

The Effects of Biocontrol and Dispersal on the Dynamics of a Two-Stage Pest Population

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Abstract

In this paper we consider two predator-prey models with a two-staged pest (prey) and its biocontroller (predator). In one model, the predator only eats the immature pest, while in the other the predator only eats the mature pest. We discuss the existence and global stability of the equilibria of these models. Each model had a trivial and a positive equilibrium, one of which must be globally asymptotically stable. Then we consider dispersal of both the pest and its biocontroller between two patches. We find that the population dispersal may significantly change the dynamics of the populations in the sense that oscillation behaviors may occur in the two-patch model for certain dispersal rates. In particular, we find that the dispersal rates of the mature prey in the first and second patches affect whether the population densities converge to an equilibrium or oscillate.

Keywords— predator-prey, stage-structured, pest, biocontroller, single patch, two patch, oscillation

1 Introduction

Pests pose a significant problem in areas such as agriculture and conservation [6]. There are many ways to deal with pests, including the use of pesticides. However, it is sometimes necessary to consider ways to remove pests without the use of pesticides. It could be that overuse of pesticides has rendered them useless against the pest, as in [1], or that the use of chemical agents and the labor associated with applying it is too expensive, as in [11]. One way to do this is to introduce a predator in order to curb the pest population. In other words, applying a biocontrol to the pest. In that case, it will be necessary to know how the populations will behave when introduced to one another. In particular, before introducing a predator, it is desirable to know if the result will be the extinction of the predator and the pest, if they will coexist at some stable point, or if the predator will outlive the pest and potentially become its own pest. The efficacy of a biocontrol in controlling a pest has been the subject of several papers, including [11], [2], [7]. For examples of biocontrol predators that become pests, see [9], [3].

The first mathematical consideration of a predator-prey system was done by Lotka-Volterra [5]. This model was based on four key assumptions: the prey always has enough food, the predator depends entirely on the prey for food, a population's rate of change is directly proportionate to its size, and there is no significant environmental change. Since then, many researchers have investigated alterations to

the Lotka-Volterra Model depending on their needs. Notable among these is the consideration of a stage-structured prey, as investigated in Shi and Chen's paper [8]. A predator may prefer a juvenile population of pest to an adult one or vice versa, based on the ability of the pest to fight back. For example, in [1], the authors investigated the habits of a predator in choosing the stage of its target prey. In practical circumstances, prey may be able to disperse between patches of an environment. Tang, Cheke and Xiao consider the effects of dispersal on a predator-prey relationship without a stage structure [10]. They find that different ranges of dispersal rates affect whether populations become extinct in both patches, become extinct in one patch, or persist in both patches, indicating that dispersal rates have a significant impact on the behavior of the models.

The effects of the stage-structure of pests and dispersal of both populations present the question this line of research aims to investigate. This paper is intended to build towards a model that considers both the effects of the stage-structure of pests and dispersal of both populations among two patches. To start, we investigate two one-patch models, one with the biocontrol attacking the immature stage of the pest and one with the biocontrol attacking the mature stage of the pest. The purpose of examining both of these models is to see if there is a qualitative or quantitative difference between the behavior of the populations depending on where the biocontrol is applied. When the models are extended to two patches, we have six equations, making it harder to analyze, so we present numerical simulations to show that dispersal rates do affect the behavior of the populations.

This paper is organized as follows: in section 2 we discuss the single patch models and their dynamics, while in section 3 we discuss the two patch model. In section 2.1 we present the single patch models, followed by an analytical discussion of the dynamics of their equilibria in section 2.2. In section 2.3 we present a numerical simulation of our models based on the life tables of carmine spider mites [4] and the predation habits of *Allothrombium Pulvinum* [1] in Matlab to justify our results. In section 3.1 we present the two patch model. We then reuse the criterion for our single patch simulation to run a numerical simulation for the two patch model in order to investigate the effects of our new parameters. We conclude with a discussion of our results that compares the behavior of the one patch models with what we discovered about the behavior of the two patch model.

2 Single-Patch Models and their Dynamics

2.1 Models

In the following, we introduce models that describe the dynamics of the pest and its bio-controller (predator) in a single patch.

Model 1: the biocontrol is on the immature stage of the pest; the predator only eats juvenile pests, with the dynamics governed by:

$$\begin{aligned}\frac{dx_1}{dt} &= rx_2 - \mu x_1 - \delta x_1 - cx_1y, \\ \frac{dx_2}{dt} &= \delta x_1 - \beta x_2, \\ \frac{dy}{dt} &= kcx_1y - dy,\end{aligned}\tag{1}$$

where x_1 , x_2 , and y are the densities of the immature pests, mature pests, and the predator, respectively, r is the intrinsic growth rate of the pest, μ is the death rate of the immature pests, δ is the graduation rate of immature pests to mature pests, c is the predation rate of pests by predators, β is the death rate of the mature pests, k is the conversion rate of the predator, d is the death rate of the predator.

Model 2: the biocontrol is on the mature stage of the pest; the predator only eats adult pests, with the dynamics governed by:

$$\begin{aligned}\frac{dx_1}{dt} &= rx_2 - \mu x_1 - \delta x_1, \\ \frac{dx_2}{dt} &= \delta x_1 - \beta x_2 - cx_2y, \\ \frac{dy}{dt} &= kcx_2y - dy,\end{aligned}\tag{2}$$

where the parameters have the same meaning as those in model 1.

2.2 Equilibria and Stability

Model 1 admits the equilibria

$$\begin{aligned}E_{10} &= (0, 0, 0) \quad \text{and} \\ E_{11} &= \left(\frac{d}{kc}, \quad \frac{\delta}{\beta} \cdot \frac{d}{kc}, \quad \frac{1}{c} \left[\frac{r\delta}{\beta} - (\mu + \delta) \right] \right).\end{aligned}$$

Lemma 1.1

The following statements are valid:

- (i) E_{10} is locally asymptotically stable if $r\delta < \beta(\mu + \delta)$.
- (ii) E_{11} is positive and locally asymptotically stable if $r\delta > \beta(\mu + \delta)$.

Proof

(i) The Jacobian matrix for E_{10} is

$$J(E_{10}) = \begin{bmatrix} -\mu - \delta & r & 0 \\ \delta & -\beta & 0 \\ 0 & 0 & -d \end{bmatrix}.$$

This has the following characteristic equation:

$$(-d - \lambda)[(-\mu - \delta - \lambda)(-\beta) - r\delta] = (-d - \lambda) \cdot \det(A_{10} - \lambda I)$$

where

$$A_{10} = \begin{bmatrix} -\mu - \delta & r \\ \delta & -\beta \end{bmatrix}.$$

Then $J(E_{10})$ has an eigenvalue $\lambda = -d$ and the eigenvalues of A_{10} . Since $d > 0$, $-d < 0$. Then, in order for the eigenvalues of $J(E_{10})$ to all have negative real parts, the eigenvalues of A_{10} must all have negative real parts. The conditions for this to be true can be determined from the trace and determinant of A_{10} :

$$\begin{aligned} \text{tr}(A_{10}) &= -\mu - \delta - \beta < 0, \\ \det(A_{10}) &= \beta(\mu + \delta) - r\delta > 0 \text{ when } r\delta < \beta(\mu + \delta). \end{aligned}$$

So E_{10} is asymptotically stable when $r\delta < \beta(\mu + \delta)$.

(ii) The Jacobian matrix for E_{11} is

$$J(E_{11}) = \begin{bmatrix} -\mu - \delta - cy & r & -\frac{d}{k} \\ \delta & -\beta & 0 \\ kcy & 0 & 0 \end{bmatrix}.$$

where $y = \frac{1}{c} \left[\frac{r\delta}{\beta} - (\mu + \delta) \right]$ as in the expression for E_{11} . This has the following characteristic equation:

$$-\lambda^3 - \lambda^2(\beta + \delta + \mu + cy) - \lambda[dcy + \beta(\mu + \delta + cy) - r\delta] - \beta dcy = 0.$$

We will use the Routh-Hurwitz criteria to determine when the solutions to this equation have negative real parts. To do this, we put the characteristic equation in the form $P(\lambda) = \lambda^n + a_1\lambda^{n-1} + \dots + a_{n-1}\lambda + a_n$. So we have the following equation

$$\lambda^3 + (\beta + \delta + \mu + cy)\lambda^2 + [dcy + \beta(\mu + \delta + cy) - r\delta] + \beta dcy = 0$$

with

$$\begin{aligned}
a_1 &= \beta + \mu + \delta + cy = \beta + \frac{r\delta}{\beta}, \\
a_2 &= dcy + \beta(\mu + \delta + cy) - r\delta = d \left[\frac{r\delta}{\beta} - (\mu + \delta) \right], \text{ and} \\
a_3 &= \beta dcy = \beta d \left[\frac{r\delta}{\beta} - (\mu + \delta) \right].
\end{aligned}$$

The final expressions for a_1, a_2, a_3 are obtained by substituting in our expression for y .

The first Routh-Hurwitz matrix $H_1 = [a_1]$ has determinant $\det(H_1) = a_1 = \beta + \frac{r\delta}{\beta}$ which is positive by definition. Then our condition for stability comes from the second Routh-Hurwitz matrix:

$$\begin{aligned}
H_2 &= \begin{bmatrix} \beta + \frac{r\delta}{\beta} & 1 \\ \beta d \left[\frac{r\delta}{\beta} - (\mu + \delta) \right] & d \left[\frac{r\delta}{\beta} - (\mu + \delta) \right] \end{bmatrix}, \\
\det(H_2) &= \frac{r\delta d}{\beta} \left[\frac{r\delta}{\beta} - (\mu + \delta) \right] > 0 \quad \text{when} \quad r\delta > \beta(\mu + \delta).
\end{aligned}$$

Then all the eigenvalues of $J(E_{11})$ have negative real parts if $r\delta > \beta(\mu + \delta)$. The conditions for which E_{11} is positive can be derived directly from the expression for E_{11} . \square

From this Lemma, we see that if there is no positive equilibrium point, the trivial equilibrium point is locally asymptotically stable and that when the positive equilibrium point exists, it is locally asymptotically stable, and the trivial equilibrium is unstable.

Before we continue our analysis, it is useful to know something about the behavior of our model given non-negative initial conditions.

Lemma 1.2

The solution of model 1 is non-negative if the initial conditions are non-negative.

Proof

Suppose the immature pest population becomes zero: i.e., $x_1 = 0$. Then

$$\frac{dx_1}{dt} = rx_2 \geq 0 \text{ when } x_2 \geq 0$$

Then the immature pest population can only stay non-negative if the mature pest population stays non-negative.

Now suppose the mature pest population becomes zero: i.e., $x_2 = 0$. Then

$$\frac{dx_2}{dt} = \delta x_1 \geq 0 \text{ when } x_1 \geq 1$$

Then the mature pest population can only stay non-negative if the immature pest population stays non-negative.

Thus, if we have positive initial conditions, neither x_1 nor x_2 can ever become negative.

Lastly, suppose the predator population becomes zero: i.e., $y = 0$. Then

$$\frac{dy}{dt} = 0 \geq 0.$$

Then y will always be zero once it becomes zero.

Then, given positive initial conditions, the solution of the model will always stay non-negative. \square

Now that we know the conditions for local asymptotic stability for E_{10} and E_{11} , we will go on to discuss the global stability of E_{10} and E_{11} .

Theorem 1.1

For model 1, the following statements are valid.

- (i) E_{10} is globally asymptotically stable for all non-negative initial conditions if $r\delta < \beta(\mu + \delta)$.
- (ii) E_{11} is globally asymptotically stable for all positive initial conditions if $r\delta > \beta(\mu + \delta)$.

Proof

(i) We will use LaSalle's Invariance Principle to determine the global stability for each equilibrium point. We'll do this by attempting to construct a strict Lyapunov function for each of the equilibria. We will check that each function satisfies the following conditions:

$$V_{ij}(E_{ij}) = 0, \tag{3}$$

$$V_{ij}(X) > 0 \text{ when } X \neq E_{ij}, \tag{4}$$

$$V'_{ij}(X) = \vec{\nabla} V_{ij} \cdot f_i(X) \leq 0, \quad (5)$$

$$V_{ij}(X) \rightarrow \infty \text{ as } d(E_{ij}, X) \rightarrow \infty, \quad (6)$$

where $X = (x_1, x_2, y) \in \mathbb{R}_+^3$, $i = 1, 2$ as an index denotes the model under investigation, $f_i(X)$ is the set of differential equations defining model i , and $j = 0, 1$ as an index denotes the extinction and persistence equilibria, respectively. When conditions (3)-(6) are satisfied, the equilibrium is globally stable. When the stronger form of condition (5)— $V'_{ij}(X) < 0$ for $X \neq E_{ij}$ —holds, the equilibrium point is globally asymptotically stable.

