Stability and invariant manifolds of a generalized Beddington host-parasitoid model

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We will investigate the stability and invariant manifolds of a new discrete host-parasitoid model. It is a generalization of the Beddington–Nicholson–Bailey model. Our study establishes analytically, for the first time, the stability of the coexistence fixed point.

Keywords: host-parasitoid; Beddington; Nicholson–Bailey; stability; centre manifold

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1. Introduction

Ecological systems and their component biological populations exhibit a broad spectrum of non-equilibrium dynamics ranging from characteristic natural cycles to more complex chaotic oscillations. One of the most well-known models for many experimental and theoretical investigations in ecology is Nicholson–Bailey host-parasitoid model \cite{4,11–13}. This is a discrete-time model of a biological system involved two insects, a parasitoid and its host. Nicholson and Bailey developed the model (1935) and applied it to the parasitoid, \textit{Encarsia formosa}, and the host, \textit{Trialeurodes vaporariorum}. The term ‘parasitoid’ refers to 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.

For the host-parasitoid model of Nicholson–Bailey, the basic variables and parameters are defined as follows:

\[
N_t = \text{density of host species in generation } t.
\]

\[
P_t = \text{density of parasitoid species in generation } t.
\]

\[
f(N_t, P_t) = \text{fraction of hosts not parasitized.}
\]

\[
r = \text{number of eggs laid by a host that survive through the larvae, pupae, and adult stages.}
\]

\[
e = \text{number of eggs laid by a parasitoid on a single host that survive through larvae, pupae, and adult stages.}
\]
The parameter $r$ and $e$ are positive. Applying these definitions, the general host-parasitoid model has the form:

$$N_{t+1} = rN_t f(N_t, P_t),$$

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

The function $f$ can be interpreted as the probability that each individual host escapes the parasites, so that the complementary term $1 - f$ in the second equation is the probability of being parasitized. Note that if $N_t = 0$, then $P_t = 0$ that is the parasitoid cannot survive without the host. That is why parasitoids are good biological control agents.

Nicholson and Bailey model assumes a simple functional form for $f(N_t, P_t)$. $f$ depends on the searching behaviour of the parasitoid. The number of encounters of the parasitoids $P_t$ with the hosts $N_t$ is directly proportional to the host density $N_t$ and thus follows the law of mass action $aN_t P_t$. The parameter $a$ is the searching efficiency of the parasitoid which is the probability that a given parasitoid will encounter a given host during its searching lifetime. Since the number of encounters are distributed randomly among the available hosts, Nicholson and Bailey used the Poisson distribution: $p(n) = e^{-\mu} \mu^n / n!$, where $n$ is the number of encounters and $\mu$ is the mean of encounters per host in one generation. Once the host is parasitized, it will not be parasitized again. Host with no encounters $N_t$ and potential limited resources. Note that Model (1) 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 (2) rectifies this situation by adopting the density-dependent Ricker model $N_{t+1} = N_t \exp[r(1 - N_t/K)]$, where $K$ is the carrying capacity of the host and is the sustainable size of the host. Moreover, in the absence of the parasitoid, the equilibrium is globally asymptotically stable for $0 < r < 2$ on $(0, \infty)$ [5]. It is assumed that the parameters $a, r, e, K$ are all positive real numbers.

Hone et al. [8] have studied the following predator-prey system, which generalizes the model in Equation (1):

$$N_{t+1} = rN_t \exp(-aP_t),$$

$$P_{t+1} = eN_t (1 - \exp(-aP_t)).$$

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

$$N_{t+1} = N_t \exp \left[ r \left( 1 - \frac{N_t}{K} \right) - aP_t \right],$$

$$P_{t+1} = eN_t [1 - \exp(-aP_t)],$$

where $K$ is the carrying capacity and represents the maximum population size that can be supported by the available and potential limited resources. Note that Model (1) 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 (2) rectifies this situation by adopting the density-dependent Ricker model $N_{t+1} = N_t \exp[r(1 - N_t/K)]$, where $K$ is the carrying capacity of the host and is the sustainable size of the host. Moreover, in the absence of the parasitoid, the equilibrium is globally asymptotically stable for $0 < r < 2$ on $(0, \infty)$ [5]. It is assumed that the parameters $a, r, e, K$ are all positive real numbers.

