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Stability Analysis of the Beddington Model with Allee Effect

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Abstract: We investigate the stability of the equilibria and the invariant manifolds of the host-parastoid model due to Beddington, Free, and Lawton [2] subject to the Allee effect.

Keywords: Allee efect, Beddington, Dicsrete dynamical systems

1 Introduction

One of the most commonly used ecology models is Nicholson-Bailey host-parasitoid model [8]. This is a discrete-time model applicable to biological systems involving two insects, a parasitoid (P_t) and its host (N_t). Nicholson and Bailey developed the model (1935) and applied it to the parasitiod, *Encarsia formosa*, and the host, *Trialeurodes vaporariorum*. The term "parasitoid" means a parasite which is free living as an adult but lays eggs in the larvae or pupae of the host. Hosts that are not parasitized give rise to their own progeny. Hosts that are successfully parasitized die, but the eggs laid by the parasitoid may survive to be the next generation of parasitoids.

The general host-parasitoid model has the form:

$$N_{t+1} = rN_t f(N_t, P_t),$$
$$P_{t+1} = eN_t(1 - f(N_t, P_t)).$$

where the parameters r (number of eggs laid by a host that survive through the larvae, pupae, and adult stages) and e (number of eggs laid by a parasitoid on a single host that survive through larvae, pupae, and adult stages) are positive. The function f can be interpreted as the probability that each individual host escapes the parasitoids, so that the complementary term $1 - f(N_t, P_t)$ in the second equation is the probability of being parasitized.

The following density-dependent predator-prey model was investigated by Beddington et al [2]:

$$\begin{aligned} N_{t+1} &= N_t \exp\left[r\left(1 - \frac{N_t}{K}\right) - aP_t\right], \\ P_{t+1} &= cN_t[1 - \exp(-aP_t)], \end{aligned} \quad (1)$$

where K is the carrying capacity. It represents maximum population size that can be supported due to availability of all the potentially limiting resources. In the term aN_tP_t, a is the searching efficiency that is, the probability that a given parasitoid will encounter a given host during its searching lifetime. Note that Nicholson-Bailey Model reduces to the density independent one-species model $N_{t+1} = rN_t$ if the parasitoid is not present. Since this is not realistic for most of the species, model (1) rectifies this by adopting the density-depending Ricker Model $N_{t+1} = N_t \exp\left[r(1 - \frac{N_t}{K})\right]$, where K is the carrying capacity of the host and is the sustainable size of the host. Moreover, in the absence of the parasitiod, the equilibrium K is globally asymptotically stable for $0 < r < 2$ on $(0, \infty)$ [5]. It is assumed that the parameters a, r, c, K are all positive real numbers.

When a population is small or its density is low, the classical view of population dynamics is that the major ecological force at work is the release from the constraints of intraspecific competition. Individual fitness, or one of its components, is positively correlated to

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population size or density. Most definitions of the Allee effect apply either to density of the population or its size. Allee effects occurs when the per capita growth rate of a species is an increasing function of the population size for a certain range of population size below which the population dies off. Allee effects may occur due to a variety of causes ranging from mating limitation, predator saturation and anti-predator defence, etc. Much of what we know about Allee effects comes from mathematical models since models help us organize, conceptualize and interpret a vast amount of complex ecological data, and predict or hypothesize when such data are not available. We refer the reader [7,10,11,**?**] and references cited therein about Allee effects.

We know that predation can create component Allee effects in prey. This requires that predator populations do not respond numerically to the target prey species and that the overall mortality rate of prey due to these predators is hyperbolic function of prey density [12]. We assume that the host population undergoes Allee effects in host-parasitoid interaction. The asymptotic dynamics of host-parasitoid model with the Allee effects will be investigated. We study the following discrete-time host-parasitoid model which is the Beddington Model with Allee effect on the parasitoid population.

$$
\begin{aligned}
N_{t+1} &= N_t \exp\left[r\left(1-\frac{N_t}{K}\right)-aP_t\right], \\
P_{t+1} &= cN_t[1-\exp(-aP_t)]\frac{P_t}{A+P_t},
\end{aligned} \tag{2}
$$

where the parameters r, K, a, c, and A is positive. Now, we eliminate some of the parameters by changing the variables. Taking $x_t = \frac{N_t}{K}$, and $y_t = aP_t$, we obtain

$$
\begin{aligned}
x_{t+1} &= x_t \exp\left[r(1-x_t)-y_t\right], \\
y_{t+1} &= mx_t[1-\exp(-y_t)]\frac{y_t}{B+y_t},
\end{aligned} \tag{$\star$}
$$

where $m = acK$ and $B = aA$.

