

Ecological Modeling of Host-Parasitoid Population Dynamics

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Abstract

Arthropod parasitoids, particularly parasitoid hymenopterans, can be used as sustainable, safe biological control (biocontrol) agents for agriculturally and ecologically relevant insect pests. While searching for effective biocontrol methods, mathematical models are a useful tool to predict the outcomes of host-parasitoid interactions. These interactions are complex and depend on many biotic and abiotic factors. Generally, host-parasite interactions have been modeled using a discrete approach, but more recently, a semi-discrete hybrid methodology has been proposed in which a host's vulnerable period is modeled continuously, and a discrete update for reproduction ensues after every vulnerable period for a constant and functional response. In this report, we propose three different models based on this semi-discrete framework. The first models a hyperparasitoid interaction with an overlapping vulnerable period. The second incorporates migration of the parasitoid as it forages for hosts between different locations, and, finally, we propose a five-dimensional model in which there is a mixed population of generalist and specialist parasitoids infecting two host populations. These models can be applied to help more effectively implement a multifaceted biocontrol strategy for insect pests.

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Introduction

The use of parasitoid hymenopterans to control insect pests is a long-known method of safe and sustainable biological control (biocontrol), but it is met with varying degrees of success. Insect

pests can cause millions of dollars in damage each year to agricultural crops, and invasive insects can be devastating to indigenous ecosystems, therefore, biocontrol methods using parasitoids that target these pests are appealing as they are cost-effective, sustainable, and avoid the application of pesticides.

Host-parasitoid interactions are a complex relationship that involve a parasitoid, its host and a multitude of other biotic (host-food abundance, competition) and abiotic (temperature, weather patterns) factors [4]. The parasitoid life cycle begins with of a female using a specialized ovipositor to lay its eggs in a host, and subsequently the parasitoid larvae will feed on the host as they develop, eventually pupating, overwintering, and eclosing as an adult, which in turn kills the host [3]. After eclosion, the female parasitoid will mate and must then forage for another suitable host to lay its eggs in. Generally, parasitoids only attack their host at one specific life stage which we refer to as the vulnerable period. For example, parasitoids that prey on hemipterans (true bugs) and coleopterans (beetles) commonly infect eggs, while parasitoids that prey on lepidopterans (moths and butterflies) commonly infect larvae.

Traditionally, because of arthropods' rigid life cycle, host-parasitoid interactions have been modeled using a discrete framework, namely the Nicholson-Bailey model [5]. More recently, a hybrid approach has been adopted and can allow room for more complex biological interactions that are occurring simultaneously [6]. This semi-discrete, hybrid approach uses a continuous framework to model the vulnerable period of the host (the egg or larval stage) with a discrete update at the end of each vulnerable period (updating population densities). In this report, we implement this hybrid framework to propose three new models.

Hyperparasitoidism is the phenomena in which a parasitoid is parasitized by another parasitoid while it is infecting a host. This phenomena is relatively understudied, but it is important because hyperparasitoidism can lead to pest outbreaks by lowering the populations of relevant parasitoids [1]. This can also be detrimental to integrated pest management (IPM) because the hyperparasitoid can mitigate the desired effects of a beneficial parasitoid. In this report, we model this relationship synchronously (overlapping vulnerable period for the host and the parasitoid within its host) and asynchronously (no overlapping vulnerable period).

Arthropod parasitoids are typically winged insects from the families Hymenoptera and Diptera, and mobility is critical for host foraging. Here, we propose a model that is mindful of multiple "patches" that the parasitoid can migrate between as it forages for a suitable host.

Parasitoids can be generalists or specialists with regards to host preference [7, 2], so our final model incorporates five-dimensional parasitoid selective competition that includes two different host populations, and three different parasitoid populations in which parasitoid populations 1 and 2 are specific to preying on host populations 1 and 2 respectively, and P3 is a generalist that can prey on either host populations.

Hyperparasitoid Overlap Model

In the hyperparasitoid model, we consider the case where a hyperparasitoid attacks the parasitoid while the parasitoid attacks the host during the parasitoid host larvae period. Here we consider two possible cases: one where we consider the vulnerable period of the host and the parasitoid are asynchronous and another where we consider the two vulnerable periods to overlap with each other.

Asynchronous Model

In the asynchronous model, assume that the vulnerable period of the parasitoid larvae will occur after the vulnerable period of the host larvae. Define the interval $[0, T]$ as the vulnerable period

of the host and the interval $[T, S]$ as the vulnerable period of the parasitoid. Define $L(\tau, t)$ as the uninfected host larvae, $I_p(\tau, t)$ and $I_q(\tau, t)$ as the infected host larvae from the parasitoid and hyperparasitoid, respectively, and $P(\tau, t)$ and $Q(\tau, t)$ as the adult female parasitoid and hyperparasitoids with eggs, respectively. For $\tau \in [0, T]$, we obtain the following system of differential equations:

$$\begin{aligned}
\frac{dL}{d\tau} &= -g_p(\cdot)LP & L(0, t) &= RH_t \\
\frac{dI_p}{d\tau} &= g_p(\cdot)LP & I_p(0, t) &= 0 \\
\frac{dP}{d\tau} &= 0 & P(0, t) &= P_t \\
\frac{dQ}{d\tau} &= 0 & Q(0, t) &= Q_t \\
\frac{dI_q}{d\tau} &= 0 & I_q(0, t) &= 0
\end{aligned} \tag{1}$$

where $g_p(\cdot)$ denotes the parasitism rate of the parasitoid. If we assume that $g_p = c_p$, where c_p is constant, we obtain the following solutions for (1):

$$\begin{aligned}
L(\tau, t) &= RH_t e^{-c_p P_t \tau} \\
I_p(\tau, t) &= RH_t (1 - e^{-c_p P_t \tau}) \\
P(\tau, t) &= P_t \\
Q(\tau, t) &= Q_t \\
I_q(\tau, t) &= 0.
\end{aligned}$$

Now we set up the system of equations for the hyperparasitoid. For $\tau \in [T, S]$, we have the following system of differential equations:

$$\begin{aligned}
\frac{dL}{d\tau} &= 0 & L(T, t) &= RH_t e^{-c_p P_t T} \\
\frac{dI_p}{d\tau} &= -g_q(\cdot)QI_p & I_p(T, t) &= RH_t (1 - e^{-c_p P_t T}) \\
\frac{dP}{d\tau} &= 0 & P(T, \tau) &= P_t \\
\frac{dQ}{d\tau} &= 0 & Q(T, \tau) &= Q_t \\
\frac{dI_q}{d\tau} &= g_q(\cdot)QI_p & I_q(T, t) &= 0
\end{aligned} \tag{2}$$

where $g_q(\cdot)$ denotes the parasitism rate of the hyperparasitoid. If we assume that $g_q = c_q$, where c_q is constant, we obtain the following solutions for (2):

$$\begin{aligned}
L(\tau, t) &= RH_t e^{-c_p P_t T} \\
I_p(\tau, t) &= RH_t (1 - e^{-c_p P_t T}) e^{-c_q Q_t (\tau - T)} \\
P(\tau, t) &= P_t \\
Q(\tau, t) &= Q_t \\
I_q(\tau, t) &= RH_t (1 - e^{-c_p P_t T}) (1 - e^{-c_q Q_t (\tau - T)})
\end{aligned}$$

From our solutions of (2), we have the following discrete update:

$$\begin{aligned}
H_{t+1} &= RH_t e^{-c_p P_t T} \\
P_{t+1} &= k_p RH_t (1 - e^{-c_p P_t T}) e^{-c_q Q_t (S-T)} \\
Q_{t+1} &= k_q RH_t (1 - e^{-c_p P_t T}) (1 - e^{-c_q Q_t (S-T)})
\end{aligned} \tag{3}$$

From our discrete update (3), this suggests that our escape responses are

$$\begin{aligned}
f(P_t) &= e^{-c_p P_t T} \\
g(Q_t) &= e^{-c_q Q_t (S-T)}
\end{aligned}$$

where both follow the Nicholson-Bailey model.

