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Research Article

An impulsively controlled pest management model with *n* predator species and a common prey

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ABSTRACT

This paper investigates the dynamics of a competitive single-prey *n*-predators model of integrated pest management, which is subject to periodic and impulsive controls, from the viewpoint of finding sufficient conditions for the extinction of prey and for prey and predator permanence. The per capita death rates of prey due to predation are given in abstract, unspecified forms, which encompass large classes of death rates arising from usual predator functional responses, both prey-dependent and predator-dependent. The stability and permanence conditions are then expressed as balance conditions between the cumulative death rate of prey in a period, due to predation from all predator species and to the use of control, and to the cumulative birth rate of prey in the same amount of time. These results are then specialized for the case of prey-dependent functional responses, their biological significance being also discussed.

1. Introduction

Recently, impulsively perturbed predator–prey models have been employed by many researchers to discuss the efficiency of integrated pest management strategies (see, for instance, Jiao et al., 2008; Liu et al., 2004; Tang et al., 2005; Mailleret and Grognard, 2009). Usually, a combination of a biological control, consisting in the release of natural predators of the prey (pest), and of a chemical control, consisting in pesticide spraying, is used, possibly together with an epidemiological control, consisting in the release of infective pest individuals, being supposed that these controls occur in periodic pulses. Further developments include considering models with stage structure for the predator (Georgescu and Zhang, 2010), delay due to pest hatching (Zhang et al., 2008), state-dependent impulsive perturbations (Tang and Cheke, 2005), age structure and defence mechanisms for pests (Zhang and Georgescu, 2010), and patch structure (Yang and Tang, 2009). Another direction was considering higher-dimensional food chains (Baek, 2010), multiple prey species (Georgescu, 2011), and multiple predator species (Pei et al., 2005). For a discussion on the optimal control of three-dimensional food chains, see Apreutesei (2011, 2012).

To understand the nature of predator–prey interactions, it is of paramount importance to quantify the effects of predation upon the growth rates of the prey and predator classes, respectively. Ultimately, for predator–prey models quantifying control problems, the predation rate determines the extent to which the prey population can be regulated and the success of the predation-based biocontrol strategy.

In this regard, the canonical form of a predator–prey interaction can be expressed as

$$\begin{cases} \dfrac{dN}{dt}(t) = N(t)f(N(t)) - P(t)F(N(t), P(t)) - d_N(N(t))N(t) \\ \dfrac{dP}{dt}(t) = P(t)G(N(t), P(t)) - d_P(P(t))P(t), \end{cases}$$

where $N = N(t)$ and $P = P(t)$ are the density of prey and predator, respectively, $f = f(N)$ is the per capita growth rate of the prey, $F = F(N, P)$ is the functional response of the predator, that is, the density of prey individuals consumed by a single predator per unit time and $G = G(N, P)$ is the numerical response of the predator, that is, the per capita growth rate of the predator class as a result of predation. Also, $d_N(N)$ and $d_P(P)$ are the natural mortalities of prey and predator, respectively.

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Following the standard Lotka–Volterra reasoning, one often assumes that the growth of the predator population is proportional with the amount of prey ingested, which leads to the numerical response being expressed as $G(N, P)=eF(N, P)$, the constant e being thought as an “efficiency” constant. If $F=F(N)$ (that is, the functional response depends only on prey density), F is termed “prey-dependent”, while if $F=F(N, P)$ (that is, the functional response depends on both prey and predator density), F is termed “predator-dependent”, as the dependence on prey density is implicit. In the particular case in which $F=F(N/P)$ (that is, F depends on predator density through the ratio between prey and predator density), F is termed “ratio-dependent”, the above terminology being introduced in Arditi and Ginzburg (1989). Also, one may denote $F(N, P)=NF_1(N, P)$, F_1 being the per capita death rate of prey due to predation.

A comparative analysis of several functional responses has been carried out in Skalski and Gilliam (2001), a case for predator-dependence being constructed. See also Ginzburg and Colyvan (2004), which point out several fallacies of both prey-dependent functional responses and predator-dependent functional responses (no predator interference, dealing with intrinsically different time scales for consumption and reproduction for prey dependence, perfect resource sharing for ratio dependence), McCallum (2000) for a modelling viewpoint and Jeschke et al. (2002), Křivan and Vrkoč (2004) for other comparative views of functional responses with a particular stress on the role of prey handling.

Recent investigations show that in typical food webs, the prey has to face many types of predators. Investigating a total of 92 food webs, Schoener (1989) found an average of 2.8 predator species preying on each prey species, a close figure (3.2) being obtained by Cohen et al. (1986). Studying a particular desert ecosystem (Coachella Valley), Polis (1991) identified a food web totalling a few thousand species which averages 9.6 predator species per prey species. See also Sih et al. (1998) for a discussion on the emergent effects of multiple predators on a single prey (risk reduction, caused by predator–predator interactions, and risk enhancement, caused by conflicting prey responses to multiple predators). Discussing the suppression of the pea aphid *Acyrtosiphon pisum*, pest of the alfalfa (lucerne) crop *Medicago sativa*, Cardinale et al. (2003) found out that when all its three natural enemies, the coccinnelid beetle *Harmonia axyridis*, the damsel bug *Nabis* sp. and the parasitic wasp *Aphidius ervi* were present, the combined effect was more than predicted from summing the impact of each species alone, which validates the view that biological control can be more effective under a multiple predator structure. In this regard, it has been suggested in Tylianakis and Romo (2010) that a diverse predator structure may be more effective when the prey has a complex life cycle and is patchily distributed in space and time, which narrows the effectiveness of this approach to arthropod control in heterogeneous environments.