2 Equilibrium Points

The fixed points of the discrete system ($\star$) are described in the following theorem:

Theorem 2.1. Let

$$F(x) = -r+(r+m)x - mx\exp\left[-r(1-x)\right]$$

and

$$\theta = \frac{(B+r)\sqrt{r}+\sqrt{B+r}\sqrt{4m+r(4+B+r)}}{2(m+r)}.$$

For the system given in ($\star$),

a. for any values of parameters, there exist two non-negative fixed points which are $(0,0)$ and $(1,0)$;
b. there exists one positive fixed point $(\theta, r(1-\theta))$ if and only if $m > 1$ and $B = F(\theta)$;
c. there exist two positive fixed points in the form $(\ell, r(1-\ell))$, if and only if $m > 1$ and $B < F(\theta)$, where $0 < \ell < 1$.

Proof. To find the fixed points of the system given in ($\star$), we solve the following system of equations:

$$
\begin{aligned}
x &= x\exp\left[r(1-x)-y\right], \\
y &= mx[1-\exp(-y)]\frac{y}{B+y}.
\end{aligned} \tag{3}
$$

If $x = 0$, we have the extinction fixed point $(0,0)$. If $x \neq 0$ and $y = 0$ we obtain the exclusion fixed point $(1,0)$. If $x \neq 0$ and $y \neq 0$ the system of equations (3) becomes

$$
\begin{aligned}
y &= r(1-x), \\
x &= \frac{B+y}{m[1-\exp(-y)]}.
\end{aligned} \tag{4}
$$

Eliminating y in (4), we obtain

$$B = -r+(r+m)x - mx\exp\left[-r(1-x)\right]. \tag{5}$$

Let us denote $z = F(x) = -r+(r+m)x - mx\exp\left[-r(1-x)\right]$. When this curve intersects with the horizontal line $z = B$, some fixed points are obtained.

Notice that F is continuous, $F(0) = -r < 0$, $F(1) = 0$, $F''(x) < 0$ for all x, $\lim_{x\to\infty} F(x) = -\infty$, $F'(0) > 0$. Since $F'(1) = r(1-m)$, we have the following cases:

i. If $m = 1$, then $F'(1) = 0$ and the only maximum point is at $x = 1$. Since $B > 0$, there is no intersection of the functions $z = B$ and $z = F(x)$ (See Figure 1(a)).
ii. If $m < 1$, then $F'(1) > 0$. We know that $F''(x) < 0$ for all x and $\lim_{x\to\infty} F(x) = -\infty$. This means that for some values of B, there exist either one (if the horizontal line is tangent to the curve $z = F(x)$) or two (if B is less than the height of the maximum point of the function $z = F(x)$) fixed points and for any of them if we denote the x-component of the any such fixed point by $x = \omega$, then $\omega > 1$. We have $y = r(1-\omega) < 0$ by the first equation of system (4) (See Figure 1(b)). Since one component of $(\omega, r(1-\omega))$ is negative, this fixed point is not of interest in biology and hence it will be omitted.
iii. If $m > 1$, then $F'(1) < 0$. We know that $F''(x) < 0$ for all x and $F(0) = -r < 0$. Hence, for some values of B there exist either one (if the horizontal line is tangent to the curve $z = F(x)$) or two (if B is less than the height of the maximum point of the function $z = F(x)$) fixed points. Let us denote the x-component of such a fixed point by $x = \ell$. Then $\ell < 1$ and hence $y = r(1-\ell) > 0$ by (4) (See Figure 1(c)). Hence, $(\ell, r(1-\ell))$ is a candidate to be a coexistence fixed point.