If we now add a functional response to the vulnerable period for the host ($g_p = c_p L^m$), we obtain the following changes to our solutions above after overall vulnerable period $[0, S]$:

$$\begin{aligned}
L(\tau, t) &= RH_t \left(\frac{1}{(1 + c_p m (RH_t)^m P_t \tau)^{1/m}} \right) \\
I_p(\tau, t) &= RH_t \left(1 - \left(\frac{1}{(1 + c_p m (RH_t)^m P_t \tau)^{1/m}} \right) \right) e^{-c_q Q_t (\tau - T)} \\
I_q(\tau, t) &= RH_t \left(1 - \left(\frac{1}{(1 + c_p m (RH_t)^m P_t \tau)^{1/m}} \right) \right) (1 - e^{-c_q Q_t (\tau - T)})
\end{aligned}$$

which will follow the discrete update in (3) where now $f(P_t) = \frac{1}{(1 + c_p m (RH_t)^m P_t \tau)^{1/m}}$. The case where we have a functional response to the vulnerable period of the hyperparasitoid is similar. The results for the asynchronous hyperparasitoid model are provided in Figures 1 and 2

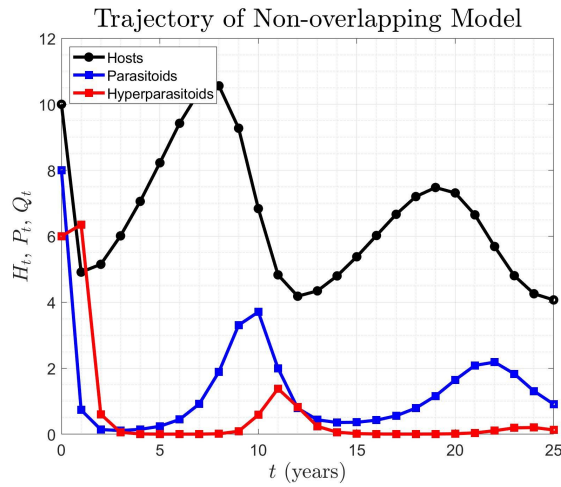


Figure 1: Trajectory Diagram with Functional Response

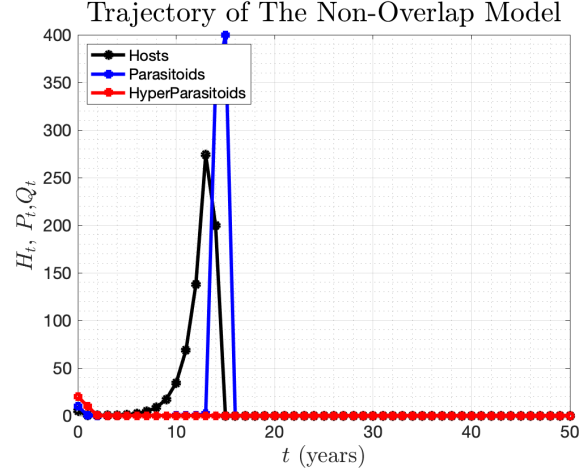


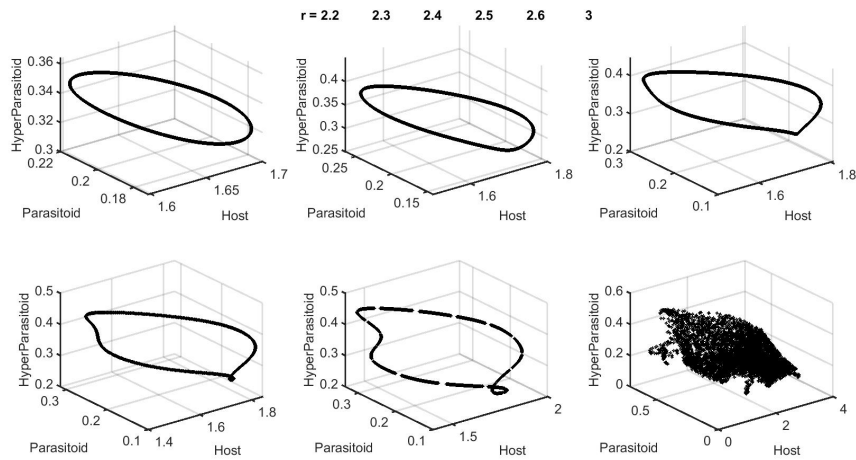
Figure 2: Trajectory Diagram with Constant Response

Considering the Beddington-Free-Lawton model, we consider a new functional response $\exp(r(1 - \frac{H_t}{k}))$ in (3), the new model has the following form:

$$\begin{aligned}
 H_{t+1} &= H_t e^{r(1 - \frac{H_t}{k}) - c_p P_t T} \\
 P_{t+1} &= k_p H_t (1 - e^{-c_p P_t T}) e^{-c_q Q_t (S-T)} \\
 Q_{t+1} &= k_q H_t (1 - e^{-c_p P_t T}) (1 - e^{-c_q Q_t (S-T)})
 \end{aligned}
 \tag{4}$$

Considering the effect of changing c_p , c_q , k and r , we have the following bifurcation diagrams (see

Figure 3: Attractors of the system (4) for different r



Figs (5)-(8):

Based on our results, when $g_p(\cdot)$ and $g_q(\cdot)$ are both constants, we conclude that the system is unstable, which makes sense since they follow the Nicholson-Bailey model. When we add functional response to the model, we conclude that the host and the parasitoid will experience coexistence while the hyperparasitoid dies out given specific values of parameter m .

Figure 4: Attractors of the system (4) for different r

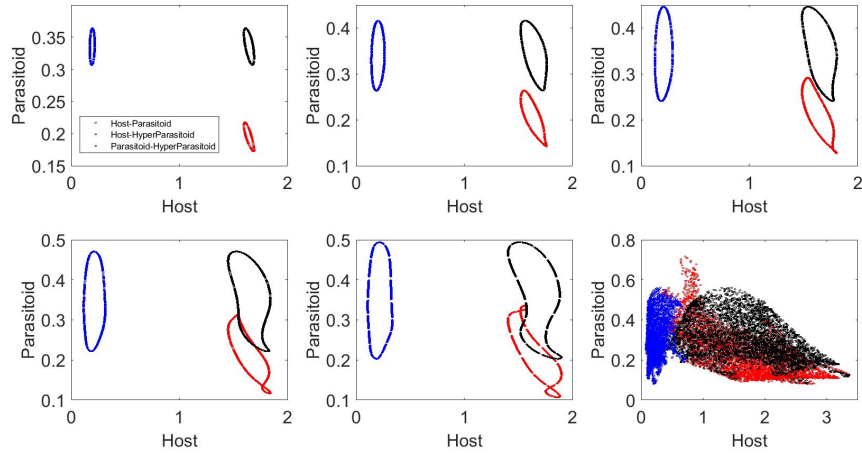
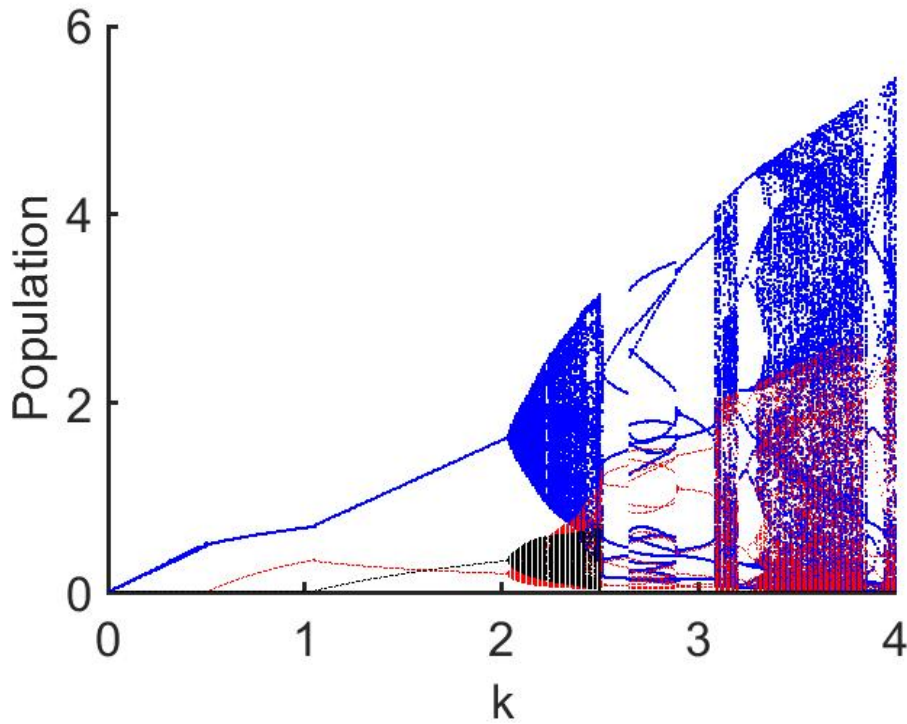


Figure 5: Bifurcation diagram with respect to k



Overlap Model

In the overlap model assume that the vulnerable periods of the parasitoid larvae and host larvae coincide for some period of time. Along with the defined functions in asynchronous model, define T_q as the starting time within the vulnerable period that the hyperparasitoid begins its attack on the parasitoid and T_p as the time where the vulnerable period for the host ends. Doing this will partition the overall vulnerable period into three sub-intervals: $[0, T_q]$, $[T_q, T_p]$, and $[T_p, T]$.

