A BIFURCATION PROBLEM IN TWO POND AMPHIBIAN POPULATION MODELING

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ABSTRACT. We present a discrete time, two pond, SI amphibian model. Partial analysis of population dynamics and equilibrium behavior for a special case of a "wild pond adjacent to a managed pond" are explored analytically. The dynamics of the non-trivial populations are explored via simulations using Mathematica.

1. INTRODUCTION

Amphibians are declining throughout the world. Biologists are unsure why, but suspect this decline may be related to climate change, fertilizer runoff, environmental chemicals, introduction of exotic species, habitat destruction, or disease [4, 5, 9]. Amphibians are more sensitive to toxins and diseases in the environment, because their skin absorbs both air and water. Thus, they may be an indicator of the overall health of the environment [9, 16, 2].

Two possible diseases associated with amphibian decline are ranavirus infection and Chytridiomycosis (chytrid fungus) [4, 5, 9, 10, 11]. Chytrid fungus is caused by an infection with *Batrachochytrium dendrobatidis* and has been linked with mass die-offs of amphibians worldwide [9, 10, 6, 2]. It is unclear if the devastating effects of chytrid fungus are due to mutations or introduction into naive hosts [9]. In [13] two hypotheses are examined, one stating that global warming plays an important part in amphibian decline, and another which indicates that the introduction of chytrid fungus is a major cause for amphibian decline.

Chytrid fungus effects amphibians differently. Some species are resistant, such as the American bullfrog, *Rana catesbeiana*; others can recover from the infection, such as tiger salamanders, *Ambystoma tigrinum* [14]; and many species rapidly die with close to 100% mortality rates not uncommon [14]. In all cases, chytrid fungus feeds off

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the keratin in an amphibian's body. Since larvae only have keratin in their mouth-parts and are relatively unaffected by the disease, they may act as reservoir hosts for the infection [5, 11], especially those with long premetamorphic states [12]. Some amphibians, such as *Rana muscosa* appear to be particularly susceptible during meta-morphosis [2, 12], exhibiting near 100% mortality rates.

Due to the importance of amphibians as indicators of environmental health, many people have modeled chytrid fungus in amphibian populations mathematically. Most models have been deterministic difference or differential equations, as in [3, 17, 18, 6, 7, 15], but there has been several published stochastic models [8, 2]. In [11], a system of differential and partial differential equations are considered which allows free-living zoospores to reproduce without an amphibian host.

2. MODEL DESCRIPTION

Our models involve amphibians that can move between two ponds, and at any given time $t = 0, 1, \ldots$, an amphibian has two possible disease states, I or S. An amphibian in disease state I is infected with chytrid fungus, while an amphibian in disease state S is susceptible to infection. For $D \in \{S, I\}$ and $K \in \{1, 2\}$, let $D_K(t)$ be the number of amphibians in pond K with disease status D at time t. For example, $S_1(t)$ is the number of susceptible amphibians in pond 1 at time t.

Rates of survival, movement among ponds, and recruitment may be affected by dis-ease status. These factors, and the rate of recovery from the disease, may also be affected by environmental differences between the ponds. With this in mind, define the following quantities:

- p_K^D is the proportion of organisms in pond K with disease status D that survive and remain in pond K as either susceptible or infected organisms.
- m_{ij}^D is the proportion of animals in pond i with disease status D that survive and move to pond j, for $i, j \in \{1, 2\}$, $i \neq j$. A disease status change is possible.
- r_K is the proportion of infected organisms in pond K that recover.

We will assume that recruitment rates are density dependent and may be affected by disease status or environmental differences between the ponds. Therefore, let B_K^D be a recruitment function with continuous first order partial derivatives satisfying the following conditions:

(1) $B_K^D(S_K, I_K) \geq 0$,
(2) $B_K^D(0, 0) = b_K^D > 0$,
(3) $\frac{\partial}{\partial S_K} B_K^D(S_K, I_K) < 0$, and
(4) $\frac{\partial}{\partial I_K} B_K^D(S_K, I_K) < 0$.

Note that b_K^D is the recruitment rate if there is no density dependence. Finally, assume that susceptible organisms in pond K contract the disease at a rate equal to $1 - e^{-w_K I_K}$, where $w_K > 0$.
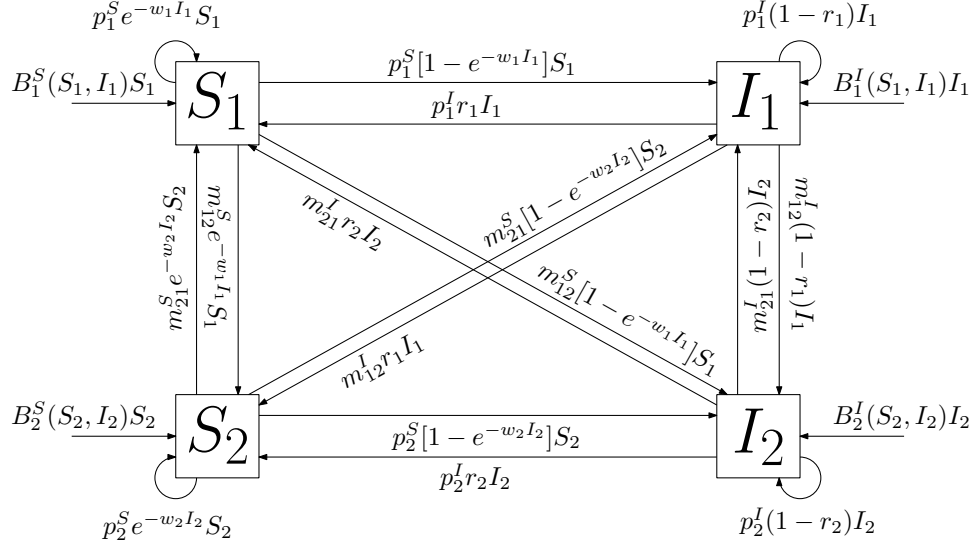

FIGURE 1. Compartmental Diagram for Model 1

Consider the compartmental diagram in Figure 1, which provides a visual representation for the transitions among the four states determined by $D \in \{S, I\}$ and $K \in \{1, 2\}$.

This leads us to the four deterministic equations that constitute our Susceptible-Infected (SI) two pond model 1.

$$
\begin{aligned}
S_1(t+1) &= B_1^S(S_1(t), I_1(t))S_1(t) + p_1^S e^{-w_1 I_1(t)} S_1(t) + p_1^I r_1 I_1(t) \\
&\quad + m_{21}^S e^{-w_2 I_2(t)} S_2(t) + m_{21}^I r_2 I_2(t) \\
I_1(t+1) &= B_1^I(S_1(t), I_1(t))I_1(t) + p_1^S(1 - e^{-w_1 I_1(t)})S_1(t) \\
&\quad + p_1^I(1 - r_1)I_1(t) + m_{21}^S(1 - e^{-w_2 I_2(t)})S_2(t) \\
&\quad + m_{21}^I(1 - r_2)I_2(t) \\
S_2(t+1) &= B_2^S(S_2(t), I_2(t))S_2(t) + p_2^S e^{-w_2 I_2(t)} S_2(t) + p_2^I r_2 I_2(t) \\
&\quad + m_{12}^S e^{-w_1 I_1(t)} S_1(t) + m_{12}^I r_1 I_1(t) \\
I_2(t+1) &= B_2^I(S_2(t), I_2(t))I_2(t) + p_2^S(1 - e^{-w_2 I_2(t)})S_2(t) \\
&\quad + p_2^I(1 - r_2)I_2(t) + m_{12}^S(1 - e^{-w_1 I_1(t)})S_1(t) \\
&\quad + m_{12}^I(1 - r_1)I_1(t)
\end{aligned}
\tag{1}
$$