Let

$$V_{10}(x_1, x_2, y) = x_1 + \frac{r}{\beta}x_2 + \frac{1}{k}y.$$

Note that $V_{10}(E_{10}) = V_{10}(0, 0, 0) = 0$ satisfies condition (3). Assume $x_1, x_2, y \geq 0$. Then, if $(x_1, x_2, y) \neq E_{10}$, it must be that one of x_1, x_2 and y is greater than zero, so $V_{10}(x_1, x_2, y) > 0$, so V_{10} satisfies condition (4).

Now we calculate $V'_{10}(X)$.

$$\begin{aligned} V'_{10}(X) &= \vec{\nabla} V_{10}(X) \cdot f_1(X) \\ &= \left(\hat{x}_1 + \frac{r}{\beta} \hat{x}_2 + \frac{1}{k} \hat{y} \right) \cdot [(rx_2 - \mu x_1 - \delta x_1 - cx_1 y) \hat{x}_1 + (\delta x_1 - \beta x_2) \hat{x}_2 + (kcx_1 y - dy) \hat{y}] \\ &= y \left[\frac{1}{k} (kcx_1 - d) - cx_1 \right] + x_1 \left[\delta \left(\frac{r}{\beta} - 1 \right) - \mu \right] + x_2 \left(r - \frac{r}{\beta} \right) \\ &= -dy + x_1 \left(\frac{\delta r}{\beta} - \mu - \delta \right) \\ &\leq 0 \quad \text{if } r\delta < \beta(\mu + \delta). \end{aligned}$$

Note that $V'_{10}(X)$ is equal to zero only for the full solution $X = E_{10}$, so V_{10} satisfies condition (5).

Our function also satisfies condition (6); since, as $d(E_{10}, X) \rightarrow \infty$, $V_{10}(X) \rightarrow \infty$.

Thus, by the LaSalle Invariance Principle, when $r\delta < \beta(\mu + \delta)$, E_{10} is globally asymptotically stable for all non-negative initial conditions. That is, if E_{10} is locally

asymptotically stable, it is also globally asymptotically stable for all non-negative initial conditions.

(ii) Let

$$V_{11}(X) = \int_{x_1^*}^{x_1} \frac{q - x_1^*}{q} dq + \frac{r}{\beta} \int_{x_2^*}^{x_2} \frac{\xi - x_2^*}{\xi} d\xi + \frac{1}{k} \int_{y^*}^y \frac{\zeta - y^*}{\zeta} d\zeta$$

where $x_1^* = \frac{d}{kc}$, $x_2^* = \frac{\delta}{\beta} \cdot \frac{d}{kc}$, $y^* = \frac{1}{c}[\frac{r\delta}{\beta} - (\mu + \delta)]$ as in E_{11} . Note that $V_{11}(E_{11}) = V_{11}(x_1^*, x_2^*, y^*) = 0$, so V_{11} satisfies condition (3). Assume $x_1, x_2, y \geq 0$. Now, if $X \neq E_{11}$, then some x_i is either greater or less than x_i^* .

If $x_i < x_i^*$, then, for $x_i < q_i < x_i^*$, $\frac{q_i - x_i^*}{q_i} \leq 0$. So

$$\int_{x_i}^{x_i^*} \frac{q_i - x_i^*}{q_i} dq_i < 0 \quad \text{and thus} \quad \int_{x_i^*}^{x_i} \frac{q_i - x_i^*}{q_i} dq_i = - \int_{x_i}^{x_i^*} \frac{q_i - x_i^*}{q_i} dq_i > 0.$$

If $x_i > x_i^*$, then, for $x_i^* < q_i < x_i$, $\frac{q_i - x_i^*}{q_i} \geq 0$. So

$$\int_{x_i^*}^{x_i} \frac{q_i - x_i^*}{q_i} dq_i > 0.$$

Since all of our coefficients are greater than zero, if $X \neq E_{11}$, it must be that $V_{11}(X) > 0$, so V_{11} satisfies condition (4).

Now we calculate $V'_{11}(X)$.

$$\begin{aligned} V'_{11}(X) &= \vec{\nabla} V_{11}(X) \cdot f_1(X) \\ &= \left[\frac{x_1 - x_1^*}{x_1} \hat{x}_1 + \frac{r}{\beta} \cdot \frac{x_2 - x_2^*}{x_2} \hat{x}_2 + \frac{1}{k} \cdot \frac{y - y^*}{y} \hat{y} \right] \cdot \\ &\quad [(rx_2 - \mu x_1 - \delta x_1 - cx_1 y) \hat{x}_1 + (\delta x_1 - \beta x_2) \hat{x}_2 + (kcx_1 y - dy) \hat{y}] \\ &= \frac{rd}{kc} \left[2\frac{\delta}{\beta} - \left(\frac{x_2}{x_1} + \frac{\delta^2}{\beta^2} \frac{x_1}{x_2} \right) \right]. \end{aligned}$$

Notate $x = \frac{x_2}{x_1}$ and $c = \frac{\delta}{\beta}$. Then

$$2\frac{\delta}{\beta} - \left(\frac{x_2}{x_1} + \frac{\delta^2}{\beta^2} \frac{x_1}{x_2} \right) = 2c - x - \frac{c^2}{x}.$$

If we multiply this expression by x , which is always positive, we have

$$2cx - x^2 - c^2 = -(x - c)^2.$$

Since $(x - c)^2$ is a square, it must always be non-negative. Then $-(x - c)^2$ must always be non-positive. Then $V'_{11}(X) \leq 0$ and is only equal to zero when $x_2 = \frac{\delta}{\beta}x_1$. If we plug this into our system of equations for model 1,

$$\frac{dx_2}{dt} = \delta x_1 - \beta x_2 = \delta x_1 - \beta \cdot \frac{\delta}{\beta} x_2 = 0.$$

Then x_2 is a constant. Since x_2 is proportional to x_1 , x_1 must also be a constant. That is,

$$\frac{dx_1}{dt} = rx_2 - \mu x_1 - \delta x_2 - cx_1 y = 0.$$

In order for this equation to hold, y must also be a constant. Then $V'_{11}(X)$ is only equal to zero for an equilibrium point of model 1. It cannot be the origin equilibrium, since $V_{11}(X)$ is not defined there. So $V'_{11}(X) = 0$ only for the full persistence solution $X = E_{11}$, satisfying condition (5).

Our function also satisfies condition (6); as $d(E_{11}, X) \rightarrow \infty$, $V_{11}(X) \rightarrow \infty$.

Then, by the LaSalle Invariance Principle, when E_{11} exists, it is globally asymptotically stable for all positive initial conditions. That is, when E_{11} is locally asymptotically stable, it is also globally asymptotically stable for all positive initial conditions. \square

We now move on to discuss model 2. Model 2 admits the equilibria

$$E_{20} = (0, 0, 0) \quad \text{and} \\ E_{21} = \left(\frac{rd}{kc(\mu + \delta)}, \frac{d}{kc}, \frac{1}{c} \left(\frac{r\delta}{(\mu + \delta)} - \beta \right) \right).$$

Lemma 2.1

The following statements are valid:

- (i) E_{20} is locally asymptotically stable if $r\delta < \beta(\mu + \delta)$.
- (ii) E_{21} is positive and locally asymptotically stable if $r\delta > \beta(\mu + \delta)$.

Proof

(i) The Jacobian matrix for E_{20} is

$$J(E_{20}) = \begin{bmatrix} -\mu - \delta & r & 0 \\ \delta & -\beta & 0 \\ 0 & 0 & -\delta \end{bmatrix}.$$

This has the following characteristic equation:

$$(-d - \lambda)[(-\mu - \delta - \lambda)(-\beta - \lambda) - r\delta] = (-d - \lambda)[\det(A_{20} - \lambda I)],$$

where

$$A_{20} = \begin{bmatrix} -\mu - \delta & r \\ \delta & -\beta \end{bmatrix}.$$

Then $J(E_{20})$ has an eigenvalue $\lambda = -d$ and the eigenvalues of A_{20} . $d < 0$ by definition, meaning $-d < 0$, so in order for the eigenvalues of $J(E_{20})$ to all have negative real parts, the eigenvalues of A_{20} must all have negative real parts. We can determine the conditions for this to be true from the trace and determinant of A_{20} :

$$\begin{aligned} \text{tr}(A_{20}) &= -\mu - \delta - \beta < 0, \\ \det(A_{20}) &= \beta(\mu + \delta) - r\delta > 0 \text{ when } r\delta < \beta(\mu + \delta). \end{aligned}$$

So E_{20} is asymptotically stable when $r\delta < \beta(\mu + \delta)$.

(ii) The Jacobian matrix for E_{21} is

$$J(E_{21}) = \begin{bmatrix} -\mu - \delta & r & 0 \\ \delta & -\beta - cy & -\frac{d}{k} \\ 0 & kcy & 0 \end{bmatrix}$$

where $y = \frac{1}{c} \left(\frac{r\delta}{(\mu + \delta)} - \beta \right)$ as defined in the expression for E_{21} . This has the following characteristic equation:

$$-\lambda^3 - (\beta + \delta + \mu + cy)\lambda^2 + [dcy + (\beta + cy)(\mu + \delta) - r\delta]\lambda + dcy(\mu + \delta)$$

We will use the Routh-Hurwitz criteria to determine when all the solutions of this equation have negative real parts. In order to do this, we must put the characteristic equation in the form $P(\lambda) = \lambda^n + a_1\lambda^{n-1} + \dots + a_{n-1}\lambda + a_n$. This gives us the following equation:

$$\lambda^3 + (\beta + \delta + \mu + cy)\lambda^2 + [dcy + (\beta + cy)(\mu + \delta) - r\delta]\lambda + dcy(\mu + \delta) = 0$$

with

$$\begin{aligned} a_1 &= \beta + \delta + \mu + cy = (\mu + \delta) + \frac{r\delta}{\mu + \delta} \\ a_2 &= dcy + (\beta + cy)(\mu + \delta) - r\delta = d \left(\frac{r\delta}{(\mu + \delta)} - \beta \right) \\ a_3 &= dcy(\mu + \delta) = (\mu + \delta) \cdot d \left(\frac{r\delta}{(\mu + \delta)} - \beta \right) \end{aligned}$$

The final expressions for a_1, a_2, a_3 are obtained by substituting in our expression for y .

The first Routh-Hurwitz matrix $H_1 = [a_1]$ has determinant $\det(H_1) = a_1 = (\mu + \delta) + \frac{r\delta}{(\mu + \delta)}$ which is positive by definition. Then our condition for stability comes from the second Routh-Hurwitz matrix.

$$\begin{aligned} H_2 &= \begin{bmatrix} (\mu + \delta) + \frac{r\delta}{(\mu + \delta)} & 1 \\ (\mu + \delta) \cdot d \left(\frac{r\delta}{(\mu + \delta)} - \beta \right) & d \left(\frac{r\delta}{(\mu + \delta)} - \beta \right) \end{bmatrix} \\ \det(H_2) &= \frac{r\delta d}{(\mu + \delta)} \left(\frac{r\delta}{(\mu + \delta)} - \beta \right) > 0 \quad \text{when} \quad r\delta > \beta(\mu + \delta) \end{aligned}$$

Then all the eigenvalues of $J(E_{21})$ have negative real parts if $r\delta > \beta(\mu + \delta)$. The condition for which E_{21} is non-negative can be derived directly from the expression for E_{21} . \square

We see from this Lemma that if there is no positive equilibrium point, the trivial equilibrium point is stable and that when the positive equilibrium exists, it is locally asymptotically stable, and the trivial equilibrium is unstable.

We would like to establish for model 2 what we have established earlier for model 1 regarding the behavior of the populations of the model given non-negative initial conditions.

Lemma 2.2

The solution of model 2 is non-negative if the initial conditions are non-negative.

Proof

Suppose the immature pest population becomes zero: i.e., $x_1 = 0$. Then

$$\frac{dx_1}{dt} = rx_2 \geq 0 \text{ when } x_2 \geq 0$$

Then x_1 only stays non-negative if x_2 stays non-negative.

Suppose the mature pest population becomes zero: i.e., $x_2 = 0$. Then

$$\frac{dx_2}{dt} = \delta x_1 \geq 0 \text{ when } x_1 \geq 0$$

Note that, as in the case with the immature population, x_2 only stays non-negative if x_1 stays non-negative. Then, if we begin with non-negative initial conditions, both populations stay non-negative.

Suppose the predator population becomes zero: i.e., $y = 0$. Then

$$\frac{dy}{dt} = 0$$

So the predator population can never become less than zero.

Then, given non-negative initial conditions, the populations of the model never become negative. \square

Now that we know the conditions for the local asymptotic stability of E_{20} and E_{21} , we will go on to discuss the global stability of E_{20} and E_{21} .

Theorem 2.1

Here we present the conditions for global stability for model 2.

- (i) E_{20} is globally asymptotically stable for all non-negative initial conditions if $r\delta < \beta(\mu + \delta)$
- (ii) E_{21} is globally asymptotically stable for all positive initial conditions if $r\delta > \beta(\mu + \delta)$.