For simplicity, assume that the parasitism rates for the parasitoid and the hyperparasitoid are

Figure 6: Bifurcation diagram with respect to r

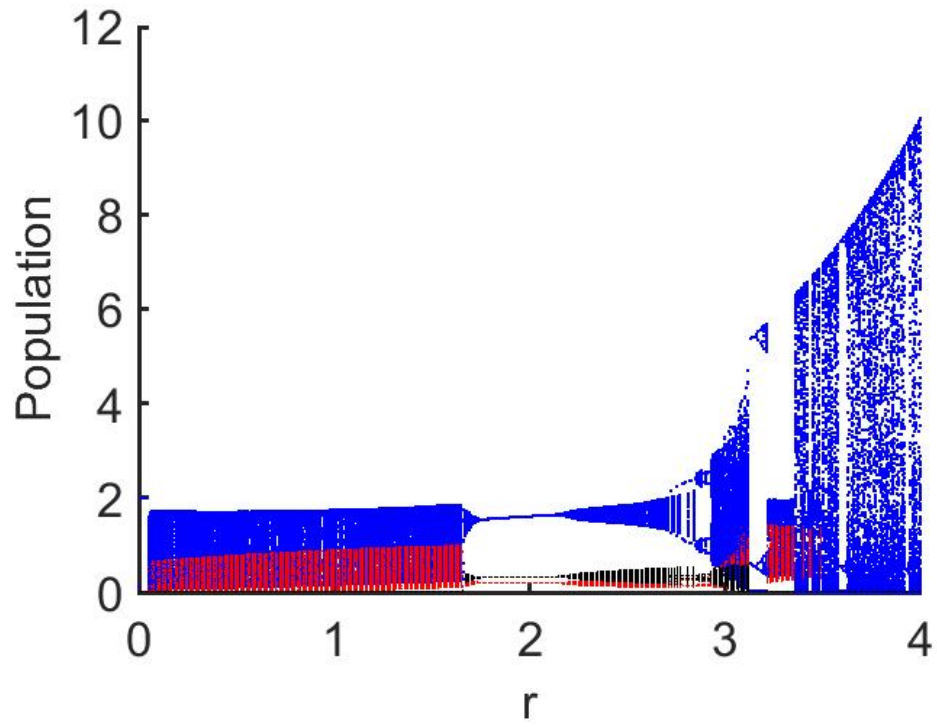


Figure 7: Bifurcation diagram with respect to c_p

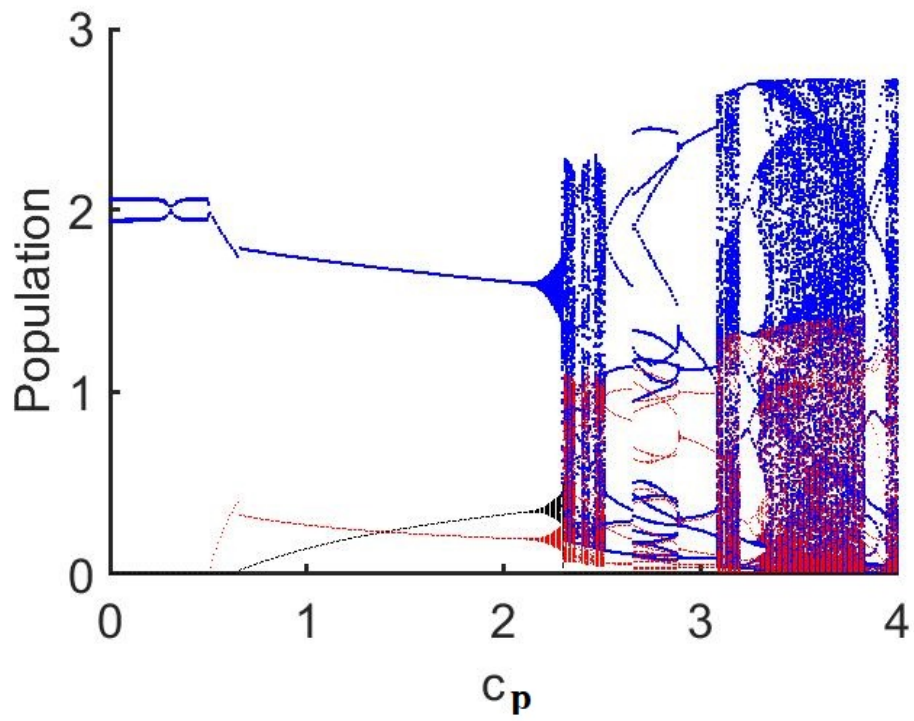
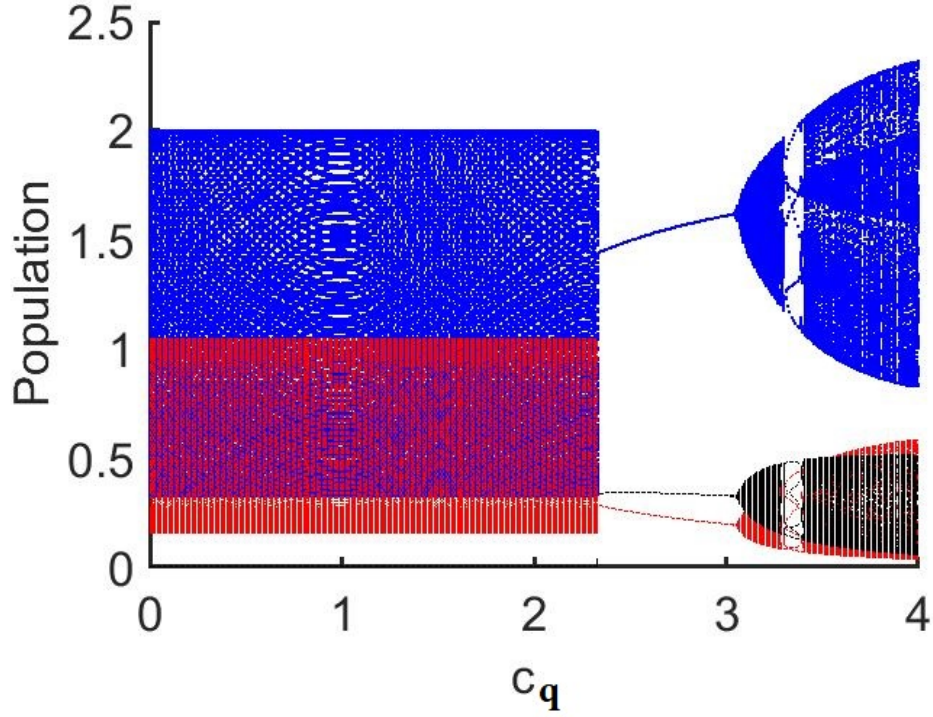


Figure 8: Bifurcation diagram with respect to c_q



constants c_p and c_q , respectively. The system of equations for subintervals $[0, T_q]$, $[T_q, T_p]$, and $[T_p, T]$ are given in equations (5)-(7), respectively:

$$\begin{aligned}
 \frac{dL}{d\tau} &= -c_p LP & L(0, t) &= RH_t \\
 \frac{dI_p}{d\tau} &= c_p LP & I_p(0, t) &= 0 \\
 \frac{dP}{d\tau} &= 0 & P(0, t) &= P_t \\
 \frac{dQ}{d\tau} &= 0 & Q(0, t) &= Q_t \\
 \frac{dI_q}{d\tau} &= 0 & I_q(0, t) &= 0
 \end{aligned} \tag{5}$$

