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► To cite this version:

Sapna Nundloll, Ludovic Mailleret, Frédéric Grognard. Two models of interfering predators in impulsive biological control. *Journal of Biological Dynamics*, Taylor & Francis Open, 2010, 4 (1), pp.102-114. 10.1080/17513750902968779 . hal-00847301

HAL Id: hal-00847301

<https://hal.inria.fr/hal-00847301>

Submitted on 23 Jul 2013

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RESEARCH ARTICLE

Two models of interfering predators in impulsive biological control

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(October 2008)

In this paper, we study the effects of Beddington-DeAngelis interference and squabbling respectively on the minimal rate of predator release required to drive a pest population to zero. A two-dimensional system of coupled ordinary differential equations is considered, augmented by an impulsive component depicting the periodic release of predators into the system. This periodic release takes place independently of the detection of the pests in the field. We establish the existence of a pest-free solution driven by the periodic releases, and express the global stability conditions for this solution in terms of the minimal predator rate required to bring an outbreak of pests to nil. In particular, we show that with the interference effects, the minimal rate will only guarantee eradication if the releases are carried out frequently enough. When Beddington-DeAngelis behaviour is considered, an additional constraint for the existence itself of a successful release rate is that the pest growth rate should be less than the predation pressure, the latter explicitly formulated in terms of the predation function and the interference parameters.

Keywords: Impulsive differential equations, prey-predator system, Beddington-DeAngelis, squabbling, global stability

AMS Subject Classification: 92D25, 34A37, 34D23

1. Introduction

The biological control of pests by their natural enemies, parasites or predators, is an integral part of organic farming and integrated pest management programs. It offers a sustainable (whether in environmental or even economic terms [20]), safe (having no harmful effects on human health, whether direct or residual) and low energy alternative to pesticide usage [4, 25].

This paper considers the case when biological control is achieved by the release of predators into a plantation under protection. The releases are carried out on a periodic basis on the assumption that the predator population naturally dies out in the absence of its food source, the pest. The control method thus presented is preventive as it takes place independently of the detection of pests. It is favoured in cases where tolerance to pest invasions is very low [11]. Inspired by works such as [14, 22] on chemotherapeutic treatment and pulse vaccination respectively, one important modelling trend of this type of biological control system has consisted of using ordinary differential equations augmented by an impulsive component to depict the instantaneous change occurring on release [15, 16, 19, 26].

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The phenomenon of interest in this paper is behavioural in nature: individual predators may interfere with each other, which is likely to affect their control efficacy. Such behaviour is observable in various species used as natural enemies [1, 9, 23], and so needs to be taken into account when formulating a control strategy.

We consider two basic ways in which interference is modelled. In the first, interference penalises predominantly the predation ability and hence appears in the trophic response [2, 6]. In the second, its effect is incorporated within a density dependent mortality rate [7, 13, 21]. Both effects are enhanced at high predator densities. Throughout this paper, we shall use the term *Beddington-DeAngelis interference* to refer to the former type of interference; *squabbling* will refer to the latter case.

To our knowledge, the literature on stability analyses with intrapredatory interference is available mainly for predator-prey systems with continuous dynamics [3, 5, 7, 8]. Conversely, work by various authors in the field of impulsive control - whether in the context of biological control or outside - has provided principally conditions for local stability [14, 22] or have focused on the conditions for the system's different chaotic rather than stable regimes [15, 24]. Likewise [18, 26], which consider interference within an impulsive model, do not give any explicit global stability condition. Finally, models for which global stability was analysed did not include interference or analogous effects [12, 19].

In allowing for a practical interpretation and a possible real-life implementation of our results, our work departs from the ones cited above in the following ways: first, we introduce the notions of a release rate (the number of predators released per unit time) and that of a release strategy (whether to release frequently a few at a time or larger numbers less frequently so). Secondly, once the existence of the pest-free solution driven by the predator releases is established, the stability conditions - both local and notably, global - of the pest-free solution of the system are expressed in terms of a minimal bound on the predator release rate required for pest eradication.

The paper is structured as follows. In Section 2, we recall results for the existence and stability of the pest-free solution in the no-interference case. Next, Beddington-DeAngelis effects and squabbling are incorporated in the system and analysed separately in Section 3. Section 4 puts into light the consequences of these effects. We demonstrate that when interference is introduced into the model, the minimal predator release rate for pest eradication becomes dependent on the release period. In particular, for a given release rate, the release period cannot be too large. With Beddington-DeAngelis interference, there is the additional constraint that the net predation pressure must be able to overcome the pest growth rate.

