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THE EFFECT OF PARTIAL CROP HARVEST ON BIOLOGICAL PEST CONTROL

S. NUNDLOLL, L. MAILLERET AND F. GROGNARD

ABSTRACT. In this paper, the effects of periodic partial harvesting of a continuously grown crop on augmentative biological control are analyzed. Partial harvesting can remove a proportion of both pests and biological control agents, so its influence on control efficiency cannot be *a priori* neglected. An impulsive model consisting of a general predator-prey model in ODE, augmented by a discrete component to depict releases of biological control agents and periodic partial harvesting is used. The periods are taken as integer multiples of each other. A stability condition for pest eradication is expressed as the minimal value of the budget per unit time to spend on predators. We consider the partial harvesting period to be fixed by both the plant's physiology and market forces so that the only manipulated variable is the release period. It is shown that varying the release period with respect to the harvest period influences the minimal budget value when the former is carried out more often than the latter and has no effect when releases take place as often as or less frequently than partial harvests.

1. Introduction. Biological control is the reduction of pest populations to harmless levels through the release of their natural enemies. The latter can include both parasitic and predatory species, which are deployed at selected locations throughout the crop and, wherever possible, to specific parts of individual plants where the pest is likely to attack. Successful control projects in the field have involved the use of only one predatory species such as in [3, 9], as well as more complex biodiverse schemes such as those suggested by [8, 14, 17] and the references therein. The target pest species and the setting, i.e., where the crop is grown, usually determine the type of control required, namely whether pest eradication is necessary or not. For an exhaustive list of definitions and applications, we refer the reader to [2, 5, 16].

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In this contribution, we consider the protection of continuously grown crops which have zero tolerance to pest invasions. There are two aspects in this type of culture.

- Firstly, inundative control which is a prophylactic method of pest control yields the most satisfactory results when implemented (see [6, 7, 13, 20] for theoretical/simulatory studies and [1, 4, 8, 9] for real life experiments). A calculated number of predators are repeatedly injected into the ecosystem, independently of the detection of pest insects. Such populations are not allowed to thrive and consist only of individuals whose main source of subsistence is the pest insect, in the absence of which, they (the predator insects) rapidly die out. The frequency of the releases and the number of predators injected each time ensures that a minimal 'sentry' population is present to reduce the damage caused by the pests on their attack.

- Secondly, over their growing period, these crops are partially harvested on a regular basis. Since it is known that harvests are likely to influence, even counterintuitively, predator-prey dynamics [15, 18], it has to be taken into account in the formulation of the problem.

We consider the simplest ditrophic case whereby one predatory species is used to eradicate a pest population. Our model consists of ODEs augmented by a discrete component to incorporate the effect of partial harvest and releases that by their very nature are discrete phenomena. This is a classical formulation that is used widely in the literature where impulsive dynamics are studied. Examples are [12, 15] in the context of agricultural ecosystems, [19] in epidemiology and [10] in pulsed chemotherapy to cite some. Few papers in the literature on impulsive crop protection, however, seem to focus on stability of the pest-free state: yet this is of practical importance especially for highly valued crop cultures.

In our work, we attempt to give an economic dimension to the solution of our problem by defining the releases in terms of the number of predators to invest in over a budget period. Using Floquet theory as presented in [19], we are able to express the stability condition as the minimal number of predators per budget period required to drive the pests to zero at a given release frequency. Mailleret and Grognard [13] showed how this number varied with the release period chosen. The worst case scenario of pest attack occurring at an intermediate stage

between two predator releases was considered, and the optimal release policy which would guarantee the most efficient protection against surges in the pest population was calculated. In particular, it is shown that the higher the frequencies of predator release, the smaller the time interval over which the pest population was above a threshold commonly referred to as the Economic Injury Level [21]—and hence the lower the damage incurred by the crops.

In line with the work of [13], we investigate how the frequency of releases is to be varied with respect to the (fixed) harvesting frequency to minimize the minimal budget value. We consider the harvest period as a reference since it is set by crop growth and market constraints. The effect of partial harvesting is similar to that of pesticide usage proposed by Liu et al. [12] in their Integrated Pest Management (IPM) strategy. Our model departs from the latter's in three ways. Firstly, both the predator and pest populations are subjected to partial harvesting when this occurs. Secondly, hypotheses made on the functions governing the population changes are weak and can encompass most of the density-dependent functions proposed in the literature. Finally, one period is taken as the integer multiple of the other. This feature is key in solving for the stability condition to obtain the minimal budget value and include the case where the frequencies are not the same.

It is shown that, for a given harvest period, when releases take place less often or as often as harvests, the minimal budget is at a calculated value which is independent of the release period. However, when releases take place more often than harvests, the minimal budget required always exceeds this value. This result runs counter with that obtained by [13]: merging the two seems to indicate that the harvest frequency is a threshold that should not be exceeded when releasing predators for efficient biological control.

In the first section of this article the system model is presented. The mathematical analysis of the system's stability and the formulation of the stability condition in terms of the minimal budget are presented in the next section. A brief interpretation of the mathematical results follows. Finally, we conclude with a discussion on their implications.

2. Model description. The model we present consists of a continuous part to depict the predator-prey interaction. We consider the case at the onset of pest invasion where the crop—the pest food supply—is in abundance. Because of this, at this stage, it is sufficient to model only the pest x and predator y species.

$$(1) \quad \begin{cases} \dot{x} = f(x) - g(x)y \\ \dot{y} = h(x)y - dy \\ x(nT_h^+) = (1 - \alpha_x)x(nT_h) & \text{for all } n \in \mathbf{N} \\ y(nT_h^+) = (1 - \alpha_y)y(nT_h) + \delta(nT_h \bmod T_r)\mu T_r & \text{for all } n \in \mathbf{N} \\ y(mT_r^+) = (1 - \delta(mT_r \bmod T_h)\alpha_y)y(mT_r) + \mu T_r & \text{for all } m \in \mathbf{N}. \end{cases}$$

The first two equations govern the intrinsic predator-prey interaction occurring in the system. The three other ones depict the impulsive phenomena that we consider with harvest taking place at nT_h and releases at mT_r .

In the continuous part, the functions discussed are not specified so they are representative of as many systems as possible. Only the following hypotheses are made.

Hypothesis 1. *Let $f(x)$, $g(x)$ and $h(x)$ be locally Lipschitz continuous in \mathbf{R}^+ such that*

- $f(0) = 0$,
- $g(0) = 0$, $g'(0) > 0$ and $g(x) > 0$ for all $x > 0$,
- $h(0) = 0$ and $h(x) > 0$ for all $x > 0$,
- $f(x)/g(x)$ and $g(x)/x$ are upper bounded for $x \geq 0$.

$f(x)$ is the growth velocity or feeding input of the pests. It represents the growth function of the pest species and, in our model, it also encompasses any nonpredatory losses of the pest population (e.g., logistic growth). We assume that the predator population is never large enough for intra-predator interaction to take place so the functional and numerical responses can be expressed solely in terms of the prey numbers, i.e, as $g(x)$ and $h(x)$, respectively.

We assume that pest growth rate, the functional and numerical responses are all nil when the ecosystem is pest-free.

The functional response is increasing for small pest population levels. We also consider that, in the presence of pests, predation always takes place with a negative impact on x , $g(x) > 0$, and a positive impact on y , $h(x) > 0$. Note that conditions can be induced as much by the predator insect foraging abilities *per se* as they can be facilitated by placing the predator insects at known locations on the plant where the pests are most likely to attack. In classical density dependent models, $g(x)$ is bounded or linear, so that $g(x)/x$ is always bounded. The boundedness of $f(x)/g(x)$ means that there is no value of x where the pest growth $f(x)$ overwhelmingly dominates the predation $g(x)$, which would render the biological control impossible.