Using similar techniques in the asynchronous hyperparasitoid model in $[0, T]$, the corresponding solutions are as follows:

$$\begin{aligned}
 L(\tau, t) &= RH_t e^{-c_p P_t \tau} \\
 I_p(\tau, t) &= RH_t (1 - e^{-c_p P_t \tau}) \\
 P(\tau, t) &= P_t \\
 Q(\tau, t) &= Q_t \\
 I_q(\tau, t) &= 0
 \end{aligned}$$

From this, we now construct the system of differential equations for the interval $[T_q, T_p]$:

$$\begin{aligned}
\frac{dL}{d\tau} &= -c_p PL & L(T_q, t) &= RH_t e^{-c_p P_t T_q} \\
\frac{dP}{d\tau} &= 0 & P(T_q, t) &= P_t \\
\frac{dQ}{d\tau} &= 0 & Q(T_q, t) &= Q_t \\
\frac{dI_p}{d\tau} &= c_p PL - c_q Q_t I_p & I_p(T_q, t) &= RH_t (1 - e^{-c_p P_t T_q}) \\
\frac{dI_q}{d\tau} &= c_q Q_t I_p & I_q(T_q, t) &= 0
\end{aligned} \tag{6}$$

The corresponding solutions for the overlap interval of the parasitoid and the hyperparasitoid are given below:

Their respective solutions using the initial conditions are:

$$\begin{aligned}
L(\tau, t) &= RH_t e^{-c_p P_t \tau} \\
I_p(\tau, t) &= RH_t (1 - e^{-c_p P_t T_q}) + \frac{c_p P_t RH_t}{c_q Q_t - c_p P_t} (e^{-c_p P_t \tau} - e^{-c_p P_t T_q}) \\
P(\tau, t) &= P_t \\
Q(\tau, t) &= Q_t \\
I_q(\tau, t) &= RH_t - L(\tau, t) - I_p(\tau, t)
\end{aligned}$$

where the solutions for I_p and I_q were obtained using an integrating factor and conservation laws. From this, we have the following system of equations on the interval $[T_p, T]$:

$$\begin{aligned}
\frac{dL}{d\tau} &= 0 & L(T_p, t) &= RH_t e^{-c_p P_t \tau} \\
\frac{dP}{d\tau} &= 0 & P(T_p, t) &= P_t \\
\frac{dQ}{d\tau} &= 0 & Q(T_p, t) &= Q_t \\
\frac{dI_p}{d\tau} &= -c_q Q_t I_p & I_p(T_p, t) &= RH_t (1 - e^{-c_p P_t T_q}) + \frac{c_p P_t RH_t}{c_q Q_t - c_p P_t} (e^{-c_p P_t T_p} - e^{-c_p P_t T_q}) \\
\frac{dI_q}{d\tau} &= c_q Q_t I_p & I_q(T_p, t) &= 0
\end{aligned} \tag{7}$$

From this, we obtain the following solutions on this subinterval:

$$\begin{aligned}
L(\tau, t) &= RH_t e^{-c_p P_t T_p} \\
I_p(\tau, t) &= U e^{c_q Q_t T_p} e^{-c_q Q_t \tau} \\
P(\tau, t) &= P_t \\
Q(\tau, t) &= Q_t \\
I_q(\tau, t) &= U + V - U e^{c_q Q_t T_p} e^{-c_q Q_t \tau}
\end{aligned}$$

From our above solutions, we have the following discrete update:

$$\begin{aligned} H_{t+1} &= RH_t e^{-c_p P_t T} \\ P_{t+1} &= k_p U e^{c_q Q_t T_p} e^{-c_q Q_t T} \\ Q_{t+1} &= k_q (U + V - U e^{c_q Q_t T_p} e^{-c_q Q_t T}) \end{aligned}$$

Our results for the overlap model with constant response rates are provided below:

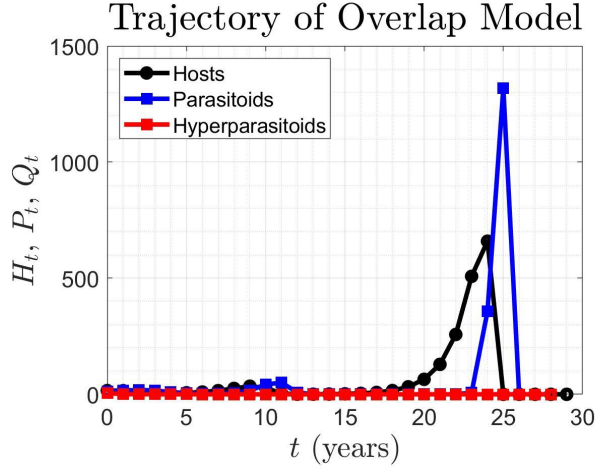


Figure 9: Trajectory Diagram of Overlap Model

During the overlapping model, we concluded that for constant response rates, we have the system being unstable. For functional response, we have the system being unstable for low number m . A further extension of the model is to try to incorporate other techniques (e.g. Beddington Model) to attempt to make the system stable.

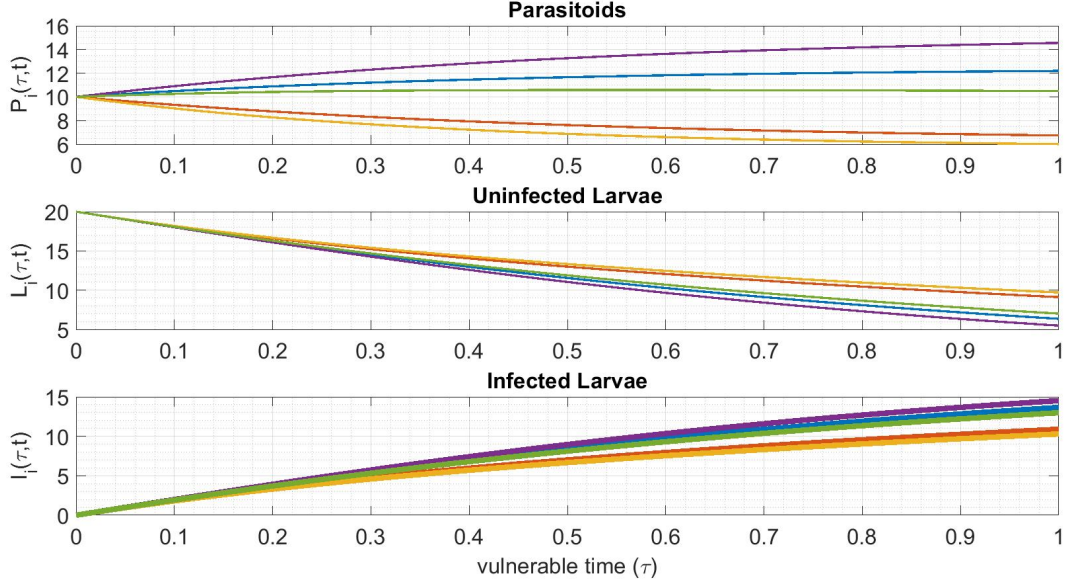
Migration Model

We are interested in looking at the vulnerable period τ (see Fig. (??)) changes from $\tau = 0$ to $\tau = T$, where the L_1 , I_1 , P_1 , P_2 and P_3 follow the following continuous system:

$$\begin{aligned} \frac{dL_1}{d\tau} &= -c L_1 P_1 \\ \frac{dI_1}{d\tau} &= c L_1 P_1 \\ \frac{dP_1}{d\tau} &= -(m_{12} + m_{13})P_1 + m_{21}P_2 + m_{31}P_3 \\ \frac{dP_2}{d\tau} &= m_{12}P_1 - (m_{21} + m_{23})P_2 + m_{31}P_3 \\ \frac{dP_3}{d\tau} &= m_{13}P_1 + m_{23}P_2 - (m_{31} + m_{32})P_3 \end{aligned}$$

Given the above system, assuming small migration size, we have shown numerically how the population of parasitoid, uninfected larvae and infected larvae are changing in the vulnerable period (see Fig. (10)).