Aside from w_K and b_K^D, which are arbitrary positive numbers, all other model parameters are elements of $(0, 1)$, unless otherwise specified. Because $p_1^D + m_{12}^D$ is the proportion of organisms in pond 1 with disease status D that survive one time step,

$$p_1^D + m_{12}^D < 1, \tag{2}$$

and similarly,

$$p_2^D + m_{21}^D < 1, \tag{3}$$

where $D = S, I$. The death rate of susceptible animals in pond one is $1 - p_1^S - m_{12}^S$, while the removal rate due to death or movement is $1 - p_1^S$. We are assuming that time steps are small enough that an amphibian cannot contract the infection and then recover in the same time step.

3. Model Analysis

Analysis for the extinction Equilibrium will be considered. The Jacobian matrix of the four equations is particularly important, because it helps us to study the stability of the model. Let J denote the Jacobian matrix of all the first order partial derivatives of the the four equations, where the order of the variables is S_1, S_2, I_1, I_2. Evaluating the Jacobian at the extinction equilibrium, $S_1 = S_2 = I_1 = I_2 = 0$, yields

$$J_{(0,0,0,0)} = \begin{pmatrix} b_1^S + p_1^S & m_{21}^S & p_1^I r_1 & m_{21}^I r_2 \\ m_{12}^S & b_2^S + p_2^S & m_{12}^I r_1 & p_2^I r_2 \\ 0 & 0 & b_1^I + p_1^I(1 - r_1) & m_{21}^I(1 - r_2) \\ 0 & 0 & m_{12}^I(1 - r_1) & b_2^I + p_2^I(1 - r_2) \end{pmatrix}.$$

This is a block triangular matrix, which can be written as

$$J = \begin{pmatrix} B_1 & * \\ \mathcal{O}_{2x2} & B_2 \end{pmatrix},$$

where

$$B_1 = \begin{pmatrix} b_1^S + p_1^S & m_{21}^S \\ m_{12}^S & b_2^S + p_2^S \end{pmatrix}, \tag{4}$$

$$B_2 = \begin{pmatrix} b_1^I + p_1^I(1 - r_1) & m_{21}^I(1 - r_2) \\ m_{12}^I(1 - r_1) & b_2^I + p_2^I(1 - r_2) \end{pmatrix}, \tag{5}$$

and $\mathcal{O}_{2x2}$ is the two by two zero matrix.

According to [1], the extinction equilibrium is locally asymptotically stable if the eigenvalues of the Jacobian matrix $J_{(0,0,0,0)}$ satisfy $|\lambda| < 1$, which occurs if and only if

(6) $$|\text{Tr}(B_i)| < 1 + \det(B_i) < 2, \text{ for } i = 1, 2.$$

The extinction equilibrium is unstable if any of the eigenvalues satisfy $|\lambda| > 1$, which occurs if and only if

(7) $$|\text{Tr}(B_i)| > 1 + \det(B_i), \text{ or } \det(B_i) > 1, \text{ for some } i = 1, 2.$$

For B_1, we have $|\text{Tr}(B_1)| = (b_1^S + p_1^S) + (b_2^S + p_2^S)$, since these model parameters are positive, and $\text{Det}(B_1) = (b_1^S + p_1^S)(b_2^S + p_2^S) - m_{12}^S m_{21}^S$. Substituting into (6) and rearranging some terms yields

$$b_1^S + p_1^S + b_2^S + p_2^S - 1 + m_{12}^S m_{21}^S < (b_1^S + p_1^S)(b_2^S + p_2^S) < 1 + m_{12}^S m_{21}^S,$$

so the eigenvalues of B_1 are less than 1 in magnitude provided

(8) $$\triangle_1^S < (b_1^S + p_1^S)(b_2^S + p_2^S) < \triangle_2^S,$$

where

$$\triangle_1^S = b_1^S + p_1^S + b_2^S + p_2^S - 1 + m_{12}^S m_{21}^S$$
(9) $$\triangle_2^S = 1 + m_{12}^S m_{21}^S.$$

Similarly, the eigenvalues of B_2 are less than 1 in magnitude provided

(10) $$\triangle_1^I < (b_1^I + p_1^I(1 - r_1))(b_2^I + p_2^I(1 - r_2)) < \triangle_2^I,$$

where

$$\triangle_1^I = b_1^I + p_1^I(1 - r_1) + b_2^I + p_2^I(1 - r_2) - 1 + m_{12}^I(1 - r_1)m_{21}^I(1 - r_2),$$
(11) $$\triangle_2^I = 1 + m_{12}^I(1 - r_1)m_{21}^I(1 - r_2).$$

These observations lead to the following theorem.

Theorem 3.1. *The extinction equilibrium is locally asymptotically stable provided*
$$\triangle_1^S < (b_1^S + p_1^S)(b_2^S + p_2^S) < \triangle_2^S$$

and
$$\triangle_1^I < (b_1^I + p_1^I(1 - r_1))(b_2^I + p_2^I(1 - r_2)) < \triangle_2^I,$$
where $\triangle_1^S$ and $\triangle_2^S$ are defined in (9), and $\triangle_1^I$ and $\triangle_2^I$ are defined in (11).

We will now investigate the case where $b_1^S = b_2^S =: b_S$. Then (8) gives us the following inequality:

$$2b_S + p_1^S + p_2^S - 1 + m_{12}^S m_{21}^S < (b_S + p_1^S)(b_S + p_2^S) < 1 + m_{12}^S m_{21}^S,$$

which is equivalent to

(12) $0 < (b_S)^2 + b_S(p_1^S + p_2^S - 2) + (1 - p_1^S)(1 - p_2^S) - m_{12}^S m_{21}^S < 2 - p_1^S - p_2^S - 2b_S.$

Let

(13) $$h(b_S) = (b_S)^2 + b_S(p_1^S + p_2^S - 2) + (1 - p_1^S)(1 - p_2^S) - m_{12}^S m_{21}^S$$

and

(14) $$k(b_S) = 2 - p_1^S - p_2^S - 2b_S.$$

We shall investigate various conditions for which $0 < h(b_S) < k(b_S)$.

The line $y = k(b_S)$ is decreasing with b_S-intercept $(2 - p_1^S - p_2^S)/2 > 0$ and y-intercept $2 - p_1^S - p_2^S$. Therefore, $k(b_S) > 0$ only when $b_S < (2 - p_1^S - p_2^S)/2$, providing a necessary condition on b_S for local asymptotic stability and an immediate corollary.

Corollary 3.2. *If $b_S = b_1^S = b_2^S$, and $b_S > \dfrac{2 - p_1^S - p_2^S}{2}$, then the extinction equilibrium is not locally asymptotically stable.*

Recall that $1 - p_1^S$ is the removal rate of susceptible animals in pond one due to death or movement to the other pond. This corollary states that extinction is unstable whenever the recruitment rate b_S is larger than the average of the removal rates from ponds one and two due to death or movement to the other pond. In Corollary 3.3, a sharper restriction is given on the recruitment rate b_S, with regards to local asymptotic stability of the extinction equilibrium.