Now, we have to determine the condition for which the horizontal line $z = B$ intersects the function $z = F(x)$ for $m > 1$. That is the condition for which the number B is less than the height of the maximum value of the curve $z = F(x)$. Let us denote the maximum point by $(\bar{x}, \bar{y})$. In order to find that point, we have

$$F'(\bar{x}) = r - m\left(-1 + e^{r(-1+\bar{x})}(1 + r\bar{x})\right) = 0.$$

We focus on the case in which the horizontal line $z = B$ is tangent to the curve $z = F(x)$, that is $F(\bar{x}) = B$:

$$-r + (r+m)\bar{x} - m\bar{x}\exp\left[-r(1-\bar{x})\right] = B.$$

Eliminating the term $e^{-r(1-\bar{x})}$, we obtain

$$-r + (m+r)\bar{x} - \frac{(m+r)\bar{x}}{1+r\bar{x}} = B. \tag{6}$$

The positive solution of equation (6) for $\bar{x}$ is as follows:

$$\bar{x} = \frac{(B+r)\sqrt{r} + \sqrt{B+r}\sqrt{4m + r(4+B+r)}}{2(m+r)}. \tag{7}$$

Hence, the condition for existence of the positive fixed point in part (b) and (c) is obtained: There exist one intersection point $(\bar{x}, r(1-\bar{x}))$ if and only if $m > 1$ and $B = F(\bar{x})$, and there exist two intersection points if and only if $m > 1$ and $B < F(\bar{x})$.

3 Stability of extinction and exclusion fixed points

Theorem 3.1. For system ($\star$), the following statements hold true:

a.The equilibrium $(0,0)$ is unstable.
b.if $0 < r \leq 2$, then the equilibrium $(1,0)$ is asymptotically stable .

Proof. The Jacobian matrix of the map

$$G(x,y) = \left(xe^{r(1-x)-y}, mx(1-e^{-y})\frac{y}{B+y}\right)$$

is

$$JG(x,y) = \begin{pmatrix} e^{r-rx-y}(1-rx) & -e^{r-rx-y}x \\ \frac{(1-e^{-y})my}{B+y} & \frac{e^{-y}mx\left(y^2+B(-1+e^y+y)\right)}{(B+y)^2} \end{pmatrix}.$$

a.The Jacobian evaluated at the point $(0,0)$ is

$$JG(0,0) = \begin{pmatrix} e^r & 0 \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues of $JG(0,0)$ are 0 and e^r. Since $r > 0$, it follows that $e^r > 1$. Thus $(0,0)$ is unstable.

b.The Jacobian evaluated at $(1,0)$ is

$$JG(1,0) = \begin{pmatrix} 1-r & -1 \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues for this matrix are $\lambda_1 = 1-r$ and $\lambda_2 = 0$. Thus, the fixed point $(1,0)$ is stable if $\rho(JG(1,0)) < 1$, that is $0 < r < 2$. If $r > 2$, the fixed point $(1,0)$ is unstable. If $r = 2$, then the eigenvalue are $\lambda_1 = -1$ and $\lambda_2 = 0$. Now, we have to apply the center manifold theorem [5]: by changing variables, let $u = x-1$ and $v = y$ in system ($\star$), we have a shift from the point $(1,0)$ to $(0,0)$. Then the new system is given by

$$\begin{aligned} u_{t+1} &= (u_t+1)\exp\left[-ru_t - v_t\right] - 1, \\ v_{t+1} &= m(u_t+1)[1-\exp(-v_t)]\frac{v_t}{B+v_t}. \end{aligned} \tag{8}$$

The Jacobian of the planar map given in (8) is

$$\tilde{J}G(u,v) = \begin{pmatrix} -e^{-ru-v}(-1+r+ru) & -e^{-ru-v}(1+u) \\ \frac{(1-e^{-v})mv}{B+v} & \frac{e^{-v}m(1+u)\left(v^2+B(-1+e^v+v)\right)}{(B+v)^2} \end{pmatrix}. \tag{9}$$