Figure 10: Time evolution of parasitoid, uninfected larvae and infected larvae during the vulnerable period

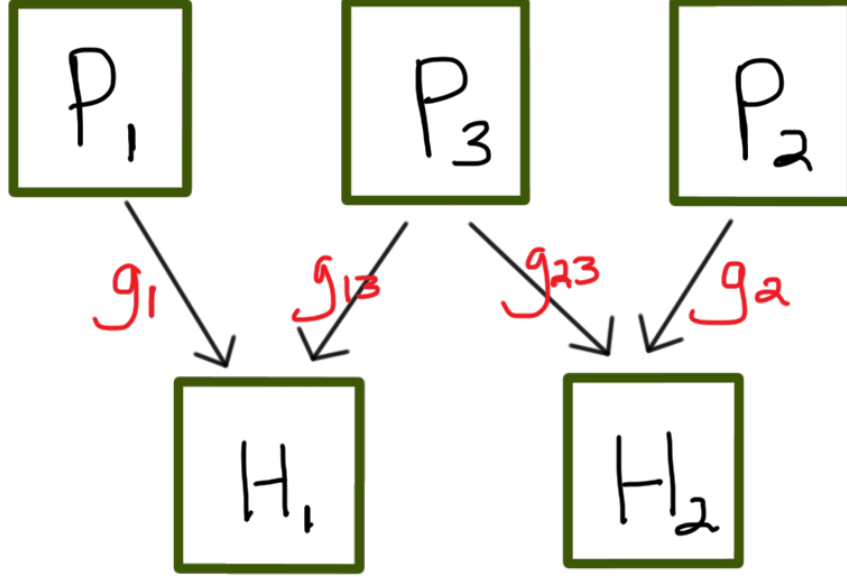


Selective Competition Model

In the selective competition model, we have three separate species of parasitoids that attack two separate species of host. As seen in Figure 11, Parasitoid 1 attacks Host 1, and Parasitoid 2 attacks Host 2. Parasitoid 3 attacks both Host 1 and Host 2. This model can be represented by the following system of differential equations:

$$\begin{aligned}
 \frac{dL_1}{d\tau} &= -c_1 P_{1t} L_1 - c_3 P_{3t} L_1 \\
 \frac{dL_2}{d\tau} &= -c_2 P_{2t} L_2 - c_3 P_{3t} L_2 \\
 \frac{dI_1}{d\tau} &= c_1 P_{1t} L_1 \\
 \frac{dI_2}{d\tau} &= c_2 P_{2t} L_2 \\
 \frac{dI_3}{d\tau} &= c_3 P_{3t} L_1 + c_3 P_{3t} L_2 \\
 \frac{dP_1}{d\tau} &= 0 \\
 \frac{dP_2}{d\tau} &= 0 \\
 \frac{dP_3}{d\tau} &= 0
 \end{aligned}$$

Figure 11: Diagram of selective competition model



where L_1 and L_2 represent the concentrations of uninfected Host 1 larvae and Host 2 larvae, respectively; I_1 , I_2 , and I_3 represent the concentrations of host larvae infected by Parasitoids 1, 2, and 3, respectively; g_1 , g_2 , and g_3 represent the general rates at which the parasitoids attack the hosts by Parasitoids 1, 2, and 3, respectively; and P_1 , P_2 , and P_3 represent the concentrations of each type of adult female parasitoids with eggs. R_1, R_2 represent the number of viable host eggs per adult host. c_1, c_2, c_3 represent the constant rates at which the parasitoids attack the hosts. Since Parasitoid 3 attacks both Hosts 1 and 2, we initially assume that it attacks them at equal rates. k_1, k_2, k_3 represent the average number of each type of parasitoid larvae that emerge from an infected host and survive to adulthood. We define the initial conditions to be $L_1(0, t) = R_1 H_{1t}$, $L_2(0, t) = R_2 H_{2t}$, $I_1(0, t) = I_2(0, t) = I_3(0, t) = 0$, $P_1(0, t) = P_{1t}$, $P_2(0, t) = P_{2t}$, and $P_3(0, t) = P_{3t}$. Since the rates of change for each parasitoid concentration is 0, those concentrations will be constant. Solving the differential equations, we find that:

$$\begin{aligned}
 L_1(\tau, t) &= R_1 H_{1t} e^{-(c_1 P_{1t} + c_3 P_{3t})\tau} \\
 L_2(\tau, t) &= R_2 H_{2t} e^{-(c_2 P_{2t} + c_3 P_{3t})\tau} \\
 I_1(\tau, t) &= \frac{c_1 P_{1t} R_1 H_{1t}}{c_1 P_{1t} + c_3 P_{3t}} (1 - e^{-(c_1 P_{1t} + c_3 P_{3t})\tau}) \\
 I_2(\tau, t) &= \frac{-c_2 P_{2t} R_2 H_{2t}}{c_2 P_{2t} + c_3 P_{3t}} (1 - e^{-(c_2 P_{2t} + c_3 P_{3t})\tau}) \\
 I_3(\tau, t) &= R_1 H_{1t} (1 - e^{-(c_1 P_{1t} + c_3 P_{3t})\tau}) + R_2 H_{2t} (1 - e^{-(c_2 P_{2t} + c_3 P_{3t})\tau}) \\
 &\quad + \frac{c_1 P_{1t} R_1 H_{1t}}{c_1 P_{1t} + c_3 P_{3t}} (e^{-(c_1 P_{1t} + c_3 P_{3t})\tau} - 1) + \frac{c_2 P_{2t} R_2 H_{2t}}{c_2 P_{2t} + c_3 P_{3t}} (e^{-(c_2 P_{2t} + c_3 P_{3t})\tau} - 1)
 \end{aligned}$$

Next, perform the discrete update:

$$H_{1,t+1} = R_1 H_{1t} f_1$$

$$\begin{aligned}
H_{2,t+1} &= R_2 H_{2t} f_2 \\
P_{1,t+1} &= \frac{k_1 c_1 P_{1t} R_1 H_{1t}}{c_1 P_{1t} + c_3 P_{3t}} (1 - f_1) \\
P_{2,t+1} &= \frac{k_2 c_2 P_{2t} R_2 H_{2t}}{c_2 P_{2t} + c_3 P_{3t}} (1 - f_2) \\
P_{3,t+1} &= k_3 \left[R_1 H_{1t} (1 - f_1) + R_2 H_{2t} (1 - f_2) + \frac{c_1 P_{1t} R_1 H_{1t}}{c_1 P_{1t} + c_3 P_{3t}} (f_1 - 1) + \frac{c_2 P_{2t} R_2 H_{2t}}{c_2 P_{2t} + c_3 P_{3t}} (f_2 - 1) \right]
\end{aligned}$$

We define $f_1 = e^{-(c_1 P_{1t} + c_3 P_{3t})T}$ and $f_2 = e^{-(c_2 P_{2t} + c_3 P_{3t})T}$.

We find the fixed points. Let $H_1^*, H_2^*, P_1^*, P_2^*, P_3^*$ be the nontrivial fixed points of the system of discrete difference equations. We find the following:

$$\begin{aligned}
H_1^* &= \frac{\ln R_1}{k_1 T C_1 (R_1 - 1)} \\
H_2^* &= \frac{\ln R_2}{k_2 T C_2 (R_2 - 1)} \\
c_1 P_1^* + c_3 P_3^* &= \frac{\ln R_1}{T} \\
c_2 P_2^* + c_3 P_3^* &= \frac{\ln R_2}{T} \\
\frac{k_3}{k_1} P_1^* + \frac{k_3}{k_2} P_2^* + P_3^* &= \frac{k_3 \ln R_1}{k_1 T C_1} + \frac{k_3 \ln R_2}{k_2 T C_2}
\end{aligned}$$

The equations in terms of P_1^* , P_2^* , and P_3^* can be solved symbolically, but the results differ drastically depending on whether we assume $k_1 = k_2 = k_3 = 1$ or not. If we make this assumption, then we find that

$$\begin{aligned}
P_1^* &= \frac{\ln R_1}{c_1 T} \\
P_2^* &= \frac{\ln R_2}{c_2 T} \\
P_3^* &= 0
\end{aligned}$$

