Dynamics of Host-Parasitoid Populations and Biological Control

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Abstract

In this article, we propose the host-parasitoid model that takes into account the duration of developing to be the mature parasitoid after the eggs were laid in host and the effect of refuge in host population for hiding from predation. The existence of critical time delay for unstable coexist equilibrium is examined. The successful biological control to suppress the abundance of an insect pest causing damage to crops is also discussed.

Keywords: Host, Parasitoid, Insects, Refuge, Time Delay, Biological Control

1. Introduction

Natural enemies of insect pests consisting of predators, parasitoids and pathogens have been introduced for controlling populations of arthropods [1-2]. Especially, parasitoid which is the beneficial insect is extensively used as agent for management strategies and considered for models of biological control [3-4]. The parasitoid lays eggs and lives in or on the body of its host during their immature stage and later destroys the host to live as free adult [5-6].

In theoretical ecology, the models of a parasitoid and its host have been developed to explore their interaction. The discrete insect host-parasitoid system proposed by Hessell in 1978 describing the population dynamics has been favoured [7-8]. In 2001, Nick J. Mills [9] proposed a discrete model represented the influence of a host refuge from parasitism on the host density.

In particular, the effect of delays to the interplay between pests and parasitoid has received apparently attention. The time delay is considered as the influence on stabilizing and/or destabilizing in host-parasitoid system [10]. In 1989, Hasting proposed the host-parasitoid model with time delays and resulted that parasitoid delays are more critical than host delays [11].

The success of controlling the insect pests by their natural enemy is the essence of classical biological control. Classically, the approach of mathematical model is used as a tool to understand the mechanism for success biological control of pest by its enemy.

In this paper, we propose the delay host-parasitoid models based on the assumptions that hosts are capable of refuge from the parasitoids in inaccessible habitats and the time delay occurs during the juvenile parasitoids occupying in a host. The dynamics and stability of coexistence equilibrium for the delay system are discussed. In addition, to consider the factors that influence the biological control of host population, we consider the equilibrium dynamic of the model.

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2. The Stability for The Host-parasitoid Model

Based on the Lotka-Volterra model of predator-prey system, we assume that the growth of host population follows a self-limiting logistic law and the predation rate obeys the mass action law. As in previous study, the model is taken into account for both the effect of refuge and the delay time of parasite needed in developing to become mature. The delay differential equation model representing the interactions between host, S(t), and mature parasitoid, P(t), is given by

$$\frac{dS(t)}{dt} = rS(t)(1 - \frac{S(t)}{K}) - \mu(1 - \alpha)S(t)P(t)$$

$$\frac{dP(t)}{dt} = \sigma\mu(1 - \alpha)S(t - \tau)P(t - \tau) - mP(t)$$
(1)

where r and K are the intrinsic growth rate and carrying capacity of host, respectively. The proportionality μ represents the efficiency at which the predator captures its prey as a host. The proportionality α represents a refuge in which hosts are concealed from parasitism, the parameter σ stands for the number of adult parasitoids emerging from an individual parasitized host, and m is the mortality rate of parasitoid. Finally, the delay τ is the duration of occupying in a host of the juvenile parasitoids stage.

We first consider the equilibrium point (S^*, P^*) of the model (1). It is easy to see that there are three equilibriums such as $E_1^* = (0,0)$, the extinction of both populations, $E_2^* = (K,0)$, only host exists in community, and the coexistence equilibrium

$$E_3^* = \left(\frac{m}{\sigma\mu(1-\alpha)}, \frac{r}{\mu(1-\alpha)}(1-\frac{m}{K\sigma\mu(1-\alpha)})\right) \cdot$$

For E_3^* to be exists, we must have the conditions

$$\alpha < 1 \text{ and } \sigma \mu (1 - \alpha) > \frac{m}{K}$$
 (2)

For the coexisting state to be occurred, the latter condition indicates that the maximum reproductive rate of parasite must be larger than its natural death rate.

