



Effects of environmental fluctuation and time delay on ratio dependent hyperparasitism model

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ABSTRACT

A model of host–parasitoid–hyperparasitoid is considered with ratio dependence between parasitoid and hyperparasitoid. First, the conditions for local stability and increasing host fitness due to the effect of hyperparasitism are deduced. Next, we study the effects of stochastic environmental fluctuations and discrete time delay on the system behavior and calculate the corresponding populations variances. Numerical simulations illustrate that populations densities oscillate randomly around equilibrium points. Also, in contrast to previous literature, the simulations carried out here indicate that populations variances oscillate with the increase of time delay.

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1. Introduction

A hyperparasitoid may act as a stabilizing agent in a host–parasitoid system. It is generally recognized that hyperparasitoids can be an important mortality factor of parasitoids, and this may reduce the overall negative impact of parasitoids on hosts [1,2]. This is usually seen in the context of hyperparasitoids suppressing the population density of the parasitoids, and thus affecting the degree of subsequent host infestation. Individual hosts may also directly benefit from the action of hyperparasitoids if parasitization of parasitoids leads to a significant reduction of their lifetime consumption [1,2].

Many literatures are devoted for prey–predator (or host–parasitoid) interactions where the models are based on prey-dependent functional response [3–6]. According to Berryman [7], this type of models is unable to satisfy the minimum biological property that states “when resources are low relative to population density, the predator per capita growth rate should decline with its density”. This is due to the fact that per capita growth rates of predator is a function of prey density only, which is independent of predator density [8].

Recently, there is a growing evidences that in many situations, a more suitable general predator–prey theory should be based on the so called ratio-dependence theory, which can be roughly stated as that the per capita predator growth rate should be a function of the ratio of prey to predator abundance [9–15].

As deterministic models in ecology do not incorporate the effect of fluctuating environment, it is always difficult to predict the future of the system accurately [8,9]. In fact, randomness or stochasticity plays a vital role in the structure and function of biological systems [9]. As a result of fluctuations in environment, the population density never attains a fixed value with advancement of time. It exhibits continuous oscillation around some average values [8,16,17]. The environmental factors are time-dependent, randomly varying and should be taken as stochastic processes [9].

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Time-delays occur so often, in almost every natural situation [18–21]. So, it is reasonable to assume that death of parasitoids is instantaneous when attacked by hyperparasitoids but its contribution to the growth of hyperparasitoid population is delayed by some discrete time lag. This type of discrete time delay is known as “gestation delay” [22,23].

The objective of this article is to study the effects of environmental fluctuations and time delay on hyperparasitism model. The functional response between the parasitoids and hyperparasitoids is ratio dependent Holling type II. The paper is structured as follows; In Section 2, local stability analysis is performed in deterministic model case. Then the effect of environmental fluctuations is considered followed by the study of environmental fluctuation with time delay. In both cases, the formulae of populations variances are deduced. In Section 3, numerical simulations are carried out to substantiate the analytical findings. Results show that populations densities oscillate randomly around equilibrium points and, in contrast to deductions in previous article, populations variances do not increase with the increase of time delay but oscillate randomly. Section 4 contains the conclusion and the general discussions of this work.

2. Mathematical Models

Let $x(t)$, $y(t)$, and $z(t)$ denote the densities of hosts, parasitoid, and hyperparasitoid populations at time t , respectively. The following assumptions are imposed in the mathematical model: in absence of parasitoid, the host population grows according to a logistic fashion with carrying capacity k and with an intrinsic birth rate constant r . The rate at which the host population is infected by the parasitoid is proportional to the product of the two population sizes. The functional response of the parasitoids and hyperparasitoids is a ratio dependent Holling type II. The parameters of the model are as follow: a denotes half capturing saturation constant, d and g denote the death rates of parasitoid and hyperparasitoid, respectively, h and m denote capturing rates of parasitoid and hyperparasitoid, respectively, e and c denote the conversion rates. In the following subsections three cases are presented: the basic deterministic model, the model subjected to environmental fluctuations, and the model subjected to environmental fluctuations and time delay.

2.1. The deterministic model

Based on the above assumptions, the basic mathematical model of the host–parasite–parasitoid system takes the form

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - hxy, \\ \frac{dy}{dt} &= exy - dy - \frac{myz}{az + y}, \\ \frac{dz}{dt} &= \frac{cyz}{az + y} - gz,\end{aligned}\tag{1}$$

Equilibrium points of this system are

$$\begin{aligned}E_1 &= (0, 0, 0), \quad E_2 = (k, 0, 0), \quad E_3 = \left(\frac{d}{e}, -\frac{dr}{ehk} + \frac{r}{h}, 0\right) \text{ and} \\ E_4 &= (x_4^*, y_4^*, z_4^*) = \left(x_4^*, \frac{r}{h} \left(1 - \frac{x_4^*}{k}\right), \frac{(c-g)r}{agh} \left(1 - \frac{x_4^*}{k}\right)\right),\end{aligned}$$

where $x_4^* = \frac{d}{e} + \frac{m}{ae} - \frac{gm}{ace}$.

Proposition 1. Positive equilibrium solution E_3 exists if $0 < \frac{d}{e} < k$ and positive equilibrium solution E_4 exists if $-\frac{d}{e} < \frac{m}{ae} \left(1 - \frac{g}{c}\right) < k - \frac{d}{e}$.

Lemma 1. To increase host fitness due to hyperparasitism we must have $c > g$. Whereas if $c \leq g$, then $\lim_{t \rightarrow \infty} z(t) = 0$ as $t \rightarrow \infty$.

Proof. At $z = 0$, which corresponds to the two-trophic system, $x_3^* = \frac{d}{e}$, while when $z \neq 0$, $x_4^* = \frac{d}{e} + \frac{m}{ae} - \frac{gm}{ace}$. $\therefore x_4^* - x_3^* > 0$ if $\frac{m}{ae} - \frac{gm}{ace} > 0$ which implies that $c > g$.

On the other hand, if $c \leq g$, then $\frac{cy}{az+y} \leq g$, and hence $\frac{dz}{dt} \leq 0$ which implies $\lim_{t \rightarrow \infty} z(t) \geq 0$.

We claim that $\exists P > 0$, such that $\lim_{t \rightarrow \infty} z(t) = P$. Then, $\exists \epsilon$ that satisfy $0 < \epsilon < P$, such that for a certain $t_0 > 0$ we have $P - \epsilon < z(t) < P + \epsilon$ for $\forall t > t_0$. In addition, $\exists y_{\max} > 0$ such that $\forall t > t_0$, $y(t) < y_{\max}$.

From the third equation in system (1), it follows that

$$z(t) = z(t_0) \exp \left[\int_{t_0}^t \left(\frac{cy}{az+y} - g \right) ds \right].\tag{2}$$

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