The b_S-coordinate of the vertex of the parabola $y = h(b_S)$ is the same as the b_S-intercept of the line $k(b_S)$, namely $(2 - p_1^S - p_2^S)/2 > 0$. The y-coordinate of the vertex of the parabola is

$$h\left(\frac{2 - p_1^S - p_2^S}{2}\right) = -\frac{(2 - p_1^S - p_2^S)^2}{4} + (1 - p_1^S)(1 - p_2^S) - m_{12}^S m_{21}^S < 0$$

$$\Leftrightarrow (p_1^S - p_2^S)^2 > -4m_{12}^S m_{21}^S.$$

Note that the last inequality is clearly true, so the y-coordinate of the vertex is always negative.

Finally, the y-intercept of the parabola is given by $(1 - p_1^S)(1 - p_2^S) - m_{12}^S m_{21}^S$. By restrictions (2) and (3) $m_{12}^S < 1 - p_1^S$ and $m_{21}^S < 1 - p_2^S$, which implies

$$(1 - p_1^S)(1 - p_2^S) > m_{12}^S m_{21}^S.$$

Thus, the y-intercept of the parabola is always positive. Now, we compare the y-intercepts of the line and parabola.

$$(2 - p_1^S - p_2^S) - ((1 - p_1^S)(1 - p_2^S) - m_{12}^S m_{21}^S) = 1 - p_1^S p_2^S + m_{12}^S m_{21}^S > 0.$$

Hence, the y-intercept of the line is always greater than the y-intercept of the parabola.

This information about the line $k(b_S)$ and parabola $h(b_S)$ is summarized in Figure 2. A necessary condition for local asymptotic stability of the extinction equilibrium is $0 < h(b_S) < k(b_S)$, which occurs when the recruitment term b_S is less than or equal to
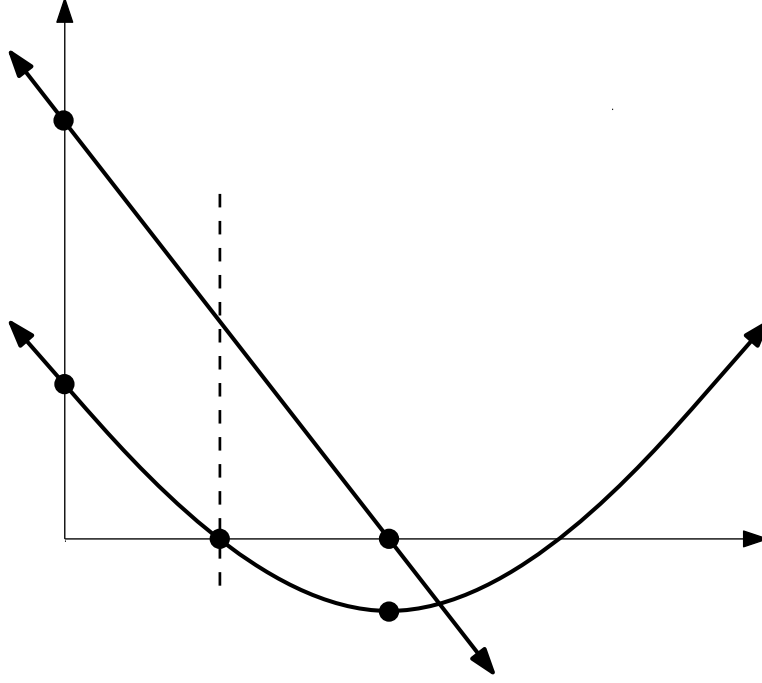
FIGURE 2. Parabola and Line. To the right of the dashed line, the extinction equilibrium is automatically unstable.

the smallest b_S-intercept of the parabola. The smaller b_S-intercept for the parabola $h(b_S)$ is

$$(15) \qquad \frac{(2 - p_1^S - p_2^S) - \sqrt{(2 - p_1^S - p_2^S)^2 - 4\left((1 - p_1^S)(1 - p_2^S) - m_{12}^S m_{21}^S\right)}}{2}.$$

Note that the placement of the vertex, in quadrant four, and the positive y-intercept ensures that both b_S-intercepts are always positive real numbers.

The preceding observations are summarized in the following corollary.

Corollary 3.3. *If $b_S = b_1^S = b_2^S$ and*

$$b_S > \frac{(2 - p_1^S - p_2^S) - \sqrt{(2 - p_1^S - p_2^S)^2 - 4\left((1 - p_1^S)(1 - p_2^S) - m_{12}^S m_{21}^S\right)}}{2},$$

then the extinction equilibrium is not locally asymptotically stable.

Similar analysis on B_2 yields:

Corollary 3.4. *If $b_I = b_1^I = b_2^I$ and*

$$b_I > \frac{2 - p_1^I(1 - r_1) - p_2^I(1 - r_2)}{2},$$

then the extinction equilibrium is not locally asymptotically stable.

Note that $1 - p_1^I(1 - r_1)$ is the removal rate of an infected animal in pond one due to movement or death, but not recovery. Therefore, this corollary states that extinction is not locally asymptotically stable if the infected recruitment rate is greater than the average of the removal rates from ponds one and two due to movement or death, but not recovery.

Next, we consider the parabola, $y = H(b_I)$, noting that the y-intercept is

$$(1 - p_1^I(1 - r_1))(1 - p_2^I(1 - r_2)) - m_{12}^I m_{21}^I(1 - r_1)(1 - r_2).$$

It is not immediately clear if the y-intercept is positive. However, by inequalities (2) and (3), $m_{12}^I < 1 - p_1^I$ and $m_{21}^I < 1 - p_2^I$. Therefore, $m_{12}^I m_{21}^I < (1 - p_1^I)(1 - p_2^I)$, and multiplying by the positive term $(1 - r_1)(1 - r_2)$, we obtain the following inequalities,

$$m_{12}^I m_{21}^I(1 - r_1)(1 - r_2) < (1 - p_1^I)(1 - p_2^I)(1 - r_1)(1 - r_2)$$
$$= \left((1 - r_1) - p_1^I(1 - r_1)\right)\left((1 - r_2) - p_2^I(1 - r_2)\right)$$
$$< \left(1 - p_1^I(1 - r_1)\right)\left(1 - p_2^I(1 - r_2)\right),$$

since $1 - r_1 < 1$ and $1 - r_2 < 1$. Hence, the y-intercept of the parabola is always positive. Subtracting the y-intercept of the parabola from the y-intercept of the line, we obtain

$$1 - p_1^I p_2^I(1 - r_1)(1 - r_2) + m_{12}^I m_{21}^I(1 - r_1)(1 - r_2),$$

which is clearly positive. Thus, the y-intercept of the parabola is always below the y-intercept of the line.