At $(0,0)$, $\tilde{J}G$ has the form

$$\tilde{J}G(0,0) = \begin{pmatrix} 1-r & -1 \\ 0 & 0 \end{pmatrix}.$$

When $r = 2$ we have

$$\tilde{J}G(0,0) = \begin{pmatrix} -1 & -1 \\ 0 & 0 \end{pmatrix}.$$

Now we can write the equations in system (8) as

$$\begin{aligned} u_{t+1} &= -u_t - v_t + \tilde{f}(u_t, v_t), \\ v_{t+1} &= \tilde{g}(u_t, v_t), \end{aligned} \tag{10}$$

where

$$\tilde{f}(u_t, v_t) = -1 + u_t + e^{-2u_t - v_t}(1+u_t) + v_t$$

and

$$\tilde{g}(u_t, v_t) = \frac{(1-e^{-v_t})m(1+u_t)v_t}{B+v_t}.$$

Let us assume that the map $v = h(u)$ takes the form

$$h(u) = \alpha u^2 + \beta u^3 + O(u^4), \quad \alpha, \beta \in \mathbb{R}.$$

Now, we compute the constants α and β. The function $v = h(u)$ must satisfy the center manifold equation

$$h\left[-u - h(u) + \tilde{f}(u, h(u))\right] - \tilde{g}(u, h(u)) = 0.$$

The Taylor series expansion at the point $u = 0$ is evaluated for the equation above. Equating the coefficients of the series, we obtain $\alpha = \beta = 0$.

Thus on the center manifold $v=0$ we have the following map

$$P(u)=-1+e^{-2u}(1+u).$$

Calculations show that $P'(0)=-1$ and Schwarzian derivative of the map P at the origin is $-\frac{4}{3}<0$. Hence, the exclusion fixed point $(1,0)$ is locally asymptotically stable (See Figure 1).

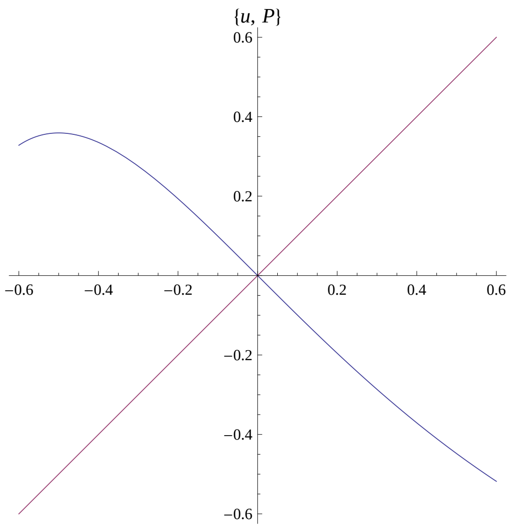

Fig. 1: The map P on the center manifold $v=h(u)$, where $r=2$

4 Stable and Unstable Manifolds of the Extinction and Exclusion Fixed Points

For the point $(0,0)$, since $|\lambda_1|=e^r>1$ and $|\lambda_2|=0<1$, the extinction fixed point is saddle for any values of parameters r and m. For this point, the x-axis is unstable and the y-axis is stable.
Now, let us focus on the exclusion fixed point $(1,0)$: By using the similar procedure that is used for the center manifold in the proof of Theorem 3, we obtain the stable and unstable manifolds. In model ($\star$) the saddle scenario for the exclusion fixed point occurs when $r>2$. Shifting the exclusion fixed point from $(1,0)$ to $(0,0)$, we have the following Jacobian matrix:

$$\tilde{J}G(0,0)=\begin{pmatrix}1-r & -1\\ 0 & 0\end{pmatrix}.$$

We can write the equations in system (8) as

$$\begin{aligned}u_{t+1}&=(1-r)u_t-v_t+\tilde{f}(u_t,v_t),\\ v_{t+1}&=\tilde{g}(u_t,v_t),\end{aligned}\qquad(11)$$

where

$$\tilde{f}(u,v)=-1+(-1+r)u+e^{-ru-v}(1+u)+v$$

and

$$\tilde{g}(u_t,v_t)=\frac{(1-e^{-v})\,m(1+u)v}{B+v}.$$

The eigenvalues of the Jacobian matrix $\tilde{J}G(0,0)$ are $\lambda_1=1-r$ and $\lambda_2=0$. Thus, at the fixed point $(1,0)$, the unstable and stable manifold must be tangent to the eigenvectors $\begin{pmatrix}1\\0\end{pmatrix}$ and $\begin{pmatrix}1\\1-r\end{pmatrix}$, respectively.