We consider the following density-dependent predator-prey model which is a generalized version of the discrete systems (1)–(3). In [8], the authors introduced the model as an open problem.

$$N_{t+1} = N_t \exp \left[ r \left( 1 - \frac{N_t}{K} \right) - aP_t \right],$$

$$P_{t+1} = eN_t [1 - \exp(-bP_t)],$$

where the parameters $a, b, e, K$, and $r$ are positive.
Notice that in Equation (4), when $a = b$ we obtain the Beddington model. With unlimited capacity, for which the term $N_t/K$ vanishes, Equation (4) becomes the model discussed by Hone et al. Further, if $a = b$ and the capacity is unlimited, we have Nicholson–Bailey model.

Now, we eliminate some of the parameters by changing the variables. Taking $x_t = N_t/K$ and $y_t = bP_t$, we obtain

\[
\begin{align*}
x_{t+1} &= x_t \exp[r(1 - x_t) - qy_t], \\
y_{t+1} &= \mu x_t[1 - \exp(-y_t)],
\end{align*}
\]

where $\mu = beK$ and $q = a/b$.

All the procedures we maintain for the case $a \neq b$ in this paper can be done for the case $a = b$ by taking $q = 1$.

2. Equilibrium points

The fixed points of the discrete system (*) are obtained:

**Lemma 2.1** For the system given in (*),

(a) if $\mu \leq 1$, then there exist two non-negative fixed points which are $(0, 0)$ and $(1, 0)$.
(b) if $\mu > 1$, there exist three fixed points which are $(0, 0)$, $(1, 0)$ and $(\ell, (r/q)(1 - \ell))$ where $0 < \ell < 1$. In this case, $(\ell, (r/q)(1 - \ell))$ is the coexistence (positive) fixed point.

**Proof** To find the fixed points of the system given in (*), the following system of equations must be solved:

\[
\begin{align*}
x &= x \exp[r(1 - x) - qy], \\
y &= \mu x[1 - \exp(-y)].
\end{align*}
\]

If $x = 0$, we have the extinction fixed point $(0, 0)$ and if $x \neq 0$, the system of Equations (5) becomes

\[
\begin{align*}
0 &= r(1 - x) - qy, \\
y &= \mu x[1 - \exp(-y)].
\end{align*}
\]

It is easy to find the exclusion fixed point $(1, 0)$ by taking $y = 0$ in the first equation of the system given in Equations (6).

Eliminating $y$ in Equations (6), we obtain

\[
r = (r + q\mu)x - q\mu x \exp\left[-\frac{r}{q}(1 - x)\right].
\]

Let us denote $z = F(x) = (r + q\mu)x - q\mu x \exp[-(r/q)(1 - x)]$. When this curve intersects the horizontal line $z = r$, some fixed points are obtained. Notice that $x = 1$ is a solution of Equation (7), i.e. the curves $z = F(x)$ and $z = r$ have an intersection at the point $(1, r)$ on $xz$-plane which corresponds to the fixed point $(1, 0)$ of the system in Equations (5).
Lemma 2.2 Let \( f : \mathbb{R} \to \mathbb{R} \) be in \( C^2 \) where \( f'(x) > 0, f''(x) < 0 \) for all \( x \in \mathbb{R} \), and let \( g(x) = ax + \beta \) where \( \alpha, \beta \in \mathbb{R} \) and \( \alpha < 0 \). Furthermore, assume that \( y = f(x) \) and \( y = g(x) \) have an intersection point at \((\tilde{x}, \tilde{y})\) (Note that, there is not another intersection point.). Take any point \((x_0, y_0)\) on the curve \( y = f(x) \) such that \( x_0 > \tilde{x} \).

Then, the line tangent to the curve \( y = f(x) \) at the point \((x_0, y_0)\) intersects \( g(x) \) at the point \((x_1, y_1)\) where \( \tilde{y} < y_1 < y_0 \).

**Proof** Firstly, let us define the regions

\[
R_1 = \{(x, y) : x < \tilde{x}, y > \tilde{y}\},
\]

\[
R_2 = \{(x, y) : x < \tilde{x}, y < \tilde{y}\},
\]

\[
R_3 = \{(x, y) : x > \tilde{x}, y < \tilde{y}\},
\]

\[
R_4 = \{(x, y) : x > \tilde{x}, y > \tilde{y}\}.
\]

Figure 2.

By using the monotonicity of the functions, it is easy to show that every point on the curve \( y = f(x) \) lay in the set \( R_2 \cup R_4 \cup \{(\tilde{x}, \tilde{y})\} \). Similarly, the line \( y = g(x) \) lays in the set \( R_1 \cup R_3 \cup \{(\tilde{x}, \tilde{y})\} \).

