/pest population.

A. *Allee effects on predation*

In [19] a model has been proposed in which Allee effects occur on predators and has repercussions on trophic functions in a biological control context. Allee effects take place due to the difficulty to find mates at low size and so to be efficient in predation. This is modelled through

$$\begin{cases} \dot{x} = rx\left(1 - \dfrac{x}{K}\right) - \dfrac{b_0}{a}\dfrac{x}{x+x_h}\dfrac{y}{y+y_h}y, \\ \dot{y} = b_0\dfrac{x}{x+x_h}\dfrac{y}{y+y_h}y - my, \end{cases} \tag{7}$$

in which x and y represent the prey and the predator densities, respectively. Pest growth is modelled by a logistic function. The mortality rate of predators m is assumed constant. In the trophic functions, the value $\frac{y}{y+y_h}$ is the probability of mating success and the term $\frac{b_0}{a}\frac{x}{x+x_h}$ is a Holling II functional response, which saturates at large x values due to predator satiation or handling time [21]. The numerical response is proportional to the functional response.

Model (7) assumes an important inefficiency in prey assimilation when predators are at low density. It predicts a higher risk of predator extinction when the Allee effect parameter, y_h, is large. Predator extinction is always stable; however, stable coexistence of both species at equilibrium or along a limit cycle is also possible for intermediate K values.

B. *Generalization*

Positive density dependence has consequences on trophic functions: at low predator density, functional and numerical reponses are less efficient. We use generic functions to model such a system:

$$\begin{cases} \dot{x} = f(x) - g(x)q(y)y, \\ \dot{y} = h(x)q(y)y - my, \end{cases} \tag{8}$$

where $f(x)$ denotes prey growth and $g(x)q(y)$ and $h(x)q(y)$ represent the predator functional and numerical response, respectively. $q(y)$ models Allee effects through a decrease of predator efficiency at low sizes. $m > 0$ is the predator mortality. We assume some general qualitative hypotheses on the functions $f(x)$, $g(x)$, $h(x)$ and $q(y)$:

Hypotheses 3.1:

(i) $f(0) = 0$ and $f'(0) > 0$.
(ii) $g(0) = 0$, $g'(0) > 0$ and $\forall x > 0$, $g(x) > 0$.
(iii) $h(0) = 0$ and $\forall x > 0$, $h(x) \geqslant 0$.
(iv) $q(0) = 0$; $\forall y > 0$, $0 < q(y) \leqslant 1$; $\lim\limits_{y \to +\infty} q(y) = 1$; $q(y)$ is increasing.
(v) $S_g = \sup\limits_{x \geqslant 0}\left(\frac{f(x)}{g(x)}\right)$.

Assumptions (i)-(iii) on pest growth and predation are classical: in absence of pest, neither growth nor predation can take place, and predation is unilateral. Assumption (iv) states that predation is low at small y values and reaches its maximum value at large y values. We also suppose that $\frac{f}{g}$ is upper bounded by some S_g for all positive values of x, which means that pest growth never overwhelms predation.

To kill pests, predators are periodically introduced into the environment, similarly to Section II:

$$\begin{cases} \left.\begin{aligned} \dot{x} &= f(x) - g(x)q(y)y \\ \dot{y} &= h(x)q(y)y - my \end{aligned}\right\}, & t \neq nT, \\ y(nT^+) = y(nT) + \mu T, & \forall n \in \mathbb{N}. \end{cases} \tag{9}$$

This kind of models has already been used in the past to understand impulsive biological control with direct competition between predators [5], [6]; however, hypotheses on $q(y)$ were different in order to represent antagonistic interactions.

C. *Stability of the pest-free solution*

Here we will demonstrate the conditions for existence and stability of a periodic pest-free solution. We first define this solution:

Proposition 3.1: Under Hypotheses 3.1, there exists a pest-free solution

$$(x_p(t), y_p(t)) = (0, y^* e^{-m(t \mod T)}) \tag{10}$$

with

$$y^* = \frac{\mu T}{1 - e^{-mT}},$$

which is a periodic solution of system (9).

