

MATHEMATICAL ANALYSIS OF A THREE-SPECIES HOST–PARASITOID–HYPERPARASITOID

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ABSTRACT. This study investigated a new three-species host–parasitoid–hyperparasitoid system, which considers the mutual interference functional response. We establish the existence and uniqueness of positive equilibrium points and demonstrate that the presence of hyperparasitoids always leads to an increase in the level of host population equilibrium. In addition, we demonstrate that the quest constant b of hyperparasitoids is proportional to the host equilibrium level, which is critical for the efficiency of biological control programs. We provide parametric conditions for the local stability of the proposed system. Some numerical simulations are performed to validate our theoretical results.

1. Introduction

When considering the parasitoid density response, the constant searching efficiency should be modified by mutual interference. Thus the two-species host–parasitoid system can be modeled as follows [1],

$$\begin{cases} H_{t+1} = \lambda H_t e^{-aP_t^{1-m}}, \\ P_{t+1} = H_t (1 - e^{-aP_t^{1-m}}), \end{cases} \quad (1)$$

where H_t and P_t represent the host and parasitoid densities at generation t , respectively; $m \in (0, 1)$ denotes the mutual interference constant; $a > 0$ is the quest constant; and $\lambda > 1$ stands for the mean quantity of eggs from a host that survives to be the subsequent generation. $f(P_t) = e^{-aP_t^{1-m}}$ is the fraction of hosts that are not parasitized by parasitoid P . The uninfected hosts generate their subsequent offspring; the next generation of parasitoids is produced due to infection of hosts.

The relationships among biological species are intricate, and one intriguing aspect of insect parasitism is the frequent occurrence of hyperparasitoids. The

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hyperparasitoid seeks out the immature stage of a primary parasitoid as its host, which results in a three-species host–primary parasitoid–hyperparasitoid system. The primary parasitoid targets the host, meanwhile, the hyperparasitoid hunts for the primary parasitoid. A typical life circle diagram of host, parasitoid, and hyperparasitoid is shown in Figure 1. Despite the increasing popularity of studying these relationships in the context of biological control, there have been limited attempts to unravel the qualitative analysis among host, parasitoid, and hyperparasitoid. In 1977, Beddington and Hammand [2] proposed a discrete-time host–parasitoid–hyperparasitoid system; they identified some critical parameters related to its feasibility and stability. Zhang and Zhao [3] modified the host–parasitoid–hyperparasitoid model by considering the effect of prolonged diapause for the host, from which many complex dynamic behaviors were observed. However, few studies give clear evidence of the important role of hyperparasitoids in the success or failure of parasitoid invasions. There is only some speculation in the biological control literature [4] where it has been argued that hyperparasitoids may badly affect the efficiency of a parasitoid as a control agent. By carrying out field and laboratory biological control programs, Broadley et al. [5] assessed the impact of hyperparasitoids on the potential success of *Cyzenis albicans* (a parasitoid) in controlling the winter moth.

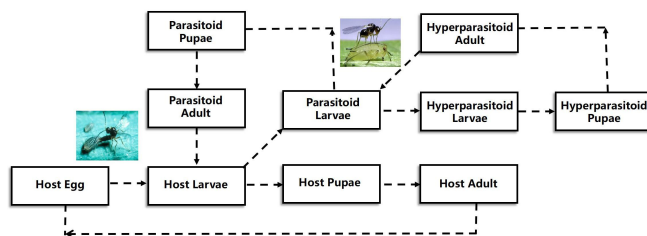


FIGURE 1. A life cycle diagram of the host, parasitoid, and the hyperparasitoid. A viable egg is laid by a parasitoid adult on a single host larvae, which is killed by the parasitoid's progeny; the hyperparasitoid adult lays an egg into the larvae of a parasitoid, which eventually leads to the parasitoid's demise. Pictures are taken from <https://en.wikipedia.org/wiki/Parasitoid> and <http://www.biologicalcontrol.info/aphid-primary-and-hyperparasitoids.html>.