Figure 1. \( z = F(x), z = r \): (a) \( \mu = 1 \), (b) \( \mu < 1 \), and (c) \( \mu > 1 \).

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

(a) If \( \mu = 1 \), then \( F'(1) = 0 \) and the only intersection point is at \( x = 1 \). From Equations (6) we obtain \( y = 0 \). Hence, the fixed points are \((0, 0)\) and \((1, 0)\). There are no positive fixed points for this case (Figure 1(a)).

If \( \mu < 1 \), then \( F'(1) > 0 \). We know that \( F''(x) < 0 \) and \( \lim_{x \to \infty} F(x) = -\infty \) for all \( x \). This means that there exists another fixed point which is different from \((1, 0)\). Let us denote the \( x \)-component of this fixed point by \( x = \omega \), then \( \omega > 1 \). We have \( y = (r/q)(1 - \omega) < 0 \) by Equations (6) (Figure 1(b)). Since one component of \((\omega, (r/q)(1 - \omega))\) is negative, this fixed point is not of interest in biology and hence it will be omitted.

(b) If \( \mu > 1 \), then \( F'(1) < 0 \). We know that \( F''(x) < 0 \) for all \( x \) and \( F'(0) > 0 \). Hence, there exists another fixed point which is different from \((1, 0)\). Let us denote the \( x \)-component of this fixed point by \( x = \ell \). Then \( \ell < 1 \) and hence \( y = (r/q)(1 - \ell) > 0 \) by Equations (6) (Figure 1(c)). Hence \((\ell, (r/q)(1 - \ell))\) is the coexistence fixed point.

\[\square\]
Take any point \((x_0, y_0)\) on the curve \(y = f(x)\) such that \(x_0 > \bar{x}\). Since \(f''(x) < 0\), except the tangent point, every point of the tangent line at \((x_0, y_0)\) is above the curve \(y = f(x)\). The tangent line and the line \(y = g(x)\) intersect at some point \((x_g, y_1)\) since the slopes of the lines have different signs. The point \((x_g, y_1)\) is above the function \(y = f(x)\). The points on the line \(y = g(x)\) which are above the curve \(y = f(x)\) must be in the set \(R_1\). Hence, the intersection occurs in that region which guaranties that \(\bar{y} < y_1\). And, since the tangent line is monotonically increasing, \(x_g < x_0\) implies \(y_1 < y_0\). So, we have the desired result, \(\bar{y} < y_1 < y_0\) (Figure 3).

Now we construct an iteration in order to approach the intersection point of the graphs of the two functions in Lemma 2.2.

Let \((x_0, y_0)\) be a point in the region \(R_4\). Now, the tangent line to the curve \(y = f(x)\) and passing through the point \((x_0, y_0)\) will intersect the line \(y = g(x)\) at a point, let us call it \((x_{1g}, y_1)\). Now the horizontal line passing through the point \((x_{1g}, y_1)\) will intersect the curve \(y = f(x)\) at a point which will be denoted by \((x_1, y_1)\). Next we find the point of intersection of the tangent line to \(y = f(x)\) passing through the point \((x_1, y_1)\) and the line \(y = g(x)\) and we call this point \((x_{2g}, y_2)\). Now the horizontal line through \((x_{2g}, y_2)\) will intersect \(y = f(x)\) at the point \((x_2, y_2)\). Hence, iteratively we
construct a sequence of points \{(x_t, y_t)\} on the curve \(y = f(x)\) in which every point \((x_t, y_t)\) lies in the Region \(R_4\). Consequently, we have a monotonically decreasing sequences \(y_0 > y_1 > y_2 > \cdots > \bar{y}\) and \(x_0 > x_1 > x_2 > \cdots > \bar{x}\). Moreover, one may show that
\[
y_1 = \frac{\beta f'(x_0) - \alpha y_0 + \alpha f'(x_0)x_0}{f'(x_0) - \alpha}.
\] (8)

The next result establishes the above iteration procedure.

**Theorem 2.3** Let \(f : \mathbb{R} \to \mathbb{R}\) be in \(C^2\) where \(f'(x) > 0, f''(x) < 0\) for all \(x \in \mathbb{R}\). Consider \(g(x) = \alpha x + \beta\) where \(\alpha, \beta \in \mathbb{R}\) and \(\alpha < 0\). Furthermore, assume that \(f\) and \(g\) intersect at the point \((\bar{x}, \bar{y})\). If \(x_0 > \bar{x}\), then for any initial value \(y_0 = f(x_0)\), \(\bar{y}\) is the only fixed point of the difference equation
\[
y_{t+1} = \frac{\beta + \alpha u(Y_t) - \alpha Y_t u(Y_t)}{1 - \alpha u(Y_t)},
\]
where \(u = f^{-1}\). Moreover, this fixed point is asymptotically stable.