Proof: In the absence of prey, the model is written as follows:

$$\begin{cases} \left.\begin{aligned} \dot{x} &= 0 \\ \dot{y} &= -my \end{aligned}\right\}, \quad t \neq nT, \\ y(nT^+) = y(nT) + \mu T, \quad \forall n \in \mathbb{N}. \end{cases} \tag{11}$$

On a period $(nT^+, (n+1)T^+)$, this yields

$$y((n+1)T^+) = y(nT^+)e^{-mT} + \mu T$$

whose fixed point y^* is

$$y^* = \frac{\mu T}{1 - e^{-mT}}.$$

Thus model (11) possesses (10) as pest-free solution. ∎

Henceforth there exists a T-periodic pest-free solution of model (11). We now must study its stability to know for what conditions biocontrol agents can control the pests.

Theorem 3.2: Pest-free solution (10) *is Locally Asymptoticaly Stable (LAS) if and only if*

$$\Psi_L(T, \mu) = \frac{g'(0)}{T} \int\limits_0^T q(y_p(\tau)) y_p(\tau) d\tau - f'(0) > 0. \tag{12}$$

Moreover, if

$$\Psi_G(T, \mu) = \frac{g'(0)}{T} \int\limits_0^T q(y_p(\tau)) y_p(\tau) d\tau - S_g g'(0) > 0 \tag{13}$$

then solution (10) *is Globaly Asymptoticaly Stable (GAS).*

Proof: To obtain global stability of the pest-free solution, we must find global attractivity conditions and local stability conditions. The strongest condition will give us global stability. We first write system (9) in deviation coordinates, that is the difference between a general solution $(x(t), y(t))$ and the pest-free solution $(x_p(t), y_p(t))$, denoted $(\widetilde{x}(t), \widetilde{y}(t))$, then the dynamics become

$$\begin{cases} \dot{\widetilde{x}} = f(\widetilde{x}) - g(\widetilde{x}) Q(y_p + \widetilde{y}), \\ \dot{\widetilde{y}} = h(\widetilde{x}) Q(y_p + \widetilde{y}) - m\widetilde{y}, \end{cases} \tag{14}$$

where $Q(y) = q(y)y$ is an increasing function of y and the impulsive component disappears since

$$\widetilde{y}(nT^+) = y(nT) + \mu T - y_p(nT) - \mu T = \widetilde{y}(nT).$$

We want to show that the deviation coordinates converge to zero. We start by dividing the x dynamics by $g(x)$ then we integrate from an initial time t_0 to t and so from $x(t_0)$ to $x(t)$ for the density:

$$\int_{\widetilde{x}(t_0)}^{\widetilde{x}(t)} \frac{du}{g(u)} = \int_{t_0}^{t} \left[\frac{f(\widetilde{x}(\tau))}{g(\widetilde{x}(\tau))} - Q(y_p(\tau) + \widetilde{y}(\tau)) \right] d\tau. \tag{15}$$

We note that the left-hand term goes to $-\infty$ if and only if $\widetilde{x}(t)$ goes to 0 because $g(x) \sim g'(0)x$ for $x \approx 0$ and $g(x) > 0$ for all $x > 0$. Thus if we can show that it goes to $-\infty$ as $t \rightarrow +\infty$, the convergence of $\widetilde{x}$ to 0 will be proved. This will be true if the right hand side of (15) diverges to $-\infty$. Consider the $\widetilde{y}$ dynamics of Equation (14); they yield $\dot{\widetilde{y}} \geqslant -m\widetilde{y}$ so that $\widetilde{y}(t) \geqslant \widetilde{y_0} e^{-m(t-t_0)}$. As $\widetilde{y} + y_p \geq 0$, we have $\widetilde{y}(t) \geqslant -y_p(t)$, $\forall t$, so that:

$$\widetilde{y} \geqslant -\max y_p(t) = -y^*.$$

Then we have $\widetilde{y_0} \geqslant -y^*$ and

$$\widetilde{y}(t) \geqslant -y^* e^{-m(t-t_0)}. \tag{16}$$

Thus for any $\varepsilon > 0$, there exists a time t_f such that after this time, $\widetilde{y}(t) > -\varepsilon$.