In this study, we are concerned with a new three-species host–parasitoid–hyperparasitoid system to describe the interaction of a host parasitized by a

primary parasitoid P , which, while developing, is subject to parasitism by the hyperparasitoid Q [6],

$$\begin{cases} H_{t+1} = \lambda H_t e^{-aP_t^{1-m}}, \\ P_{t+1} = H_t(1 - e^{-aP_t^{1-m}})e^{-bQ_t^{1-n}}, \\ Q_{t+1} = H_t(1 - e^{-aP_t^{1-m}})(1 - e^{-bQ_t^{1-n}}), \end{cases} \tag{2}$$

where $m \in (0, 1)$ and $n \in (0, 1)$ respectively denote mutual interference of parasitoids and hyperparasitoids; $a > 0$ and $b > 0$ represent two quest constants. $f_1(P_t) = e^{-aP_t^{1-m}}$ is the fraction of hosts not parasitized by parasitoids, and $f_2(Q_t) = e^{-bQ_t^{1-n}}$ is the fraction of parasitoids that are not parasitized by hyperparasitoids.

By investigating the existence and local stability of positive equilibrium points of system (2), we verify that hyperparasitism always increases the host equilibrium level in biological control and thereby decreases the efficiency of a parasitoid. Moreover, we provide convincing evidence on the mechanism of the effects of hyperparasitoids. Specifically, we highlight the critical role of the quest constant b of hyperparasitoids in determining the degree to which pest populations can be suppressed.

2. Qualitative Analysis

2.1. Existence and Uniqueness

The existence and uniqueness of equilibrium points in a population model signifies that there are certain conditions under which a balance can be achieved. This could suggest a clear and defined state of balance for the population in its environment. Note that the unique positive equilibrium point $(H_1^*, P_1^*) = \left(\frac{\lambda(\frac{\ln\lambda}{a})^{\frac{1}{1-m}}}{\lambda-1}, (\frac{\ln\lambda}{a})^{\frac{1}{1-m}} \right)$ can be easily obtained by setting $H_{t+1} = H_t = H_1^*$ and $P_{t+1} = P_t = P_1^*$ in system (1). The following theorem gives the existence and uniqueness of positive equilibrium points of system (2):

Theorem 2.1. *If $\left(\frac{n}{b(1-n)}\right)^{\frac{1}{1-n}} > \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}} (e^{\frac{n}{1-n}} - 1)$, there exists a unique positive equilibrium $(H^*, P^*, Q^*) \in \left(\frac{\lambda(\frac{\ln\lambda}{a})^{\frac{1}{1-m}}}{\lambda-1}, \frac{\lambda(\frac{\ln\lambda}{a})^{\frac{1}{1-m}}}{\lambda-1} e^{\frac{n}{1-n}}\right) \times \left\{ \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}} \right\} \times \left(0, \left(\frac{n}{b(1-n)}\right)^{\frac{1}{1-n}}\right)$ of the system (2).*

Proof. In the system (2), $P^* = \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}$ and $\frac{Q^*}{P^*} = e^{bQ^{*1-n}} - 1$. If we define

$$f(Q^*) = \frac{Q^*}{P^*} = \frac{Q^*}{\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}},$$

and

$$g(Q^*) = e^{bQ^{*1-n}} - 1,$$

it follows that $f(0) = g(0) = 0$, $f' > 0$, and $g' > 0$. Furthermore, $f'' = 0$ and $g'' = b(1-n)Q^{*-n}e^{bQ^{*1-n}}\frac{b(1-n)Q^{*1-n}-n}{Q^*} < 0$ for $Q^* \in \left(0, \left(\frac{n}{b(1-n)}\right)^{\frac{1}{1-n}}\right)$. Therefore, if $f\left(\left(\frac{n}{b(1-n)}\right)^{\frac{1}{1-n}}\right) > g\left(\left(\frac{n}{b(1-n)}\right)^{\frac{1}{1-n}}\right)$, that is $\left(\frac{n}{b(1-n)}\right)^{\frac{1}{1-n}} > \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}(e^{\frac{n}{1-n}} - 1)$, then two functions f and g have a unique intersection. The system (2) has a unique solution Q^* in $\left(0, \left(\frac{n}{b(1-n)}\right)^{\frac{1}{1-n}}\right)$. It follows that there exists a unique $H^* \in \left(\frac{\lambda\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}}{\lambda-1}, \frac{\lambda\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}}{\lambda-1}e^{\frac{n}{1-n}}\right)$. \square