**Proof** In order to find the fixed points we solve the following equation:
\[
Y = \frac{\beta + \alpha u(Y) - \alpha Y u'(Y)}{1 - \alpha u'(Y)}.
\] (9)

Hence, we obtain
\[
Y = \alpha f^{-1}(Y) + \beta.
\] (9)

It is clear that \(\bar{y}\) is a solution. Since the function \(f\) is increasing \((f'(x) > 0)\), so is \(f^{-1}\). Hence, by the fact that the function at the left-hand side of Equation (9) is increasing and the one on the right-hand side is decreasing, there can be only one solution. We conclude that \(Y = \bar{y}\) is the only solution, which is the \(y\)-component of the intersection point.

By Lemma 2.2, \(Y_t\) is decreasing and bounded below. Hence, its limit is the fixed point \(Y = \bar{y}\). ■

Now, we are ready to focus on the isoclines of system (⋆):
\[
y = -\frac{r}{q}x + \frac{r}{q},
\] (10)
\[
y = \mu x(1 - e^{-\gamma}).
\]

By Theorem 2.3 we have
\[
g(x) = -\frac{r}{q}x + \frac{r}{q},
\]
\[
f^{-1}(y) = \frac{y}{\mu(1 - e^{-\gamma})}.
\] (11)

By Lemma 1, if \(\mu > 1\) we have a positive fixed point which means that the isoclines have a point of intersection. We have \(\alpha = -\frac{r}{q} + 0\) and \(\beta = \frac{r}{q}\). Moreover, \(f'(x) > 0\) and \(f''(x) < 0\). Hence, by Theorem 2.3, the difference equation that have \(\bar{y}\) as its fixed point is given by
\[
y_{t+1} = \frac{r(\mu + e^{2\gamma}\mu - e^{\gamma}(\gamma^2 + 2\mu))}{q\mu + e^{2\gamma}(r + q\mu) - e^{\gamma}(r + ry_t + 2q\mu)} = G(y_t).
\] (12)

The graph of the function \(y_{t+1} = G(y_t)\), in Equation (12), is given in Figure 4 for some particular values of parameters.
The iteration is shown in Figure 5.

The iteration in Equation (12) gives rise to the sequence \( \{(X_t, Y_t)\} \) with \( Y_t > y^* \), where \( y^* \) is the \( y \)-component of the coexistence fixed point of the system \( (\ast) \). We now create a new sequence \( \{(X_t, \tilde{Y}_t)\} \), where \( \tilde{Y}_t \) is the \( y \)-component of the point on the isocline \( y = (r/q)(1 - x) \) with the \( x \)-component equals to \( X_t \).

Now \( X_t = f^{-1}(Y_t) = Y_t/\mu(1 - e^{-Y_t}) \). Hence, the equation for \( \tilde{Y}_t \) is given by

\[
\tilde{Y}_t = \frac{r}{q} \left( 1 - \frac{Y_t}{\mu(1 - e^{-Y_t})} \right).
\]

So for \( Y_0 > y^* \), we have

\[
\tilde{Y}_t < y^* < Y_t \quad \text{for all } t \geq 0. \tag{13}
\]

We will use this fact in studying the stability of the coexistence fixed point \( (x^*, y^*) \).

3. Stability of system \( (\ast) \)

3.1. Stability of extinction and exclusion fixed points

**Theorem 3.1** For system \( (\ast) \), the following statements hold true:

(a) \( (0, 0) \) is unstable.
(b) \( (1, 0) \) is asymptotically stable if \( 0 < \mu < 1 \) and \( 0 < r \leq 2 \) or \( 0 < \mu \leq 1 \) and \( 0 < r < 2 \).

**Proof** The Jacobian matrix of the map

\[G(x, y) = (x \exp[r(1 - x) - qy], \mu x[1 - \exp(-y)])\]

is

\[
JG(x, y) = \begin{pmatrix}
 e^{r-rx-qy}(1 - rx) & -q e^{r-rx-qy}x \\
 -q e^{r-rx-qy} & \mu - e^{-\gamma} \mu x
\end{pmatrix}.
\]
Figure 5. Isoclines and the iterations of $y_t = G(y_t)$.