Partial crop harvests and predator releases occur respectively every T_h and T_r . α_x and α_y represent the respective proportions of the prey and predator populations affected at each harvest. These parameters are allowed to be different since, in reality, it is very likely that each species tends to occupy different parts of the plant. We also assume that the insects are uniformly distributed throughout our plantation so that the effect of partial harvesting is directly correlated with the number of plants harvested. We assume linear maturation of the crop so the proportion of crops harvested each time and hence insects removed is considered as fixed. The δ -function is defined thus to identify instants of simultaneous partial harvest and predator release.

$$(2) \quad \delta(\theta) = \begin{cases} 1 & \text{if } \theta = 0 \\ 0 & \text{otherwise.} \end{cases}$$

Finally, we presume that we have a fixed budget of predators over a designated time period that is distributed evenly among the releases that are carried out. μ refers to the total number of predators purchased per time unit. Expressing T_r in the same units as the budget period gives the control μT_r as the number of predators released every T_r .

3. Mathematical analysis. In our analysis, we restrict ourselves to the case where either one of the periods (release or partial harvests) is the integer multiple of the other. Note however that the model (1) formalism is more general. We study the system in the absence of pests, i.e., when $x = 0$. In addition to being invariant, it is the target state of our system. The stability of the system around that state is therefore of interest. Our analysis takes place separately for the case

when releases are more frequent than harvests, and when they are less frequent.

We show that in the absence of pests at the initial time, the predator population converges towards a positive periodic solution. We then demonstrate that when preys are present at the initial time, convergence of the predator population also takes place to that same periodic solution, while the preys go extinct provided some condition on the parameters is verified.

3.1. Pest-free stability analysis.

Releases more frequent than harvests.

Proposition 1. *Let $T_h = kT_r$ where $k \in \mathbf{N}^*$ and Hypotheses 1 be satisfied. Then, in the absence of pests, model (1) possesses a globally stable periodic solution*

$$(3) \quad (x_{ph}(t), y_{ph}(t)) = \left(0, y^* e^{-d(t \bmod T_h)} + \mu T_r e^{-d(t \bmod T_r)} \sum_{j=0}^{\lfloor (t \bmod T_h)/T_r \rfloor - 1} e^{-jdT_r} \right)$$

where

$$(4) \quad y^* = \frac{((1 - e^{-dT_h})/(1 - e^{-dT_r}))(1 - \alpha_y) + \alpha_y}{1 - (1 - \alpha_y)e^{-dT_h}} \mu T_r.$$

Proof. When $T_h = kT_r$, in the absence of pests and using Hypotheses 1, the system is simplified to

$$(5) \quad \begin{cases} \dot{x} = 0 \\ \dot{y} = -dy \\ x(mT_r^+) = (1 - \delta(m \bmod k)\alpha_x)x(mT_r) \\ y(mT_r^+) = (1 - \delta(m \bmod k)\alpha_y)y(mT_r) + \mu T_r \end{cases} \text{ for all } m \in \mathbf{N}.$$

The pest population stays nil since, in the absence of pests, their population does not change either. The solution

$$x_{ph}(t) = 0$$

is trivial.

On the other hand, the predator population will vary according to the number of predators manually injected into the system and, since the population is nonzero, according to the partial harvest effect. The absence of their source of food will cause an exponential decay of the population. We demonstrate that these forces will provoke the predator population to reach a periodic pattern of period equal to T_h , which we shall refer to as the *period of reference*. The instant following a coinciding partial harvest and release is taken as the *point of reference*.

To prove Proposition 1, we first show by induction that the predator population right after a release can be expressed in terms of the point of reference as follows

$$(6) \quad y(nT_h + iT_r^+) = y(nT_h^+)e^{-idT_r} + \mu T_r \sum_{j=0}^{i-1} e^{-jdT_r}$$

where $i \in [0, 1, \dots, (k - 1)]$.

It is seen that (6) is valid for $i = 0$ since it is equal to

$$y(nT_h^+) = y(nT_h^+)e^0 + \mu T_r \sum_{j=0}^{-1} e^{-jdT_r} = y(nT_h^+).$$

Now suppose that (6) holds for $i = q$ where $q \in [0, 1, \dots, k - 2]$, i.e.,

$$(7) \quad y(nT_h + qT_r^+) = y(nT_h^+)e^{-qdT_r} + \mu T_r \sum_{j=0}^{q-1} e^{-jdT_r}.$$

We will now show that (6) is valid for $i = q + 1$. We calculate $y(nT_h + (q + 1)T_r^+)$ from $y(nT_h + qT_r^+)$ using (5), and get

$$\begin{aligned} y(nT_h + (q + 1)T_r^+) &= y(nT_h + qT_r^+)e^{-dT_r} + \mu T_r \\ &= \left(y(nT_h^+)e^{-qdT_r} + \mu T_r \sum_{j=0}^{q-1} e^{-jdT_r} \right) e^{-dT_r} + \mu T_r \end{aligned}$$

$$\begin{aligned}
 &= y(nT_h^+)e^{-(q+1)dT_r} + \mu T_r \sum_{j=1}^q e^{-jdT_r} + \mu T_r \\
 &= y(nT_h^+)e^{-(q+1)dT_r} + \mu T_r \sum_{j=0}^q e^{-jdT_r},
 \end{aligned}$$

so that (6) holds true for $i \in [0, 1, \dots, k - 1]$.

To evaluate the evolution of y according to the period of reference T_h , we need to calculate the value of $y((n + 1)T_h^+)$, which is equivalent to $y(nT_h + kT_r^+)$, in terms of $y(nT_h^+)$. At this point however, partial harvesting takes place before predator release; so we first express it in terms of $y(nT_h + (k - 1)T_r^+)$, then expand the expression using (6) as follows

$$\begin{aligned}
 y((n + 1)T_h^+) &= y(nT_h + (k - 1)T_r^+) e^{-dT_r} (1 - \alpha_y) + \mu T_r \\
 &= \left(y(nT_h^+)e^{-d(k-1)T_r} + \mu T_r \sum_{j=0}^{k-2} e^{-jdT_r} \right) e^{-dT_r} (1 - \alpha_y) + \mu T_r \\
 &= y(nT_h^+)e^{-dT_h} (1 - \alpha_y) + \mu T_r (1 - \alpha_y) \sum_{j=1}^{k-1} e^{-jdT_r} + \mu T_r \\
 &= y(nT_h^+)e^{-dT_h} (1 - \alpha_y) + \mu T_r \left((1 - \alpha_y) \sum_{j=0}^{k-1} e^{-jdT_r} + \alpha_y \right).
 \end{aligned}$$

Note that the summation term can also be evaluated so the sequence is expressible as

$$\begin{aligned}
 (8) \quad y((n + 1)T_h^+) &= (1 - \alpha_y)y(nT_h^+)e^{-dT_h} \\
 &\quad + \mu T_r \left((1 - \alpha_y) \frac{1 - e^{-dT_h}}{1 - e^{-dT_r}} + \alpha_y \right).
 \end{aligned}$$

In this linear dynamical system, the coefficient of $y(nT_h^+)$, $(1 - \alpha_y)e^{-dT_h}$ is less than one in magnitude, so the sequence will converge to a limit, the equilibrium of (8). This equilibrium yields (4) and the convergence of $y(t)$ to a periodic solution $y_{ph}(t)$ based on y^* .

Now that we have established the existence of the periodic solution $y_{ph}(t)$, we seek to formulate it. We focus on a reference period over

$nT_h < t \leq (n + 1)T_h$ during which $y_{ph}(t)$ is piecewise continuous, with the continuous components separated by predator releases. The continuous intervals are defined over $nT_h + iT_r < t \leq nT_h + (i + 1)T_r$ where $i \in [0, 1, \dots, k - 1]$. For a given value of t , the value of i is easily identified as being $i = \lfloor (t \bmod T_h) / T_r \rfloor$. The value of $y_{ph}(t)$ is then of the form

$$y_{ph}(t) = y_{ph}(nT_h + iT_r^+)e^{-d(t \bmod T_r)},$$

and, from (6) with $y(nT_h^+) = y^*$, we have that

$$y_{ph}(nT_h + iT_r^+) = y^*e^{-idT_r} + \mu T_r \sum_{j=0}^{i-1} e^{-jdT_r}$$

so that

$$\begin{aligned} y_{ph}(t) &= \left(y^*e^{-idT_r} + \mu T_r \sum_{j=0}^{i-1} e^{-jdT_r} \right) e^{-d(t \bmod T_r)} \\ &= y^*e^{-d(t \bmod T_h)} + \mu T_r e^{-d(t \bmod T_r)} \sum_{j=0}^{i-1} e^{-jdT_r} \\ &= y^*e^{-d(t \bmod T_h)} + \mu T_r e^{-d(t \bmod T_r)} \sum_{j=0}^{\lfloor (t \bmod T_h) / T_r \rfloor - 1} e^{-jdT_r}. \end{aligned}$$

This is the form proposed in (3), thereby completing our proof. □

The form of the y_{ph} function is illustrated in Figure 1.