2. No interference model

The biological control system is modelled by a pair of coupled ordinary differential equations augmented by an impulsive component to depict predator releases.

$$\left\{ \begin{array}{l} \dot{x} = rx \left(1 - \frac{x}{K}\right) - \frac{ax}{c+x}y \\ \dot{y} = \frac{\gamma ax}{c+x}y - my \\ y(nT^+) = y(nT) + \mu T, \quad \forall n \in \mathbb{N} \end{array} \right\} t \neq nT \tag{H}$$

where x and y are the pest and predator respectively. The continuous part corresponds to the Rosenzweig-MacArthur description. The pest growth follows a

classical logistic formulation, parameterised by a growth rate $r \geq 0$ and a carrying capacity $K \geq 0$. The functional and numerical responses are Holling Type II [10], defined by $a > 0$, the half-saturation constant $c > 0$, and the conversion factor $\gamma > 0$. The predator population has a linear mortality rate $m > 0$ and hence decays exponentially if not replenished from an external source in the absence of prey. The discrete component models the discontinuity that occurs upon the periodic release of predators, with μ representing the rate of predator release per unit time, and T the release period, such that their product gives the predator population size released at the start of each cycle.

This system possesses a periodic pest-free solution driven by the periodic predator release.

$$(x_p(t), y_p(t)) = \left(0, \frac{\mu T}{1 - e^{-mT}} e^{-m(t \bmod T)} \right)$$

This zero-pest solution is locally asymptotically stable (LAS), if and only if [15]

$$\mu > \frac{r m c}{a} \quad (1a)$$

If, in addition, the following condition is satisfied,

$$\mu > \frac{r m S}{a} \quad (1b)$$

where

$$S = \begin{cases} \frac{(K + c)^2}{4K} & \text{for } 0 \leq c \leq K \\ c & \text{for } c \geq K \end{cases} \quad (1c)$$

the solution is globally asymptotically stable (GAS)[17]. We notice that the LAS and GAS conditions are equivalent at small carrying capacity and hold for all release periods.

3. Models with interference

3.1. Beddington-DeAngelis interference

When the access to food is impeded by the presence of additional predators, interference is prominent in the trophic response. It can encompass competitive effects or the fact that predators in guarding their territories spend less time engaging in hunting and food consumption. The Holling Type II trophic response is modified into a decreasing function of the predator population, referred to as the Beddington-DeAngelis response [2, 6].

$$\left\{ \begin{array}{l} \dot{x} = r x \left(1 - \frac{x}{K} \right) - \frac{a x}{c + x + b y} y \\ \dot{y} = \frac{\gamma a x}{c + x + b y} y - m y \\ y(nT^+) = y(nT) + \mu T, \quad \forall n \in \mathbb{N} \end{array} \right\} t \neq nT \quad (\mathcal{H}_b)$$

b is the penalty coefficient on the predation efficiency. We note that the state variables initiated at $t = t_0 \in [0, T)$ at some non-negative values remain non-negative.

Straightforward arguments lead to the following proposition on pest growth limitation.

Proposition 3.1: *Let $t_0 \geq 0$ and $x(t_0), y(t_0) \geq 0$. Then for all $\epsilon > 0$, there exists a finite time $t_f(\epsilon) \geq 0$ such that for all $t \geq t_f(\epsilon)$, $x(t, x(t_0), y(t_0)) \in [0, K(1 + \epsilon)]$.*

We have the following result on the existence and stability of a pest-free solution.

Theorem 3.2: *Model \mathcal{H}_b possesses a periodic solution that corresponds to pest-eradication:*

$$(x_{pb}(t), y_{pb}(t)) = (0, y^* e^{-m(t \bmod T)}) \tag{2a}$$

where

$$y^* = \frac{\mu T}{1 - e^{-mT}} \tag{2b}$$

which is LAS if and only if

$$r < \frac{a}{b} \quad \text{and} \quad \mu > \underline{\mu}_{b(i)} = \frac{c}{b} \left(\frac{1 - e^{-r \frac{b}{a} mT}}{e^{-r \frac{b}{a} mT} - e^{-mT}} \right) \frac{1 - e^{-mT}}{T} \tag{2c}$$

and is GAS if, in addition,

$$\mu > \underline{\mu}_{b(ii)} = \frac{c + K}{b} \left(\frac{1 - e^{-r \frac{b}{a} mT}}{e^{-r \frac{b}{a} mT} - e^{-mT}} \right) \frac{1 - e^{-mT}}{T} \tag{2d}$$

Proof: We consider the establishment of the periodic solution in the absence of pests; so $x(0) = 0$ and system (\mathcal{H}_b) is simplified to

$$\begin{cases} \dot{x} = 0 \\ \dot{y} = -my \\ y(nT^+) = y(nT) + \mu T \end{cases} \tag{3}$$

The solution $x_{pb}(t) = 0$ is trivial. To calculate the evolution of $y_{pb}(t)$, we consider a period $(nT^+, (n+1)T^+)$. From the second equation in (3), the population decays exponentially from the start of the release period until the subsequent release whereupon it increases by μT . The sequence of post-release points is thus

$$y((n+1)T^+) = y(nT^+) e^{-mT} + \mu T \tag{4}$$

This is an exponentially stable discrete dynamical system that converges to

$$y^* = \frac{\mu T}{1 - e^{-mT}} \tag{5}$$

as $n \rightarrow \infty$. The existence of $(x_{pb}(t), y_{pb}(t))$ has been proved.