We divide the right-hand side of (15) in three integrals of the same integrand:

$$\left(\int_{t_0}^{(\lfloor \frac{t_f}{T} \rfloor + 1)T} + \int_{(\lfloor \frac{t_f}{T} \rfloor + 1)T}^{\lfloor \frac{t}{T} \rfloor T} + \int_{\lfloor \frac{t}{T} \rfloor T}^{t} \right) \left[\frac{f(\widetilde{x}(\tau))}{g(\widetilde{x}(\tau))} - Q(y_p(\tau) + \widetilde{y}(\tau)) \right] d\tau.$$

In this equation, the first and third integral are bounded so that we concentrate on the second:

$$\begin{aligned} &\int_{(\lfloor \frac{t_f}{T} \rfloor + 1)T}^{\lfloor \frac{t}{T} \rfloor T} [S_g - Q(y_p(\tau) + \widetilde{y}(\tau))] d\tau \\ &\leqslant \sum_{n = \lfloor \frac{t_f}{T} \rfloor + 1}^{\lfloor \frac{t}{T} \rfloor - 1} \int_{nT}^{(n+1)T} [S_g - Q(y_p(\tau) - \varepsilon)] d\tau \\ &= \left(\lfloor \frac{t}{T} \rfloor - \lfloor \frac{t_f}{T} \rfloor - 1 \right) \int_0^T [S_g - Q(y_p(\tau) - \varepsilon)] d\tau, \end{aligned} \tag{17}$$

because $Q(y)$ is an increasing function and $\widetilde{y}(\tau) > -\varepsilon$. Since $\left(\lfloor \frac{t}{T} \rfloor - \lfloor \frac{t_f}{T} \rfloor - 1 \right)$ is positive and goes to $+\infty$, if it is multiplied by some negative constant, (17) goes to $-\infty$ as $t \longrightarrow +\infty$. So $\widetilde{x}(t)$ converges to 0 if there exists some $\varepsilon > 0$ such that

$$S_g T - \int_0^T Q(y_p(\tau) - \varepsilon) d\tau < 0. \tag{18}$$

Since (18) multiplied by $-\frac{g'(0)}{T}$ is a small perturbation of (13), the latter ensures that (18) is satisfied for ε small enough. Thus condition (13) is a sufficient condition to obtain the global convergence of $x(t)$ to $x_p(t) = 0$.

We now demonstrate the convergence of $\widetilde{y}$ to zero when (13) is satisfied by studying the second equation of (14). First consider $\widetilde{y} > 0$. Since $\dot{\widetilde{y}} \geq 0$ when $\widetilde{y} = 0$, $\widetilde{y}$ cannot become negative from there. Since $\widetilde{x}$ tends asymptotically to zero, there exists a time t_g so that $h(\widetilde{x}) < \frac{m}{2}$ for any $t > t_g$:

$$\dot{\widetilde{y}} < h(\widetilde{x})(\widetilde{y} + y_p) - m\widetilde{y} \text{ because } q(y) \leq 1, \forall\ y > 0$$

and

$$\dot{\widetilde{y}} < h(\widetilde{x}) y_p - \frac{m}{2} \widetilde{y} < 0, \text{ for } t \geq t_g.$$

We know that $h(\widetilde{x}) y_p$ converges to zero, so that $\widetilde{y}$ does too.

When $\widetilde{y}(0) < 0$, either $\widetilde{y}$ becomes positive at some time and the preceding reasoning applies, or it does not and (16) shows that $\widetilde{y}$ goes to 0. Thus we have demonstrated the global attractivity of the pest-free solution of model (9) under condition (18).