Releases less frequent than harvests. When harvesting is more frequent than the release of predators, we have a similar result about the existence of a periodic solution.

Proposition 2. *Let $T_r = kT_h$ where $k \in \mathbf{N}^*$ and Hypotheses 1 be satisfied. Then, in the absence of pests, model (1) possesses a globally stable periodic solution*

$$(9) \quad (x_{pr}(t), y_{pr}(t)) = \left(0, y^*e^{-d(t \bmod T_r)}(1 - \alpha_y)^{\lfloor (t \bmod T_r) / T_h \rfloor} \right)$$

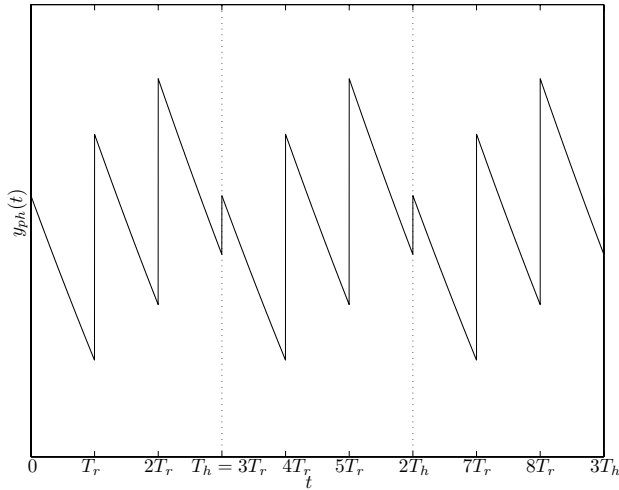


FIGURE 1. Form of the periodic solution $y_{ph}(t)$ in the case where $k = 3$. Releases of predators are apparent at every mT_r instant, while the cumulative effect of harvest and release leads to an apparent smaller release at every nT_h instant. Between those instants, the population decays exponentially since it has no prey to feed on.

where

$$(10) \quad y^* = \frac{\mu T_r}{1 - (1 - \alpha_y)^k e^{-dT_r}}.$$

Proof. When $T_r = kT_h$, in the absence of pests and using Hypotheses 1, the system is simplified to

$$(11) \quad \begin{cases} \dot{x} = 0 \\ \dot{y} = -dy \\ x(nT_h^+) = (1 - \alpha_x)x(nT_h) \\ y(nT_h^+) = (1 - \alpha_y)y(nT_h) + \mu T_r \delta(n \bmod k) \end{cases} \text{ for all } n \in \mathbf{N}.$$

As previously explained, $x_{pr}(t)$ is solved for trivially as being

$$x_{pr}(t) = 0$$

We prove that the predator population again reaches a periodic solution. This time, however, the *period of reference* is T_r . The *point*

of reference is the instant after a coinciding harvest and release. We show by induction that the population after a harvest can be expressed as

$$(12) \quad y(mT_r + iT_h^+) = y(mT_r^+)e^{-idT_h}(1 - \alpha_y)^i$$

where $i \in [0, 1, \dots, (k - 1)]$.

It is seen that (12) is valid for $i = 0$ since it resumes to

$$y(mT_r^+) = y(mT_r^+)e^0(1 - \alpha_y)^0.$$

Suppose (12) holds for $i = q$ where $q \in [0, 1, \dots, k - 2]$, i.e.,

$$(13) \quad y(mT_r + qT_h^+) = y(mT_r^+)e^{-qdT_h}(1 - \alpha_y)^q.$$

We will now show that (12) is valid for $i = q + 1$. We calculate the value of y when $i = q + 1$ in terms of $y(nT_h + qT_r^+)$, knowing from $\dot{y} = -dy$ in (11) that it will be an exponential decay with the added component for the harvest. We then get

$$(14) \quad \begin{aligned} y(mT_r + (q + 1)T_h^+) &= y(mT_r + qT_h^+)e^{-dT_h}(1 - \alpha_y) \\ &= (y(mT_r^+)e^{-qdT_h}(1 - \alpha_y)^q) e^{-dT_h}(1 - \alpha_y) \\ &= y(mT_r^+)e^{-d(q+1)T_h}(1 - \alpha_y)^{q+1}. \end{aligned}$$

This is clearly the same form given from the expression in (12), thereby validating it.

y^* is given as the fixed point of the sequence representing post-release instants. Therefore, using (12) for $i = k$ and model (11), we next calculate $y((m + 1)T_r^+)$ as

$$(15) \quad \begin{aligned} y((m + 1)T_r^+) &= y(mT_r + kT_h^+) \\ &= y(mT_r^+)e^{-kdT_h}(1 - \alpha_y)^k + \mu T_r \\ &= y(mT_r^+)e^{-dT_r}(1 - \alpha_y)^k + \mu T_r. \end{aligned}$$

In this linear dynamical system, the coefficient of $y(mT_r^+)$, $e^{-dT_r}(1 - \alpha_y)^k$ is less than one in magnitude, which confirms the existence of the fixed point y^* to which the sequence converges. This equilibrium yields (10) and the convergence of $y(t)$ to a periodic solution $y_{pr}(t)$.

Now that we have established the existence of the periodic solution $y_{pr}(t)$, we seek to formulate it. We focus on a reference period over $mT_r < t \leq (m + 1)T_r$ during which $y_{pr}(t)$ is piecewise continuous, with the continuous components separated by harvests. The intervals of continuity span $mT_r + iT_h < t \leq mT_r + (i + 1)T_h$ where $i \in [0, 1, \dots, k - 1]$. For a given value of t , the value of i is easily identified as being $i = \lfloor (t \bmod T_r) / T_h \rfloor$. The value of $y_{pr}(t)$ is then of the form

$$y_{pr}(t) = y_{pr}(mT_r + iT_h^+)e^{-d(t \bmod T_h)}$$

and, from (12) with $y(mT_r^+) = y^*$, we have that

$$y_{pr}(mT_r + iT_h^+) = y^*e^{-idT_h}(1 - \alpha_y)^i$$

so that

$$\begin{aligned} y_{pr}(t) &= (y^*e^{-idT_h}(1 - \alpha_y)^i) e^{-d(t \bmod T_h)} \\ &= y^*e^{-d(t \bmod T_r)}(1 - \alpha_y)^{\lfloor (t \bmod T_r) / T_h \rfloor}, \end{aligned}$$

which is exactly the expression given in (9) and completes the proof. \square

The form of the y_{pr} function is illustrated in Figure 2.

3.2. Global stability analysis. Since we will study the convergence of the solutions to $(0, y_p(t))$ (where the p subscript stands as well for ph or pr), it will be convenient to describe the system in terms of the deviation coordinates with respect to the reference periodic solution:

$$\begin{aligned} \tilde{x}(t) &= x(t) - x_p(t) \\ \tilde{y}(t) &= y(t) - y_p(t). \end{aligned}$$

This yields

$$(16) \quad \dot{\tilde{x}} = f(x) - g(x)y = f(\tilde{x}) - g(\tilde{x})(\tilde{y} + y_p(t))$$

and

$$(17) \quad \dot{\tilde{y}} = h(x)y - dy - h(x_p)y_p + dy_p = h(\tilde{x})(\tilde{y} + y_p(t)) - d\tilde{y}.$$

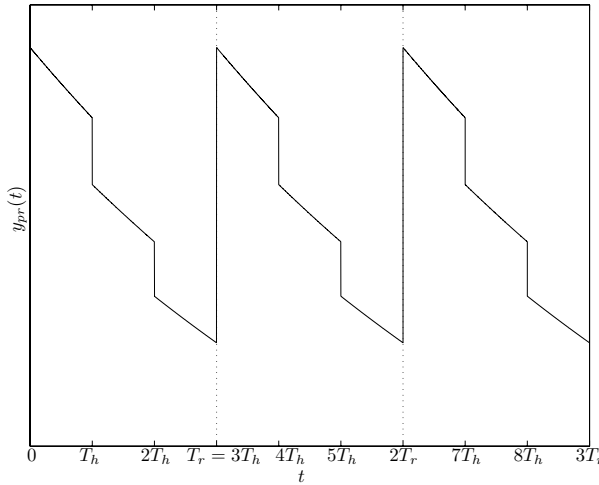


FIGURE 2. Form of the periodic solution $y_{pr}(t)$ in the case where $k = 3$. Harvests are apparent at every nT_h instant, while the release of predators dominates the harvest at every mT_r instant. Between those instants, the population decays exponentially since it has no prey to feed on.