From Theorem 1 in [14], the conditions for local stability of (x_{pb}, y_{pb}) in system (\mathcal{H}_b) are $e^{\int_0^T \left(r - \frac{ay_{pb}(\tau)}{c + by_{pb}(\tau)} \right) d\tau} < 1$ and $e^{-\int_0^T m d\tau} < 1$. The latter condition is trivial,

and the former yields

$$\int_0^T a \frac{y^* e^{-m\tau}}{c + by^* e^{-m\tau}} d\tau > rT \quad (6)$$

$$\Leftrightarrow (e^{-r\frac{b}{a}mT} - e^{-mT})by^* > (1 - e^{-r\frac{b}{a}mT})c$$

At this point, we note that the right-hand side of the inequality is positive. The left-hand side is therefore required to be positive too; this imposes

$$e^{-r\frac{b}{a}mT} - e^{-mT} > 0$$

which is equivalent to $r < \frac{a}{b}$. Using (2b) and isolating μ in (6), we get

$$\mu > \frac{c}{b} \left(\frac{1 - e^{-r\frac{b}{a}mT}}{e^{-r\frac{b}{a}mT} - e^{-mT}} \right) \frac{1 - e^{-mT}}{T}$$

so that $(x_{pb}(t), y_{pb}(t))$ is LAS iff (2c) holds.

To demonstrate the global asymptotic stability condition, we suppose that we start at some state value away from the periodic solution, then consider how the deviations from the periodic solution vary with time. This new set of coordinates is defined as $\tilde{x} = x - x_{pb} = x$ and $\tilde{y} = y - y_{pb}$ respectively, and subjected to the dynamics in (\mathcal{H}_b) . This results in the equivalent system

$$\begin{cases} \dot{\tilde{x}} = r\tilde{x} \left(1 - \frac{\tilde{x}}{K} \right) - \frac{a\tilde{x}}{c + \tilde{x} + b(y_{pb} + \tilde{y})} (y_{pb} + \tilde{y}) \\ \dot{\tilde{y}} = \frac{\gamma a \tilde{x}}{c + \tilde{x}} (\tilde{y} + y_{pb}) - m\tilde{y} \end{cases} \quad (7)$$

where the impulsive component disappears since

$$\tilde{y}(nT^+) = y(nT) + \mu T - y_{pb}(nT) - \mu T = \tilde{y}(nT)$$

Let initial conditions be $(\tilde{x}_0, \tilde{y}_0)$ at $t = t_0$. The \tilde{x} -dynamics are obtained by integrating $\frac{\dot{\tilde{x}}}{\tilde{x}}$ as

$$\int_{\tilde{x}_0}^{\tilde{x}(t)} \frac{1}{s} ds = \int_{t_0}^t r \left(1 - \frac{\tilde{x}(\tau)}{K} \right) - \frac{a(y_{pb}(\tau) + \tilde{y}(\tau))}{c + \tilde{x}(\tau) + b(y_{pb}(\tau) + \tilde{y}(\tau))} d\tau \quad (8)$$

In order to show that $\lim_{t \rightarrow +\infty} \tilde{x}(t) = 0$, we will investigate the divergence of $\int_{\tilde{x}_0}^{\tilde{x}(t)} \frac{1}{s} ds$ towards $-\infty$ as t goes to infinity. For any $\epsilon > 0$ and t large enough we have

$$\begin{aligned} \int_{\tilde{x}_0}^{\tilde{x}(t)} \frac{1}{s} ds &= \int_{t_0}^{(\lfloor \frac{t_f(\epsilon)}{T} \rfloor + 1)T} r \left(1 - \frac{\tilde{x}(\tau)}{K} \right) - \frac{a(y_{pb}(\tau) + \tilde{y}(\tau))}{c + \tilde{x}(\tau) + b(y_{pb}(\tau) + \tilde{y}(\tau))} d\tau \\ &+ \int_{\lfloor \frac{t}{T} \rfloor T}^{(\lfloor \frac{t_f(\epsilon)}{T} \rfloor + 1)T} r \left(1 - \frac{\tilde{x}(\tau)}{K} \right) - \frac{a(y_{pb}(\tau) + \tilde{y}(\tau))}{c + \tilde{x}(\tau) + b(y_{pb}(\tau) + \tilde{y}(\tau))} d\tau \quad (9) \\ &+ \int_{\lfloor \frac{t}{T} \rfloor T}^t r \left(1 - \frac{\tilde{x}(\tau)}{K} \right) - \frac{a(y_{pb}(\tau) + \tilde{y}(\tau))}{c + \tilde{x}(\tau) + b(y_{pb}(\tau) + \tilde{y}(\tau))} d\tau \end{aligned}$$