In other words, Parasitoid 3, which can attack either host, will die out. This scenario is not desirable, so we examine the scenario in which k_1, k_2, k_3 are not all equal to 1. In this case the fixed point becomes

$$\begin{aligned}
P_1^* &= \frac{c_2 c_3 k_2 \ln R_1 + c_1 c_3 k_1 k_3 \ln R_1 + c_1 c_3 k_1 \ln R_2 - c_1 c_3 k_1 k_2 \ln R_2 - c_1 c_2 k_1 k_2 \ln R_1}{c_1 T (c_1 c_3 k_1 k_3 + c_2 k_2 (c_3 k_3 - c_1 k_1))} \\
P_2^* &= -\frac{c_2 c_3 k_2 k_3 \ln R_1 - c_2 c_3 k_2 \ln R_1 - c_2 c_3 k_2 k_3 \ln R_2 - c_1 c_3 k_1 \ln R_2 + c_1 c_2 k_1 k_2 \ln R_2}{c_2 T (c_1 c_3 k_1 k_3 + c_2 k_2 (c_3 k_3 - c_1 k_1))} \\
P_3^* &= \frac{c_1 k_1 k_3 \ln R_2 + c_2 k_2 k_3 \ln R_1 - c_2 k_2 \ln R_1 - c_1 k_1 \ln R_2}{T (c_1 c_3 k_1 k_2 + c_2 k_2 (c_3 k_3 - c_1 k_1))}
\end{aligned}$$

We analyze the eigenvalues of the Jacobian of this system of differential equations in order to test for stability. In order to do this, we will fix various parameters and vary others. Initially, we

will vary R_1 for fixed values of the other parameters, and selected values of c_{13} and c_{23} . These values are displayed in Table 1.

In Figure 15, we examine the stability of the system when the value $c_{23} > c_{13}$; i.e., Parasitoid 3 is more likely to attack Host 2 than Host 1, and as R_1 varies from 1 to 4. We see that the maximum eigenvalue is never less than 1, so the fixed point is not stable. The populations of each parasitoid and host are calculated by evaluating the fixed points for each parameter, and these are shown for scenario A as R_1 varies from 1 to 4. As Host 1 increases the number of eggs laid from 1 to 4, the population of host 1 will decrease, while the population of host 2 will remain essentially constant, the populations of Parasitoids 1 and 3 will increase, and the population of Parasitoid 2 will decrease.

In Figure 19, we examine the stability of the system when the value $c_{13} = c_{23}$; i.e., Parasitoid 3 is equally likely to attack both hosts, and as R_1 varies from 1 to 4. We see that the maximum eigenvalue is never less than 1, so again the fixed point is not stable. The populations of each parasitoid and host are calculated by evaluating the fixed points for each parameter, and these are shown for scenario B as R_1 varies from 1 to 4. The populations of each host and each parasitoid will change in the same ways as they did in scenario A: Host 1 decreases, Host 2 stays constant, Parasitoids 1 and 3 increase, and parasitoid 2 decreases.

In Figure 23, we examine the stability of the system when the value $c_{13} > c_{23}$; i.e., Parasitoid 3 is more likely to attack Host 1 than Host 2, and as R_1 varies from 1 to 4. We see that the maximum eigenvalue is never less than 1, so again the fixed point is not stable. The populations of each parasitoid and host are calculated by evaluating the fixed points for each parameter, and these are shown for scenario C as R_1 varies from 1 to 4. The populations of each host and each parasitoid will change in the same ways as they did in scenarios A and B: Host 1 decreases, Host 2 stays constant, Parasitoids 1 and 3 increase, and Parasitoid 2 decreases.

Next, we examine the impact on the eigenvalues, host population, and parasitoid population when we vary k_3 and c_{13} . k_3 represents the average number of Parasitoid 3 larvae that emerge from an infected host and survive to adulthood, and we vary k_3 from 0.5 to 2. Here we do not differentiate between whether these larvae emerge from Host 1 or 2. c_{13} represents the constant rate at which Parasitoid 3 attacks Host 1, ranging from 10^{-2} to 10^2 , and the rate at which Parasitoid 3 attacks Host 2 remains fixed.

In Figure 27, we analyze the stability of this scenario. The three-dimensional plot of the maximum eigenvalues demonstrates that there is no situation with these parameters that results in the fixed point being stable. Both Host 1 and Host 2's populations remain constant as k_3 changes, and the populations of Parasitoids 2 and 3 remain constant while Parasitoid 1's population decreases as k_3 increases. These graphs are generated at the last value of c_{13} in the range, 10^2 .

Finally, we examine the impact on the eigenvalues, host populations, and parasitoid populations when we vary R_1 and c_{13} . As in the previous examples, we will vary c_{13} from 10^{-2} to 10^2 , and R_1 from 1 to 4. The values of the other fixed parameters are displayed in Table 3.

We analyze the stability of the scenario in Figure 31. From the three-dimensional plot of the maximum eigenvalues, we can see that there is no situation with these parameters that results in stability. The population of Host 1 decreases, while the population of Host 2 remains constant as R_1 varies from 1 to 4. The population of Parasitoid 1 increases as R_1 varies from 1 to 4, while the populations of Parasitoid 2 and 3 remain constant. These graphs are generated at the last value of c_{13} in the range, 10^2 .

Table 1: Values of parameters for selective competition model for varying R_1

	R_1 A	R_1 B	R_1 C
c1	0.1	0.1	0.1
c2	0.1	0.1	0.1
c13	0.1	0.1	0.2
c23	0.2	0.1	0.1
k1	1	1	1
k2	1	1	1
k3	1.5	1.5	1.5
r1	[1.01,4,100]	[1.01,4,100]	[1.01,4,100]
r2	2	2	2
t	1	1	1

Table 2: Values of parameters for selective competition model for varying k_3 and c_{13}

	k3 c13
c1	0.1
c2	0.1
c13	logspace(-2,2,100)
c23	0.1
k1	1
k2	2
k3	[.5,2,100]
r1	2
r2	2
t	1