The impulsive effects on \tilde{x} are obviously unchanged compared to those on x . On the other hand, the release effects on y disappear in \tilde{y} ; indeed, we have

$$\begin{aligned} \tilde{y}(mT_r^+) &= y(mT_r^+) - y_p(mT_r^+) \\ &= y(mT_r) + \mu T_r - (y_p(mT_r) + \mu T_r) \\ &= \tilde{y}(mT_r). \end{aligned}$$

The harvesting impulses are preserved in the expression of \tilde{y}

$$\begin{aligned} \tilde{y}(nT_h^+) &= y(nT_h^+) - y_p(nT_h^+) \\ &= (1 - \alpha_y)y(nT_h) - (1 - \alpha_y)y_p(nT_h) \\ &= (1 - \alpha_y)\tilde{y}(nT_h). \end{aligned}$$

In the sequel, we will perform a global and a local stability analysis. For the latter, we will need the computation of the linear approximation of the deviation system around the periodic solution $(0, y_p(t))$:

$$(18) \quad \begin{cases} \dot{\tilde{x}} = (f'(0) - g'(0)y_p(t))\tilde{x} \\ \dot{\tilde{y}} = h'(0)y_p(t)\tilde{x} - d\tilde{y}. \end{cases}$$

Releases more frequent than harvests. We will first prove our result in the case where releases take place more often than harvests. We obtain two different constraints for the Local Asymptotic Stability (LAS) and Global Asymptotic Stability (GAS) of the periodic solution in system (1). The latter is obviously stronger than the former, which is sufficient in the case where pests outbreaks do not immediately take large proportions.

In order to state the following theorem, we first need to define the function

$$\begin{aligned} \underline{\mu}_h(S, r) = & d \left(S + \frac{\ln(1 - \alpha_x)}{rT_h} \right) \\ & \times \frac{1}{1 - ((\alpha_y(1 - e^{-dT_h})) / (1 - (1 - \alpha_y)e^{-dT_h})) ((e^{-dT_h/k}) / (k(1 - e^{-dT_h/k})))}. \end{aligned}$$

This function is increasing in S and r because the sign of the partial derivatives is determined by the sign of the last factor, which can be shown to be positive. Indeed, this factor is positive when

$$\left(\frac{\alpha_y(1 - e^{-dT_h})}{1 - (1 - \alpha_y)e^{-dT_h}} \right) \left(\frac{e^{-dT_h/k}}{k(1 - e^{-dT_h/k})} \right) < 1,$$

and we have $\alpha_y e^{-(dT_h)/k} \leq \alpha_y$ and $1 - (1 - \alpha_y)e^{-dT_h} > \alpha_y$, so that

$$\frac{\alpha_y e^{-dT_h/k}}{1 - (1 - \alpha_y)e^{-dT_h}} < 1.$$

Also, $k(1 - e^{-dT_h/k}) \geq (1 - e^{-dT_h})$ since both sides of the inequality have the same value in $T_h = 0$, and

$$\frac{d}{dT_h} \left(k(1 - e^{-dT_h/k}) \right) = de^{-dT_h/k} \geq de^{-dT_h} = \frac{d}{dT_h} (1 - e^{-dT_h}),$$

which shows that $\underline{\mu}_h(S, r)$ is increasing in S and r .

Theorem 1. *When $T_h = kT_r$ with $k \in \mathbf{N}^*$, the solution $(x(t), y(t)) = (0, y_{ph}(t))$ of (1) is LAS if and only if*

$$(19) \quad \mu > \underline{\mu}_h \left(\frac{f'(0)}{g'(0)}, g'(0) \right)$$

and is GAS if

$$(20) \quad \mu > \underline{\mu}_h \left(\sup_{x \geq 0} \frac{f(x)}{g(x)}, \sup_{x \geq 0} \frac{g(x)}{x} \right).$$

Proof. We start with the proof of global convergence under condition (20). In this proof, we will first show that \tilde{x} goes to zero, from which we will derive that \tilde{y} goes to 0 also (so that $y(t)$ converges to $y_{ph}(t)$).

Let the initial condition for system (16)–(17) be $(\tilde{x}_0, \tilde{y}_0)$ at $t_0 = 0^+$, that is, after the harvest and the predator release that take place at the initial time. Analyzing (17) and noting that $y_{ph}(t) + \tilde{y} = y(t) \geq 0$, we have

$$\dot{\tilde{y}} \geq -d\tilde{y}$$

so that $\tilde{y}(t) \geq \min(0, \tilde{y}_0)e^{-dt}$.

In order to analyze the $\dot{\tilde{x}}$ equation, we define the function

$$(21) \quad G(\tilde{x}) = \int_{x_0}^{\tilde{x}} \frac{1}{g(s)} ds,$$

which can easily be seen to be an increasing function of \tilde{x} since $g(s) > 0$. Since we also have that

$$g(s) < \left(\sup_{x \geq 0} \frac{g(x)}{x} \right) s,$$

it is straightforward that $\lim_{\tilde{x} \rightarrow 0} G(\tilde{x}) = -\infty$. In order to show the extinction of the pests we will then prove that $G(\tilde{x})$ goes to $-\infty$ as t goes to infinity. Therefore, we write the G dynamics:

$$\begin{aligned} \frac{dG(\tilde{x})}{dt} &= \frac{1}{g(\tilde{x})} \dot{\tilde{x}} = \frac{f(\tilde{x})}{g(\tilde{x})} - \tilde{y} - y_{ph}(t) \\ &\leq \frac{f(\tilde{x})}{g(\tilde{x})} - \min(0, \tilde{y}_0)e^{-dt} - y_{ph}(t). \end{aligned}$$

We will now consider the evolution of G between two successive harvests, that is, the evolution of G between the times nT_h^+ and $(n+1)T_h$ for a given n :

$$\begin{aligned} G(\tilde{x}((n+1)T_h)) &\leq G(\tilde{x}(nT_h^+)) \\ &\quad + \int_{nT_h^+}^{(n+1)T_h} \left[\frac{f(\tilde{x}(\tau))}{g(\tilde{x}(\tau))} - \min(0, \tilde{y}_0)e^{-d\tau} - y_{ph}(\tau) \right] d\tau. \end{aligned}$$

Since no impulse is present inside the integral, we can drop the $+$ superscript in its lower extremity.