One can notice that the first and third terms are bounded; we therefore focus on the second one. To upper bound this term, it is useful to lower bound $y_{pb} + \tilde{y}$, as given by the system dynamics. Since $y_{pb}(t) + \tilde{y}(t) = y(t) \geq 0$, we have from (7)

$$\dot{\tilde{y}} \geq -m\tilde{y} \tag{10}$$

so that if $\tilde{y}(t)$ is not negative for some t , it remains so for all subsequent times. Furthermore, $\tilde{y}(t) \geq -y_{pb}(t) \geq -y^*$ implies that $\tilde{y}_0 \geq -y^*$. Therefore,

$$\tilde{y}(t) \geq -y^* e^{-m(t-t_0)}, \quad \forall t \geq t_0$$

Hence

$$y_{pb}(t) + \tilde{y}(t) \geq y^*(e^{-m(t \bmod T)} - e^{-m(t-t_0)})$$

Finally, from Proposition 3.1, $\tilde{x} \in [0, K(1 + \epsilon)]$ over the interval considered in the second term of (9). So, this term is bounded by

$$\int_{(\lfloor \frac{t_f(\epsilon)}{T} \rfloor + 1)T}^{\lfloor \frac{t}{T} \rfloor T} r - \frac{ay^*(e^{-m(\tau \bmod T)} - e^{-m(\tau-t_0)})}{c + K(1 + \epsilon) + by^*(e^{-m(\tau \bmod T)} - e^{-m(\tau-t_0)})} d\tau \tag{11}$$

which we can rewrite as $\sum_{n=\lfloor \frac{t_f(\epsilon)}{T} \rfloor + 1}^{\lfloor \frac{t}{T} \rfloor - 1} I(n)$, where

$$\begin{aligned} I(n) &= \int_{nT}^{(n+1)T} r - \frac{ay^*(e^{-m(\tau-nT)} - e^{-m(\tau-t_0)})}{c + K(1 + \epsilon) + by^*(e^{-m(\tau-nT)} - e^{-m(\tau-t_0)})} d\tau \\ &= rT + \frac{a}{bm} \ln \left(\frac{c + K(1 + \epsilon) + by^* e^{-mT}(1 - e^{-m(nT-t_0)})}{c + K(1 + \epsilon) + by^*(1 - e^{-m(nT-t_0)})} \right) \end{aligned}$$

We notice that $I(n)$ is a decreasing function of n . Moreover, if $\lim_{n \rightarrow \infty} I(n) < 0$, there exists $\alpha > 0$ and a finite n_0 such that $\forall n > n_0, I(n) < -\alpha$ and

$$\lim_{t \rightarrow \infty} \sum_{n=\lfloor \frac{t_f(\epsilon)}{T} \rfloor + 1}^{\lfloor \frac{t}{T} \rfloor - 1} I(n) = -\infty$$

Thus from (9) we have that $\lim_{t \rightarrow \infty} \tilde{x}(t) = 0$ if

$$\lim_{n \rightarrow \infty} I(n) = rT + \frac{a}{bm} \ln \left(\frac{c + K(1 + \epsilon) + by^* e^{-mT}}{c + K(1 + \epsilon) + by^*} \right) < 0 \tag{12}$$

Replacing y^* with (5) in (12), and extracting μ yields

$$\mu > \frac{c + K(1 + \epsilon)}{b} \left(\frac{1 - e^{-r \frac{b}{a} mT}}{e^{-r \frac{b}{a} mT} - e^{-mT}} \right) \frac{1 - e^{-mT}}{T} \tag{13}$$

GAS is obtained when this condition is satisfied for any $\epsilon > 0$. Because of the strict inequality in (13), we can directly conclude that GAS is achieved with this

condition for $\epsilon = 0$, which yields (2d).

One can now prove that \tilde{y} converges to zero as well. Indeed, from (10) either $\tilde{y}(t)$ converges to zero in infinite time from below, or it reaches the positively invariant region where $\tilde{y} \geq 0$ in finite time. Translating the initial time t_0 as required, we then have to consider the positive \tilde{y}_0 only. Since \tilde{x} converges to zero, it is clear that there exists a time t_m such that

$$\forall t > t_m, \frac{\gamma a \tilde{x}}{c + \tilde{x} + by} \leq \frac{m}{2} \Rightarrow \forall t > t_m, \dot{\tilde{y}} \leq \frac{\gamma a \tilde{x}}{c + \tilde{x} + by} y_{pb}(t) - \frac{m}{2} \tilde{y}.$$

Since $\frac{\gamma a \tilde{x}}{c + \tilde{x} + by} y_{pb}(t)$ goes to zero as t goes to infinity, so does \tilde{y} . We have shown that $(0, 0)$ is globally attractive for system (7), i.e. $(x_{pb}(t), y_{pb}(t))$ is globally attractive for \mathcal{H}_b . \square

The necessary condition obtained when the Beddington-DeAngelis coefficient is introduced into the model highlights the interplay between two antagonistic forces involved in biological control: r , the pest growth rate and $\frac{a}{b}$, which is related to the predation pressure. In fact, if the interference effect in the predator population is past the threshold given by the condition, i.e. if $b > \frac{a}{r}$, no matter how large the predator population, it will not be able to suppress even low pest invasions.