The remaining part of this paper is organized as follows. In Section 2, we introduce the mathematical model to be discussed and indicate the biological relevance of the assumptions on which the model is based upon. Several auxiliary notions relating to the Floquet theory of impulsively perturbed differential systems are given in Section 3, where the biological well-posedness of the model is also established. In Section 4, several quantitative properties of the so-called prey-free periodic solution are indicated and the relationship between its stability properties and the success of the pest management strategy is pointed out. Sufficient conditions for the local and global stability of the prey-free periodic solution are established in Section 5. Section 6 is devoted to discussing the permanence of the system, while in Section 7 the previously obtained results are contextualized for the case of prey-dependent functional responses. Finally, a biological interpretation of our results is provided in Section 8, together with a few concluding remarks.

2. The Mathematical Model and its Biological Well-posedness

Following the previously mentioned considerations, we are now ready to formulate the mathematical model which is of concern in this paper in the following form

$$\begin{cases} \dfrac{dx}{dt}(t)=x(t)(r-ax(t)) & \\ \quad -\displaystyle\sum_{i=1}^{n} x(t)y_i(t)\varphi_i(x(t),\mathbf{y}(t)) & t\neq(n+l-1)T,\ \ t\neq nT;\\ \dfrac{dy_i}{dt}(t)=c_ix(t)y_i(t)\varphi_i(x(t),\mathbf{y}(t)) & \\ \quad -d_iy_i(t) & t\neq(n+l-1)T,\ \ t\neq nT,\\ & 1\le i\le n;\\ \Delta x(t)=-\delta_x x(t), & t=(n+l-1)T;\\ \Delta y_i(t)=-\delta_i y_i(t), & t=(n+l-1)T,\\ & 1\le i\le n;\\ \Delta x(t)=0, & t=nT;\\ \Delta y_i(t)=\mu_i, & t=nT,\ \ 1\le i\le n. \end{cases} \tag{S}$$

In the above model, $x=x(t)$ represents the density of prey, being understood that all prey individuals belong to the same species, while $y_i=y_i(t)$ represents the density of the predator species i, $1\le i\le n$, and $\mathbf{y}=(y_1, y_2, \ldots, y_n)$ is the vector of all predator densities, where $n\in\mathbb{N}^*$ represents the number of predator species. Generally, bold letters will be used in this paper to denote vector-valued functions or their particular values. The constants r and a denote the intrinsic birth rate of the prey and the effects of intraspecific competition among the prey individuals, respectively, while the constants c_i and d_i, $1\le i\le n$, represent the efficiency of prey conversion into newborn predators of species i and the natural mortality of predator species i, respectively. Also, T is the common periodicity of the impulsive perturbations and $0<l<1$ is a parameter used to describe the time lag lT between predator release and pesticide spraying, which do not occur simultaneously. Here, $\Delta\psi(t)=\psi(t+)-\psi(t)$, $\psi\in\{x, y_i, 1\le i\le n\}$, represent the instantaneous jumps of the populations sizes each time the controls are used, $0\le\delta_x<1$ and $0\le\delta_i<1$, $1\le i\le n$, are the fixed proportions of the prey and predator populations, respectively, which are removed from the environment each time the pesticides are sprayed and μ_i is the constant amount of predators from species i, $1\le i\le n$, which are released each time.

The prey death rates due to predation by predator species i, $\varphi_i:[0,\ \infty)^{n+1}\to[0,\ \infty)$, $\varphi_i\in C([0,\ \infty)^{n+1})$, $1\le i\le n$, are assumed to satisfy the following monotonicity assumptions.

- (H0) For all $1\le i\le n$, $(x, \mathbf{y})\to xy_i\varphi_i(x, \mathbf{y})$ is locally Lipschitz.
- (H1) For all $1\le i\le n$, $x\to\varphi_i(x, \mathbf{y})$ is nonincreasing for fixed $\mathbf{y}\in[0,\ \infty)^n$.
- (H2a) For all $1\le i\le n$, $y_i\to y_i\varphi_i(x, \mathbf{y})$ is nondecreasing for fixed x and y_k, $k\neq i$.
- (H2b) For all $1\le i\le n$, $y_j\to\varphi_i(x, \mathbf{y})$ is nonincreasing for fixed x and y_k, $k\neq j$, for all $1\le j\le n$.

Hypothesis (H1), (H2a), (H2b) are satisfied, for instance, if the functional responses of the predators species are prey-dependent of Holling type I, for which $\varphi(x,\ \mathbf{y})=a$, of Holling type II, for which $\varphi(x,\ \mathbf{y})=(a/1+bx)$, or of Holling type IV, for which $\varphi(x,$