We will now analyze how the harvest that takes place at time $(n+1)T_h$ impacts G . We have

(22)

$$\begin{aligned}
 G(\tilde{x}((n+1)T_h^+)) &= \int_{x_0}^{\tilde{x}((n+1)T_h^+)} \frac{1}{g(s)} ds \\
 &= \int_{x_0}^{\tilde{x}((n+1)T_h)} \frac{1}{g(s)} ds + \int_{\tilde{x}((n+1)T_h)}^{\tilde{x}((n+1)T_h^+)} \frac{1}{g(s)} ds \\
 &\leq G(\tilde{x}(nT_h^+)) \\
 &\quad + \int_{nT_h}^{(n+1)T_h} \left[\frac{f(\tilde{x}(\tau))}{g(\tilde{x}(\tau))} - \min(0, \tilde{y}_0)e^{-d\tau} - y_{ph}(\tau) \right] d\tau \\
 &\quad + \int_{\tilde{x}((n+1)T_h)}^{\tilde{x}((n+1)T_h^+)} \frac{1}{g(s)} ds.
 \end{aligned}$$

The last term represents the influence of harvest on G and can easily be approximated because

$$\tilde{x}((n+1)T_h) > \tilde{x}((n+1)T_h^+) = (1 - \alpha_x)\tilde{x}((n+1)T_h).$$

Denoting $S_g = \sup_{x \geq 0} f(x)/g(x)$ and $r_g = \sup_{x \geq 0} g(x)/x$, we have

(23)

$$\int_{\tilde{x}((n+1)T_h)}^{(1-\alpha_x)\tilde{x}((n+1)T_h)} \frac{1}{g(s)} ds \leq \int_{\tilde{x}((n+1)T_h)}^{(1-\alpha_x)\tilde{x}((n+1)T_h)} \frac{1}{r_g s} ds = \frac{\ln(1 - \alpha_x)}{r_g}.$$

Introducing (23) into (22) then yields a bound on the application between successive moments after harvest.

(24)

$$\begin{aligned}
 G(\tilde{x}((n+1)T_h^+)) &\leq G(\tilde{x}(nT_h^+)) \\
 &\quad + \int_{nT_h}^{(n+1)T_h} \left[\frac{f(\tilde{x}(\tau))}{g(\tilde{x}(\tau))} - \min(0, \tilde{y}_0)e^{-d\tau} - y_{ph}(\tau) \right] d\tau \\
 &\quad + \frac{\ln(1 - \alpha_x)}{r_g}.
 \end{aligned}$$

We can now evaluate an upper-bound for G at any time $t \geq 0$. Defining l as the integer part of t/T_h , we have:

$$\begin{aligned} G(\tilde{x}(t)) - G(x_0) &\leq \int_0^t \left[\frac{f(\tilde{x}(\tau))}{g(\tilde{x}(\tau))} - \min(0, \tilde{y}_0)e^{-d\tau} - y_{ph}(\tau) \right] d\tau \\ &\quad + l \frac{\ln(1 - \alpha_x)}{r_g} \\ &\leq \int_0^t [S_g - \min(0, \tilde{y}_0)e^{-d\tau} - y_{ph}(\tau)] d\tau + l \frac{\ln(1 - \alpha_x)}{r_g} \\ &= - \int_0^t \min(0, \tilde{y}_0)e^{-d\tau} d\tau + \int_{lT_h}^t [S_g - y_{ph}(\tau)] d\tau \\ &\quad + l \int_0^{T_h} [S_g - y_{ph}(\tau)] d\tau + l \frac{\ln(1 - \alpha_x)}{r_g} \\ &= \frac{\min(0, \tilde{y}_0)}{d} (e^{-dt} - 1) + \int_{lT_h}^t [S_g - y_{ph}(\tau)] d\tau \\ &\quad + l \int_0^{T_h} [S_g - y_{ph}(\tau)] d\tau + l \frac{\ln(1 - \alpha_x)}{r_g}. \end{aligned}$$

The first two terms are bounded (the first one is obvious and the second one is upper-bounded by $S_g T_h$). We then have to analyze the third one, which has been obtained through the periodicity of $y_{ph}(t)$ and the fourth in order to know if $G(\tilde{x}(t))$ goes to $-\infty$ when t goes to infinity. In fact, it suffices to have

$$\int_0^{T_h} [S_g - y_{ph}(\tau)] d\tau + \frac{\ln(1 - \alpha_x)}{r_g} < 0$$

to achieve this. It is more cleanly rewritten in the form

$$(25) \quad \int_0^{T_h} y_{ph}(\tau) d\tau > S_g T_h + \frac{\ln(1 - \alpha_x)}{r_g}.$$

In order to obtain (20), we are now left with the computation of $\int_0^{T_h} y_{ph}(\tau) d\tau$, which is detailed in Proposition 3 of the Appendix:

$$\begin{aligned} (26) \quad \int_0^{T_h} y_{ph}(\tau) d\tau &= \frac{\mu T_h}{d} \left(1 - \left(\frac{\alpha_y (1 - e^{-dT_h})}{1 - (1 - \alpha_y) e^{-dT_h}} \right) \left(\frac{e^{-dT_h/k}}{k (1 - e^{-dT_h/k})} \right) \right). \end{aligned}$$

Introducing (26) into (25) then yields (20), which shows that this last condition is sufficient to have \tilde{x} go to 0 as t goes to ∞ .

Since \tilde{x} goes to zero, there exists a finite time t_f after which $h(\tilde{x}) \leq d/2$ for all times. Therefore, after this time, we have

$$\dot{\tilde{y}} = h(\tilde{x})(y_{ph}(t) + \tilde{y}) - d\tilde{y} \leq h(\tilde{x})y_{ph}(t) - \frac{d}{2}\tilde{y}.$$

We have seen that $h(\tilde{x})y_{ph}(t)$ goes to zero as t goes to infinity; so also \tilde{y} does.

In order to have global asymptotic stability, we are only left with local asymptotic stability to prove. In order to do that, we only have to consider the discrete system that maps the state at time nT_h^+ onto the state at time $(n + 1)T_h^+$ with respect to the linear equation (18) and the discrete part. After some computations, we obtain:

$$(27) \quad \begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix} ((n + 1)T_h^+) = \mathbf{B} \begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix} (nT_h^+)$$

where

$$\mathbf{B} = \begin{pmatrix} (1 - \alpha_x)e^{\int_{nT_h}^{(n+1)T_h} f'(0) - g'(0)y_{ph} d\tau} & 0 \\ \ddagger & (1 - \alpha_y)e^{-d \int_{nT_h}^{(n+1)T_h} d\tau} \end{pmatrix}.$$

Note that \ddagger is a term that we do not use in our analysis; therefore, it is not expressed. Indeed, since the matrix is triangular and $|B_{22}| < 1$, it is stable if and only if $|B_{11}| < 1$, i.e.,

$$(28) \quad \int_{nT_h}^{(n+1)T_h} y_{ph} d\tau > \frac{f'(0)T_h + \ln(1 - \alpha_x)}{g'(0)}.$$

Similarly to what was done earlier, it can be shown that (28) is equivalent to (19), so that the necessary and sufficient condition for local stability is proven.

It is directly seen that (28) is satisfied when (20) is because $\underline{\mu}_h(S, r)$ is increasing in S and r , and we have

$$(29) \quad \frac{f'(0)}{g'(0)} = \lim_{x \rightarrow 0} \frac{f(x)}{g(x)} \leq \sup_{x \geq 0} \frac{f(x)}{g(x)} \quad \text{and} \quad g'(0) = \lim_{x \rightarrow 0} \frac{g(x)}{x} \leq \sup_{x \geq 0} \frac{g(x)}{x}.$$

This completes the proof of global stability, since we have shown global convergence and local stability when (20) is satisfied. \square

Releases less frequent than harvests. If we now consider the case where predator releases take place less often than harvests, we also obtain global and local stability results based on the following function

$$\underline{\mu}_r(S, r) = d \left(S + \frac{\ln(1 - \alpha_x)}{rT_h} \right) \frac{1 - (1 - \alpha_y)e^{-dT_h}}{1 - e^{-dT_h}},$$

which is nondecreasing in S and r since the last fraction is positive and $\alpha_x \in [0, 1]$.

Theorem 2. *When $T_r = kT_h$ with $k \in \mathbf{N}^*$, the solution $(x(t), y(t)) = (0, y_{pr}(t))$ of (1) is LAS if and only if*

$$(30) \quad \mu > \underline{\mu}_r \left(\frac{f'(0)}{g'(0)}, g'(0) \right)$$

and is GAS if

$$(31) \quad \mu > \underline{\mu}_r \left(\sup_{x \geq 0} \frac{f(x)}{g(x)}, \sup_{x \geq 0} \frac{g(x)}{x} \right).$$

Proof. This proof does not depart very much from the one of Theorem 1. The only difference is that the reference period is now T_r . We use the same function $G(\tilde{x})$ as in (21), and an analysis similar to the one of the previous theorem leads to

$$\begin{aligned} G(\tilde{x}(mT_r + (l + 1)T_h^+)) &\leq G(\tilde{x}(mT_r + lT_h^+)) \\ &+ \int_{mT_r + lT_h}^{mT_r + (l+1)T_h} \left[\frac{f(\tilde{x}(\tau))}{g(\tilde{x}(\tau))} - \min(0, \tilde{y}_0)e^{-d\tau} - y_{pr}(\tau) \right] d\tau \\ &+ \frac{\ln(1 - \alpha_x)}{r_g}, \end{aligned}$$

which has the same form as (24) (where y_{ph} is replaced by y_{pr}) since it is depicting the behavior of the system between two harvesting instants.