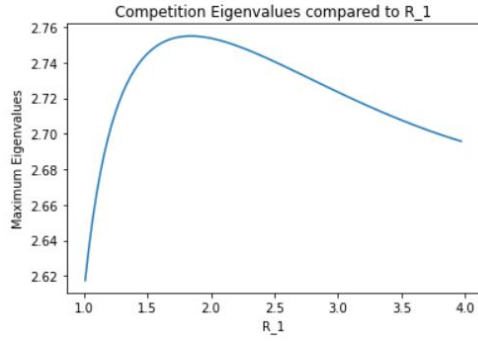


Figure 12: Maximum eigenvalues

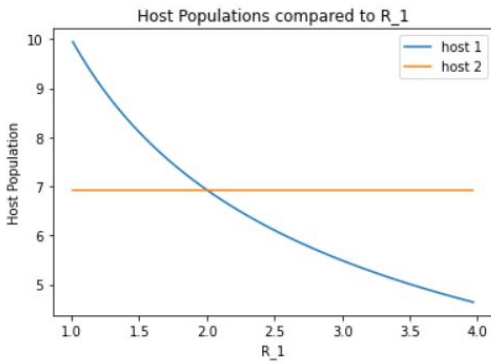


Figure 13: Host population

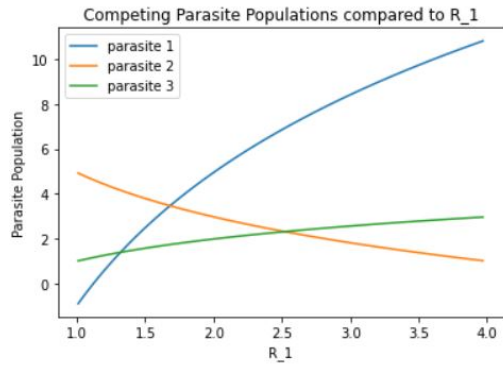


Figure 14: Parasitoid population

Figure 15: Stability analysis for scenario A as R_1 varies

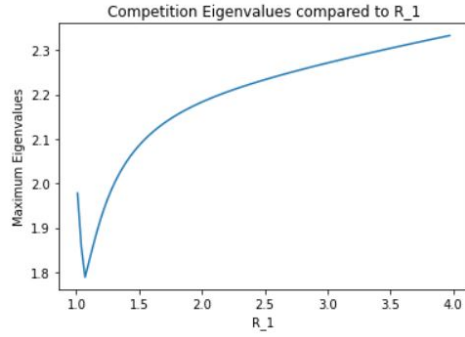


Figure 16: Maximum eigenvalues

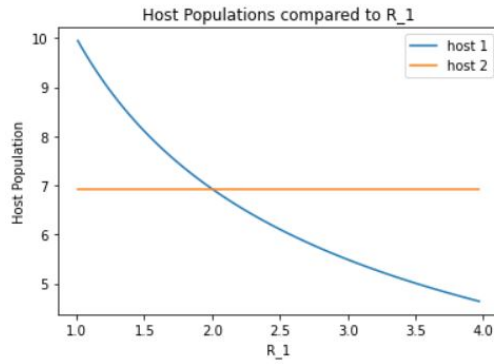


Figure 17: Host population

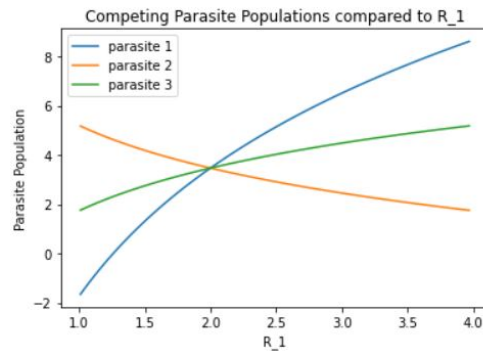


Figure 18: Parasitoid population

Figure 19: Stability analysis for scenario B as R_1 varies

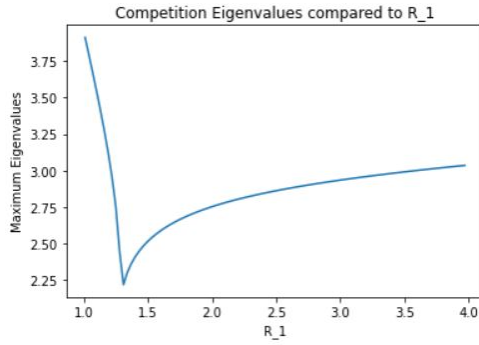


Figure 20: Maximum eigenvalues

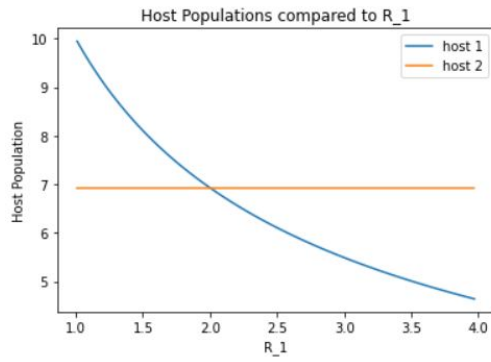


Figure 21: Host population

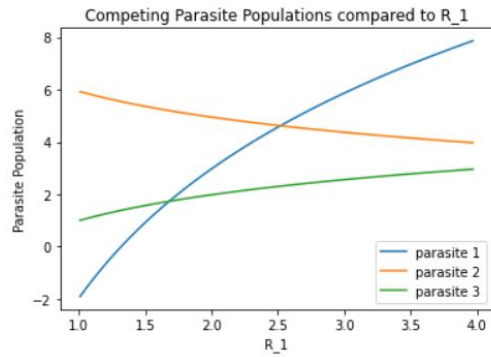


Figure 22: Parasitoid population

Figure 23: Stability analysis for scenario C as R_1 varies

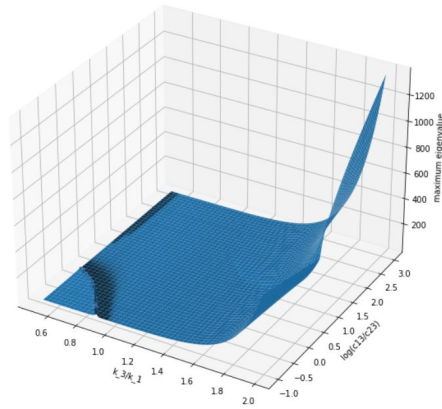


Figure 24: Maximum eigenvalues

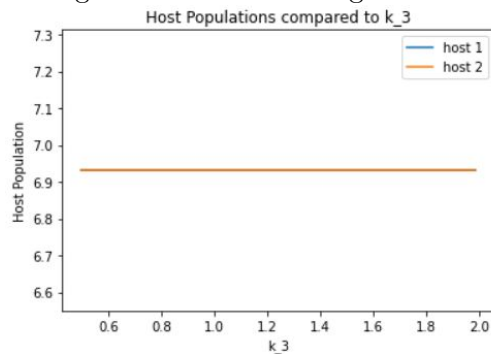


Figure 25: Host population

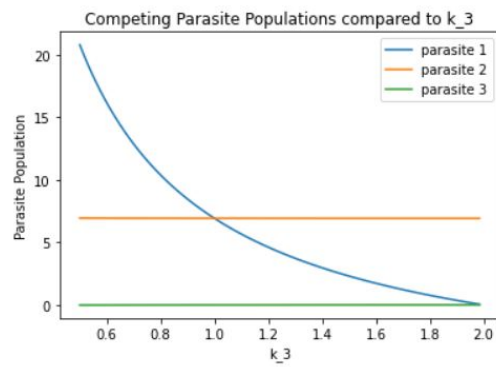


Figure 26: Parasitoid population

Figure 27: Stability analysis for varying k_3 and c_{13}

Table 3: Values of parameters for selective competition model for varying R_1 and c_{13}

	r1 c13
c1	0.1
c2	0.1
c13	logspace(-2,2,100)
c23	0.1
k1	1
k2	1
k3	1.1
r1	[1.01,4,100]
r2	2
t	1

Functional Response

Next, we implement a functional response, where instead of the rates of parasitoid attacks on the hosts being constant, we assume the rates of attacks are functions of the density of the uninfected host larvae. Assume that the functions are $g_1 = c_1 L^m$, $g_2 = c_2 L^m$, $g_{13} = c_{13} L^m$, and $g_{23} = c_{23} L^m$. The solutions to the differential equations will thus be

$$\begin{aligned}
 L_1(\tau, t) &= R_1 H_{1t} \left[\frac{1}{[1 + m(c_1 P_{1t} + c_{13} P_{13t})(RH_{1t})^{m\tau}]^{1/m}} \right] \\
 L_2(\tau, t) &= R_2 H_{2t} \left[\frac{1}{[1 + m(c_2 P_{2t} + c_{23} P_{23t})(RH_{2t})^{m\tau}]^{1/m}} \right] \\
 I_1(\tau, t) &= \frac{c_1 P_{1t} R_1 H_{1t}}{c_1 P_{1t} + c_3 P_{3t}} \left(1 - \frac{1}{[1 + m(c_1 P_{1t} + c_{13} P_{13t})(RH_{1t})^{m\tau}]^{1/m}} \right) \\
 I_2(\tau, t) &= \frac{-c_2 P_{2t} R_2 H_{2t}}{c_2 P_{2t} + c_3 P_{3t}} \left(1 - \frac{1}{[1 + m(c_2 P_{2t} + c_{23} P_{23t})(RH_{2t})^{m\tau}]^{1/m}} \right) \\
 I_3(\tau, t) &= R_1 H_{1t} \left(1 - \frac{1}{[1 + m(c_1 P_{1t} + c_{13} P_{13t})(RH_{1t})^{m\tau}]^{1/m}} \right) \\
 &\quad + R_2 H_{2t} \left(1 - \frac{1}{[1 + m(c_2 P_{2t} + c_{23} P_{23t})(RH_{2t})^{m\tau}]^{1/m}} \right) \\
 &\quad + \frac{c_1 P_{1t} R_1 H_{1t}}{c_1 P_{1t} + c_3 P_{3t}} \left(\frac{1}{[1 + m(c_1 P_{1t} + c_{13} P_{13t})(RH_{1t})^{m\tau}]^{1/m}} - 1 \right) \\
 &\quad + \frac{c_2 P_{2t} R_2 H_{2t}}{c_2 P_{2t} + c_3 P_{3t}} \left(\frac{1}{[1 + m(c_2 P_{2t} + c_{23} P_{23t})(RH_{2t})^{m\tau}]^{1/m}} - 1 \right)
 \end{aligned}$$