3.2. Squabbling

Squabbling predators are characterised by a density dependent mortality rate. It can be representative of general factors, other than food that are limiting at high predator densities (see for instance [13] and references therein, and [21]). [8], considers it to be related to overcrowding. It is also an elementary description of cannibalism. In this paper, this effect is modelled by adding a quadratic component to an otherwise linear mortality.

$$\left\{ \begin{array}{l} \dot{x} = rx \left(1 - \frac{x}{K}\right) - \frac{ax}{c+x}y \\ \dot{y} = \frac{\gamma ax}{c+x}y - (m + qy)y \\ y(nT^+) = y(nT) + \mu T, \quad \forall n \in \mathbb{N} \end{array} \right\} t \neq nT \tag{\mathcal{H}_q}$$

where $q \geq 0$ is the degree of squabbling.

As previously, note the state variables initiated at $t = t_0 \in [0, T)$ at some non-negative values will remain non-negative.

Theorem 3.3: *Model \mathcal{H}_q possesses a periodic solution that corresponds to pest eradication:*

$$(x_{pq}(t), y_{pq}(t)) = \left(0, \frac{my^* e^{-m(t \bmod T)}}{m + (1 - e^{-m(t \bmod T)})qy^*}\right) \tag{14a}$$

where

$$y^* = \frac{1}{2} \left(\mu T - \frac{m}{q} + \sqrt{\left(\mu T - \frac{m}{q}\right)^2 + \frac{4\mu m T}{q(1 - e^{-mT})}} \right) \tag{14b}$$

which is LAS if and only if

$$\ln \left(1 + \frac{q}{m} (1 - e^{-mT}) y^* \right) > \frac{rcTq}{a} \tag{14c}$$

and is GAS if, in addition,

$$\ln \left(1 + \frac{q}{m} (1 - e^{-mT}) y^* \right) > \frac{rSTq}{a} \tag{14d}$$

where S is as defined in (1c).

Proof: In the absence of pests, $x(t_0) = 0$ and system (\mathcal{H}_q) is simplified to

$$\begin{cases} \dot{x} = 0 \\ \dot{y} = -(m + qy)y \\ y(nT^+) = y(nT) + \mu T \end{cases} \tag{15}$$

As previously, $x_{pq}(t) = 0$ is a trivial solution. We consider the time interval between two releases $t \in [nT^+, (n + 1)T]$ to calculate the variation of $y_{pq}(t)$ over the continuous interval. The quadratic component in the mortality requires some additional computations in the integration of the \dot{y} dynamics. So, separating variables, we obtain

$$\begin{aligned} \int_{y(nT^+)}^{y(t)} \frac{1}{(m + qs)s} ds &= \frac{1}{m} \int_{y(nT^+)}^{y(t)} \left(\frac{1}{s} - \frac{q}{m + qs} \right) ds = - \int_{nT^+}^t d\tau \\ \Leftrightarrow \ln \left(\frac{y(t)}{y(nT^+)} \left(\frac{m + qy(nT^+)}{m + qy(t)} \right) \right) &= -m(t - nT) \\ \Leftrightarrow y(t) &= \frac{my(nT^+)e^{-m(t-nT)}}{m + (1 - e^{-m(t-nT)})qy(nT^+)} \end{aligned} \tag{16}$$

After release at $t = (n + 1)T$, we obtain the sequence

$$y((n + 1)T^+) = \frac{my(nT^+)e^{-mT}}{m + (1 - e^{-mT})qy(nT^+)} + \mu T \tag{17}$$

It is clear that this non-linear mapping has a unique and stable positive equilibrium $y^* = y((n + 1)T^+) = y(nT^+)$ which can be computed as (14b). The existence of (14a) is thus proved.

To prove the condition for local stability, we evoke once again Theorem 1 from [14], and obtain the necessary and sufficient conditions $e^{-\int_0^T (m + qy_{pq}(\tau))d\tau} < 1$, which is trivial, and $e^{\int_0^T (r - \frac{a}{c}y_{pq}(\tau))d\tau} < 1$. Recalling $y_{pq}(t)$ from (14a), the latter yields

$$\begin{aligned} rT - \frac{a}{c} \int_0^T y_{pq}(\tau) d\tau &< 0 \\ \Leftrightarrow \int_0^T \frac{my^*e^{-m\tau}}{m + (1 - e^{-m\tau})qy^*} d\tau &> \frac{rcT}{a} \\ \Leftrightarrow \ln \left(1 + \frac{q}{m} (1 - e^{-mT}) y^* \right) &> \frac{rcTq}{a} \end{aligned}$$

which is the LAS condition (14c).