To analyze the stability of such equilibriums, we first consider the case when the delay is absent. Setting, $\tau=0$, the Jacobian matrix of (1) reads

$$J = \begin{pmatrix} r - \frac{2rS}{K} - \mu(1 - \alpha)P & -\mu(1 - \alpha)S \\ \sigma\mu(1 - \alpha)P & \sigma\mu(1 - \alpha)S - m \end{pmatrix}.$$
 (3)

It follows that the equilibrium points E_1^* is always unstable, while E_2^* is stable when $\sigma\mu(1-\alpha) < m \ / \ K$, and E_2^* is stable when the condition (2) is satisfied.

Next, we consider the effect of time delay on the dynamics of the two species. From the model (1) by letting $S(t)=S^*+u(t)$ and $P(t)=P^*+v(t)$, we have a linearized system

$$u'(t) = \left(-\frac{2rS^*}{K} + r - \mu(1 - \alpha)P^*\right)u(t) - \mu(1 - \alpha)S^*v(t)$$

$$v'(t) = -mv(t) + \sigma\mu(1 - \alpha)P^*u(t - \tau) + \sigma\mu(1 - \alpha)S^*v(t - \tau).$$
(4)

Focusing on the coexistence equilibrium, the characteristic equation for $\,E_3^{\ast}\,$ is given by

$$\lambda^{2} - m\lambda e^{-\lambda\tau} + \left(\frac{rm}{K\sigma\mu(1-\alpha)} + m\right)\lambda - \left(\frac{2rm^{2}}{K\sigma\mu(1-\alpha)} - rm\right)e^{-\lambda\tau} + \frac{rm^{2}}{K\sigma\mu(1-\alpha)} = 0.$$
 (5)

We have shown that E_3^* is stable when $\tau=0$. We now treat the delay as a bifurcation parameter and assume that the eigenvalue λ is a function of τ . Since the real part of λ is negative

at $\tau=0$, the bifurcation occurs at the eigenvalue crosses its imaginary axis. At this point, there must be a critical delay such that $\lambda=i\omega$ where $\omega\in\mathbb{R}^+$, and resulting in E_3^* becomes unstable.

After substituting $\lambda = i\omega$ into (5) and then working on algebraic procedure, we then obtain the quartic equation

$$\omega^4 + b\omega^2 + c = 0 \tag{6}$$

where

$$b = \left(\frac{rm}{K\sigma\mu(1-\alpha)}\right)^{2},$$

$$c = -r^{2}m^{2}\left(\frac{3m}{K\sigma\mu(1-\alpha)} - 1\right)\left(\frac{m}{K\sigma\mu(1-\alpha)} - 1\right).$$
(7)

Since

$$\omega^2 = \frac{-b \pm \sqrt{b^2 - c}}{2},\tag{8}$$

(6) has only one positive real root for ω when c < 0. In other words, the conditions that allows for the existence of pure imaginary root of (5) are the condition (2) and,

$$\sigma\mu(1-\alpha) > \frac{3m}{K}.\tag{9}$$

Using ω^2 from (8), we can compute the critical delay using the traditional method. To see this, after substituting $\lambda=i\omega$ into (5), we obtain the couple equations for real part and imaginary part, and these two equations are expressed in the algebraic form of $\sin(\omega\tau)$ and $\cos(\omega\tau)$. From this point we can solve them for critical time delay so that its formula is given by

$$\tau^* = \frac{1}{\omega} \tan^{-1} \left\{ \frac{\omega \left[(rm - \omega^2)(K\sigma\mu(1 - \alpha))^2 + (r^2m - rm^2)K\sigma\mu(1 - \alpha) - 2r^2m^2 \right]}{\omega^2 (r + m)(K\sigma\mu(1 - \alpha))^2 - (r^2m^2 + rm\omega^2)K\sigma\mu(1 - \alpha) + 2r^2m^3} \right\}$$
(10)

This is the first critical value of time delay, τ^* , for unstable $E_{_q}^*$. If the delay increases passing through this critical point, then the stability of E_3^* is changed from stable fixed point to the unstable spiral.

3. Parameters Analysis and Numerical Results

In this section, we examine the effects of the parameters σ , μ and α on the dynamics pattern. To do this, we fix the parameters K=500 and r=0.5 while the mortality rate of parasitoid m=0.5 which is referred from Holt and Polis [12] and Nakazawa and Yamamura [13].