In order to find the unstable manifold for the exclusion fixed point, we assume that the map $v=h(u)$ takes the form

$$h(u)=\alpha u^2+\beta u^3+O(u^4),\quad \alpha,\beta\in\mathbb{R}.$$

The map h must satisfy the following center manifold equation

$$h\left((1-r)u-h(u)+\tilde{f}(u,h(u))\right)-\tilde{g}(u,h(u))=0.$$

The Taylor expansion at the point $(0,0)$ yields

$$\alpha(-1+r)^2u^2-(-1+r)\left(-2\alpha^2+\beta(-1+r)^2+\alpha(-2+r)r\right)u^3+O[u]^4=0.$$

Thus, we obtain $\alpha=\beta=0$. Hence, the unstable manifold is $h(u)=0$ and the map on the unstable manifold is

$$Q(u)=-1+e^{-ru}(1+u).$$

Notice that $|Q'(0)|=|1-r|>1$ when $r>2$.

In order to find the stable manifold for the exclusion fixed point, we assume that map h takes the form

$$h(v)=\frac{1}{1-r}v+\alpha v^2+\beta v^3+O(v^4),\quad \alpha,\beta\in\mathbb{R}.$$

Hence, the center manifold equation is

$$h\left(\tilde{g}(h(v),v)\right)-(1-r)h(v)+v-f(h(\tilde{v}),v)=0.$$

By using the Taylor series expansion at the point $(0,0)$ and equating the coefficient of the polynomials to 0, we obtain

$$\alpha=\frac{2m+B(-3+r)}{2B(-1+r)^2}$$

and

$$\beta=-\frac{6m(-1+r)^2+3Bm(-1+r)^2+B^2\left(-9+21r-9r^2+r^3\right)}{6B^2(-1+r)^4}.$$

Hence, the map on the center manifold is obtained as

$$R(v)=\frac{(1-e^{-v})\,mv\left(1+\frac{v}{1-r}+\alpha v^2+\beta v^3\right)}{B+v},$$

and the stable manifold is

$$h(v)=\frac{v}{1-r}+\alpha v^2+\beta v^3,$$

where α and β are given above. Notice that $R'(0)=0$ which makes the fixed point $(1,0)$ locally asymptotically stable (See Figure 2).

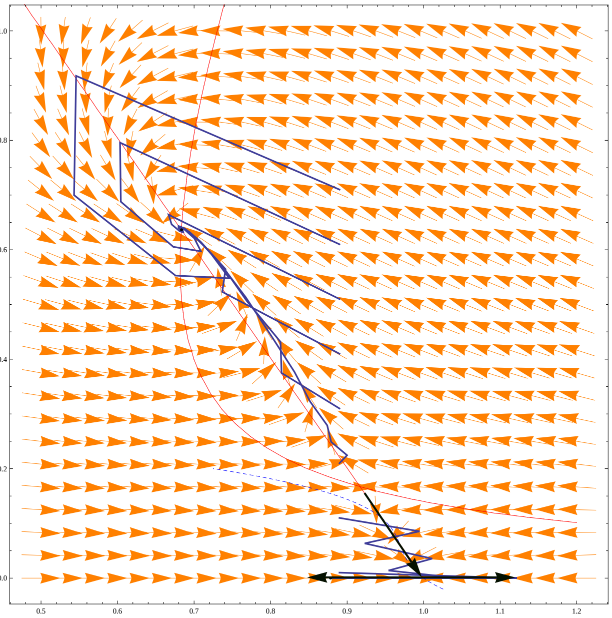

Fig. 2: Stable and unstable manifolds for the exclusion fixed point $(1,0)$, where $m = 2.6$, $B = 0.2$, and $r = 2.01$. The red curves represent the isoclines and the dashed curve represents the stable manifold.

5 Conclusion

We investigate the stability and bifurcation of Beddington model with Allee effect. The condition for the existence of the fixed points are found. We also obtained the invariant manifolds for extinction and exclusion fixed points. In the future study, we will examine the host-parasite models with Allee effects for both host and parasite using the Ricker, the logistic, and Hassell models.

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