To obtain the global stability condition, we consider the deviation from the periodic solution as $\tilde{x} = x - x_{pq} = x$ and $\tilde{y} = y - y_{pq}$ respectively. The equivalent system is given as

$$\begin{cases} \dot{\tilde{x}} = r\tilde{x} \left(1 - \frac{\tilde{x}}{K}\right) - \frac{a\tilde{x}}{c + \tilde{x}}(y_{pq} + \tilde{y}) \\ \dot{\tilde{y}} = \frac{\gamma a\tilde{x}}{c + \tilde{x}}(\tilde{y} + y_{pq}) - (m + 2qy_{pq} + q\tilde{y})\tilde{y} \end{cases} \quad (18)$$

As previously, the impulsive term disappears.

We divide the \tilde{x} -dynamics this time by $\frac{a\tilde{x}}{c + \tilde{x}}$ throughout, then integrate

$$\int_{\tilde{x}_0}^{\tilde{x}(t)} \frac{c + s}{as} ds = \int_{t_0}^t \frac{r}{a} \left(1 - \frac{\tilde{x}(\tau)}{K}\right) (c + \tilde{x}(\tau)) - (\tilde{y}(\tau) + y_{pq}(\tau)) d\tau \quad (19)$$

In order to show the convergence of $\lim_{t \rightarrow +\infty} \tilde{x}(t) \rightarrow 0$, we seek to establish the

divergence of $\int_{\tilde{x}_0}^{\tilde{x}(t)} \frac{c + s}{as} ds$ to $-\infty$ as $t \rightarrow +\infty$.

Since x and y are always non-negative

$$\dot{\tilde{y}} \geq -(m + 2qy_{pq} + q\tilde{y})\tilde{y} = -(m + qy_{pq} + qy)\tilde{y} \quad (20)$$

There are two possible lower bounds on the variation of \tilde{y} depending on the initial values \tilde{y}_0 . Indeed, the positivity of \tilde{y} can be seen from (20), so that when $\tilde{y}_0 \geq 0$, $\tilde{y}(t) \geq 0$ for all $t \geq 0$. Conversely, when $\tilde{y}_0 < 0$, $\dot{\tilde{y}} \geq -(m + qy_{pq} + qy)\tilde{y} \geq -m\tilde{y}$, so that $\tilde{y}(t) \geq \tilde{y}_0 e^{-mt}$. Therefore

$$\tilde{y}(t) \geq \min(0, \tilde{y}_0 e^{-m(t-t_0)})$$

If we separate the \tilde{y} from the rest of the integral, the remaining integral has a T -periodic argument, so we can split the time domain as follows.

$$\begin{aligned} \int_{\tilde{x}_0}^{\tilde{x}(t)} \frac{c + s}{as} ds &= \int_{t_0}^{(\lfloor \frac{t_0}{T} \rfloor + 1)T} \left(\frac{r}{a} \left(1 - \frac{\tilde{x}(\tau)}{K}\right) (c + \tilde{x}(\tau)) - y_{pq}(\tau) \right) d\tau \\ &+ \left(\lfloor \frac{t}{T} \rfloor - \lfloor \frac{t_0}{T} \rfloor - 1 \right) \int_0^T \frac{r}{a} \left(1 - \frac{\tilde{x}(\tau)}{K}\right) (c + \tilde{x}(\tau)) - y_{pq}(\tau) d\tau \\ &+ \int_{\lfloor \frac{t}{T} \rfloor T}^t \frac{r}{a} \left(1 - \frac{\tilde{x}(\tau)}{K}\right) (c + \tilde{x}(\tau)) - y_{pq}(\tau) d\tau \\ &- \int_{t_0}^t \min(0, \tilde{y}_0 e^{-m(\tau-t_0)}) d\tau \end{aligned} \quad (21)$$

The first, third and fourth integrals of (21) are bounded. The coefficient of the second integral clearly tends to infinity as $t \rightarrow +\infty$. So for stability, we require that

$$\int_0^T \frac{r}{a} \left(1 - \frac{\tilde{x}(\tau)}{K}\right) (c + \tilde{x}(\tau)) - y_{pq}(\tau) d\tau < 0 \quad (22)$$

The first term of the integrand is upper bounded by $\frac{rS}{a}$ with

$$S = \max_{x \geq 0} \left(1 - \frac{\tilde{x}(\tau)}{K} \right) (c + \tilde{x}(\tau)) = \begin{cases} \frac{(K+c)^2}{4K} & \text{for } 0 \leq c \leq K \\ \frac{c}{c} & \text{for } c \geq K \end{cases}$$

Thus, (22) holds provided

$$\begin{aligned} & \int_0^T \frac{rS}{a} - y_{pq}(\tau) d\tau < 0 \\ \Leftrightarrow & \int_0^T \frac{my^* e^{-m\tau}}{m + (1 - e^{-m\tau})qy^*} d\tau > \frac{rST}{a} \tag{23} \\ \Leftrightarrow & \ln \left(1 + \frac{q}{m} (1 - e^{-mT})y^* \right) > \frac{rSTq}{a} \end{aligned}$$

which is condition (14d). The convergence of \tilde{y} to zero follows in a similar fashion as in Section 3.1. \square

The formulation (14c) and (14d) are not explicit enough at this level for a practical read-off of the mathematical result. At this level, the dependence of the left-hand side of these inequalities in μ and the non-dependence of the right-hand side only indicate that provided μ is large enough, the stability condition can be satisfied. To extract μ , we can however consider the following.