We first examine the relationship between the predation's coefficient and the emerging rate of parasite. In Figure 1, the shaded area is the region that the stability of E_3^* can be induced by the delay parameter. The region between dot line and solid line shows the stable region of E_3^* for all value of time delay. We observe that at the small emerging rate, the predation rate must be high enough so that the coexistence equilibrium can be destabilized.

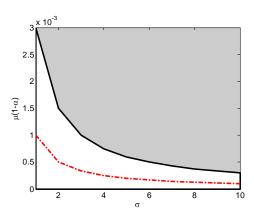


Figure 1 Plots of area of $\ \sigma\mu(1-\alpha)>m\ /\ K$ (upper dot line) and $\ \sigma\mu(1-\alpha)>3m\ /\ K$ (upper solid line) where $\ \sigma$ is varied when $\ K=500$, $\ r=0.5$, and $\ m=0.5$.

If the number of adult parasitoids form individual host is two ($\sigma=2$), we can choose $\mu(1-\alpha)=0.002$ that is satisfied with the area in Figure 1. Further, in order to find the relationship between μ and α where $\mu(1-\alpha)=0.002$, for example, we plot μ versus α in Figure 2 that shows that the captures ability increases if the refuge is increased.

We observe that the predator efficiency becomes 0.002 ($\mu=0.002$) when there is no any refuge for the hosts ($\alpha=0$). Here, substituting K=500, r=0.5, m=0.5, $\sigma=2$, $\alpha=0.5$, and $\mu=0.004$ obtained from Figures 1 and 2 in (10), we get the critical time delay $\tau^*=1.5$.

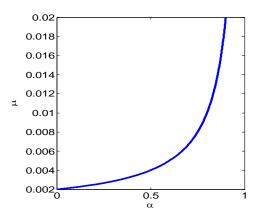


Figure 2 Plot of μ versus α for the relationship $\mu(1-\alpha)=0.002$.

The following figures present the dynamics of host and parasitoid and their orbits when $\tau=1,\,1.5$ and 3, respectively.

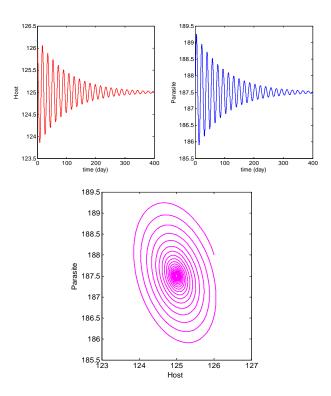


Figure 3 The dynamics of host and parasitoid where $\,K=500$, $\,r=0.5$, $\,m=0.5$, $\,\sigma=2$,

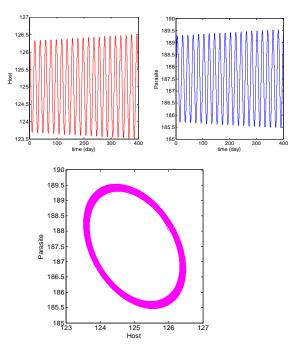


Figure 4 The dynamics of host and parasitoid where K=500, r=0.5, m=0.5, $\sigma=2$, $\alpha=0.5$, $\mu=0.004$, and $\tau=1.5$.

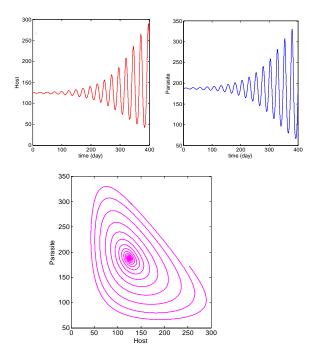


Figure 5 The dynamics of host and parasitoid where K=500, r=0.5, m=0.5, $\sigma=2$, $\alpha=0.5$, $\mu=0.004$, and $\tau=3$.

In figure 3, the direction of the orbit return to the equilibrium point since τ is less than the critical time delay. While for figure 4 and figure 5, we find that the directions of the orbits tend to move away from their equilibriums since τ is greater than the critical time delay.

In addition, we examine the effect of refuge for hosts on the critical time delay. We first illustrate the region of existence of critical time delay in parametric plane for σ and α (see Figure 6). Only refuge parameter is usually not known in nature. The role of present model is to gain insight into the cause of oscillatory pattern between host and parasite.