Theorem 2.2. *The quest constant b of hyperparasitoids in system (2) can be represented as a function of the host equilibrium H^* , that is*

$$b = \frac{\ln\left[\left(1 - \frac{1}{\lambda}\right)H^*\right] - \frac{1}{1-m}\ln\frac{\ln\lambda}{a}}{\left[\left(1 - \frac{1}{\lambda}\right)H^* - \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}\right]^{1-n}},$$

where b is an increasing function of H^* ; on the other hand, H^* will increase with the parameter b .

Proof. In equations $P^* = H^*(1 - e^{-aP^{*1-m}})e^{-bQ^{*1-n}}$ and $Q^* = H^*(1 - e^{-aP^{*1-m}})(1 - e^{-bQ^{*1-n}})$ of system (2), we can obtain $Q^{*1-n} = \frac{1}{b}\ln\frac{\left(1 - \frac{1}{\lambda}\right)H^*}{\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}}$ and $Q^* = \left(1 - \frac{1}{\lambda}\right)H^* - \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}$. Thus, $\frac{1}{b}\ln\frac{\left(1 - \frac{1}{\lambda}\right)H^*}{\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}} = \left[\left(1 - \frac{1}{\lambda}\right)H^* - \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}\right]^{1-n}$.

If we define a function

$$F(H^*) = \frac{\ln\left[\left(1 - \frac{1}{\lambda}\right)H^*\right] - \frac{1}{1-m}\ln\frac{\ln\lambda}{a}}{\left[\left(1 - \frac{1}{\lambda}\right)H^* - \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}\right]^{1-n}},$$

it follows that

$$F'(H^*) = \frac{-\frac{\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}}{H^*} + \left(1 - \frac{1}{\lambda}\right)\{1 - (1-n)\ln\left[\left(1 - \frac{1}{\lambda}\right)H^*\right] + (1-n)\frac{1}{1-m}\ln\frac{\ln\lambda}{a}\}}{\left[\left(1 - \frac{1}{\lambda}\right)H^* - \left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}\right]^{2-n}}.$$

We notice that $-\frac{\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}}{H^*} + \left(1 - \frac{1}{\lambda}\right)\{1 - (1-n)\ln\left[\left(1 - \frac{1}{\lambda}\right)H^*\right] + (1-n)\frac{1}{1-m}\ln\frac{\ln\lambda}{a}\} > 0$ always holds for $H^* \in \left(\frac{\lambda\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}}{\lambda-1}, \frac{\lambda\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}}{\lambda-1}e^{\frac{n}{1-n}}\right)$, which shows that $F'(H^*) > 0$. \square

2.2. Stability Analysis

Next, we investigate the local stability of positive equilibrium points of systems (1) and (2). Stability suggests that the population has adapted to its surroundings and can persist without significant fluctuations. This may indicate effective resource utilization, successful reproduction, and an overall well-adapted population. The Jacobian matrix J of system (1) evaluated at the

equilibrium (H_1^*, P_1^*) is given by

$$J_{(H_1^*, P_1^*)} = \begin{pmatrix} 1 & -\frac{\lambda(1-m)\ln\lambda}{\lambda-1} \\ \frac{\lambda-1}{\lambda} & \frac{(1-m)\ln\lambda}{\lambda-1} \end{pmatrix}. \tag{3}$$

The corresponding Jacobian matrix J of system (2) calculated at equilibrium (H^*, P^*, Q^*) is

$$J_{(H^*, P^*, Q^*)} = \begin{pmatrix} 1 & -a(1-m)H^*P^{*-m} & 0 \\ P^*/H^* & a(1-m)P^{*-m}(H^*e^{-bQ^{*1-n}} - P^*) & -b(1-n)Q^{*-n}P^* \\ Q^*/H^* & a(1-m)P^{*-m}[H^*(1 - e^{-bQ^{*1-n}}) - Q^*] & b(1-n)Q^{*-n}P^* \end{pmatrix}. \tag{4}$$