Proof

(i) Let

$$V_{20}(X) = x_1 + \left(\frac{\mu}{\delta} + 1\right)\left(x_2 + \frac{1}{k}y\right).$$

Note that $V_{20}(E_{20}) = V_{20}(0, 0, 0) = 0$, satisfying condition (3). Assume $x_1, x_2, y \geq 0$. Then, if $X \neq E_{20}$, it must be that one of x_1, x_2 and y is greater than zero, so $V_{20}(X) > 0$, satisfying condition (4).

Now we calculate $V'_{20}(X)$.

$$\begin{aligned}
V'_{20}(X) &= \vec{\nabla} V_{20}(X) \cdot f_2(X) \\
&= [\hat{x}_1 + (\frac{\mu}{\delta} + 1)\hat{x}_2 + \frac{1}{k}(\frac{\mu}{\delta} + 1)\hat{y}] \cdot [(rx_2 - \mu x_1 - \delta x_1)\hat{x}_1 + (\delta x_1 - \beta x_2 - cx_2y)\hat{x}_2 + (kcx_2y - dy)\hat{y}] \\
&= [r - \beta(\frac{\mu}{\delta} + 1)]x_2 - \frac{d}{k}(\frac{\mu}{\delta} + 1)y \\
&\leq 0 \quad \text{if } r\delta < \beta(\mu + \delta)
\end{aligned}$$

Note that $V'_{20}(X) = 0$ only for the full solution $X = E_{20}$, so V_{20} satisfies condition (5).

Our function also satisfies condition (6); as $d(E_{20}, X) \rightarrow \infty$, $V_{20}(X) \rightarrow \infty$.

Thus, by the LaSalle Invariance Principle, when $r\delta < \beta(\mu + \delta)$, E_{20} is globally asymptotically stable for all non-negative initial conditions. That is, if E_{20} is locally asymptotically stable, it is also globally asymptotically stable for all non-negative initial conditions.

(ii) Let

$$V_{21}(X) = \int_{x_1^*}^{x_1} \frac{q - x_1^*}{q} dq + \frac{\mu + \delta}{\delta} \int_{x_2^*}^{x_2} \frac{\xi - x_2^*}{\xi} d\xi + \frac{\mu + \delta}{k\delta} \int_{y^*}^y \frac{\zeta - y^*}{\zeta} d\zeta.$$

where $x_1^* = \frac{rd}{kc(\mu + \delta)}$, $x_2^* = \frac{d}{kc}$, and $y^* = \frac{1}{c} \left(\frac{r\delta}{(\mu + \delta)} - \beta \right)$. Note that $V_{21}(E_{21}) = 0$, satisfying condition (3). By the logic used for $V_{11}(X)$, $V_{21}(X) > 0$ for $X \neq E_{21}$, satisfying condition (4).

Now we calculate $V'_{21}(X)$.

$$\begin{aligned}
V'_{21}(X) &= \vec{\nabla} V_{21}(X) \cdot f_2(X) \\
&= -r \frac{rd}{kc(\mu + \delta)} \frac{x_2}{x_1} + \frac{rd}{kc} - (\mu + \delta) \frac{d}{kc} \frac{x_1}{x_2} + \frac{\mu + \delta}{k\delta} d \frac{1}{c} \left(\frac{r\delta}{\mu + \delta} - \beta \right) \\
&= \frac{2rd}{kc} - \frac{r^2d}{kc(\mu + \delta)} \frac{x_2}{x_1} - \frac{(\mu + \delta)d}{kc} \frac{x_1}{x_2}
\end{aligned}$$

We then use the inequality $a^2 + b^2 \geq 2ab$ (and thus $-a^2 - b^2 \leq -2ab$) to claim

$$-\frac{r^2d}{kc(\mu + \delta)} \frac{x_2}{x_1} - \frac{(\mu + \delta)d}{kc} \frac{x_1}{x_2} \leq -2\sqrt{\frac{r^2d}{kc(\mu + \delta)} \cdot \frac{(\mu + \delta)d}{kc}} = -\frac{2rd}{kc},$$

meaning $V'_{21} \leq 0 \forall X$ fulfilling condition (5). In particular, $V'_{21} = 0$ if $\frac{x_1}{x_2} = \frac{r}{\mu + \delta}$. Then we can write $x_1 = \frac{r}{\mu + \delta}x_2$ and substitute this into $F_2(X)$. This gives the equation

$$\frac{dx_1}{dt} = rx_2 - \frac{r}{\mu + \delta}x_2 - \delta \frac{r}{\mu + \delta}x_2 = 0,$$

meaning x_1 is a constant. Since x_2 must be proportional to x_1 , x_2 must also be a constant. Then it must be true that

$$\frac{dx_2}{dt} = \delta x_1 - \beta x_2 - cx_2y = 0.$$

This equation holds when $y = \frac{1}{c}(\frac{r\delta}{\mu + \delta} + \beta) = y^*$. Then we are left with the last equation of $F_2(X)$, which must be equal to zero since we see that y is a constant. This makes $x_2 = \frac{d}{kc} = x_2^*$. Applying the required relation between x_1 and x_2 gives us $x_1 = \frac{rd}{kc(\mu + \delta)} = x_1^*$. Then $V'_{21}(X) = 0$ if and only if $X = E_{21}$.

Our function also satisfies condition (6); as $d(E_{21}, X) \rightarrow \infty$, $V_{21}(X) \rightarrow \infty$.

Then, by the LaSalle Invariance Principle, when E_{21} exists, it is globally asymptotically stable. That is, when E_{21} is locally asymptotically stable, it is also globally asymptotically stable for all positive initial conditions. \square

2.3 Case Study

We would like to apply our model to a specific case, with *Allothrombium pulvinum* as a biocontroller for the spider mite pest. Spider mites are a considerable pest to many agricultural crops [1], but overuse of pesticides during World War II rendered them ineffective against spider mites [4]. The predatory mite *Allothrombium pulvinum* is known to prey on the spider mite, with its preferences recorded in [1]. We use this paper to provide the predation parameter in our model for the simulation. Information on the life tables of the carmine spider mite (*Tetranychus cinnabarinis*) was readily available for us to use in the paper [4]. While this is not

the same spider mite that is preyed upon by *Allothrombium pulvinum* in the paper [1], (that spider mite being *Tetranychus urticae*), we considered the mites to be nearly related enough to justify the use of the complete and readily available life tables in [4]. The spider mite has more four life stages: egg, larvae, protonymph and deutonymph. Since our model only accounts for two life stages, the egg and larvae stages were grouped together as the immature stage of the pest and the protonymph and deutonymph stages were grouped together as the mature stage of the pest. We used the Matlab command ode45 to simulate our models.

The life tables of the Carmine spider mite are grouped by temperature in degrees Celsius and relative humidity. The percent of spider mites that die between stages is listed in the table. We chose the percentage of deaths after the larvae stage to be the value of the immature pest death parameter μ , depending on whether we wanted to display the extinction behavior of the models or the coexistence behavior. A similar process was used to find the mature pest death parameter β . The graduation parameter was based on the percent of pests surviving the larvae stage. Again, values under different temperatures and relative humidity were chosen based on whether we wanted the model to display extinction behavior or coexistence behavior. The predation parameter was obtained from [?] based on the information that *Allothrombium pulvinum* consumed 3.66 eggs out of 20 available within a 24 hour period. The rest of the parameters were invented to be on a similar scale to the others and fulfill the conditions for global asymptotic stability for either the trivial or positive equilibrium.

We summarize the parameters used in our simulation and their origins in Table 1 and Table 2. In fact, the parameters in Table 1 lead to extinction of both the pests and their predators. The parameters in Table 2 lead to the persistence of both the pests and their predators.

Table 1

Parameter	Value (per bug per day)	Source
r	0.05	Invented to cause extinction
μ	0.117	A. Hazan, U. Gerson, and A.S. Tahori, Life History and Life Tables of the Carmine Spider Mite, <i>Acarologia</i> , vol. 15 no.3, (1973), 414-440. [4] [at 24 degrees celsius, 80% RH]
δ	0.708	[4] [at 19 degrees celsius, 80% RH]
β	0.064	[4] [at 19 degrees celsius, 38% RH]
c	0.183*	A. Ashouri, Predation by <i>Allothribium Pulvinum</i> on the Spider Mites <i>Tetranychus Urticae</i> and <i>Amphitetranychus Viennensis</i> : Predation Rate, Prey Preference and Functional Response, <i>Experimental and Applied Acarology</i> vol. 37, (2005), 173-181. [1]
k	0.01	Invented
d	0.0905	Invented

Table 2

Parameter	Value (per bug per day)	Source
r	.07	Invented to cause persistence
μ	0.079	[4] [at 24 degrees celsius, 38% RH]
δ	0.770	[4] [at 19 degrees celsius, 38%RH]
β	0.048	[4] [at 19 degrees celsius, 80% RH]
c	0.183	[1]
k	0.01	Invented
d	0.0905	Invented

The initial conditions for the extinction cases were meant to approximate the conditions used in the paper [1]. To see the persistence phenomenon, we chose initial conditions near the positive equilibrium.

Results - Extinction Case

We take parameters in table 1 for model 1 and model 2. The parameters satisfy the relation $r\delta < \beta(\mu + \delta)$. By Theorems 1.1 and 2.1, there is no positive equilibria for either model and the zero solution is globally asymptotically stable. Thus, both populations die out for both models.

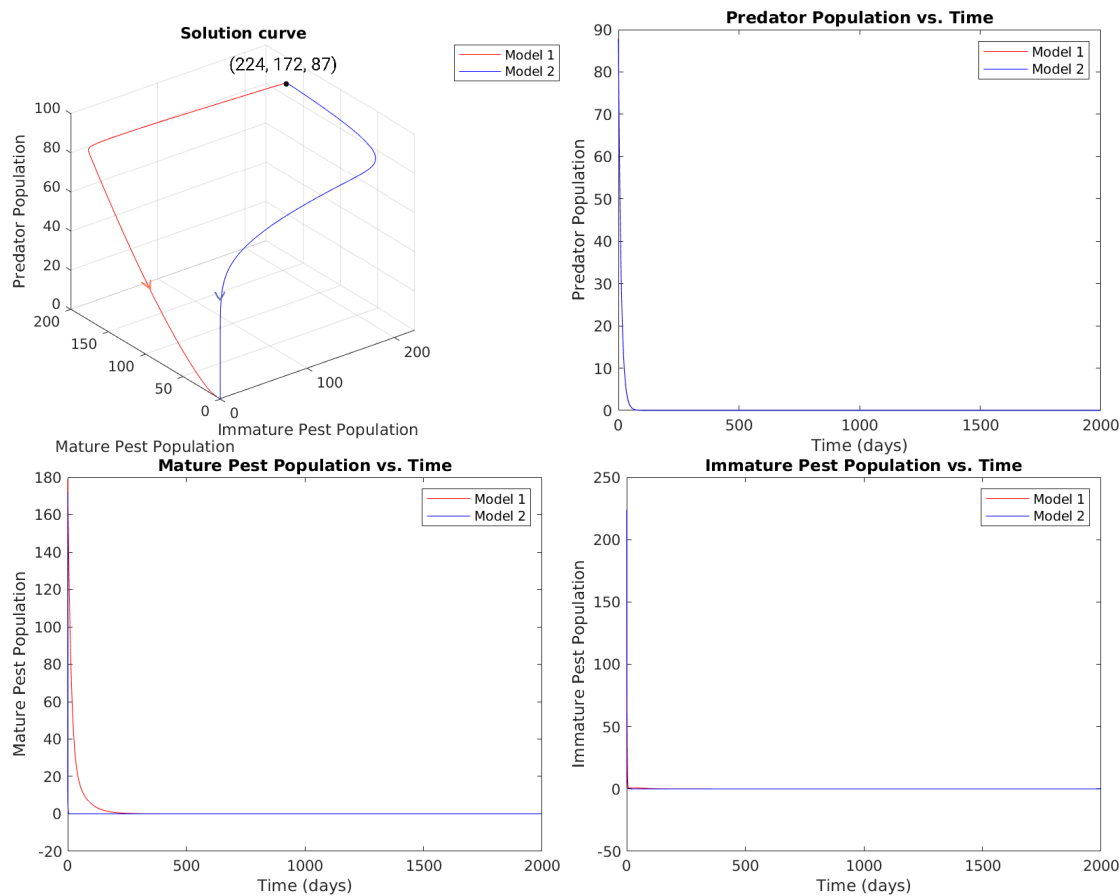


Figure 1: The solutions of model 1 and model 2 with initial conditions: $(x_1, x_2, y) = (224, 172, 87)$, Equilibria: $E_{10} = E_{20} = (0, 0, 0)$, Run Time: 2,000 days. Parameters given in Table 1.

The differences in population change are difficult to see on the scale of 2,000 days for the immature and predator populations, so I re-scaled the graphs to show the difference between models one and two. In particular, I show the predator population between 40 and 100 days rather than the full length of simulated time, and I show the immature pest population for the first 500 days rather than the full simulated time (2,000 days).