Now we have to study the local stability of the solution. For this, we compute Floquet's characteristic multipliers of the monodromy matrix built on the linearization of (14) around the pest-free solution.

$$\begin{cases} \dot{\widetilde{x}} = \widetilde{x}(f'(0) - g'(0)q(y_p)y_p), \\ \dot{\widetilde{y}} = \widetilde{x}h'(0)q(y_p)y_p - m\widetilde{y}. \end{cases}$$

We obtain the following matrix equation

$$\begin{pmatrix} \dot{\widetilde{x}} \\ \dot{\widetilde{y}} \end{pmatrix} = \begin{pmatrix} f'(0) - g'(0)q(y_p)y_p & 0 \\ h'(0)y_p q(y_p) & -m \end{pmatrix} \begin{pmatrix} \widetilde{x} \\ \widetilde{y} \end{pmatrix}$$

and we got the post-release mapping

$$\begin{pmatrix} \widetilde{x} \\ \widetilde{y} \end{pmatrix} ((n+1)T^+) = B \begin{pmatrix} \widetilde{x} \\ \widetilde{y} \end{pmatrix} (nT^+) \tag{19}$$

with B the matrix such that

$$B = \begin{pmatrix} e^{\int_{nT^+}^{(n+1)T^+} (f'(0) - g'(0)q(y_p)y_p)d\tau} & 0 \\ \cdots & e^{-m \int_{nT^+}^{(n+1)T^+} d\tau} \end{pmatrix}$$

whose bottom-left term does not influence the eigenvalues because the matrix is triangular. The analysis of system (19) indicates that the eigenvalues (or characteristic multipliers) of B, which are read on the diagonal, must be smaller than 1 in norm to obtain local stability of the pest-free solution. It is trivial for the second one and is achieved for the first if and only if the following inequality:

$$\frac{f'(0)}{g'(0)} T - \int_{nT^+}^{(n+1)T^+} q(y_p(\tau))y_p(\tau)d\tau < 0$$

is satisfied. This is equivalent to (12) because y_p is T-periodic.

Since $\lim_{x \to 0} \frac{f(x)}{g(x)} = \frac{f'(0)}{g'(0)}$, thanks to L'Hospital rule, we know that $\frac{f'(0)}{g'(0)} \leqslant S_g$. Therefore the global attractivity condition is stronger than the local stability condition and global asymptotic stability is achieved with (13). ■

The conditions for local and global stability of the pest-free solution (10) are very similar. We note that the global stability condition is only sufficient: if $\Psi_L(T, \mu) > 0$ and $\Psi_G(T, \mu) < 0$, the pest-free solution might be GAS, but this situation is not identified by Theorem 3.2.

IV. NUMERICAL RESULTS

A. *Single species dynamics*

We can illustrate Theorem 2.1 by taking the explicit growth function:

$$g(y) = -r_y y \left(1 - \frac{y}{A}\right). \tag{20}$$

It is represented in Figure 2. It satisfies Hypotheses 2.1 and is an approximation of (2) for $K_y \gg A$ over $(0, A]$. Computing (6) explicitely, we obtain:

$$\frac{F_T(y(0^+))(A - y(0^+))}{y(0^+)(A - F_T(y(0^+)))} = e^{-r_y T},$$

then we get $y(0^+)$ from the first equation of (5):

$$y(0^+) = Ae^{\frac{r_y T}{2}} \frac{(e^{\frac{r_y T}{2}} - 1)}{e^{r_y T} - 1},$$

and from the second equation of (5), we have

$$\mu_s(T) = \frac{A(e^{\frac{r_y T}{2}} - 1)}{T(e^{\frac{r_y T}{2}} + 1)}. \tag{21}$$

This equation is represented in Figure 3. If the introduction rate is strong (superior to $\mu_s(0) = \frac{r_y A}{4}$), population establishment will always be possible. Otherwise the period must be large enough to overcome the Allee effect and install the population.

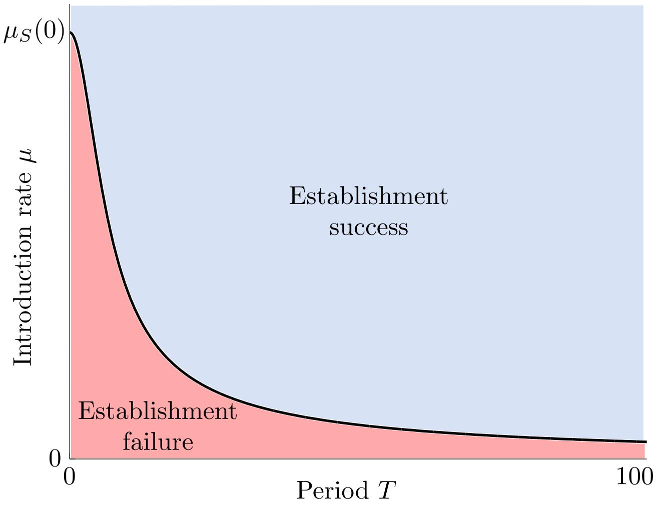

Fig. 3. Introduction rate threshold $\mu_s(T)$. In the red area, the installation of the population is impossible and the blue area gives couples (T, μ) with which the installation will be possible in a finite time.