(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 $r > 0$, $e^r > 1$. Thus $(0, 0)$ is unstable. We also notice that any point with the form $(0, y)$ is eventually fixed point, because starting with $(0, y)$, we get $G(0, y) = (0, 0)$.

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

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

The eigenvalues for this matrix are $\lambda_1 = 1 - r$ and $\lambda_2 = \mu$. Thus $\rho(JG(1, 0)) < 1$ if and only if $0 < r < 2$ and $0 < \mu < 1$. Hence $(1, 0)$ is locally asymptotically stable if $0 < r < 2$ and $0 < \mu < 1$.

Two issues remain unresolved. The first is the case when $\mu = 1$ and $r < 2$ in which the eigenvalue $|\lambda_1| < 1$ and $\lambda_2 = 1$. The second case is when $\mu < 1$ and $r = 2$ in which the eigenvalue $\lambda_1 = -1$ and $|\lambda_2| < 1$.

Let us now consider the first case. In order to apply the center manifold theorem [3,5,7,10], it is more convenient to make a change of variables in system (⋆) so we can have a shift from the point $(1, 0)$ to $(0, 0)$. Let $u = x - 1$ and $v = y$. Then the new system is given by

$$u_{t+1} = (u_t + 1) \exp[-ru_t - qv_t] - 1,$$
$$v_{t+1} = \mu(u_t + 1)[1 - \exp(-v_t)].$$

(14)

The Jacobian of the planar map given in Equations (14) is

$$\tilde{J}G(u, v) = \begin{pmatrix} cc - e^{-ru - qv}(-1 + r + ru) & -e^{-ru - qv}(1 + u) \\ \mu - e^{-v} & e^{-v}(1 + u) \mu \end{pmatrix}.$$  

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

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

When $\mu = 1$, we have

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

Now we can write the equations in system (14) as

$$u_{t+1} = (1 - r)u_t - qv_t + \tilde{f}(u_t, v_t),$$
$$v_{t+1} = v_t + \tilde{g}(u_t, v_t),$$

(15)

where

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

and

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

Let us assume that the map $h$ takes the form

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

Now we are going to compute the constants $\alpha$ and $\beta$. The function $h$ must satisfy the center manifold equation

$$h(v + \tilde{g}(h(v), v)) - [(1 - r)h(v) - qv + \tilde{f}(h(v), v)] = 0.$$
The Taylor series expansions, at the point $v = 0$, are evaluated for the equation above. Equating the coefficients of the series, we obtain the system of equations

$$\frac{q^2}{r^2} + \frac{q}{2r} + \alpha r = 0$$

and

$$3q^2 + 6r^2(\alpha - \beta r) + qr(1 + 6\alpha(3 + r)) = 0.$$ 

Solving the system we get

$$\alpha = -\frac{q(2q + r)}{2r^3}, \quad \beta = \frac{q(-15qr + (3 + r)r^2 - 6q^2(3 + r))}{6r^5}. \quad (16)$$

Thus on the center manifold $u = h(v)$ we have the following map:

$$P(v) = \frac{1}{6} \left( 6 - \frac{6qv}{r} - \frac{3q(2q + r)v^2}{r^3} + \frac{q(-15qr + (3 + r)r^2 - 6q^2(3 + r))v^3}{r^5} \right) \times (1 - e^{-v}).$$

Calculations show that $P'(0) = 1$ and $P''(0) = -1 - 2q/r < 0$. Hence, for the map $P$, the origin is semistable from the right (Figure 6).

The numerical evidence that $u = h(v)$ is a good candidate for a center manifold is shown in Figure 7.

![Figure 6](image-url)

Figure 6. The map $P$ on the center manifold $u = h(v)$ where $\mu = 1$, $q = 1.6$, and $r = .8$. 
Thus, for this case the exclusion fixed point is asymptotically stable.

Note that the actual center manifold at the point \((1, 0)\) which is given in Figure 7 is following:

\[ x = 1 - \frac{q}{r} y + \alpha y^2 + \beta y^3 + O(y^4), \]

where \(\alpha\) and \(\beta\) are given in Equation (16).

Now, let us consider the case that \(\mu < 1\) and \(r = 2\) in which the eigenvalue \(\lambda_1 = -1\) and \(|\lambda_2| < 1\).