The b_I-coordinate of the vertex of the parabola $y = H(b_I)$ is given by

$$\frac{2 - p_1^I(1 - r_1) - p_2^I(1 - r_2)}{2} > 0,$$

which equals the b_I-intercept of the line $y = K(b_I)$. A simple calculation shows that the y-coordinate of the vertex of the parabola,

$$-\frac{1}{4}(p_1^I(1 - r_1) - p_2^I(1 - r_2))^2 - m_{12}^I m_{21}^I(1 - r_1)(1 - r_2),$$

is always negative. Once again, the parabola has a positive y-intercept and a vertex in the fourth quadrant, and we need only concern ourselves with the smaller of the positive real solutions to the equation $H(b_I) = 0$ when determining equivalent conditions for $0 < H(b_I) < K(b_I)$. See Figure 2 for a graphical interpretation of this situation.

The smaller root of the equation $H(b_I) = 0$ is given by

(16)
$$\frac{\left(2 - p_1^I(1 - r_1) - p_2^I(1 - r_2)\right) - \sqrt{R}}{2},$$

where

$$(17) \qquad R = \left(2 - p_1^I(1 - r_1) - p_2^I(1 - r_2)\right)^2$$
$$- 4\left((1 - p_1^I(1 - r_1))(1 - p_2^I(1 - r_2)) - m_{12}^I m_{21}^I(1 - r_1)(1 - r_2)\right),$$

providing the following corollary.

Corollary 3.5. *If $b_I = b_1^I = b_2^I$ and*

$$b_I > \frac{\left(2 - p_1^I(1 - r_1) - p_2^I(1 - r_2)\right) - \sqrt{R}}{2},$$

where R is given by equation (17), then the extinction equilibrium is not locally asymptotically stable.

Finally, assembling the information for both block matrices B_1 and B_2, we obtain the following sufficient condition for stability of the extinction equilibrium.

Corollary 3.6. *Assume that $b_S = b_1^S = b_2^S$ and $b_I = b_1^I = b_2^I$. Then the extinction equilibrium is locally asymptotically stable provided the following conditions hold*

$$b_S < \frac{(2 - p_1^S - p_2^S) - \sqrt{(2 - p_1^S - p_2^S)^2 - 4\left((1 - p_1^S)(1 - p_2^S) - m_{12}^S m_{21}^S\right)}}{2}$$

$$b_I < \frac{\left(2 - p_1^I(1 - r_1) - p_2^I(1 - r_2)\right) - \sqrt{R}}{2},$$

where R is given by equation (17).

4. Managed Pond vs Wild Pond

Here we consider the case where pond 2 has survival parameters that are a constant multiple of the parameters in pond 1. This situation could correspond to a wild pond

1 and a nearby managed pond 2. The model then becomes

$$S_1(t+1) = B^S(S_1(t), I_1(t))S_1(t) + p^S e^{-w_1 I_1(t)} S_1(t) + p^I r I_1(t)$$
$$+ \alpha m^S e^{-w_2 I_2(t)} S_2(t) + \alpha m^I r I_2(t)$$
$$I_1(t+1) = B^I(S_1(t), I_1(t))I_1(t) + p^S(1 - e^{-w_1 I_1(t)})S_1(t)$$
(18)
$$+ p^I(1-r)I_1(t) + \alpha m^S(1 - e^{-w_2 I_2(t)})S_2(t)$$
$$+ \alpha m^I(1-r)I_2(t)$$
$$S_2(t+1) = \alpha B^S(S_2(t), I_2(t))S_2(t) + \alpha p^S e^{-w_2 I_2(t)} S_2(t) + \alpha p^I r I_2(t)$$
$$+ m^S e^{-w_1 I_1(t)} S_1(t) + m^I r I_1(t)$$
$$I_2(t+1) = \alpha B^I(S_2(t), I_2(t))I_2(t) + \alpha p^S(1 - e^{-w_2 I_2(t)})S_2(t)$$
$$+ \alpha p^I(1-r)I_2(t) + m^S(1 - e^{-w_1 I_1(t)})S_1(t)$$
$$+ m^I(1-r)I_1(t)$$

where α is a non-negative parameter. In this case we have the following theorem concerning the extinction equilibrium.

Theorem 4.1. *Given that $b^S > 2$, the extinction equilibrium for system* (18) *is not locally asymptotically stable for any positive value of α.*

The analysis for this theorem proceeds in a similar fashion to the general model with the following modifications. The restriction (2) and (3) on p and m are still in effect, but addtitionally we have

(19) $$\alpha p^D + m^D < 1 \text{ and } p^D + \alpha m^D < 1,$$

where $D = S, I$. This in turn imposes restrictions on α of

(20) $$\alpha < \frac{1 - m^D}{p^D} \text{ and } \alpha < \frac{1 - p^D}{m^D},$$

where $D = S, I$. With these restrictions, we consider the Jacobian evaluated at the extinction equilibrium:

$$J = \begin{pmatrix} B_1 & * \\ \mathcal{O}_{2x2} & B_2 \end{pmatrix},$$

where

(21) $$B_1 = \begin{pmatrix} b^S + p^S & \alpha m^S \\ m^S & \alpha b^S + \alpha p^S \end{pmatrix},$$

(22) $$B_2 = \begin{pmatrix} b^I + p^I(1-r) & \alpha m^I(1-r) \\ m^I(1-r) & \alpha b^I + \alpha p^I(1-r) \end{pmatrix}.$$

To begin the analysis, observe that $\mathrm{Tr}(B_1) = (1 + \alpha)(b^S + p^S) > 0$ and $\det(B_1) = \alpha \left((b^S + p^S)^2 - (m^S)^2\right)$. Since we still have $p^S + m^S < 1$, it is easy to show that $-m^S > -p^S - 1$. Then $(b^S + p^S)^2 - (m^S)^2 = (b^S + p^S + m^S)(b^S + p^S - m^S) > (b^S + p^S + m^S)(b^S - 1)$. So with $b^S > 1$, then $1 + \det(B_1) < 2$ is equivalent to

$$1 + \alpha \left((b^S + p^S)^2 - (m^S)^2\right) < 2,$$

(23) $$0 < (b^S + p^S)^2 - (m^S)^2 < \frac{1}{\alpha}$$

and $|\mathrm{Tr}(B_1)| < 1 + \det(B_1)$ implies

$$(1 + \alpha)(b^S + p^S) < 1 + \alpha \left((b^S + p^S)^2 - (m^S)^2\right),$$

$$b^S + p^S - 1 < \alpha \left((b^S + p^S)^2 - (m^S)^2 - (b^S + p^S)\right),$$

(24) $$\frac{1}{\alpha} < \frac{(b^S + p^S)^2 - (m^S)^2 - (b^S + p^S)}{b^S + p^S - 1}.$$

Now, with the assumption of $b^S > 2$, then in the following inequality, the left side is negative and the right side is positive, so

$$-\frac{b^S + p^S}{(b^S + p^S)^2 - (m^S)^2} < b^S + p^S - 2,$$

$$1 - \frac{b^S + p^S}{(b^S + p^S)^2 - (m^S)^2} < b^S + p^S - 1,$$

$$\frac{(b^S + p^S)^2 - (m^S)^2 - (b^S + p^S)}{(b^S + p^S)^2 - (m^S)^2} < b^S + p^S - 1,$$

(25) $$\frac{1}{\alpha} < \frac{(b^S + p^S)^2 - (m^S)^2 - (b^S + p^S)}{b^S + p^S - 1} < (b^S + p^S)^2 - (m^S)^2 < \frac{1}{\alpha}.$$

The last inequality follows from (23) and (24), and the resulting contradiction shows that the extinction equilibrium is not locally asymptotically stable when $b^S > 2$.