Population dynamics as a function of the release period T can be investigated further by considering the term $F_T(y(0^+)) + \mu T - y(0^+)$. It describes population increase over one period $(0^+, T^+)$ for an initial density $y(0^+) < A$, encompassing both population decline because of Allee effects and the release. Dividing it by T, we obtain its increase per unit time. The computation of the average of the latter over $y(0^+)$ values between 0 and A yields thus an indicator of the mean population growth over the strong Allee effects zones, which is positively correlated with the swiftness of population establishment. We define mean population growth as:

$$\Phi(T, \mu) = \frac{1}{A} \int_0^A \frac{F_T(y(0^+)) + \mu T - y(0^+)}{T} dy(0^+),$$

which becomes:

$$\Phi(T, \mu) = \frac{A}{2T} \frac{2r_y T e^{r_y T} - e^{2r_y T} + 1}{(e^{r_y T} - 1)^2} + \mu, \tag{22}$$

for model (4) with growth function (20). Differentiating Φ with respect to T, we obtain a function whose denominator is positive and whose numerator sign needs to be assessed. This numerator and its first five derivatives being 0 in $T = 0$ and its sixth derivative being positive for all positive T, the numerator is positive so that $\Phi(T,\mu)$ is an increasing function of the period T, as illustrated in Figure 4. Thus, for a given μ, the larger the T, the faster biocontrol agents establishment.

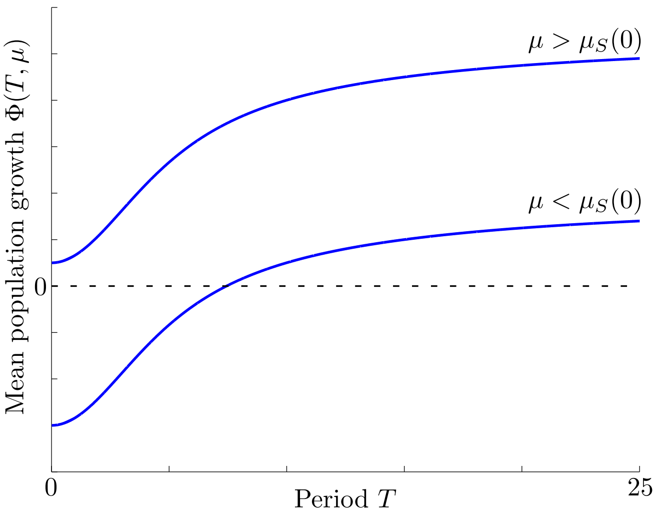

Fig. 4. Mean population growth $\Phi(T,\mu)$ increases with the release period T. If $\mu < \mu_S(0)$ only large release periods lead to population establishment.

B. Predator-prey dynamics

To illustrate our results on the pest-free solution, we return to model (7) which satisfies Hypotheses 3.1. There are two possibilities depending on parameters x_h and K: if $x_h < K$, we have $\frac{f'(0)}{g'(0)} = S_g = \frac{arx_h}{b_0}$ but if $x_h > K$, $S_g = \frac{ar}{4Kb_0}(K + x_h)^2$. In the former case, the local and global stability conditions are identical, while they differ in the latter.

In order to evaluate the convergence rate of x to 0, we note that system (19) and matrix B indicate that, locally,

$$\begin{aligned} x(nT^+) &= \left(e^{\int_{nT^+}^{(n+1)T^+}(f'(0)-g'(0)y_p q(y_p))d\tau}\right)^n x(0^+) \\ &= e^{-\Psi_L(T,\mu)nT}x(0^+), \end{aligned}$$

so that $\Psi_L(T,\mu)$ is the mean convergence-rate of x to 0. The more it is positive, the faster the convergence of x to 0.