Corollary 3.4: *Provided T is small enough, the periodic solution (14a) of model \mathcal{H}_q is LAS if*

$$\mu > \underline{\mu}_{q(i)} = \frac{rc}{a} \left(\frac{rcq}{a} + m \right) \tag{24a}$$

and is GAS if

$$\mu > \underline{\mu}_{q(ii)} = \frac{rS}{a} \left(\frac{rSq}{a} + m \right) \tag{24b}$$

Proof: In order to extract the condition (24a) from (14c), we compare the functions on either side of the inequality in terms of their dependence on the period of release T . Defining $\Omega(T, y^*(T)) = \ln \left(1 + \frac{q}{m} (1 - e^{-mT})y^*(T) \right)$ and noting that both sides of (14c) cancel at $T = 0$, this inequality can be shifted to the derivatives of the functions in the limit as $T \rightarrow 0^+$.

$$\lim_{T \rightarrow 0^+} \frac{d}{dT} \Omega(T, y^*(T)) = \lim_{T \rightarrow 0^+} \frac{\partial \Omega}{\partial T} + \lim_{T \rightarrow 0^+} \frac{\partial \Omega}{\partial y^*} \frac{\partial y^*}{\partial T} > \frac{rcq}{a} \tag{25}$$

We first calculate $\lim_{T \rightarrow 0^+} y^*(T) = \frac{1}{2q} \left(-m + \sqrt{m^2 + 4q\mu} \right)$. Hence

$$\begin{aligned} \lim_{T \rightarrow 0^+} \frac{\partial \Omega}{\partial T} &= \lim_{T \rightarrow 0^+} \frac{me^{-mT} \frac{q}{m} y^*(T)}{1 + (1 - e^{-mT}) \frac{q}{m} y^*(T)} \\ &= \frac{1}{2} \left(-m + \sqrt{m^2 + 4q\mu} \right) \end{aligned}$$

and $\lim_{T \rightarrow 0^+} \frac{\partial \Omega}{\partial y^*} \frac{\partial y^*}{\partial T} = 0$ (see Appendix A for details). So, the stability condition

Table 1. Summary of results for the dependence on the release period, T , for a given release rate, μ

Interference type	Parameter value	Period	Rate	Stability*
None	–	any	$\mu > \underline{\mu}$	OK
Beddington DeAngelis	$0 < b < \frac{a}{r}$	small	$\mu > \underline{\mu}_b(T)$	OK
		large	$\mu < \underline{\mu}_b(T)$	None
	$b \geq \frac{a}{r}$	any	impossible	None
Squabbling	$q > 0$	small	$\mu > \underline{\mu}_q(T)$	OK
		large	$\mu < \underline{\mu}_q(T)$	None

*Stability of the pest-free solution.

(25) becomes

$$\lim_{T \rightarrow 0^+} \frac{d}{dT} \Omega(T, y^*(T)) = \frac{1}{2} \left(-m + \sqrt{m^2 + 4q\mu} \right) > \frac{rcq}{a}$$

$$\Leftrightarrow \mu > \frac{\left(\frac{2rcq}{a} + m \right)^2 - m^2}{4q} = \frac{rc}{a} \left(\frac{rcq}{a} + m \right)$$

which is condition (24a). The global condition (24b) on μ follows from the fact that the inequality (14d) has exactly the same form as (14c), with c substituted by S . \square

4. Discussion

A stable pest-free solution implies that the biological control agents are capable of bringing the pest population down to zero, hence that the zero-pest system is resilient to a sudden pest invasion. The stability conditions were expressed in terms of explicit lower bounds on the release rate of the biological control agents. In this contribution we first recalled the existing results concerning non-interfering biocontrol agents (conditions (1a) and (1b)). We then investigated the effects of two types of intrapredatory interference on the biological control efficacy. The results of our analysis are summarised in Table 1.

When interference does not take place, we note that both local and global stability conditions may coincide if the carrying capacity of the pest species is small enough. It is found that pest eradication is always possible provided the release rate is large enough. Moreover the stability conditions are independent of the release period T . Thus an identified minimal release rate will be able to combat a pest invasion and bring down its population to zero whether the predators are spread over several frequent releases or released in larger numbers over longer periods.

Similarly, when we account for squabbling, we show that it is also always possible to choose a large enough biocontrol agents release rate that ensures pest eradication (see Theorem 3.3 and Corollary 3.4). For Beddington-DeAngelis interference however, a necessary condition must be fulfilled first: it is not possible to eradicate the pest population if the interference intensity is too large with respect to the pest growth rate (condition $r < \frac{a}{b}$). Thus, whether interference acts upon the trophic response or the mortality rate of the predators result thus in different outcomes for the possible success of a biological control program.