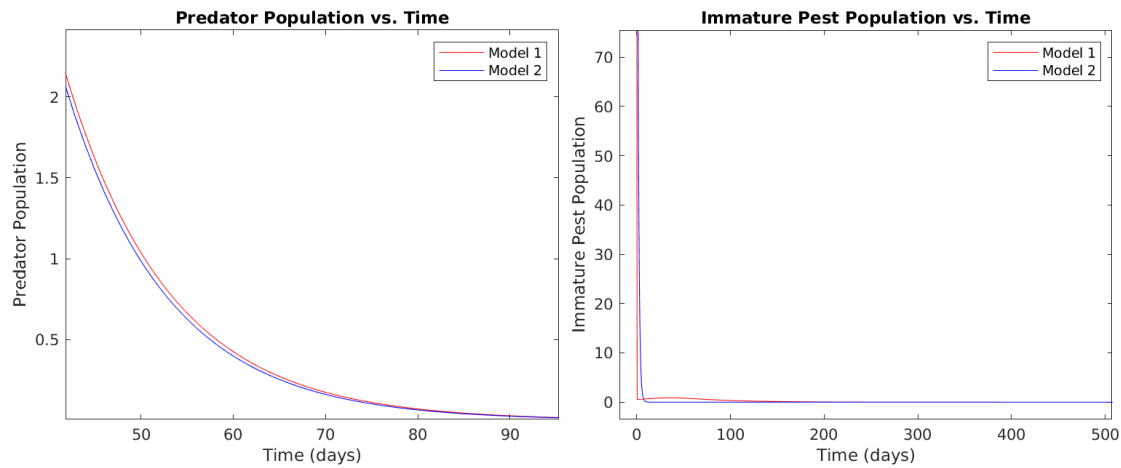


Figure 2: Predator and Immature Pest Populations on the periods 40 to 100 days and 0 to 500 days, respectively.

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The models are asymptotically approaching the equilibrium at the origin. It appears that model 2 is the more efficient method. Although the immature population in model 1 appears to reach extinction before model 2, it plateaus a bit before reaching zero, and by the time model 1 rests at zero, model 2 has already reached zero.

Results - Persistence Case

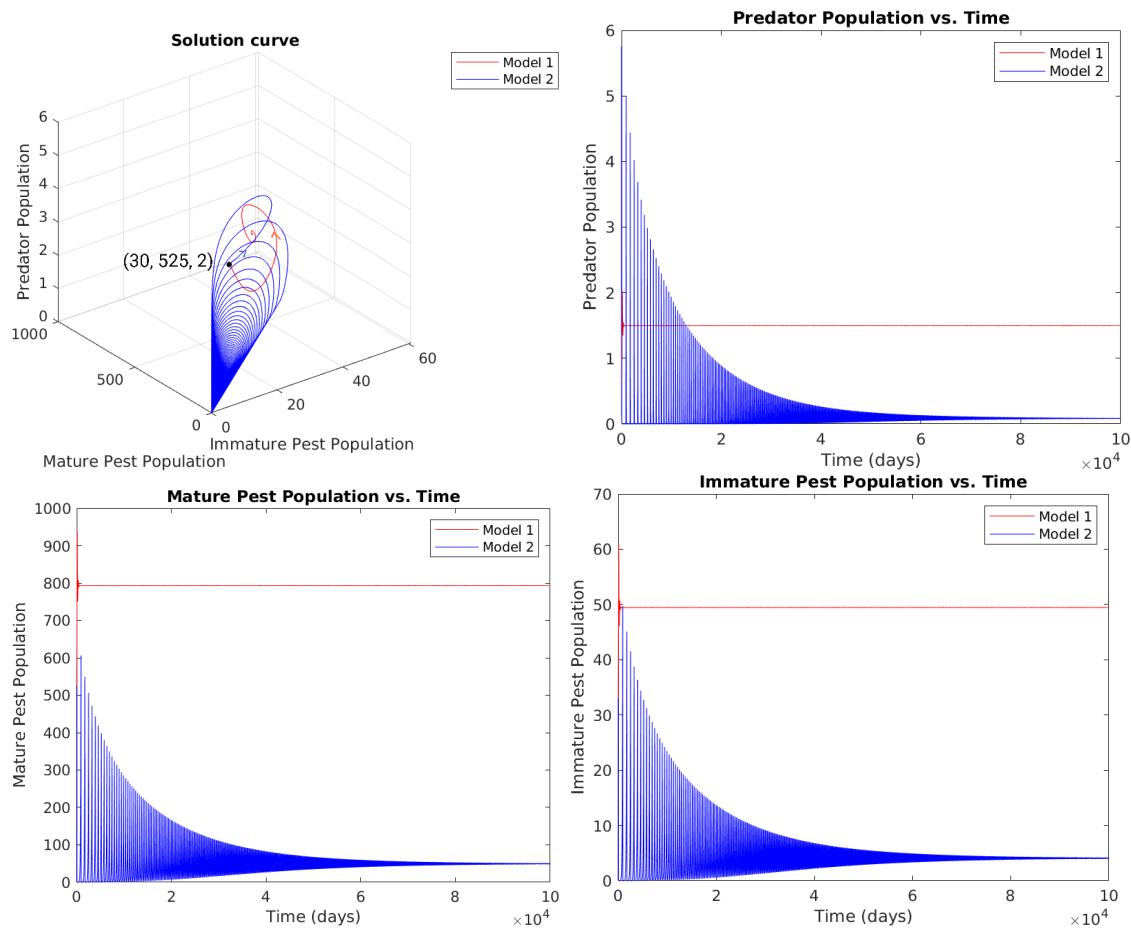


Figure 3: The solutions of model 1 and model 2 with initial conditions: $(x_1, x_2, y) = (30, 525, 2)$, Equilibria: $E_{11} = (49.453, 793, 317, 1.4968)$, $E_{21} = (4.077, 49.453, 0.0846)$, Run time: 10,000 days. Parameters given in Table 2.

We see that the solution of model 1 reaches the equilibrium point much faster than the solution of model 2, which oscillates as it approaches equilibrium. Both models asymptotically approach their positive equilibria, as predicted. However, the densities of the matured and immature pest populations in the equilibrium of model 1 is much larger than in model 2. Thus, biocontrol on the adults (model 2) lowers the total pest population density more significantly than biocontrol on juveniles (model 1).

3 Two-Patch Model

3.1 Models

In this section we assume that the predator and the prey can disperse between two patches and consider two-patch models. We first introduce the two-patch model where in each patch the predator only eats the juvenile prey.

$$\begin{aligned}
 \frac{dx_1}{dt} &= r_1x_2 - \mu_1x_1 - \delta_1x_1 - c_1x_1y - a_1x_1 + b_1X_1, \\
 \frac{dx_2}{dt} &= \delta_1x_1 - \beta_1x_2 - a_2x_2 + b_2X_2, \\
 \frac{dy}{dt} &= k_1c_1x_1y - d_1y - a_3y + b_3Y, \\
 \frac{dX_1}{dt} &= r_2X_2 - \mu_2X_1 - \delta_2X_1 - c_2X_1Y + a_1x_1 - b_1X_1, \\
 \frac{dX_2}{dt} &= \delta_2X_1 - \beta_2X_2 + a_2x_2 - b_2X_2, \\
 \frac{dY}{dt} &= k_2c_2X_1Y - d_2Y + a_3y - b_3Y.
 \end{aligned} \tag{7}$$

In this model, the variables mean the same things as they did in the single patch models, with subscripts 1 and 2 indicating which patch they describe. The parameters a_1, a_2, a_3 are the dispersal rates of the immature pest, mature pest, and predator populations, respectively, in patch 1, while b_1, b_2, b_3 are the dispersal rates of the immature pest, mature pest, and predator populations, respectively, in patch 2. We introduce new variables in this model, X_1, X_2 , and Y , which indicate the immature pest, mature pest, and predator populations in the second patch.

In the following, we intend to find the equilibria of this model and the local and global stability conditions for those equilibria, using computer programming as an aid. In the meantime, we used Matlab to simulate the long-term behavior of this model.

We assume that in one patch, all populations will die out, i.e., the zero solution is globally asymptotically stable, while in the other patch, all populations will co-exist, i.e., the positive equilibria is globally asymptotically stable. Thus, one patch was assigned the parameters that lead to extinction from Table 1, while the other was assigned the parameters that lead to persistence from Table 2. The initial conditions for each test were $(x_1, x_2, y, X_1, X_2, Y) = (4, 49, 1, 4, 49, 1)$ to show long-term behavior.

In order to investigate how dispersal rates affect population dynamics in the two-patch model, the dispersion parameters were changed one at a time, with the rest being kept as constants. We present the results of this investigation for each dispersal rate in the next section.

3.2 Case Study

Effect of Dispersal Rate a_1

We first consider the effects of the dispersal of juveniles from patch 1 to patch 2, i.e., a_1 . Figures 4-6 were obtained by setting all the dispersal rates to 0.1 with the exception of a_1 . The value of a_1 is chosen as 0.6, 0.9.

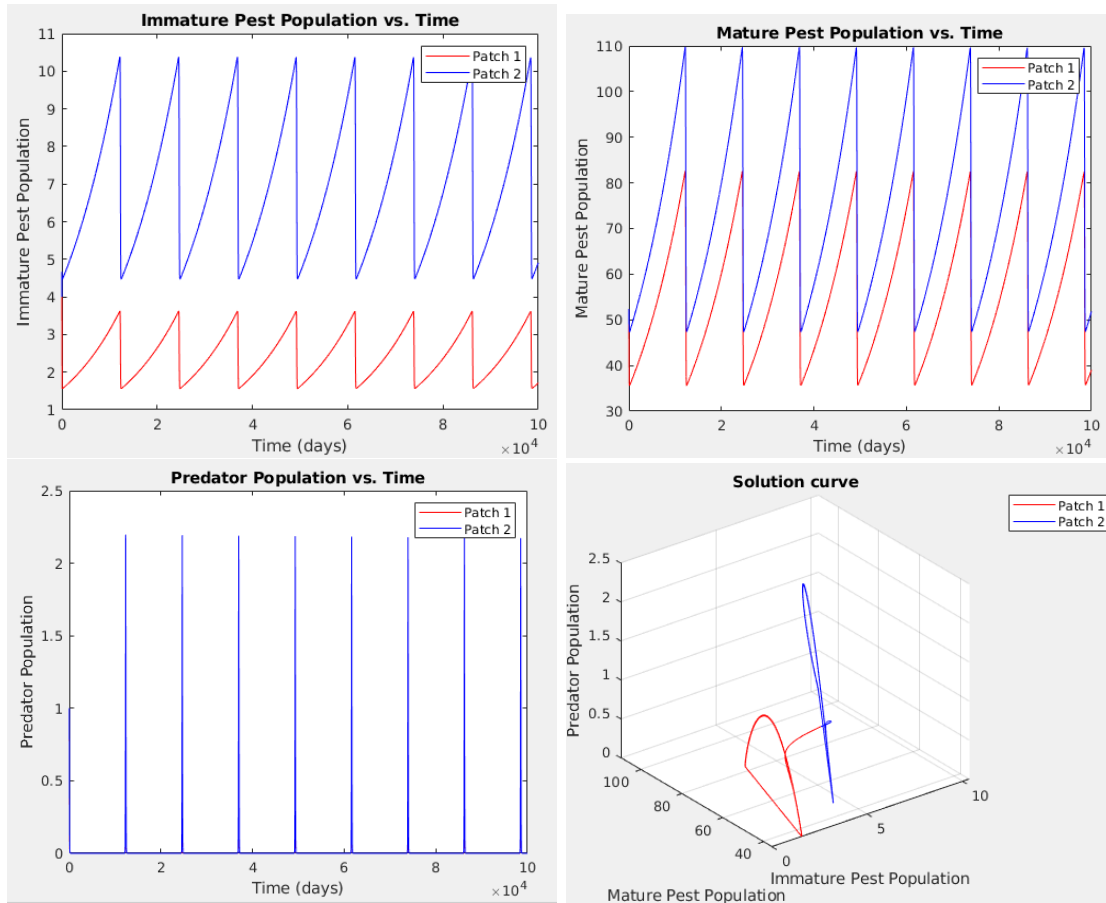


Figure 4: The solution of model 7. Parameters: $a_1 = 0.6$, $a_2 = a_3 = b_1 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 1,000 days

We see what appears to be a cyclical solution, where both stages of pest and predator repeatedly arrive at the same populations. We increase the run time to 1,000,000 to check that this is the case.