For model (7), it writes:

$$\Psi_L(T,\mu) = \frac{b_0}{ax_h}\frac{1}{T}\int_0^T \frac{y^{*2}e^{-2m\tau}}{y^* e^{-m\tau} + y_h} d\tau - r,$$

which becomes

$$\Psi_L(T,\mu) = \frac{b_0}{ax_h m}\left(\mu + \frac{y_h}{T}\ln\left[\frac{y^* e^{-mT} + y_h}{y^* + y_h}\right]\right) - r.$$

This should be positive for LAS of the pest-free solution. Neither T nor μ can easily be isolated from $\Psi_L(T,\mu) > 0$ since y^* depends on both. By maintaining the introduction rate μ constant, we compute the value of Ψ_L for small and large periods T. For large periods, it is studied through L'Hospital rule:

$$\lim_{T\to+\infty}\frac{\Psi_L(T,\mu)T}{T} = \lim_{T\to+\infty}\frac{d}{dT}\left(\Psi_L(T,\mu)T\right),$$

which yields

$$\lim_{T\to+\infty}\Psi_L(T,\mu) = \frac{\mu b_0}{ax_h m} - r.$$

The local stability condition for large periods is then

$$\mu > \mu_{Lb} = \frac{arx_h m}{b_0}. \tag{23}$$

For small periods, we show that

$$\Psi_L(T,\mu) \underset{T\to0^+}{\simeq} \frac{b_0}{ax_h m}\left(\mu + \frac{\mu y_h}{m + y_h} - \frac{\mu_{Lb}}{m}\right),$$

So that, for short periods, the condition to obtain local stability is a quadratic inequation in μ:

$$\mu^2 - \mu\mu_{Lb} - my_h\mu_{Lb} > 0, \tag{24}$$

which yields

$$\mu > \mu_{La} = \mu_{Lb}\frac{1 + \sqrt{1 + \frac{4my_h}{\mu_{Lb}}}}{2} > \mu_{Lb}. \tag{25}$$

The same reasoning is used for the global stability condition (when $x_h > K$) and we find respectively for large and small periods the following conditions:

$$\mu > \mu_{Gb} = mS_g, \tag{26}$$

$$\mu > \mu_{Ga} = \mu_{Gb}\frac{1 + \sqrt{1 + \frac{4my_h}{\mu_{Gb}}}}{2} > \mu_{Gb}. \tag{27}$$

Simulations have been performed with model (7) and the parameters given in the caption of Figure 5. These values correspond to the situation where model (7) has only one globally stable equilibrium, $(K,0)$ leading to the extinction of predators. Since $x_h > K$, the global and local stability are different.

Figure 5 illustrates the stability of the pest-free solution as a function of parameters μ and T. Compared with model (7) where prey were always present at equilibrium, it is now possible to eradicate the pest population (blue area). The green area only guarantees that the pest-free solution is LAS while it is unstable in the red area. The aforementioned μ_{La}, μ_{Lb}, μ_{Ga} and μ_{Gb} are illustrated in Figure 5. For an introduction rate too small (under μ_{Lb}), the solution is unstable for any T and if μ is large enough (above μ_{Ga}), the solution is always GAS.

Intermediate introduction rates μ allow to obtain different situations as a function of the release period T: for small periods, the pest-free solution is unstable, while it is GAS for large T-values. The upper hand of larger T values over smaller ones is further illustrated in Figure 6, where $\Psi(T,\mu)$, the convergence rate of the pest population to 0, is plotted against T for different μ values. Small introduction rates μ never lead to pest control, but as soon as μ is large enough, larger T values clearly accelerate pest eradication.