Extending this to the whole T_r interval, we obtain

$$\begin{aligned}
 G(\tilde{x}((m+1)T_r^+)) &\leq G(\tilde{x}(mT_r^+)) \\
 &+ \int_{mT_r}^{(m+1)T_r} \left[\frac{f(\tilde{x}(\tau))}{g(\tilde{x}(\tau))} - \min(0, \tilde{y}_0) e^{-d\tau} - y_{pr}(\tau) \right] d\tau \\
 &+ k \frac{\ln(1 - \alpha_x)}{r_g}.
 \end{aligned}$$

We now see that this expression is identical to (24) with the exception of the presence of a k factor and the expression of $y_{pr}(t)$, which comes from (9) instead of (3).

Condition (25) then becomes

$$(32) \quad \int_0^{T_r} y_{pr}(\tau) d\tau > S_g T_r + k \frac{\ln(1 - \alpha_x)}{r_g},$$

and the computation of $\int_0^{T_r} y_{pr}(\tau) d\tau$ with $y_{pr}(t)$ as in (9) yields (see Proposition 4 in the Appendix)

$$(33) \quad \int_0^{T_r} y_{pr}(\tau) d\tau = \frac{\mu T_r}{d} \frac{1 - e^{-dT_h}}{1 - (1 - \alpha_y) e^{-dT_h}}.$$

This leads to condition (31). Global convergence of (\tilde{x}, \tilde{y}) to $(0, 0)$ is then concluded by using the same argument as in the proof of Theorem 1 to show the convergence of \tilde{y} to 0.

The local stability condition (30) then directly arises from the analysis of the stability of the discrete linearized system that maps $\tilde{y}(mT_r^+)$ onto $\tilde{y}((m+1)T_r^+)$.

$$(34) \quad \begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix} ((m+1)T_r^+) = \mathbf{B} \begin{pmatrix} \tilde{x} \\ \tilde{y} \end{pmatrix} (mT_r^+)$$

where

$$(35) \quad \mathbf{B} = \begin{pmatrix} (1 - \alpha_x)^k e^{\int_{mT_r}^{(m+1)T_r} f'(0) - g'(0) y_{pr} d\tau} & 0 \\ \ddagger & (1 - \alpha_y)^k e^{-d \int_{mT_r}^{(m+1)T_r} d\tau} \end{pmatrix}.$$

Again, since the system matrix is lower triangular, for stability we simply require that $|B_{11}| < 1$ and $|B_{22}| < 1$. The latter yields a trivial condition, so we calculate the former:

$$(36) \quad \int_{mT_r}^{(m+1)T_r} y_{pr} \, d\tau > \frac{f'(0)T_r + k \ln(1 - \alpha_x)}{g'(0)},$$

which directly leads to condition (30) for local stability and the proof of global stability is also complete because $\underline{\mu}_r$ is increasing in S and r and (29) is still satisfied. \square

Comment. As we have seen, when condition (20) or (31) is satisfied, the extinction of the pests is GAS. When the local condition (19) or (30) is not verified, the extinction of the pests is not stable and a bifurcation analysis similar to what is done in [10, 12] would show the presence of a limit cycle when μ is close to the limit. When μ satisfies condition (19) or (30) only, the pests' extinction is locally stable, and we cannot rule out that it is globally stable (since our global condition is only sufficient). Such a budget has the advantage of being smaller than the one that guarantees global stability. It allows for good control of limited pest invasions; however, the culture is at risk of being destroyed by a large pest outbreak.

Since, in both cases, the conditions for local and global stability are identical up to two different parameters, any analysis of the consequences of one of those conditions will immediately translate to the other. The interpretation of conditions (19)–(20) and (30)–(31) will be given in the next section.

4. Interpretation of results. It is easy to see that $\underline{\mu}_r$ is independent of T_r . The influence of T_r on $\underline{\mu}_h$ is trickier to identify so we shall analyze it. We then present graphically the variation of both $\underline{\mu}_r$ and $\underline{\mu}_h$ with respect to T_r for a typical set of parameter values and attempt to give a practical interpretation of these results.

4.1. Mathematical analysis. We first need to note that when $S + (\ln(1 - \alpha_x))/(rT_h) < 0$, for any of the local or global conditions, the condition is trivially verified. Indeed, it implies simply that no biological control is needed for exterminating the pests; in fact, the

partial harvesting is effective enough for this purpose (as α_x is large enough). We now evaluate how the release frequency influences the minimal budget when this condition is not trivial.

We have already seen that $\underline{\mu}_r$ is independent of T_r . We will now study the latter's influence on $\underline{\mu}_h$.

Theorem 3. *Let $T_h = kT_r$ where $k \in \mathbf{N}^*$.*

The minimal budget is monotonically decreasing with respect to the release period T_r for nonnegative values of $\underline{\mu}_h$, i.e.,

$$(37) \quad \frac{\partial \underline{\mu}_h}{\partial T_r} < 0.$$

Proof. Knowing that T_r is equal to T_h/k , it is possible to identify the sign of $\partial \underline{\mu}_r / \partial T_r$ noting that

$$\frac{\partial \underline{\mu}_h}{\partial T_r} = \frac{\partial \underline{\mu}_h}{\partial k} \frac{\partial k}{\partial T_r} = \frac{\partial \underline{\mu}_h}{\partial k} \left(\frac{-k^2}{T_h} \right).$$

So

$$(38) \quad \text{sgn} \left(\frac{\partial \underline{\mu}_h}{\partial T_r} \right) = -\text{sgn} \left(\frac{\partial \underline{\mu}_h}{\partial k} \right);$$

$\underline{\mu}_h$ is expressed as the product of two distinctive parts, one of which is independent of k and which, for the nontrivial stability condition, is positive,

$$S + \frac{\ln(1 - \alpha_x)d}{rT_h} > 0,$$

where S and r are the parameters required for the local or global conditions, as defined previously.

The second part is viewed as a composite function of k so that (38) can be evaluated as

$$(39) \quad \text{sgn} \left(\frac{\partial \underline{\mu}_h}{\partial T_r} \right) = -\text{sgn} \left(\frac{\partial}{\partial k} \left(\frac{1}{1 - ((\alpha_y(1 - e^{-dT_h}))/ (1 - (1 - \alpha_y)e^{-dT_h})) \sigma(k)} \right) \right)$$

where $\sigma(k) = (e^{-dT_h/k}/k(1 - e^{-dT_h/k}))$. Then, we get

$$\begin{aligned}
 (40) \quad & \operatorname{sgn} \left(\frac{\partial \underline{\mu}_h}{\partial T_r} \right) \\
 &= -\operatorname{sgn} \left(\frac{(\alpha_y(1 - e^{-dT_h})/(1 - (1 - \alpha_y)e^{-dT_h}))}{(1 - (\alpha_y(1 - e^{-dT_h})/(1 - (1 - \alpha_y)e^{-dT_h}))) \sigma(k)^2} \frac{\partial \sigma}{\partial k} \right) \\
 &= -\operatorname{sgn} \left(\frac{\partial \sigma}{\partial k} \right) \\
 &= -\operatorname{sgn} \left(\frac{e^{-dT_h/k}}{k^2(1 - e^{-dT_h/k})^2} \left(\frac{dT_h}{k} - 1 + e^{-dT_h/k} \right) \right) \\
 &= -\operatorname{sgn} \left(ke^{-dT_h/k} + dT_h - k \right).
 \end{aligned}$$

Since

$$\frac{\partial}{\partial k} (ke^{-dT_h/k} + dT_h - k) = \left(1 + \frac{dT_h}{k} \right) e^{-dT_h/k} - 1 \leq 0,$$

and using l'Hospital's rule,

$$\begin{aligned}
 \lim_{k \rightarrow \infty} (ke^{-dT_h/k} + dT_h - k) &= dT_h + \lim_{k \rightarrow \infty} \left(\frac{e^{-dT_h/k} - 1}{1/k} \right) \\
 &= dT_h + \lim_{k \rightarrow \infty} \left(\frac{(dT_h/k^2)e^{-dT_h/k}}{-1/k^2} \right) \\
 &= 0,
 \end{aligned}$$

we deduce that $\operatorname{sgn}(ke^{-dT_h/k} + dT_h - k) > 0$. Therefore,

$$(41) \quad \operatorname{sgn} \left(\frac{\partial \underline{\mu}_h}{\partial T_r} \right) < 0. \quad \square$$

We can deduce that we hit the smallest minimal value for the budget for the largest possible T_r in this case that corresponds to when $k = 1$. This happens when the release frequency equals the partial harvest frequency.