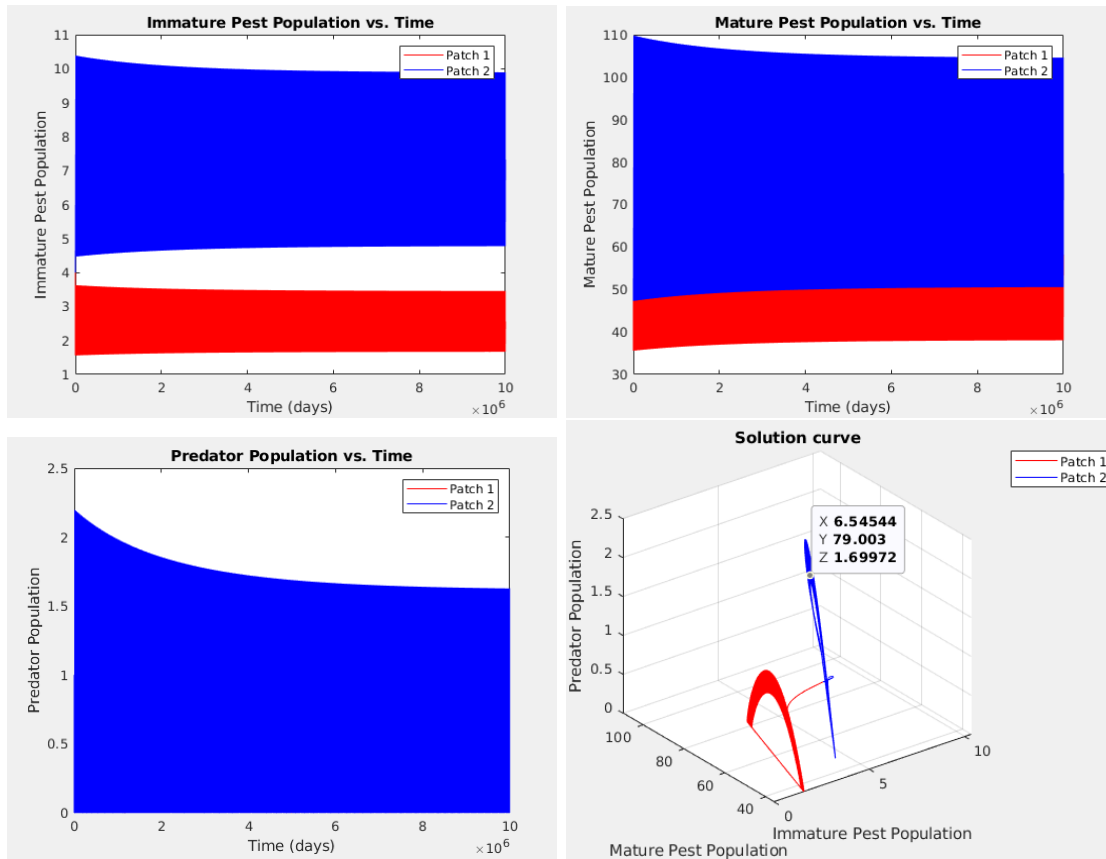


Figure 5: The solution of model 7. Parameters: $a_1 = 0.6$, $a_2 = a_3 = b_1 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 1,000,000 days

While it may be that this is approaching an equilibrium by slightly damped oscillations, it seems to be displaying a periodic solution.

In the next set of figures, we see the result of setting a_1 equal to 0.90.

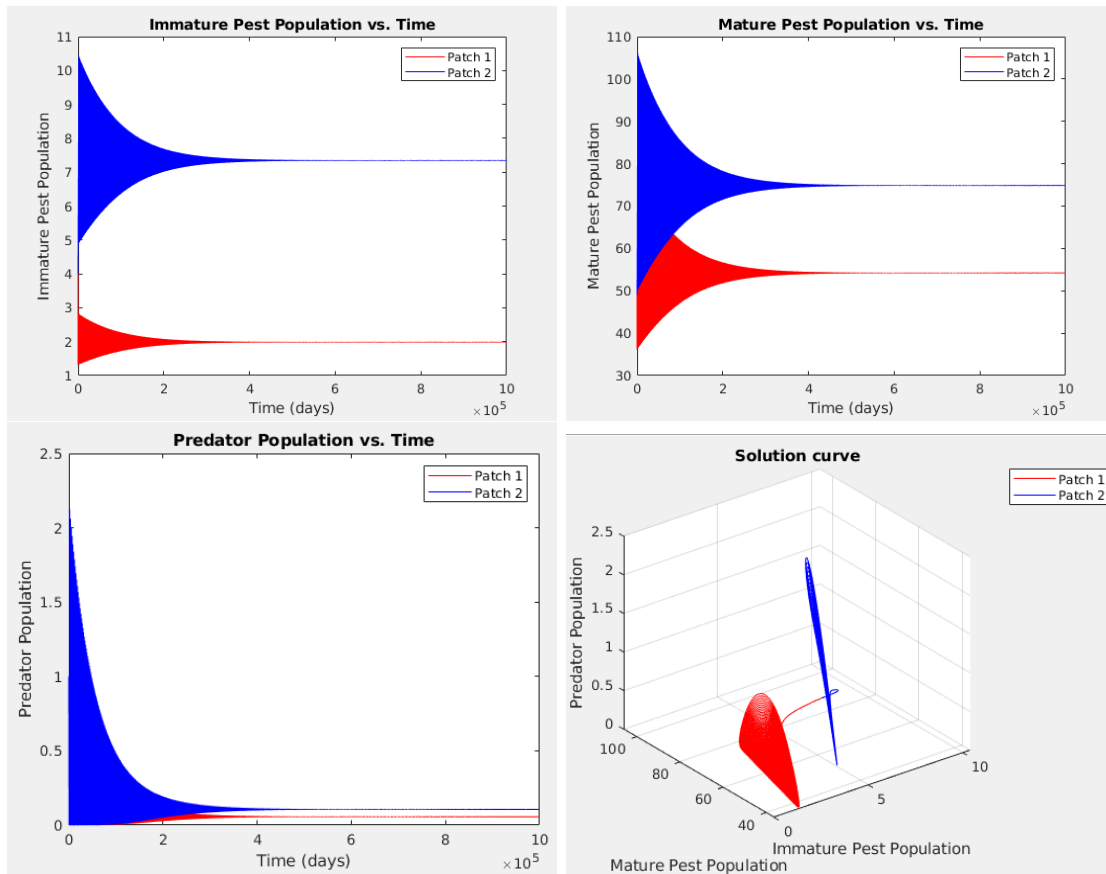


Figure 6: The solution of model 7. Parameters: $a_1 = 0.9$, $a_2 = a_3 = b_1 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 1,000,000

Thus, changing the value of a_1 may decide whether the solution asymptotically reaches some equilibrium or a periodic solution.

Effect of Dispersal Rate a_2

Now we consider the effects of the dispersal of the adult population from patch 1 to patch 2, i.e., a_2 . Set a_2 to 0.12. The solutions of model 7 are shown in Figures 7 and 8.

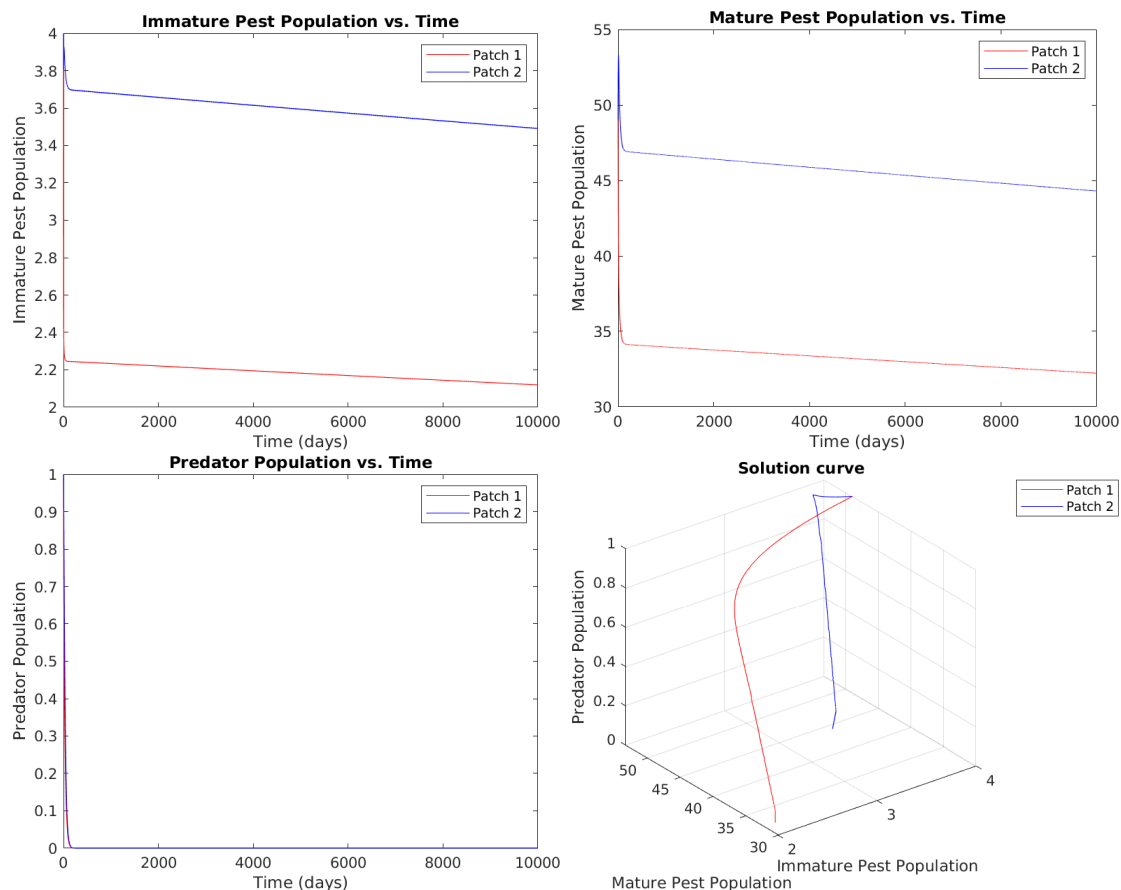


Figure 7: The solution of model 7. Parameters: $a_2 = 0.12$, $a_1 = a_3 = b_1 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

The predator population drops to zero fairly quickly. It is difficult to see over this shorter period how the pest populations behave, so we include simulations over a longer run time of 500,000 days to show that they slowly approach some equilibrium point; see Figure 8.

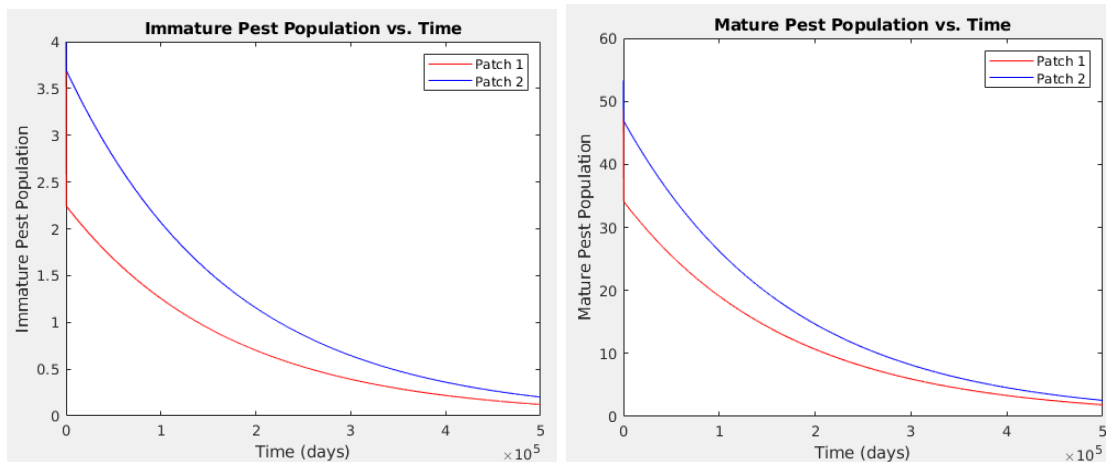


Figure 8: Immature and Mature Pest Populations over 500,000 day period, $a_2 = 0.12$

However, if we set a_2 to be a very large value, like 0.99, we get clearly oscillatory behavior over the shorter period of 10,000 days. See Figure 9. We wanted to see if the oscillatory behavior changed over the long term, but Matlab would not run the program for longer the specified length 50,000 days, killing Matlab instead. The behavior remained the same for a simulated run time of 40,000 days, though, with oscillating behavior diverging over time.