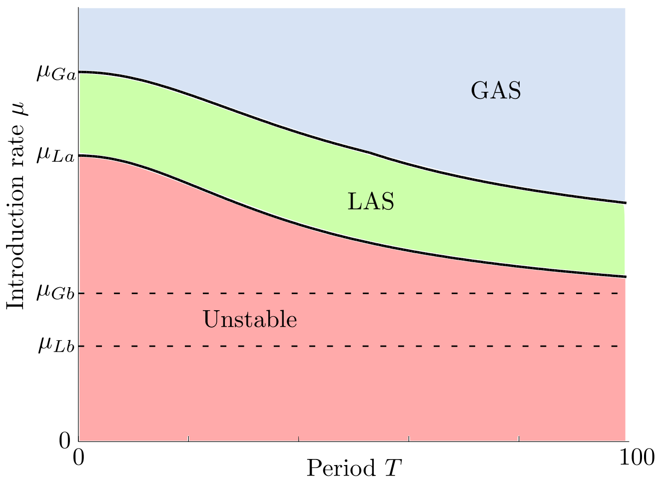

Fig. 5. Local and global stability conditions in function of parameters μ and T. The red area represents couples (T,μ) such that the solution does not converge to the pest-free solution. The green area give only the local stability. Blue part is a zone where the pest-free solution is GAS. Parameters are from [19]: $b_0 = 0.936$, $a = 0.214$, $r = 0.9$, $x_h = 0.8$, $y_h = 1$ and we consider a small value of the carrying capacity $K = 0.2$.

These numerical results have been confirmed through formal calculations performed on Maple [22] that $\Psi_L(T,\mu)$ is an increasing function of T. Thus, larger T can make pest eradication possible, and when the latter is possible, the larger the T the faster the convergence of the pest population to 0.

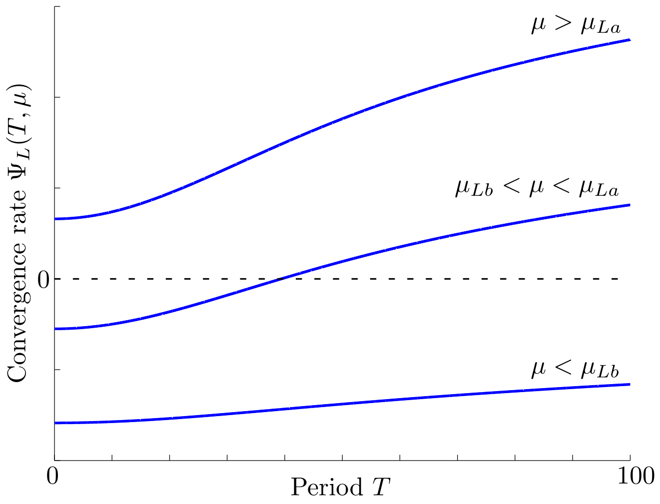

Fig. 6. Convergence rate of the pest population to 0 $\Psi(T,\mu)$, as a function of the release period for three introduction rates μ. When μ is too small, pest control is never achieved, while it is achieved for any T when μ is large enough. For intermediate values of μ, only large T yield to pest eradication.

V. DISCUSSIONS

Allee effects affect numerous animal and vegetal populations. They are acknowledged as important drivers of population establishment and can also have repercussions on interspecific interactions such as in predator-prey systems [18], [19], [20].

In line with [20], we considered biocontrol agents subject to Allee effects. We specifically focused on the introduction strategies of biocontrol agents in terms of sizes and frequency of the introductions, as *e.g.* in [16], [5], [6]. We used two different population models, the first one concentrating on the biocontrol agents population, while the second explicitly considered predator-prey interactions. In the former model, biological control efficacy has been evaluated through an indicator of biocontrol agents population establishment swiftness, and in the latter, through a measure of the pest eradication rate.

Our results are clear-cut in both approaches: for a given introduction rate, the most efficient strategies are to very rarely release massive amounts of biocontrol agents (Figures 4 and 6). Depending on how large the introduction rate is, more frequent, and thus smaller, releases may still succeed, but may also fail: in fact, in both models there exist a release rate - release period threshold under which either biocontrol agents do not establish (single species model) or pest control is disrupted (predator-prey model). The only important difference in our conclusions is that, in the predator-prey model, there is a threshold introduction rate under which any release strategy will fail, while such threshold does not exist in the single species model.

Disregarding density dependence in the predator population, previous modelling studies on augmentative biological control [16] concluded that, due to stochasticity in the timing of pest invasions, small and frequent biocontrol agents introductions were to be preferred over larger and rarer ones. This conclusion has also been reached by [5], [6] as a result of intraspecific competition (negative density dependence) among biocontrol agents. This contribution makes it clear that positive density dependence in biocontrol agents has to be experimentally assessed, as it can revert recommendations on the release strategies.