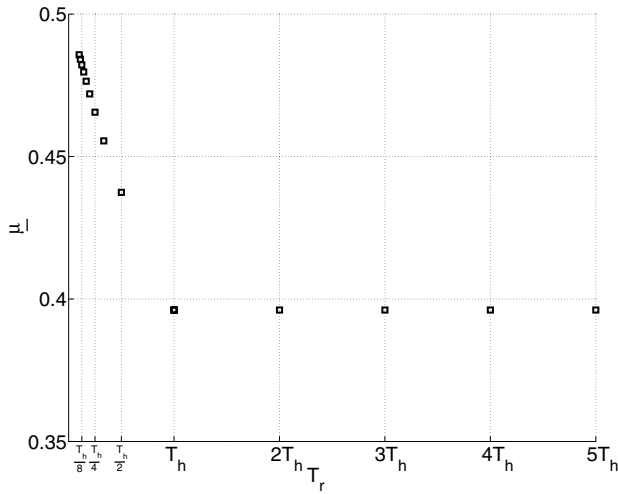


FIGURE 3. Variation of the minimal number of predators required per budget year $\underline{\mu}$ as a function of release to harvest period ratio. Parameters are given the values (in arbitrary units): $\alpha_x = \alpha_y = 0.5$, $d = 1$, and the rate of growth $f'(0)$, functional response $g'(0)$ and numerical response $h'(0)$ with respect to time when the ecosystem is pest-free, i.e., $x_p(t) = 0$, are all equal to 1.

4.2. Discussion. Figure 3 represents the analytical results obtained in the previous sections for a chosen set of parameters. The plot includes the two cases studies: either one of the partial harvest and the release period is an integer multiple of the other.

Under this set of possible scenarios, increasing the frequency of release beyond the frequency of harvest requires that the total number of predators to invest in be higher than that when releases take place less or as often as partial harvests. In the latter case, to ensure pest eradication, the total budget of predators to invest in is fixed, independently of the release period.

These results imply that it is clearly less costly to protect a crop for lower frequencies of release. Of additional economic interest, in this case, the biological treatment is always combined with partial harvesting, so that there is little or no extra cost linked to the presence of workers on-site. However, we recall that [13] previously demonstrated that the higher the release frequency, the smaller the worst-case damages. Combining the results from both studies seems to indicate that

the most profitable release strategy among the possibilities that have been considered is the one where releases are synchronized with partial harvests.

5. Conclusion. The results obtained in this paper for the stability of the system are yet another confirmation that inundative control can be an effective means of suppressing low pest invasions in agricultural crops. This requires that a sufficient number of predators be introduced in the system as in, for instance, [7, 9].

Our study aimed to provide a control strategy in the protection of continuously grown crops that are partially harvested on a regular basis. We demonstrated that partial harvesting had a nonnegligible effect on biological control and needed to be taken into account when devising a control strategy in the case of such crops.

We thus investigated the combined effects of releases and partial harvests in terms of the relative frequencies of their implementation. We considered the case where these two events occurred at periods such that one was the integer multiple of the other, and with the two events coinciding over the longer period. In particular, we found when releases were as frequent as or less than the partial harvests, the minimal budget did not depend on the period of release but instead on the harvest parameters, the growth function of the pest population, the mortality of the predators and the functional response. When releases were more frequent than partial harvests however, the minimal budget value increased with the increasing frequency of the releases, exceeding the constant value obtained for the less frequent case. Combined with the findings of [13] which pointed out that higher release frequencies led to the optimal control policy, we concluded that for the set of possibilities that was studied, the current best strategy is when release and harvest frequencies are equal.

This approach, however, has its shortcomings. Since the integer multiple factor is key to calculating the minimal budget which would satisfy the stability conditions, it is not yet generalized to other scenarios where neither period is the integer multiple of the other. This would happen for instance at other rational noninteger ratios as well as irrational ones. It is highly likely that these intermediate ratios might induce other dynamics in the system. Whether they might stabilize it

given even lower minimal budget values or favor chaos remains to be seen. Moreover, it would be interesting to extend the results to the case where the two controls never coincide in spite of following a periodic pattern. This would be in the line of the work, for instance, of [11], where pesticide spraying—which is analogous to harvests—and releases are not synchronized.

Nevertheless, we consider that our simplification already has its practical economical advantage. Indeed, coinciding periods imply little or no additional costs incurred in terms of labor: the task of predator release can be assigned to workers in charge of partial harvesting. Field-testing is now the next step required to validate the results of this paper.

APPENDIX

Proposition 3. *Let Hypothesis 1 hold. Then*

$$\int_0^{T_h} y_{ph}(t) dt = \frac{\mu T_h}{d} \left(1 - \left(\frac{\alpha_y (1 - e^{-dT_h})}{1 - (1 - \alpha_y) e^{-dT_h}} \right) \left(\frac{e^{-dT_h/k}}{k (1 - e^{-dT_h/k})} \right) \right).$$

Proof. In order to compute the integral, we describe $y_{ph}(t)$ as $y_{ph}(iT_r^+)e^{-d(t-iT_r)}$ in each time interval $[iT_r, (i+1)T_r]$, with $y_{ph}(iT_r^+)$ given by (6) when $y(nT_h^+) = y^*$. This yields:

$$\begin{aligned} & \int_0^{T_h} y_{ph}(t) dt \\ &= \sum_{i=0}^{k-1} y_{ph}(iT_r^+) \int_{iT_r}^{(i+1)T_r} e^{-d(t-iT_r)} dt \\ &= \sum_{i=0}^{k-1} \left(y^* e^{-idT_r} + \mu T_r \sum_{j=0}^{i-1} e^{-jdT_r} \right) \int_0^{T_r} e^{-dt} dt \\ &= \left(y^* \frac{1 - e^{-kdT_r}}{1 - e^{-dT_r}} + \mu T_r \sum_{i=0}^{k-1} \frac{1 - e^{-idT_r}}{1 - e^{-dT_r}} \right) \frac{1 - e^{-dT_r}}{d} \\ &= \frac{y^*}{d} (1 - e^{-kdT_r}) + \frac{\mu T_r}{d} \left(k - \frac{1 - e^{-kdT_r}}{1 - e^{-dT_r}} \right) \end{aligned}$$