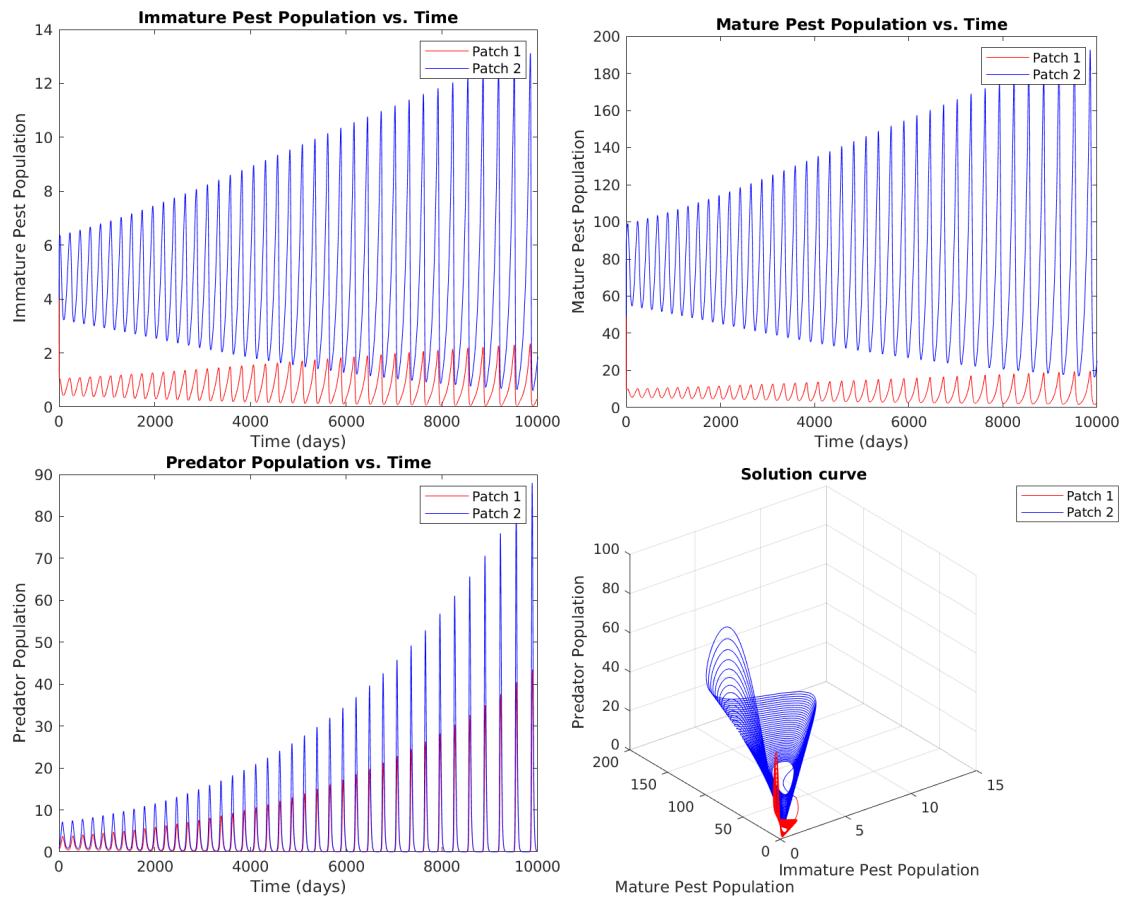


Figure 9: The solution of model 7. Parameters: $a_2 = 0.99$, $a_1 = a_3 = b_1 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

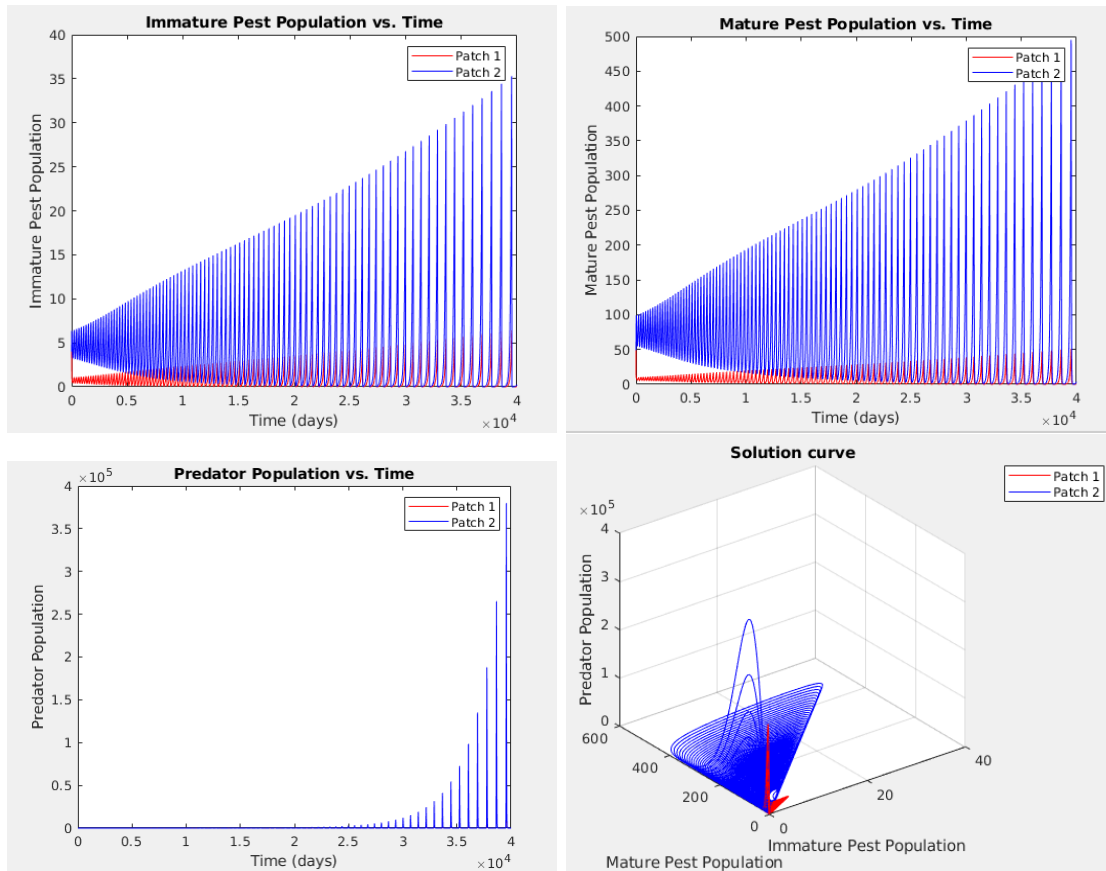


Figure 10: The solution of model 7. Parameters: $a_2 = 0.99$, $a_1 = a_3 = b_1 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 40,000 days

Effect of Dispersal Rate a_3

Then we vary the dispersal rate of the predator from patch 1 to patch 2, but observe that changing a_3 had no obvious effect on the behavior of our model for certain values of a_3 . To illustrate this, we show the behavior of our model for $a_3 = 0.01$ and $a_3 = 0.99$ in Figures 11 and 12, run for a simulated time of 10,000 days. We see that in both cases the solutions approaches the zero solution as time becomes large.

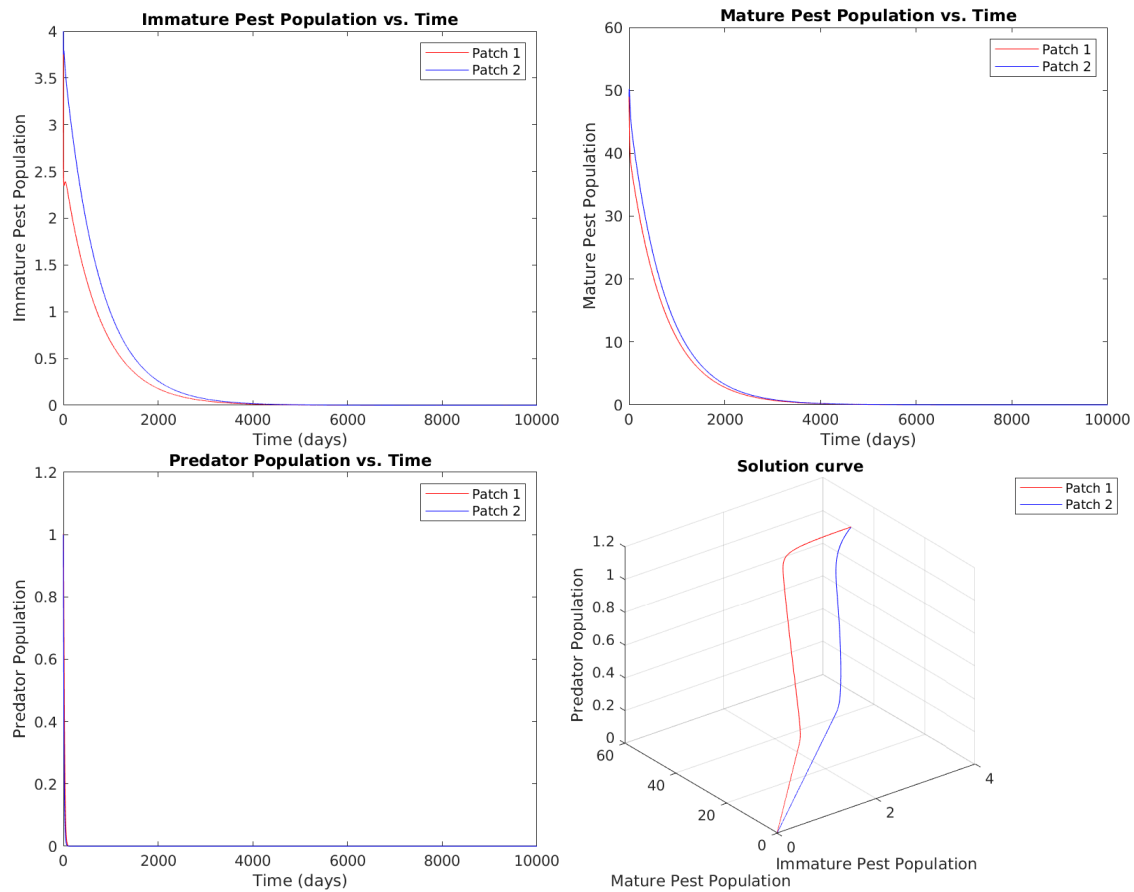


Figure 11: The solution of model 7. Parameters: $a_3 = 0.01$, $a_1 = a_2 = b_1 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

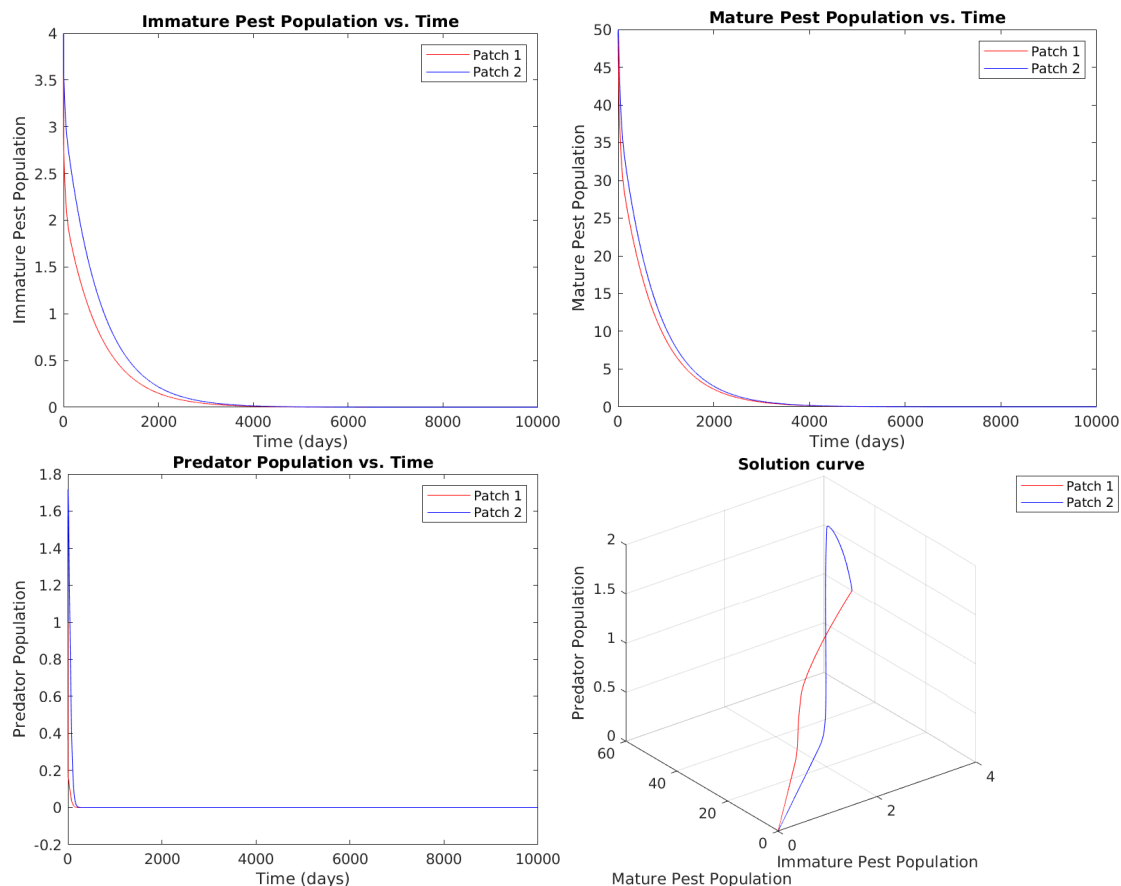


Figure 12: The solution of model 7. Parameters: $a_3 = 0.99$, $a_1 = a_2 = b_1 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

Effect of Dispersal Rate b_1

When we vary the dispersal rate b_1 , we see that the model approaches extinction both when b_1 is small and when it is large. The values chosen are again $b_1 = 0.01$, $b_1 = 0.99$, run for a simulated time of 10,000 days. See Figures 13-14.