When \(r = 2\) we have

\[ \tilde{J}G(0, 0) = \begin{pmatrix} -1 & -q \\ 0 & \mu \end{pmatrix}. \]

Now we can write the equations in system (14) as

\[ u_{t+1} = -u_t - q v_t + \tilde{f}(u_t, v_t), \]
\[ v_{t+1} = \mu v_t + \tilde{g}(u_t, v_t), \]

where

\[ \tilde{f}(u_t, v_t) = -1 + u_t + e^{-2u_t-qv_t}(1 + u_t) + q v_t \]

and

\[ \tilde{g}(u_t, v_t) = (1 - e^{-v_t})\mu(1 + u_t) - \mu v_t. \]

Let us assume that the map \(h\) takes the form

\[ h(u) = \alpha u^2 + \beta u^3 + O(u^4), \quad \alpha, \beta \in \mathbb{R}. \]
Now we are going to compute the constants $\alpha$ and $\beta$. The function $h$ must satisfy the center manifold equation

$$h(-u - qh(u) + \tilde{f}(u, h(u))) - \mu h(u) - \tilde{g}(u, h(u)) = 0.$$ 

Solving the above functional equation yields:

$$\alpha - \alpha \mu = 0$$

and

$$2\alpha^2 q - \alpha \mu - \beta (1 + \mu) = 0.$$ 

Hence, $\alpha = \beta = 0$. Hence $h(u) = 0$. Thus on the center manifold $v = 0$, we have the following map:

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

Simple calculations show that $Q'(0) = -1$. The Schwarzian derivative of the map $Q$ at the origin is $-4 < 0$. Hence, the exclusion fixed point $(1, 0)$ is asymptotically stable.

Notice that the center manifolds estimated are only locally defined.

3.2. The estimation of the stability region of the coexistence fixed point in the parameter space

In this section, the estimation of the stability region of the coexistence fixed point in $r-\mu$ parameter space is presented.

**Lemma 3.2** For the functions $f, g, \tilde{f}, \tilde{g} : \mathbb{R}^2 \to \mathbb{R}$, let

$$A = \{(a, b) : f(a, b) < g(a, b)\},$$

$$\tilde{A} = \{(a, b) : \tilde{f}(a, b) < \tilde{g}(a, b)\}.$$ 

If $f(a, b) < \tilde{f}(a, b)$ and $\tilde{g}(a, b) < g(a, b)$ for all $a, b \in \mathbb{R}$, then $\tilde{A} \subset A$.

**Proof** For $\tilde{A} = \emptyset$, it is trivial. Now let $\tilde{A} \neq \emptyset$. Take $(x_0, y_0) \in \tilde{A}$. Then $\tilde{f}(x_0, y_0) < \tilde{g}(x_0, y_0)$. Hence, $f(x_0, y_0) < \tilde{f}(x_0, y_0) < \tilde{g}(x_0, y_0) < g(x_0, y_0)$ from which we conclude that $(x_0, y_0) \in A$. Thus, $\tilde{A} \subset A$. 

In Section 2, we give a symbolic approximation of the coexistence fixed point. To obtain the stability region for the fixed point, we use Equation (13), Lemma 3.2 and the following Trace-Determinant Formula [5]:

$$|\text{Tr}(J^*)| - 1 < \text{Det}(J^*) < 1,$$

where $J^*$ is the Jacobian matrix evaluated at the coexistence fixed point.
It is equivalent to
\[
\text{Det}(J^*) < 1 \wedge \text{Det}(J^*) > \text{Tr}(J^*) - 1 \wedge \text{Det}(J^*) > -\text{Tr}(J^*) - 1.
\]

Firstly, we convert the Jacobian of the system at the coexistence fixed point \((x^*, y^*)\) to the following form in which, \(x^*\) is eliminated:
\[
J^* = \begin{pmatrix}
1 - r + qy^* & -q + \frac{q^2y^*}{r} \\
\frac{r_y^*}{r - qy^*} & \mu - y^* - \frac{\mu qy^*}{r}
\end{pmatrix}.
\]
The determinant and the trace of \(J^*\) are
\[
\text{Det}(J^*) = \frac{1}{r} [r^2(y^* - \mu) - qy^*(1 + qy^*)\mu + r(-qy^* + \mu) + y^*(-1 + q + 2q\mu)],
\]
\[
\text{Tr}(J^*) = 1 - r + (-1 + q)y^* + \mu - \frac{qy^*\mu}{r}.
\]

3.2.1. Case 1. \(\text{Det}(J^*) < 1\)

The region on \(r-\mu\) parameter space for the condition \(\text{Det}(J^*) < 1\) is given by
\[
A = \{(r, \mu) : \mu r - \mu r^2 - r + (2\mu qr + r^2 + qr)y^* < (qr + q^2\mu)y^* + (r + q\mu)y^*\}.
\]
Let
\[
A_t = \{(r, \mu) : \mu r - \mu r^2 - r + (2\mu qr + r^2 + qr)Y_t < (qr + q^2\mu)Y_t^2 + (r + q\mu)Y_t\}. \tag{18}
\]