REFERENCES

[1] P. DeBach, *The scope of biological control*. Chapman and Hall Ltd., 1964.
[2] S. M. Smith, "Biological control with trichogramma: Advances, successes, and potential of their use," *Annual Review of Entomology*, vol. 41, pp. 375–406, 1996.
[3] G. K. Roderick, R. Hufbauer, and M. Navajas, "Evolution and biocontrol," *Evolutionary Applications*, vol. 5, pp. 419–423, 2012.
[4] T. S. Bellows, "Restoring population balance through natural ennemy introductions," *Biological Control*, vol. 21, pp. 199–205, 2001.
[5] S. Nundloll, L. Mailleret, and F. Grognard, "Two models of interfering predators in impulsive biological control," *Journal of Biological Dynamics*, vol. 00, pp. 1–14, 2008.
[6] ——, "Influence of intrapredatory interferences on impulsive biological control efficiency," *Bulletin of Mathematical Biology*, vol. 72, pp. 3264–3272, 2010.
[7] W. C. Allee, *Animal aggregations: a study in general sociology*. University of Chicago Press, 1931.
[8] ——, *Principles of animal ecology*. W. B. Saunders Company, 1949.
[9] F. Courchamp, L. Berec, and J. Gascoigne, *Allee effects in ecology and conservation*. Oxford University Press, 2008.
[10] A. M. Kramer, B. Dennis, A. M. Liebhold, and J. M. Drake, "The evidence for allee effects," *Population Ecology*, vol. 51, pp. 541–354, 2009.
[11] X. Fauvergue and K. R. Hopper, "French wasps in the new world: experimental biological control introductions reveal a demographic allee effect," *Population Ecology*, vol. 51, pp. 385–397, 2009.

[12] L. Mailleret and V. Lemesle, “A note on semi-discrete modelling in the life sciences,” *Philosophical Transactions of the Royal Society A-Mathematical Physical and Engineering Sciences*, vol. 367, pp. 2113–2138, 2009.

[13] F. Courchamp, T. Clutton-Brock, and B. Grenfell, “Inverse density dependence and the allee effect,” *Trends in Ecology and Evolution*, vol. 14, pp. 405–410, 1999.

[14] D. Boukal and L. Berec, “Single-species models of the allee effect: extinction boundaries, sex ratios and mate encounters,” *Journal of Theoretical Biology*, vol. 218, pp. 375–394, 2002.

[15] Y. Gruntfest, R. Arditi, and Y. Dombrovsky, “A fragmented population in a varying environment,” *Journal of Theoretical Biology*, vol. 185, pp. 539–547, 1997.

[16] L. Mailleret and F. Grognard, “Global stability and optimisation of a general impulsive biological control model,” *Mathematical Biosciences*, vol. 221, pp. 91 – 100, 2009.

[17] H. Guo, L. Chen, and X. Song, “Mathematical models of restoration and control of a single species with allee effect,” *Applied Mathematical Modelling*, vol. 34, pp. 2113–2138, 2010.

[18] S.-R. Zhou, Y.-F. Liu, and G. Wang, “The stability of predator-prey systems subject to the allee effects,” *Theoretical Population Biology*, vol. 67, pp. 23 – 31, 2005.

[19] A. Verdy, “Modulation of predator-prey interactions by the allee effect,” *Ecological Modelling*, vol. 221, pp. 1098–1107, 2010.

[20] A. Bompard, I. Amat, X. Fauvergue, and T. Spataro, “Host-parasitoid dynamics and the success of biological control when parasitoids are prone to allee effects,” *PLoS ONE*, vol. 8, p. e76768, 10 2013.

[21] C. S. Holling, “The components of predation as revealed by a study of small-mammal predation of the european pine sawfly1,” *The Canadian Entomolgist*, vol. 91, pp. 293–320, 1959.

[22] “Maple 16.00,” Maplesoft, a division of Waterloo Maple Inc., Waterloo, Ontario.