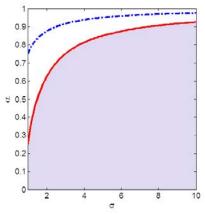


Figure 6 Plot of area of $\sigma\mu(1-\alpha) > m \ / \ K$ (below dot line) and $\sigma\mu(1-\alpha) > 3m \ / \ K$ (below solid line) where σ is varied and K=500, r=0.5, m=0.5, and $\mu=0.004$.

The area between curves (below the dot line and above the solid line) is the parameters choice for the stable coexistence equilibrium neglecting how large the delay is. This could be possible for example, when the refuge is high and the number of adult parasitoid emerging from host is low. The shaded area is the presence of critical time delay possibly leading to oscillatory pattern. It is seen that if the refuge is too low, the critical time delay always exists.

Next, by using K = 500, r = 0.5, m = 0.5, $\sigma = 4$, $\mu = 0.004$ and letting α be satisfied with the shaded area of existence in Figure 6, we plot α versus τ^* as shown in Figure 7.

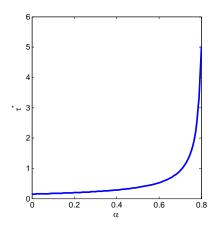


Figure 7. Plot of α versus τ^*

We observe from figure 7 that if the refuge for hosts is high, the time for breaking stability of coexistent species will be taken longer.

4. Biological controlling of prey population

Since spreading out of pest population is the main cause of plant damage, in this section we discuss about the factors that effect to the control of these insects. In ecology, the success of controlling pest by their enemies such as parasitoid is an essence of the biological control [3], [9]. To study the success of biological control of plant damage suppression caused by pest, we can consider from the equilibrium dynamic of the model or the ratio between the equilibrium of pest to its carrying capacity in the absence of parasitism [9], [14-16]. From our model, we obtain that ratio in the form of

$$\rho = \frac{S^*}{K} = \frac{m}{\sigma \mu (1 - \alpha)K}.$$
 (11)

This ratio can be a measure of the success of biological control [14-16]. Observe from (11) that $\rho>0$ when $\alpha<1$ and that the ratio of this equilibrium abundance decreases when the refuge from parasitism α also decreases.

In addition, we see from the representation of (11) that under the conditions that the number of parasitoids emerging from an individual parasitized host σ , and the efficiency at which the predator captures its prey as a host μ are high while the refuge from parasitism α and the mortality rate of parasitoid m is low, it may lead to the success of biological control.

5. Conclusions

The model for describing the dynamics between two kinds of insect which are parasitoids and their host is proposed. In this model, time delay is considered for the duration of developing to be the mature parasitoid after the eggs were laid in host. We investigate the critical time delay causing of breaking the stability of coexistence equilibrium when that duration reached the critical value. We showed that the critical time delay exists under two parameter conditions (see Figure 6). The formula for the first critical delay is presented. Thus, the bifurcation exists as the time delay increases crossing the critical value.

We also consider the effect of refuge for hiding of host from its enemy on the predation rate and the critical time delay. If the refuge is high, the parasitoid will increase its effort to prey the host. In biological control, the host that has high refuge could be controlled by the parasitoid that takes long time in the juvenile stage.

In the latter section, we examine the success of biological control measured by the ratio of the equilibrium abundance of the host in the absence of parasitism. The results show that the biological control will success when the number of mature parasitoids emerging from an individual parasitized host and the predator rate are high while the refuge from parasitism and the mortality rate of parasitoid is low. The understanding such mechanisms will lead to the success strategy of suppressing the abundance of a pest through parasitoids.

There are several possible perspectives for model development. For example, beyond the mass action law, the predation rate may be either Holling type II or type III, depending on the purpose of analysis and the empirical evidence. In terms of biological control, the suppression of abundance strategy may not be suitable for describing the temporal dynamics. In order to cope with the transient effect, analysts developed the reproductive ratio which is used as the threshold parameter that describes the potential of parasitoids to establish in their host at the beginning state. This concept is similar to the basic reproduction number in epidemiology [17-18].

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