By Lemma 3.2 and the bounds in Equation (13), we have \(A_t \subset A\) for all \(t \geq 0\). Similarly, we obtain \(A_0 \subset A_1 \subset A_2 \subset \cdots \subset A_t \subset \cdots \subset A\). Hence, for every point \((r, \mu)\) in the region \(A_t\), the condition \(\text{Det}(J^*) < 1\) is satisfied for any \(t\).

3.2.2. Case 2. \(\text{Tr}(J^*) < 1 + \text{Det}(J^*)\)

By using the similar idea as Case 1, we convert this inequality to the form where both sides are monotonic functions with respect to \(y^*\) and use the bounds in Equation (13) to obtain the region
\[
B_t = \{(r, \mu) : r^2 - \mu r^2 + (2\mu qr + r^2)Y_t > (\mu q^2 + qr)Y_t^2\}. \tag{19}
\]

3.2.3. Case 3. \(-1 - \text{Det}(J^*) < \text{Tr}(J^*)\)

For this case, similarly we obtain the region
\[
C_t = \{(r, \mu) : -2r - 2\mu r + r^2 + (2\mu qr + 2r)Y_t + (mq^2 + qr)Y_t^2 < (2mqr + r^2 + 2qr)Y_t\}. \tag{20}
\]

In order to obtain the stability region in the \((r, \mu)\) plane, let us take \(q = 1.6\). By numeric computations, we obtain the regions \(A_5, B_5,\) and \(C_5\) which are subsets of the regions satisfying \(\text{Det}(J^*) < 1, \text{Det}(J^*) > \text{Tr}(J^*) - 1\) and \(\text{Det}(J^*) > -\text{Tr}(J^*) - 1\), respectively. Since the intersection of the sets \(A_5, B_5,\) and \(C_5\) is a subset of the stability region, finally, we obtain the approximated stability region of the coexistence fixed point. Furthermore, on the borderline of
For the point \((0, 0)\), since \(|\lambda_1| = e^r > 1\) and \(|\lambda_2| = 0 < 1\), the extinction fixed point is a saddle for all values of the parameters \(r\) and \(\mu\). For this point, the \(x\)-axis is the unstable manifold and the \(y\)-axis is the stable manifold.

Now, let us focus on the exclusion fixed point, \((1, 0)\); by using a similar procedure to that used for the center manifold in the proof of Lemma 3.1, we obtain the stable and unstable manifolds which are locally defined. In model \((\ast)\), the saddle scenario for the exclusion fixed point occurs when \(r > 2\), \(\mu < 1\), or \(r < 2\), \(\mu > 1\).

4.1.1. Case 1. \(r > 2\) and \(\mu < 1\)

Shifting the exclusion fixed point from \((1, 0)\) to \((0, 0)\) we have the following Jacobian matrix:

\[
\tilde{J}G(0, 0) = \begin{pmatrix} 1 - r & -q \\ 0 & -\mu \end{pmatrix}.
\]
Figure 9. Approximated stability region for coexistence fixed point: (a) $q = 0.00001$, (b) $q = 0.01$, (c) $q = 0.1$, (d) $q = 0.15$, (e) $q = 0.5$, (f) $q = 0.6$, (g) $q = 1$, (h) $q = 2.4$, and (i) $q = 10$.

Now we can write the equations in system (14) as

\begin{align}
    u_{t+1} &= (1 - r)u_t - qv_t + \tilde{f}(u_t, v_t), \\
    v_{t+1} &= \mu v_t + \tilde{g}(u_t, v_t),
\end{align}

(21)

where

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

and

$$\tilde{g}(u_t, v_t) = (1 - e^{-v_t})\mu (1 + u_t) - \mu v_t.$$
Figure 10. Stable manifold for the exclusion fixed point $(1, 0)$ (the dashed curve). $r = 2.03 > 2$, $\mu = .9 < 1$, and $q = 1.2$.

Notice that since $\mu < 1$, the stable manifold is tangent to the corresponding eigenspace at the fixed point. The function $h$ must satisfy the equation

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

In order to solve the functional equation, the Taylor series expansions of required functions are calculated and solving the system we get $\alpha$ and $\beta$ which locally determine the stable manifold $u = h(v)$ for the exclusion fixed points. Due to the big size of the formulas for the constants $\alpha$ and $\beta$ we omit them. In Figure 10, the stable manifold is presented. There are two orbits with initial points (.888, .2) and (.98, .2). The first initial point is on the stable manifold.