$$\begin{aligned}
 &= \frac{((1 - e^{-dT_h})/(1 - e^{-dT_r}))(1 - \alpha_y) + \alpha_y \frac{\mu T_r}{d}(1 - e^{-kdT_r})}{1 - (1 - \alpha_y)e^{-dT_h}} \\
 &\quad + \frac{\mu T_r}{d} \left(k - \frac{1 - e^{-kdT_r}}{1 - e^{-dT_r}} \right) \\
 &= \mu \frac{T_h}{dk} \frac{((1 - e^{-dT_h})(1 - \alpha_y) + \alpha_y(1 - e^{-dT_h/k}))(1 - e^{-dT_h})}{(1 - e^{-dT_h/k})(1 - (1 - \alpha_y)e^{-dT_h})} \\
 &\quad + \mu \frac{T_h}{dk} \frac{(k(1 - e^{-dT_h/k}) - (1 - e^{-dT_h}))(1 - (1 - \alpha_y)e^{-dT_h})}{(1 - e^{-dT_h/k})(1 - (1 - \alpha_y)e^{-dT_h})} \\
 &= \mu \frac{T_h}{dk} \frac{((1 - (1 - \alpha_y)e^{-dT_h}) - \alpha_y e^{-dT_h/k})(1 - e^{-dT_h})}{(1 - e^{-dT_h/k})(1 - (1 - \alpha_y)e^{-dT_h})} \\
 &\quad + \mu \frac{T_h}{dk} \frac{(k(1 - e^{-dT_h/k}) - (1 - e^{-dT_h}))(1 - (1 - \alpha_y)e^{-dT_h})}{(1 - e^{-dT_h/k})(1 - (1 - \alpha_y)e^{-dT_h})} \\
 &= \mu \frac{T_h}{dk} \frac{(-\alpha_y e^{-dT_h/k})(1 - e^{-dT_h}) + (k(1 - e^{-dT_h/k}))(1 - (1 - \alpha_y)e^{-dT_h})}{(1 - e^{-dT_h/k})(1 - (1 - \alpha_y)e^{-dT_h})} \\
 &= \frac{\mu T_h}{d} \left(1 - \left(\frac{\alpha_y (1 - e^{-dT_h})}{1 - (1 - \alpha_y)e^{-dT_h}} \right) \left(\frac{e^{-dT_h/k}}{k(1 - e^{-dT_h/k})} \right) \right). \quad \square
 \end{aligned}$$

Proposition 4. *Let Hypothesis 1 hold. Then*

$$\int_0^{T_r} y_{pr}(t) dt = \frac{\mu T_r}{d} \frac{1 - e^{-dT_h}}{1 - (1 - \alpha_y)e^{-dT_h}}.$$

Proof. In order to compute the integral, we describe $y_{pr}(t)$ as $y_{pr}(iT_h^+)e^{-d(t-iT_h)}$ in each time interval $[iT_h, (i + 1)T_h]$, with $y_{pr}(iT_h^+)$ given by (12) when $y(mT_r^+) = y^*$. This yields:

$$\begin{aligned}
 \int_0^{T_r} y_{pr}(t) dt &= \sum_{i=0}^{k-1} y_{pr}(iT_h^+) \int_{iT_h}^{(i+1)T_h} e^{-d(t-iT_h)} dt \\
 &= \sum_{i=0}^{k-1} y^* e^{-idT_h} (1 - \alpha_y)^i \int_0^{T_h} e^{-dt} dt \\
 &= y^* \frac{(1 - e^{-dT_h})}{d} \sum_{i=0}^{k-1} e^{-idT_h} (1 - \alpha_y)^i
 \end{aligned}$$

$$\begin{aligned}
&= \frac{\mu T_r}{1 - (1 - \alpha_y)^k e^{-dT_r}} \frac{(1 - e^{-dT_h})}{d} \frac{1 - (1 - \alpha_y)^k e^{-kdT_h}}{1 - (1 - \alpha_y)e^{-dT_h}} \\
&= \frac{\mu T_r (1 - e^{-dT_h})}{d(1 - (1 - \alpha_y)e^{-dT_h})}. \quad \square
\end{aligned}$$

REFERENCES

1. M.E. De Courcy Williams, *Biological control of thrips on ornamental crops: Interactions between the predatory mite Neoseiulus Cucumeris* (acari: phytoseiidae) and western flower thrips *Frankliniella Occidentalis* (thysanoptera : thripidae) on cyclamen, *Biocontrol Science Technology* **11** (2001), 41–55.
2. L.E. Ehler, *Introduction strategies in biological control of insects*, in *Critical issues in biological control*, M. Mackauer, L.E. Ehler and J. Roland, eds., Intercept Limited, Andover, UK, 1990.
3. ———, *Biological control of Melanopsis obscura in oaks in northern California*, *BioControl* **50** (2005), 739–749.
4. L.E. Ehler, R.F. Long, M.G. Kinsey and S.K. Kelley, *Potential for augmentative biological control of black bean aphid in California sugarbeet*, *Entomophaga* **42** (1997), 241–256.
5. J. Eilenberg, A. Hajek and C. Lomer, *Suggestions for unifying the terminology in biological control*, *BioControl* **46** (2001), 387–400.
6. A. Fenton, R.L. Gwynn, A. Gupta, R. Norman, J.P. Fairbairn and P.J. Hudson, *Optimal application strategies for entomopathogenic nematodes: Integrating theoretical and empirical approaches*, *J. Appl. Ecol.* **39** (2002), 481–492.
7. A. Fenton, R. Norman, J.P. Fairbairn and P.J. Hudson, *Evaluating the efficacy of entomopathogenic nematodes for the biological control of crop pests: A nonequilibrium approach*, *American Naturalist* **158** (2001), 408–425.
8. R.J. Jacobson, D. Chandler, J. Fenlon and K.M. Russell, *Compatibility of Beauveria bassiana (Balsamo vuillemin with Amblyseius cucumeris Oudemans (Acarina : Phytoseiidae) to control Frankliniella occidentalis Pergande (Thysanoptera : Thripidae) on cucumber plants*, *Biocontrol Science Technology* **11** (2001), 391–400.
9. R.J. Jacobson, P. Croft and J. Fenlon, *Suppressing establishment of frankliniella occidentalis pergande (thysanoptera : Thripidae) in cucumber crops by prophylactic release of amblyseius cucumeris oudemans (acarina : Phytoseiidae)*, *Biocontrol Science Technology* **11** (2001), 27–34.
10. A. Lakmeche and O. Arino, *Bifurcation of non-trivial periodic solutions of impulsive differential equations arising chemotherapeutic treatment*, *Dynamics Continuous, Discrete Impulsive Systems* **7** (2000), 265–287.
11. B. Liu, L.S. Chen and Y.J. Zhang, *The dynamics of a prey-dependent consumption model concerning impulsive control strategy*, *Applied Math. Comp.* **169** (2005), 305–320.
12. B. Liu, Y.J. Zhang and L.S. Chen, *The dynamical behaviors of a Lotka-Volterra predator-prey model concerning integrated pest management*, *Nonlinear Anal.* **6** (2005), 227–243.

13. L. Mailleret and F. Grognaud, *Optimal release policy for prophylactic biological control*, in *Positive systems*, Springer, New York, 2006.
14. W.W. Murdoch, J. Chesson and P.L. Chesson, *Biological control in theory and practice*, *The American Naturalist* **125** (1985), 344–366.
15. K. Negi and S. Gakkhar, *Dynamics in a Beddington-DeAngelis prey-predator system with impulsive harvesting*, *Ecological Modelling* **206** (2007), 421–430.
16. G.K. Roderick and M. Navajas, *Genes in new environments: Genetics and evolution in biological control*, *Nature Reviews Genetics* **4** (2003), 889–898.
17. J.A. Rosenheim, H.K. Kaya, L.E. Ehler, J.J. Marois and B.A. Jaffee, *Intraguild predation among biological control agents: Theory and evidence*, *Biological Control* **5** (1995), 303–335.
18. F.M. Scudo and J.R. Ziegler, *The golden age of theoretical ecology: 1923–1940*, *Lecture Notes Biomath.* **22**, Springer-Verlag, New York, 1978.
19. B. Shulgin, L. Stone and Z. Agur, *Pulse vaccination strategy in the sir epidemic model*, *Bulletin Math. Biol.* **60** (1998), 1123–1148.
20. D.J. Skirvin, M.E. De Courcy Williams, J.S. Fenlon and K.D. Sunderland, *Modelling the effects of plant species on biocontrol effectiveness in ornamental nursery crops*, *J. Applied Ecol.* **39** (2002), 469–480.
21. V.M. Stern, R.F. Smith, R. Van den Bosch and K.S. Hagen, *The integrated control concept*, *Hilgardia* **29** (1959), 81–101.
22. J.C. Van Lenteren and J. Woets, *Biological and integrated pest control in greenhouses*, *Annual Review Entom.* **33** (1988), 239–269.

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