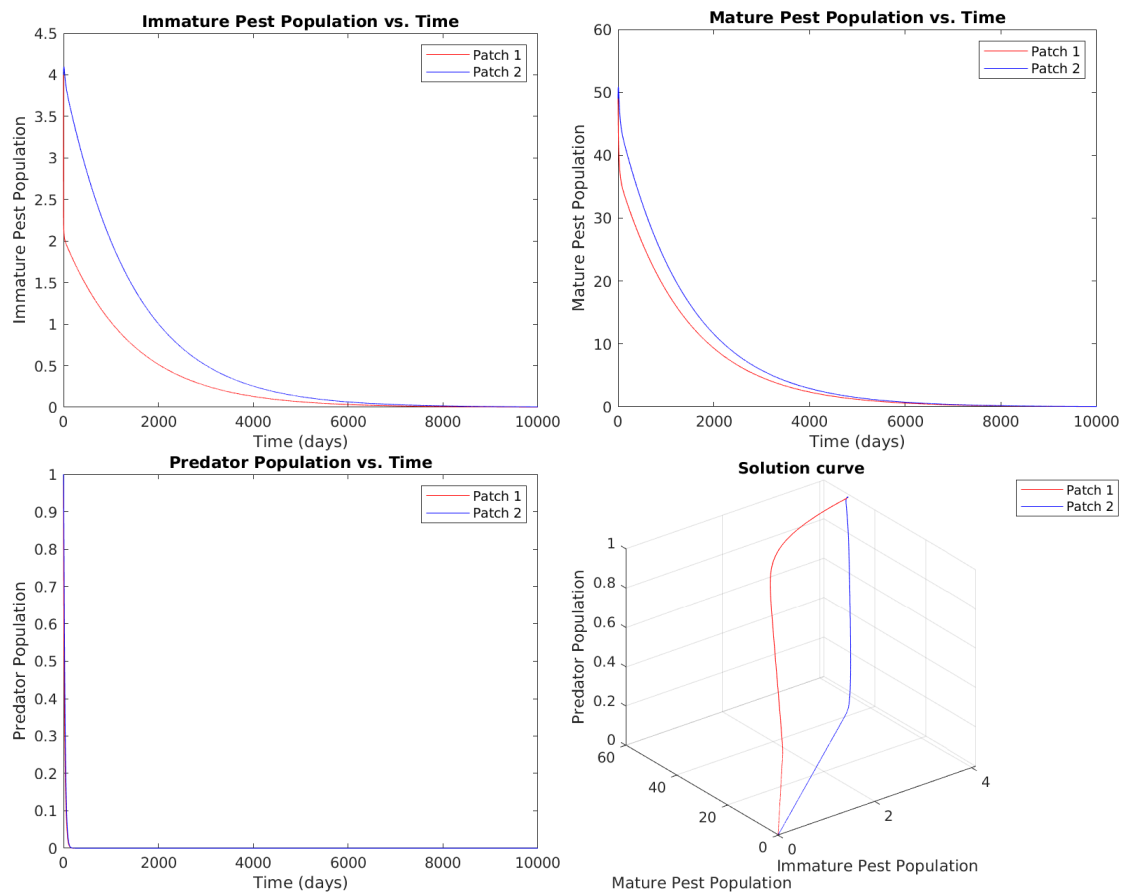


Figure 13: The solution of model 7. Parameters: $b_1 = 0.01$, $a_1 = a_2 = a_3 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

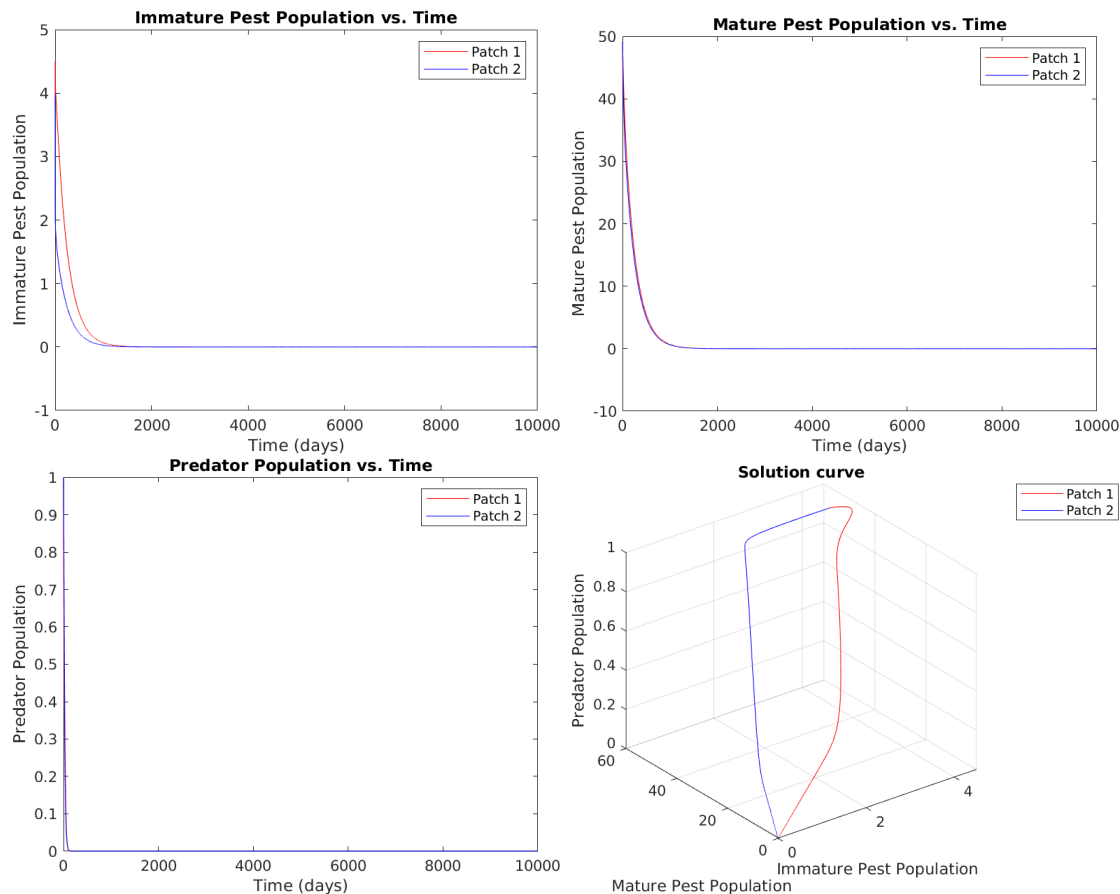


Figure 14: The solution of model 7. Parameters: $b_1 = 0.99$, $a_1 = a_2 = a_3 = b_2 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

Effect of Dispersal Rate b_2

Changing the dispersal rate b_2 has a similar effect to changing the dispersal rate a_2 , except that the divergent oscillatory behavior is exhibited when b_2 is very small rather than very large. In Figure 15, b_2 has been set to 0.01 and the simulation was allowed to run for a period of 10,000 days. We attempted to carry the simulation on farther, to make sure that the behavior didn't change, but Matlab was killed automatically after trying to run the time period 40,000 days. However, the behavior did not change for a simulated run time of 30,000 days, still showing the populations diverging. See Figure 16.

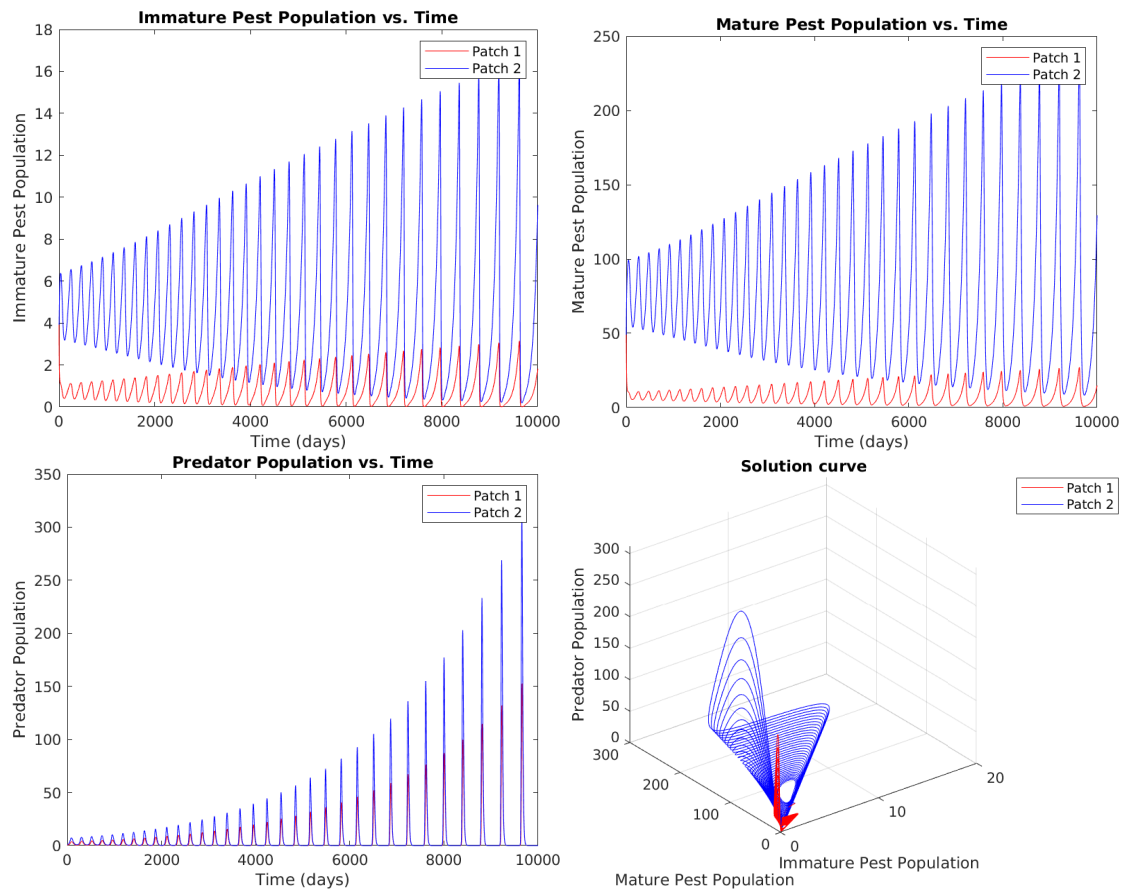


Figure 15: The solution of model 7. Parameters: $b_2 = 0.01$, $a_1 = a_2 = a_3 = b_1 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

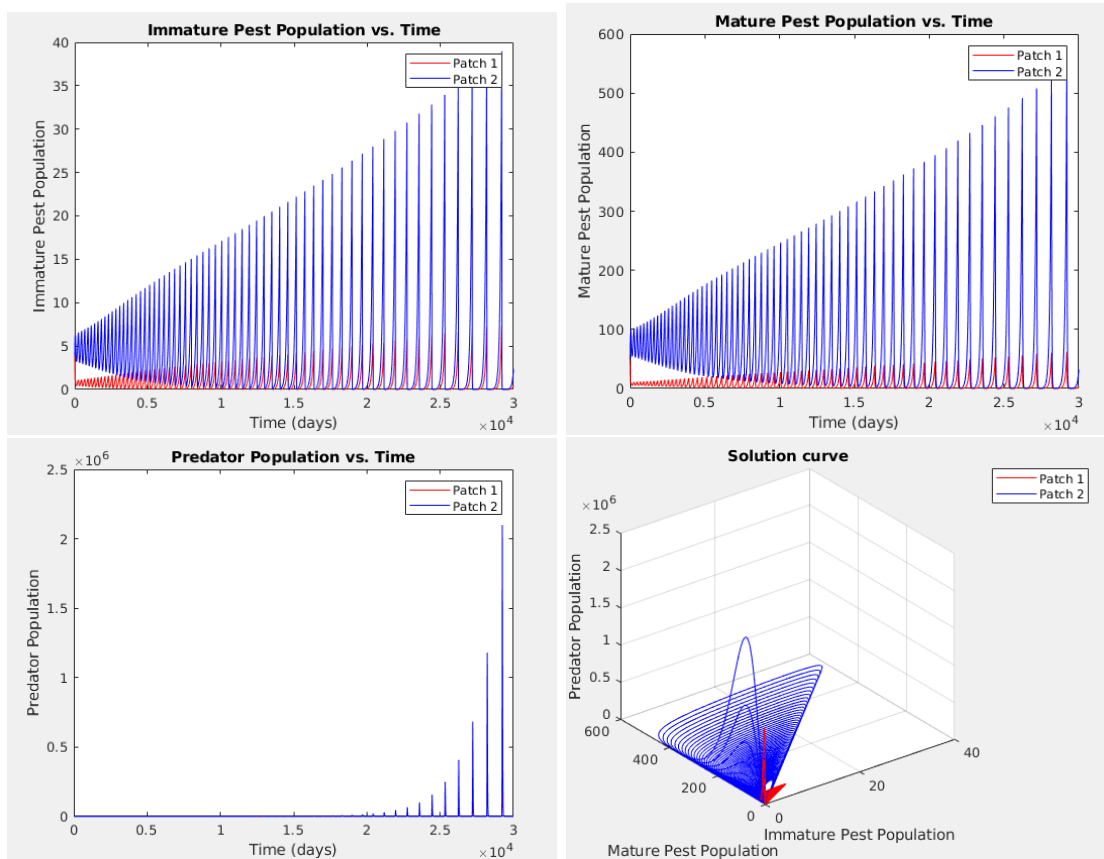


Figure 16: The solution of model 7. Parameters: $b_2 = 0.01$, $a_1 = a_2 = a_3 = b_1 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 30,000 days

In contrast, when b_2 is set to a larger value, like 0.5, all populations drop off to extinction quickly. See Figure 17.