5. SIMULATIONS

In this section we performed numerical simulations using Mathematica. For non-trivial equilibria of the managed pond vs wild pond, system (18) is too complicated to solve. Thus, we will investigate numerical approximations to equilibria and the corresponding eigenvalues and match these to simulations. We fix all parameters to similar values used earlier (see Table 1) and let α vary over the allowed values given.

TABLE 1. Parameter values used in simulations.

Pond One		Pond Two	
$b^S = 5, 20, 60$	$b^I = 5, 20, 60$	$b^S = 5, 20, 60$	$b^I = 5, 20, 60$
$p^S = 0.4$	$p^I = 0.3$	$p^S = 0.4$	$p^I = 0.3$
$m^S = 0.3$	$m^I = 0.2$	$m^S = 0.3$	$m^I = 0.2$
$r = 0.15$	$w_1 = 1$	$r = 0.15$	$w_2 = 1$

(A) Approximate equilibrium of S_1.

(B) Approximate equilibrium of I_1.

(C) Approximate equilibrium of S_2.

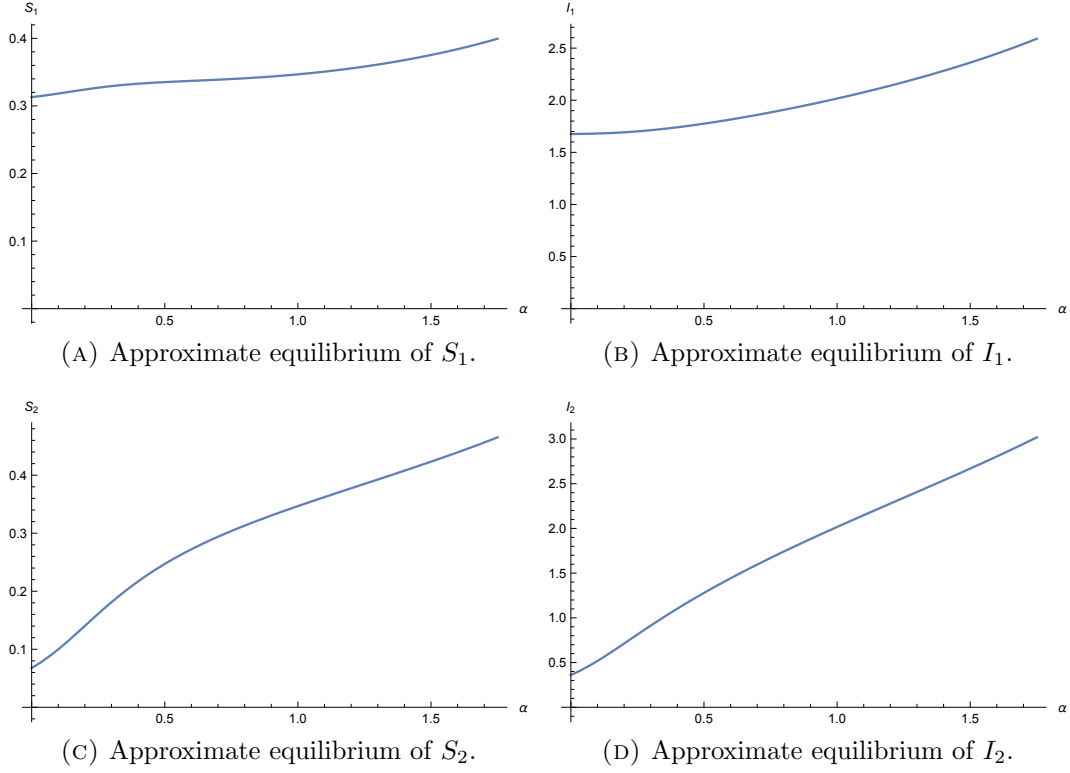(D) Approximate equilibrium of I_2.

FIGURE 3. Approximate equilibrium when $b^S = b^I = 5$ and $0 \leq \alpha \leq$ $\min\{(1 - m^S)/p^S, (1 - m^I)/p^I, (1 - p^S)/m^S, (1 - p^I)/m^I\}$.
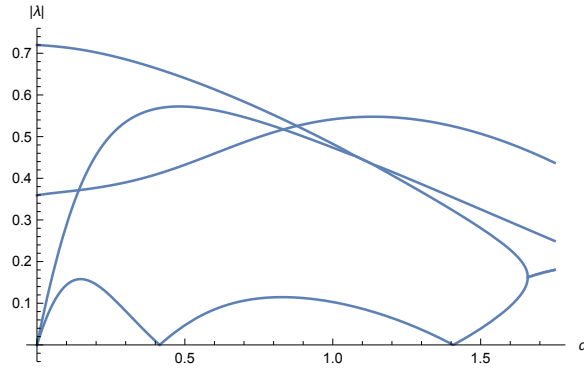

FIGURE 4. Approximate magnitudes of eigenvalues of Jacobian, evaluated at the approximate equilibrium, $b = 5$.

In Figures 3 and 4, approximations to the equilibrium solutions for the given parameters (with $b = 5$) and the corresponding eigenvalues of the Jacobian Matrix are shown as a function of the allowable values of α. For this case we see that all of the eigenvalues have magnitude less than one, so the population's equilibrium should be locally asymptotically stable. A typical bifurcation simulation, Figure 5, bears this out. For

(A) Bifurcation simulation of S_1.

(B) Bifurcation simulation of I_1.

(C) Bifurcation simulation of S_2.
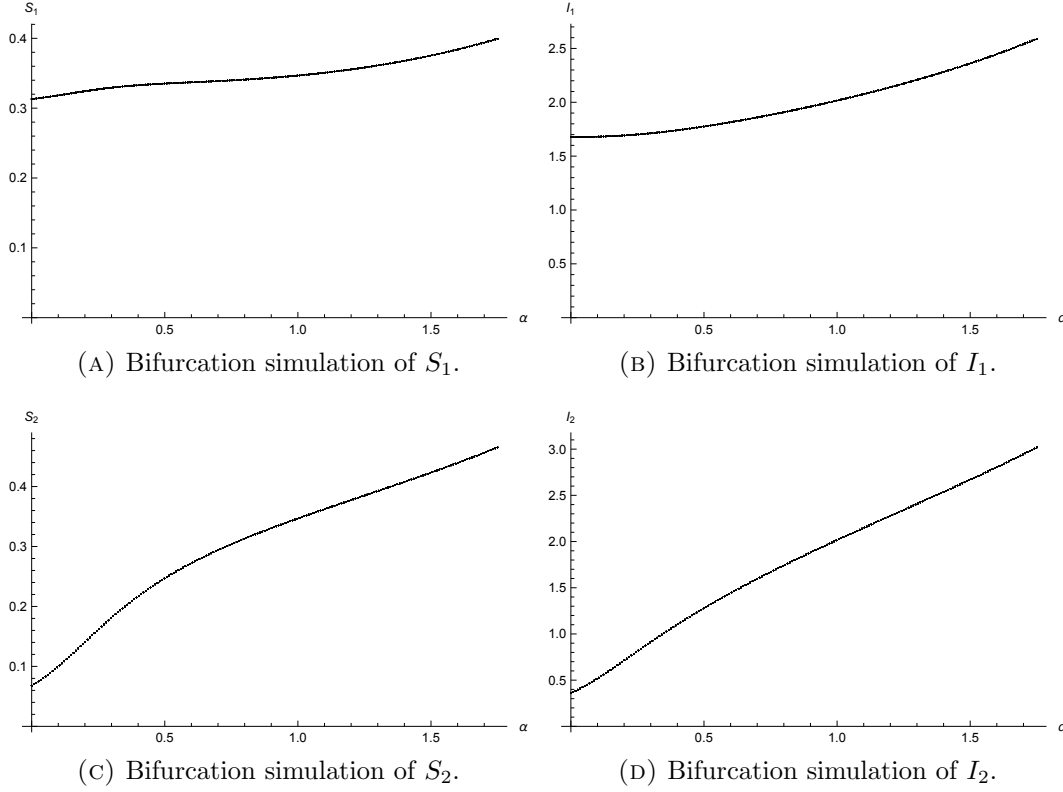

(D) Bifurcation simulation of I_2.