When we perform the discrete update, we find that these equations have the same form as the difference equations in the original selective competition model,

$$H_{1,t+1} = R_1 H_{1t} f_1$$

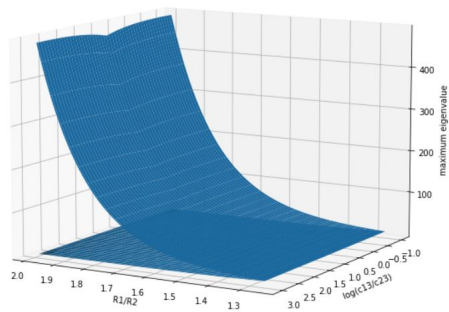


Figure 28: Maximum eigenvalues

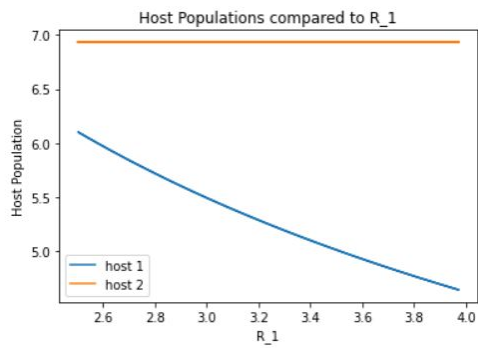


Figure 29: Host population

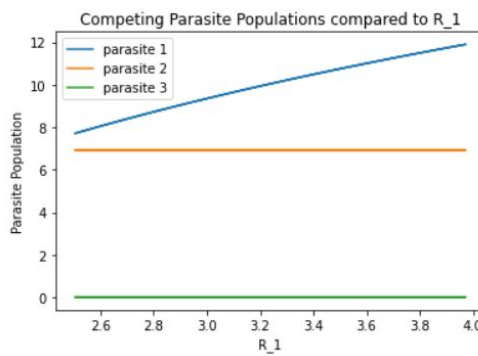


Figure 30: Parasitoid population

Figure 31: Stability analysis for varying R_1 and c_{13}

$$H_{2,t+1} = R_2 H_{2t} f_2$$

$$P_{1,t+1} = \frac{k_1 c_1 P_{1t} R_1 H_{1t}}{c_1 P_{1t} + c_3 P_{3t}} (1 - f_1)$$

$$P_{2,t+1} = \frac{k_2 c_2 P_{2t} R_2 H_{2t}}{c_2 P_{2t} + c_3 P_{3t}} (1 - f_2)$$

$$P_{3,t+1} = k_3 \left[R_1 H_{1t} (1 - f_1) + R_2 H_{2t} (1 - f_2) + \frac{c_1 P_{1t} R_1 H_{1t}}{c_1 P_{1t} + c_3 P_{3t}} (f_1 - 1) + \frac{c_2 P_{2t} R_2 H_{2t}}{c_2 P_{2t} + c_3 P_{3t}} (f_2 - 1) \right]$$

with updated functions for f_1 and f_2 . In this case, $f_1 = \frac{1}{[1+m(c_1 P_{1t} + c_3 P_{3t})(R H_{1t})^m T]^{1/m}}$ and $f_2 = \frac{1}{[1+m(c_2 P_{2t} + c_3 P_{3t})(R H_{2t})^m T]^{1/m}}$.

We also find that the trajectory of the functional response depends on m . Namely if $m < 1$, the population is oscillatory with an increasing amplitude, whereas if $m = 1$ the population has consistent oscillations. If $m > 1$ the populations stabilize. This is shown in Figure 32. The values of the fixed parameters are shown in Table 4.

Table 4: Fixed parameters for functional response model

Parameter	Value
r1	2
r2	2
c1	0.5
c2	0.4
c13	0.05
c23	0.01
t	1

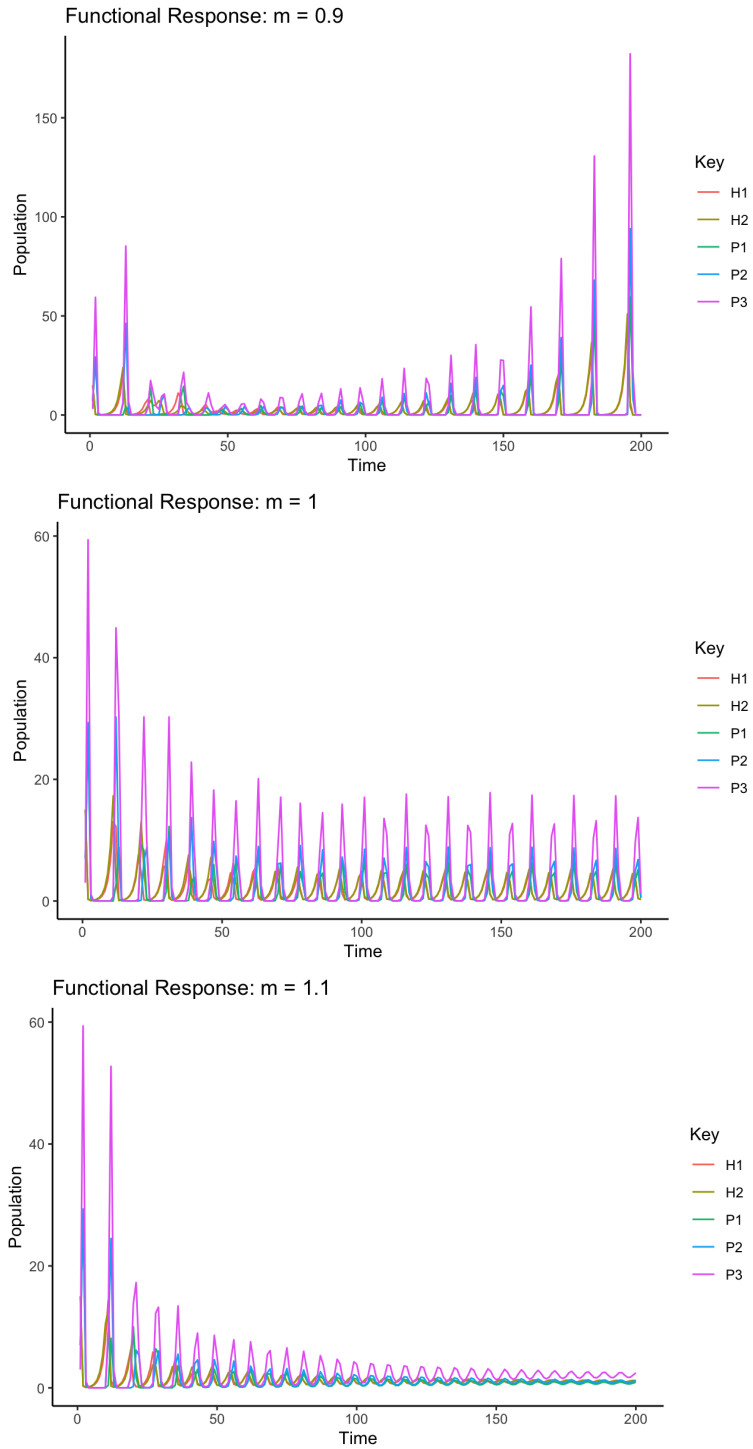


Figure 32: Functional response trajectory at varying m values

Conclusion

This paper presents three variations on a standard host-parasitoid relationship model. The first model working with the hyperparasitoid evaluates an asynchronous and synchronous timeframe for the two infections. The asynchronous model provides a basis for the more realistic synchronous time frame, where the two parasitoids' vulnerable phase transiently overlap. In the model working with the migration of parasitoids between patch locations, up to five locations were used to migrate between and are shown to give different results depending on the migration rates, as expected. It is not generalized yet for n locations, but this is an extension to the two location model. Finally, the third model demonstrates selective competition between three parasitoid populations and two hosts. As it stands, the model is unstable for all currently tested values, but a major discovery was the significance of the average number of emerging parasitoids in this particular version of the model in order to ensure that the third population does not die out. This is different compared to the other model variations where the average number of emergence of the parasitoid populations do not impact stability.

The model extensions as described in the sections above demonstrate an attempt to model the different complex aspects that make up the reality of the host-parasitoid relationship, which can then help us conceive feasible biocontrol methods. For the overlap model, there is more work to be done in examining the synchronous overlap of the hyperparasitoid and parasitoid infections. In the model about migration, a generalization to n locations would be the next step. The selective competition model can also be more generalized to include more host and parasitoid populations with different preferences and selections than chosen in this model. In addition, the functional response model could be altered such that the exponents on the g_1 and g_{13} functions are different than the exponents on the g_2 and g_{23} functions. Other factors that could be considered for future model extensions are the effects of intentional release of a population of parasitoids, incorporation of hymenopteran specific sex ratio determination, and modeling species-specific defense behaviors.

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