The characteristic polynomials of (3) and (4) can be respectively represented as

$$p_1(\gamma) = \gamma^2 - \left(1 + \frac{(1-m)\ln\lambda}{\lambda-1}\right)\gamma + \frac{\lambda(1-m)\ln\lambda}{\lambda-1} \tag{5}$$

and

$$p_2(\gamma) = \gamma^3 + a_1\gamma^2 + a_2\gamma + a_3, \tag{6}$$

where $a_1 = -\left[1 + \frac{(1-m)\ln\lambda}{\lambda-1} + b(1-n)\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}Q^{*-n}\right]$, $a_2 = \frac{(1-m)\lambda\ln\lambda}{\lambda-1} + b(1-n)\left(\frac{\ln\lambda}{a}\right)^{\frac{1}{1-m}}Q^{*-n} + \frac{b(1-m)(1-n)\ln\lambda}{\lambda}H^*Q^{*-n}$, and $a_3 = -b(1-m)(1-n)\ln\lambda H^*Q^{*-n}$.

Here, we note that the equilibrium point of system (1) is locally asymptotically stable [7] if all eigenvalues of the characteristic polynomial (5) lie inside the unit disk iff

$$|Tr(J)| < 1 + det(J) < 2,$$

and from this and [1], we get that the unique positive equilibrium point (H_1^*, P_1^*) of system (1) is locally asymptotically stable if and only if $\lambda(1-m)\ln\lambda < \lambda-1$.

Lemma 2.3. [8] (*Jury conditions, Schur-Cohn criteria, $n = 3$*). *The equilibrium point of system (2) is locally asymptotically stable if all eigenvalues of the characteristic polynomial (6) lie inside the unit disk iff*

- (1) $p(1) = 1 + a_1 + a_2 + a_3 > 0,$
- (2) $p(-1) = -1 + a_1 - a_2 + a_3 < 0,$
- (3) $D_2^+ = 1 + a_2 - a_3(a_1 + a_3) > 0,$
- (4) $D_2^- = 1 - a_2 + a_3(a_1 - a_3) > 0.$

By directly applying Lemma 2.3, we can establish the stability of positive equilibrium points of system (2)(also see [9]):

Theorem 2.4. *The unique positive equilibrium point (H^*, P^*, Q^*) of system (2) is locally asymptotically stable if and only if*

$$1 + a_1 + a_2 + a_3 > 0, \quad 1 - a_1 + a_2 - a_3 > 0, \quad |a_2 - a_1a_3| < 1 - a_3^2.$$

3. Results

The potential for hyperparasitism to destroy biological control is illustrated by [10] under a variety of ecological insect species. From the point of view of mathematics, Theorem 2.1 gives the corresponding theoretical support. Host equilibrium level $H_1^* = \frac{\lambda(\frac{ln\lambda}{a})^{\frac{1}{1-m}}}{\lambda-1}$ of system (1) is always smaller than $H^* \in \left(\frac{\lambda(\frac{ln\lambda}{a})^{\frac{1}{1-m}}}{\lambda-1}, \frac{\lambda(\frac{ln\lambda}{a})^{\frac{1}{1-m}}}{\lambda-1} e^{-\frac{n}{1-n}} \right)$ of system (2). This suggests that the host equilibrium level will be increased if the hyperparasitoid is introduced. Because biological control prefers a lower pest density, the introduction of a hyperparasitoid can result in inefficient biological control and even failure. Our numerical simulation in Figure 2 shows that two-species equilibrium point $(H_1^*, P_1^*) = (125.38, 73.14)$ is locally stable before $t = 50$. However, after the introduction of hyperparasitoids $Q = 50$ at $t = 50$, the system eventually transitions into a three-species steady state $(H^*, P^*, Q^*) = (172.47, 73.14, 27.47)$. In comparison to the pre-introduction phase, the host population's equilibrium level shows a significant improvement. This observation further supports the notion that hyperparasitoids are not conducive to effective biological control.