FIGURE 5. Bifurcation simulation when $b^S = b^I = 5$ and $0 \leq \alpha \leq \min\{(1 - m^S)/p^S, (1 - m^I)/p^I, (1 - p^S)/m^S, (1 - p^I)/m^I\}$.

the simulation random initial conditions were used, the model was then iterated 500 times and the graphs show the 50 iterations that followed that conditioning.

Two more interesting cases are when $b = 20$ and $b = 60$. In Figures 6 and 7, note that the nontrivial equilibrium is unstable, based on the size of the eigenvalues, until approximately $\alpha = 1.5$. For the larger values of α all of the eigenvalues have magnitude less that one. Thus, in this case of $b = 20$, beneficial "management" seems to stabilize the populations. This is supported by the bifurcation simulation shown in Figure 8 where we see a 2-cycle for values of α between 0 and about 1.5, and stable populations for larger values of α.

For $b = 60$, Figures 9 and 10 show that for all allowed values of α, there is at least one eigenvalue with magnitude greater than one. Thus, the equilibria in this case are not locally asymptotically stable for any allowed values of α. This is supported by the bifurcation simulation shown in Figure 11. However, even in this case it appears that beneficial "management" still seems to make the populations more stable, while values of α at or below one produce high-period oscillation in the populations.

(A) Approximate equilibrium of S_1.

(B) Approximate equilibrium of I_1.

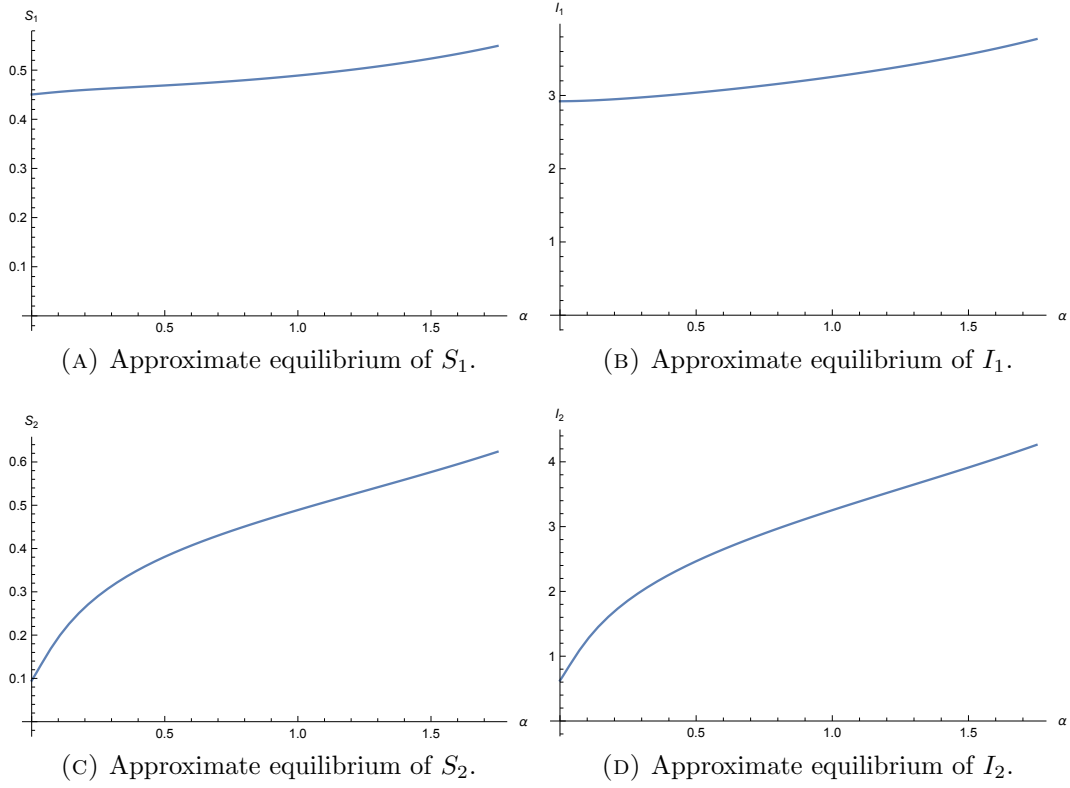(C) Approximate equilibrium of S_2.

(D) Approximate equilibrium of I_2.

FIGURE 6. Approximate equilibrium when $b^S = b^I = 20$ and $0 \leq \alpha \leq \min\{(1-m^S)/p^S, (1-m^I)/p^I, (1-p^S)/m^S, (1-p^I)/m^I\}$.
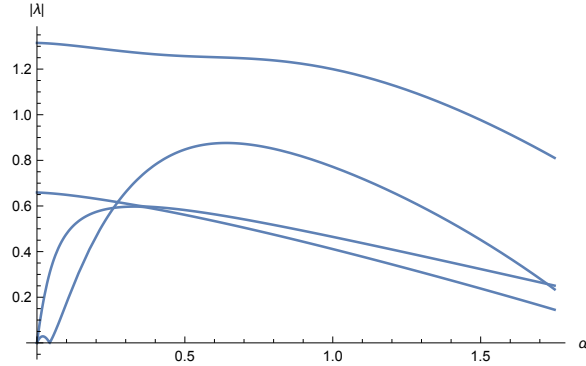

FIGURE 7. Approximate magnitudes of eigenvalues of Jacobian, evaluated at the approximate equilibrium, $b = 20$.

(A) Bifurcation simulation of S_1.

(B) Bifurcation simulation of I_1.