As for the influence of the release period T and contrary to the no-interference case, both types of interferences result in a T -dependent stability condition for

pest eradication; furthermore, the use of large periods T disrupts biological control. Indeed, in the Beddington-DeAngelis case, we note that condition (2d) yields

$$\lim_{T \rightarrow +\infty} \mu_b = \lim_{T \rightarrow +\infty} \frac{(c + K)(1 - e^{-r \frac{b}{a} m T})(1 - e^{-m T})}{b(1 - e^{-m(1 - r \frac{b}{a}) T})} \frac{e^{r \frac{b}{a} m T}}{T} = +\infty$$

so that for a given μ , the stability condition (2d) does not hold with large T . We have the same result for (2c).

In the squabbling scenario, we note that y^* is essentially linear in T for $T \rightarrow +\infty$:

$$y^*(T) = \mu T + o(\mu T)$$

so that for a given μ neither the local (14c) nor the global stability (14d) conditions are fulfilled for T large.

Hence, for both types of interference between biocontrol agents one can conclude that a given release rate is likely to work over a finite range of release periods only.

The insights of our work for biological control practitioners is thus to prefer squabbling-like biocontrol agents to Beddington-DeAngelis-like ones. If this is not possible, it is then advised to investigate at first the actual interference intensity with respect to the targeted pest growth rate to be sure that pest eradication may be achieved. In both cases though, it is always preferable to use small and frequent biocontrol agent releases rather than large and infrequent ones.

Acknowledgements

This research was supported by the Lutins&Co COLOR project of INRIA Sophia Antipolis-Méditerranée and the IA2L project of the SPE department of INRA.

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Appendix A. Calculation of $\lim_{T \rightarrow 0^+} \begin{pmatrix} \frac{\partial \Omega}{\partial y^*} & \frac{\partial y^*}{\partial T} \end{pmatrix} = 0$

The second expression on the right-hand side of (25) is a product of two partial derivatives:

$$\frac{\partial \Omega}{\partial y^*} = \frac{q(1 - e^{-mT})}{m + q(1 - e^{-mT})y^*}$$

and

$$\frac{\partial y^*}{\partial T} = \frac{\mu}{2} + \frac{1}{2q} \left(\frac{q\mu^2 T - m\mu + 2m\mu \frac{1 - e^{-mT} - mT e^{-mT}}{(1 - e^{-mT})^2}}{\sqrt{\left(\frac{m}{q} - \mu T\right)^2 + \frac{4m\mu}{q} \frac{T}{(1 - e^{-mT})}}}\right)$$

In the limit as $T \rightarrow 0^+$, the product $\frac{\partial \Omega}{\partial y^*} \frac{\partial y^*}{\partial T}$ can be written as the sum of three terms as follows

$$\begin{aligned} \lim_{T \rightarrow 0^+} \frac{\partial \Omega}{\partial y^*} \frac{\partial y^*}{\partial T} &= \frac{q\mu}{2} \lim_{T \rightarrow 0^+} \left(\frac{1 - e^{-mT}}{m + q(1 - e^{-mT})y^*(T)} \right) \\ &+ \frac{q\mu^2}{2} \lim_{T \rightarrow 0^+} \left(\frac{(1 - e^{-mT})T}{(m + q(1 - e^{-mT})y^*(T)) \sqrt{\left(\frac{m}{q} - \mu T\right)^2 + \frac{4m\mu}{q} \frac{T}{(1 - e^{-mT})}}} \right) \\ &+ \frac{m\mu}{2} \lim_{T \rightarrow 0^+} \left(\frac{(1 - e^{-mT}) \left(-1 + 2 \frac{1 - e^{-mT} - mT e^{-mT}}{(1 - e^{-mT})^2}\right)}{(m + q(1 - e^{-mT})y^*(T)) \sqrt{\left(\frac{m}{q} - \mu T\right)^2 + \frac{4m\mu}{q} \frac{T}{(1 - e^{-mT})}}} \right) \end{aligned}$$

It is easily seen that the denominators are bounded away from zero when $T \rightarrow 0^+$, since $m + q(1 - e^{-mT})y^*(T) \geq m$ and

$$\sqrt{\left(\frac{m}{q} - \mu T\right)^2 + \frac{4m\mu}{q} \frac{T}{(1 - e^{-mT})}} = 2y^*(T) - \mu T + \frac{m}{q}$$

which is larger than $\frac{m}{2q}$ when T is small. We are then left with considering the numerators and checking their convergence to zero: it can be seen directly that this is the case for the first two terms. For the third term, we note that

$$\lim_{T \rightarrow 0^+} \frac{1 - e^{-mT} - mTe^{-mT}}{(1 - e^{-mT})^2} = \lim_{T \rightarrow 0^+} \frac{mT}{2(1 - e^{-mT})} = \lim_{T \rightarrow 0^+} \frac{1}{2e^{-mT}} = \frac{1}{2}$$

This brings the numerator of the third term to zero, which proves that $\frac{\partial \Omega}{\partial y^*} \frac{\partial y^*}{\partial T} = 0$.