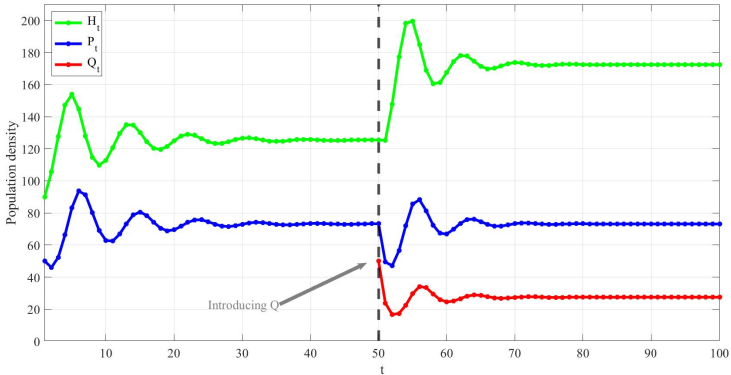


FIGURE 2. Simulation of systems (1) and (2) with $\lambda = 2.4$, $m = 0.47$, $n = 0.65$, $a = 0.09$, $b = 0.1$, and the initial condition $(H_0, P_0) = (90, 50)$. At $t = 50$, the hyperparasitoids $Q_{50} = 50$ are introduced resulting in a new three-species stable equilibrium state.

Although the fact that hyperparasitoids have adverse effects on biological control is indeed, the influence mechanism is still a concern to many ecologists [11] because the influence mechanism of hyperparasitoids concerns the efficiency of biological control. Theorem 2.2 demonstrates that the quest constant b of hyperparasitoids is proportional to the host equilibrium level H^* . The larger the value of b , the higher the host equilibrium level H^* . As shown in Figure

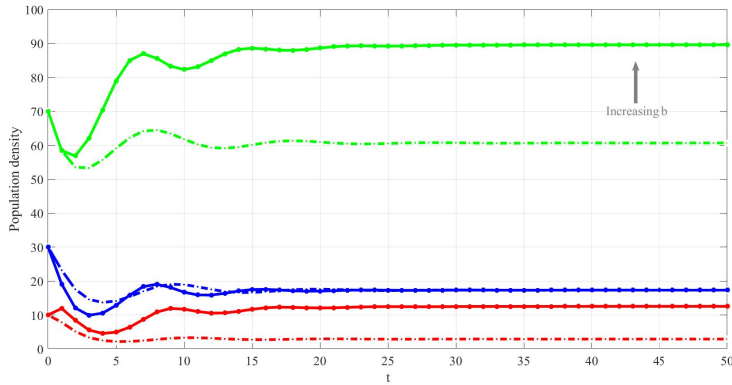


FIGURE 3. Simulation of system (2) with $\lambda = 1.5$, $m = 0.33$, $n = 0.49$, $a = 0.06$, and the initial condition $(H_0, P_0, Q_0) = (70, 30, 10)$. Where green, blue, and red lines respectively represent host H_t , parasitoid P_t , and hyperparasitoid Q_t . $b = 0.09$ for dashed lines, and $b = 0.15$ for solid lines.

3, the positive equilibrium is $(H^*, P^*, Q^*) = (60.67, 17.32, 2.90)$ when $b = 0.09$ (three dashed lines). If b is increased to 0.15, the unique equilibrium point becomes $(H^*, P^*, Q^*) = (89.60, 17.32, 12.55)$ (three solid lines). This suggests that the quest constant b increases the host equilibrium level.

4. Conclusion

We investigate a three-dimensional host–parasitoid–hyperparasitoid system to explore positive equilibrium points' existence, uniqueness, and local stability. Theorems 2.1 and 2.4 show that the conditions for achieving a stable three-species equilibrium in system (2) are stricter than in a single parasitoid–host system (1). Furthermore, the equilibrium states show that introducing hyperparasitoids always raises the host equilibrium level, which is not an ideal outcome for biological control programs. This finding is further supported by the numerical simulations in Figure 2. Theorem 2.2 and Figure 3 show that the quest constant b of hyperparasitoids is proportional to the host equilibrium level, emphasizing that a lower b value may be beneficial for biological control programs.

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