(C) Bifurcation simulation of S_2.
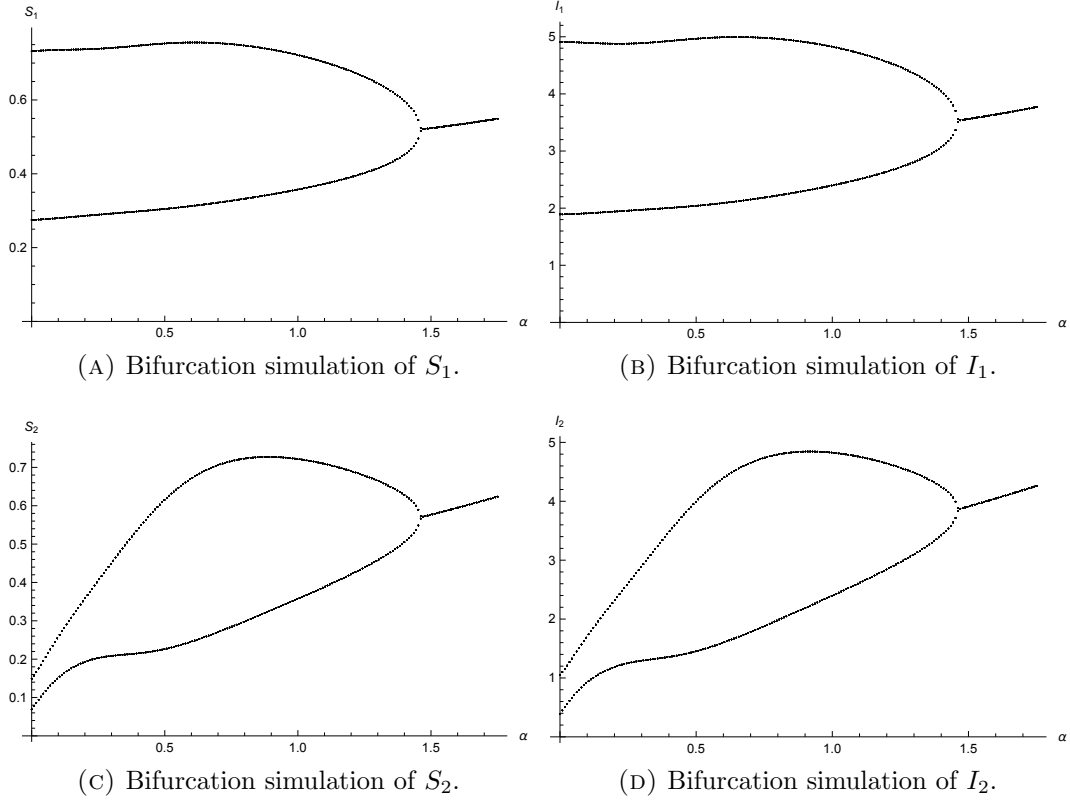

(D) Bifurcation simulation of I_2.

FIGURE 8. Bifurcation simulation when $b^S = b^I = 20$ and $0 \leq \alpha \leq \min\{(1 - m^S)/p^S, (1 - m^I)/p^I, (1 - p^S)/m^S, (1 - p^I)/m^I\}$.
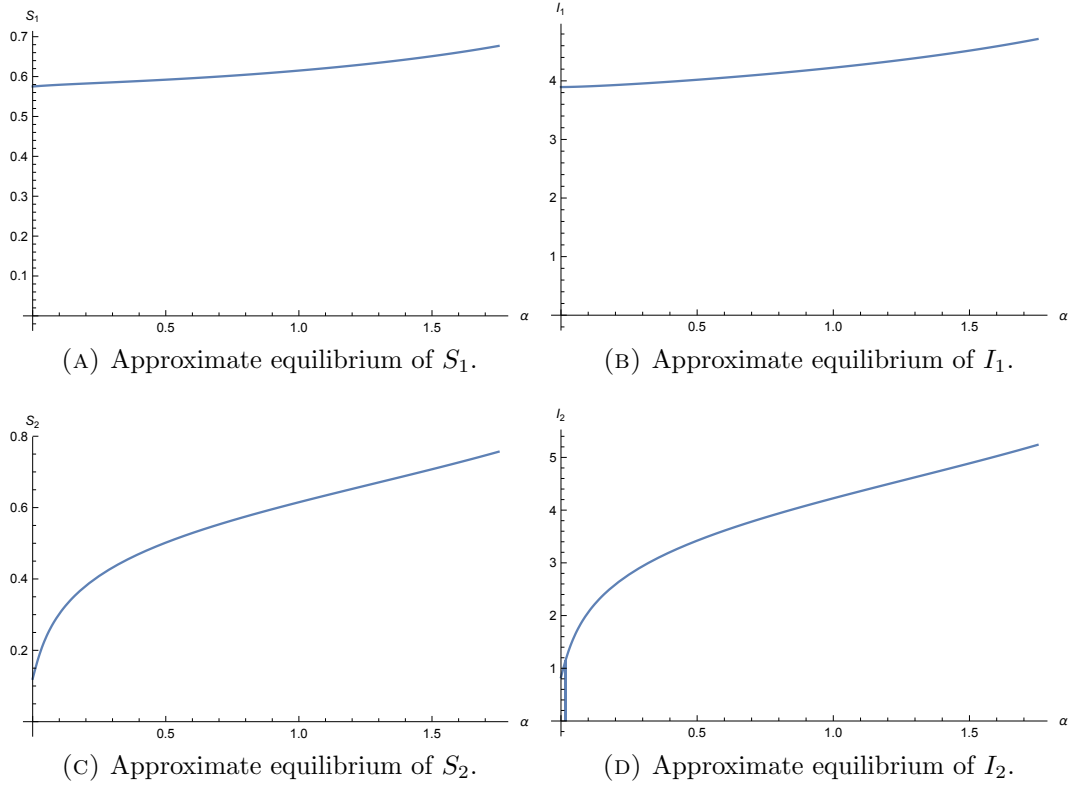
(A) Approximate equilibrium of S_1.

(B) Approximate equilibrium of I_1.

(C) Approximate equilibrium of S_2.

(D) Approximate equilibrium of I_2.

FIGURE 9. Approximate equilibrium when $b^S = b^I = 60$ and $0 \leq \alpha \leq \min\{(1-m^S)/p^S, (1-m^I)/p^I, (1-p^S)/m^S, (1-p^I)/m^I\}$.
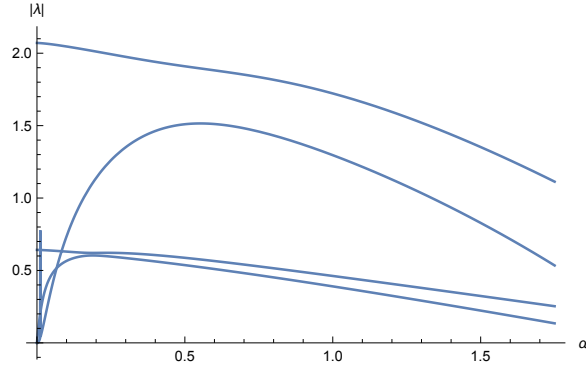

FIGURE 10. Approximate magnitudes of eigenvalues of Jacobian, evaluated at the approximate equilibrium, $b = 60$.

(A) Bifurcation simulation of S_1.

(B) Bifurcation simulation of I_1.