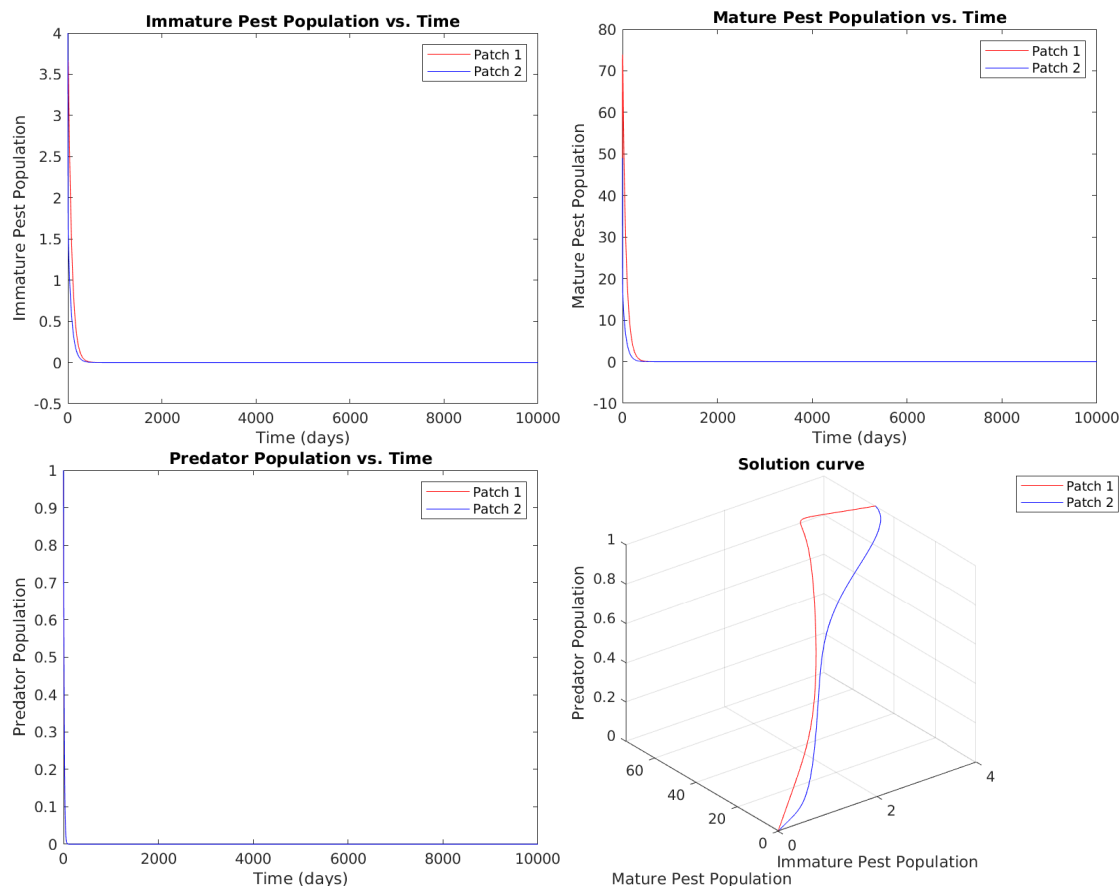


Figure 17: The solution of model 7. Parameters: $b_2 = 0.5$, $a_1 = a_2 = a_3 = b_1 = b_3 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

Effect of Dispersal Rate b_3

Last, we vary the dispersal rate b_3 and find that changing the dispersal rate b_3 does not appear to alter the behavior of the model and results in the extinction of all populations. We again display $b_3 = 0.01$ and $b_3 = 0.99$ as evidence, with a simulated run time of 10,000 days. See Figures 18 and 19.

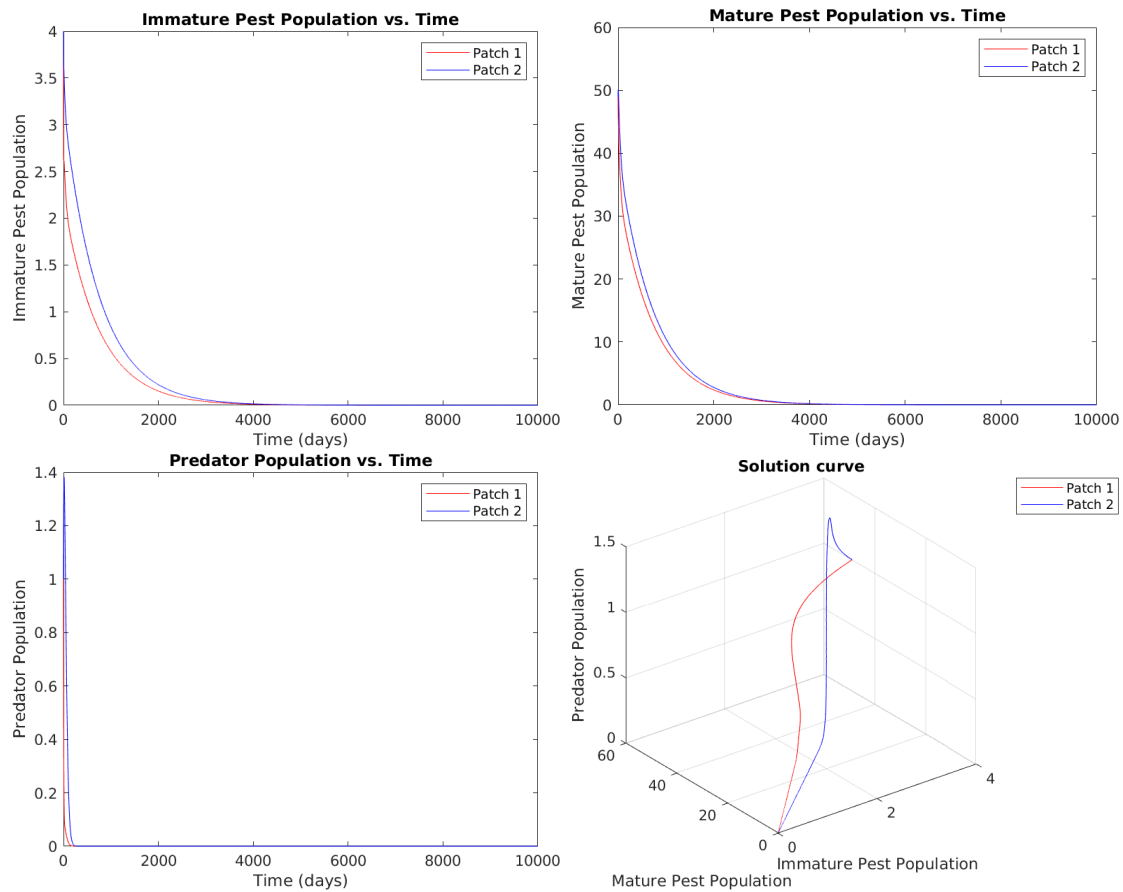


Figure 18: The solution of model 7. Parameters: $b_3 = 0.01$, $a_1 = a_2 = a_3 = b_1 = b_2 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

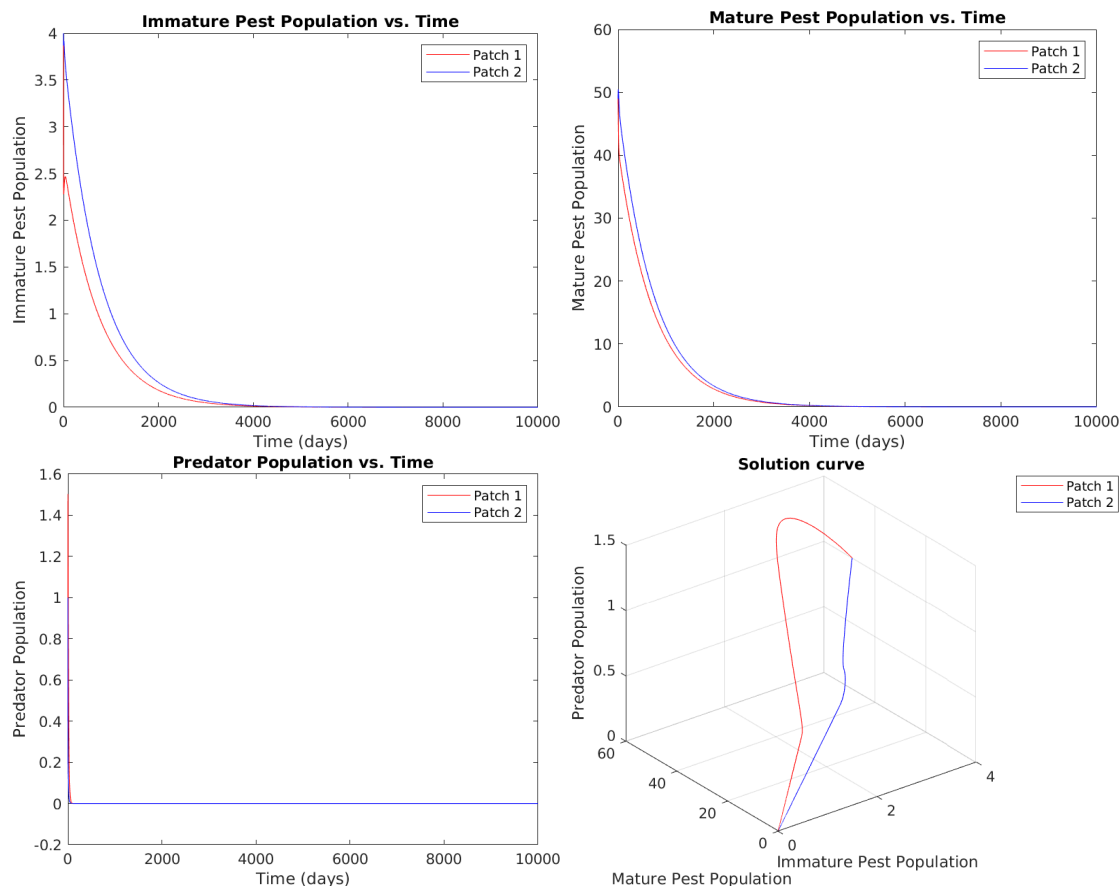


Figure 19: The solution of model 7. Parameters: $b_3 = 0.99$, $a_1 = a_2 = a_3 = b_1 = b_2 = 0.1$. Other parameters in patch 1 are from Table 1 and in patch 2 are from Table 2. Run Time: 10,000 days

4 Discussion

In this work, we considered some models for a two-stage pest and its biocontroller, both in a single patch and in two patches. We considered that the biocontroller can be applied on the immature pests or on the mature pests.

In the single patch models, we find that the trivial or positive equilibrium is always globally asymptotically stable. However, we found that applying the biocontrol meant extinction was achieved much faster than model 1 when extinction was globally asymptotically stable and achieved a lower coexistence equilibrium

than model 1 when coexistence was globally asymptotically stable. Then, for a two-stage pest in a single patch, applying biocontrol to the mature stage is more effective.

When both the pest and its biocontroller can disperse between two patches, we consider a model where biocontrol is applied to the immature population. This shows populations can oscillate between two patches, which is very different from the behavior of the single patch models.

We apply our model to the species *Allothrombium pulvinum* and *Tetranychus cinnabarinis* as a biocontroller and a pest, respectively. Our results show that applying the biocontroller to the mature stage is a more effective form of biocontrol than applying the biocontroller to the immature stage.

We hope to provide a better analysis of the behavior of the solution of our two-patch model in future research, including an expression for the equilibria of the model and their stability. Perhaps we may analyze another two-patch model in which the biocontrol is applied to the mature stage and analyze whether this proves more effective, as it did in the single patch case.

Pest control is an interesting field of study in ecology and agriculture. Our work provides a specific point of view and set of analyses that can be expanded or altered depending on the unique needs of other researchers. This could include the analysis of a pest with more than two stages, accounting more closely for the example of the spider mite.

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