(C) Bifurcation simulation of S_2.
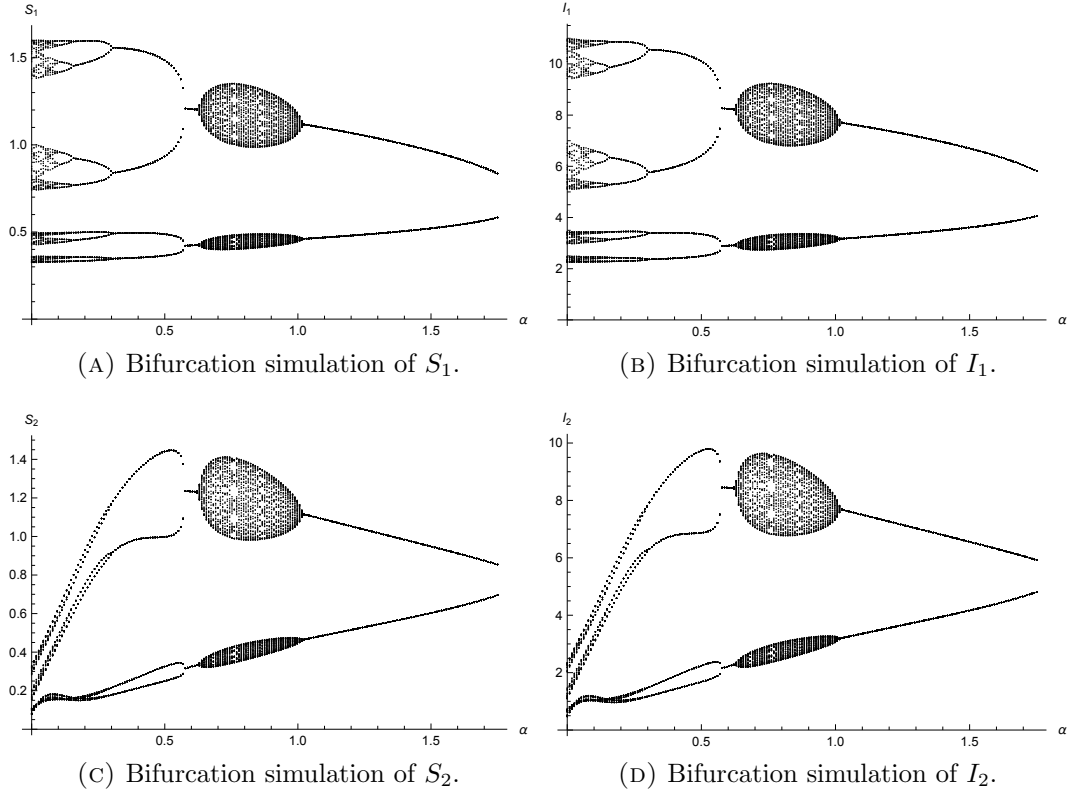

(D) Bifurcation simulation of I_2.

FIGURE 11. Bifurcation simulation when $b^S = b^I = 60$ and $0 \leq \alpha \leq$ $\min\{(1 - m^S)/p^S, (1 - m^I)/p^I, (1 - p^S)/m^S, (1 - p^I)/m^I\}$.

6. Conclusions and Future Directions

The two pond, SI amphibian model presented here has lead to both expected and unexpected results. In particular according to this model, the case of the wild pond adjacent to a managed pond can never have a stable extinction equilibrium despite the effects of negative management, provided the natural recruitment is sufficiently large. Simulations in this case also seem to indicate that beneficial management of one pond can tend to stabilize the overall population dynamics.

Future research is needed to explore analytically the stability of the non-trivial equilibrium as well as the extension of the model to more than two ponds and/or an age structured population. In this work we have used an SI amphibian model. The dynamics of a SIS or SIR model may differ. Lastly, the model could be expanded to include multiple amphibian species in a competitive and/or predator-prey model.

All Mathematica code used in the simulations can be found at:

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`http://faculty.tarleton.edu/white/ictcmindex.html`.

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References

[1] Linda J. S. Allen. *An Introduction to Mathematical Biology*. Pearson Education, Inc., 2007.

[2] Cheryl J Briggs, Vance T Vredenburg, roland A Knapp, and Lara J Rachowicz. Investigating the population-level effects of chytridiomycosis: an emerging infectious diseasse of amphibians. *Ecology*, 86:3149–3159, 2005.

[3] E. E. Brucks. Non-standard discretization methods for systems of differential equations with applications to barred tiger salamanders. Master's thesis, Tarleton State University, Stephenville, TX, 2006.

[4] C. Carey, W. R. Heyer, J. Wilkinson, R. A. Alford, J. W. Arntzen, T. Halliday, L. Hungerford, K. R. Lips, E. M. Middleton, S. A. Orchard, and A. S. Rand. Amphibian declines and environmental change: use of remote-sensing data to identify environmental correlates. *Conservation Biology*, 15:903 – 913, 2001.

[5] P. Daszak, L. Berger, A. A. Cunningham, A. D. Hyatt, D. E. Green, and R. Speare. Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases*, 5:735–748, 1999.

[6] A. J. Drew, E. J. Allen, and L. J. S. Allen. An investigation of climatic and geographic factors on the presence of chytrid fungus on amphibian populations in australia. *Diseases of Aquatic Organisms*, 2006.

[7] K. E. Emmert. *Deterministic and Stochastic Discrete-Time epidemic Models with Applications to Amphibians*. Ph.D. dissertation, Texas Tech University, Lubbock, TX, 2004.

[8] K. E. Emmert and L. J. S. Allen. Population extinction in deterministic and stochastic discrete-time epidemic models with periodic coefficients with applications to amphibian populations. *Natural Resource Modelling*, 19(2):117 – 164, 2006.

[9] J.M. Kiesecker, L. K. Belden, K. Shea, and M. J. Rubbo. Amphibian decline and emerging disease: what can sick frogs teach us about new and resurgent diseases in human populations and other species of wildlife. *American Scientist*, 92:138 – 147, 2004.

[10] R. Mazzoni, A. A. Cunningham, P. Daszak, A. Apolo, E. Perdomo, and G. Speranza. Emerging pathogen of wild amphibians in frogs *(rana catesbeiana)* farmed for international trade. *Emerging Infectious Diseases*, 9:995 – 998, 2003.

[11] Kate M Mitchell, Thomas S Churcher, Trenton W J Gqarner, and Mattchew C Fisher. Persistence of the emerging pathogen *Batrachochytrium dendrobatidis* outside the amphibian host greatly increases the probability of host extinction. *Proceedings of the Royal Society Biological Sciences*, 275:329–334, February 2008.

[12] Lara J Rachowicz and Vance T Vredenburg. Transmission of *Batrachochytruim dendrobatidis* within and between amphibian life stages. *Diseases of Aquatic Organisms*, 61:75–83, October 2004.

[13] Jason R Rohr, Thomas R Raffel, John M Romansic, Hamish McCallum, and Peter J Hudson. Evaluating the links between climate, disease spread, and amphibian declines. *Proceedings of the National Academy of Sciences*, 105(45):17436–17441, November 2008.

[14] L. A. Rollins-Smith. Neuroendocrine-immune system interactions in amphibians: implications for understanding global amphibian declines. *Immunologic Research*, 923–2/3:273–280, 2001.

[15] Paul Leonard Salceanu and Hal L Smith. Persistence in a discrete-time, stage-structured epidemic model. *Journal of Difference Equations and Applications*, 16(1):73–103, January 2010.

[16] D. Sparling and G. Fellers. Contaminant studies in the sierra nevadas. *People, Land & Water*, page 33, August 2002.

[17] E. M. Stock. Deterministic discrete-time epidemic models with applications to amphibians. Master's thesis, Tarleton State University, Stephenville, TX, 2006.

[18] J. L. Zuehlke. Deterministic modeling of the effect of reservoir hosts on the spread of chytrid fungus within the barred tiger salamander population. Master's thesis, Tarleton State University, Stephenville, TX, 2006.