In order to find the unstable manifold for the exclusion fixed point, we use the same idea. However, we assume here that the map $h$ takes the form

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

We obtain that $\alpha = 0$ and $\beta = 0$.

When $y_i = 0$ in Equation (*), the dynamics of population $x_n$ is determined by the one-dimensional Ricker map. If $2 < r < r_2$, where $r_2 \approx 2.5264$, the fixed point $(1, 0)$ loses its stability and a new asymptotically periodic orbit $\{\bar{x}_1, \bar{x}_2\}$ of period 2 is born. The unstable manifold is the open interval $[\bar{x}_1, \bar{x}_2]$ that lies on the $x$-axis. As $r$ increases, period-doubling bifurcation occurs until $r \approx 2.6294$, after which we enter the chaotic region. Hence, the boundary of the unstable manifold shrinks to 0 as $r > 2$ increases. More details on the periodic points of the Ricker map and the basin of attractions of its periodic orbits may be found in [6].
Figure 11. Stable and unstable manifolds for the exclusion fixed point \((1, 0)\). \(\mu = 1.2 > 1, r = 0.5 < 2, \) and \(q = 0.5\)

4.1.2. Case 2. \(r < 2\) and \(\mu > 1\)

In order to find the unstable manifold for this case, let us assume that the map \(h\) takes the form

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

Since \(\mu > 1\), the unstable manifold is tangent to the corresponding eigenvector at the fixed point.

Since the method we use for this case is the same as in the previous case, we omit the details.

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

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

Figure 11.

5. Bifurcation scenarios

In this section, a bifurcation diagram for the positive fixed point is presented. In Figure 12, Tr–Det Diagram for a general system is shown. We give the corresponding regions for system (\(\ast\)) in Figure 13: \(B_i\) is the corresponding region for \(A_i\).

We can see from these figures that on the border between the stability region and region \(B_3\), we have period-doubling bifurcation. The saddle-node bifurcation occurs when the point \((r, \mu)\) moves from the stability region to region \(B_7\). We find that the map \(u = P(v)\) obtained by the center manifold theorem satisfies the conditions

\[
\frac{\partial P}{\partial \mu}(\mu^*, v^*) = 0 \quad \text{and} \quad \frac{\partial^2 P}{\partial \mu^2}(\mu^*, v^*) = 0,
\]

where \(\mu^* = 1\) and \(v^* = 0\) for the case. Hence, this bifurcation is a transcritical bifurcation [5].

The system also possesses a Neimark-Sacker bifurcation [5] when the parameters are on the border between the stability region and region \(B_1\), as shown in Figure 14.
Figure 12. Tr–Det diagram for general two-dimensional discrete-time system.

Figure 13. Corresponding regions for system (•).
Figure 14. Types of bifurcation on the borderline of the stability region $q = 1.6$.

Figure 15. $(r, \mu)$ is inside the stability region: (a) bifurcation diagram, (b) phase diagram.

Figure 15 depicts the phase-space diagram and regions in the parameter space when $(r, \mu)$ is in the stability region and close to the border of the Neimark-Sacker bifurcation. The case when the point $(r, \mu)$ passes the bifurcation curve is given in Figure 16. The black points in Figures 15(a) and 16(a) represent the point $(r, \mu)$. 
6. Conclusions

In this paper, we investigated the stability and bifurcation of a generalized Beddington host-parasitoid model. We were able to study the stability of the coexistence fixed point without actually computing it. This is accomplished by using upper and lower sequences approaching the coexistence fixed point. By this, we have established the mathematical analysis and provided novel tools to study the stability of of models where there is no explicit formula for the fixed points. Our results confirmed the known results in the literature for the special case $a = b$ that were obtained via simulation. The invariant manifolds for the extinction and exclusion fixed points were obtained. Due to the lack of an explicit formula of the coexistence fixed point, we were not able to investigate the Neimark-Sacker bifurcation and the other types of bifurcations. The presence of Sacker-Neimark bifurcation was shown via numerical simulations. Moreover, the global dynamics of the system has not been determined and needs further study. Future research will include the investigation of the global stability of our system via the newly established tools and techniques that have been recently developed by Balreira et al. [1]. It is expected that for certain values of the parameters, our system is monotone. In that case, one may utilize the theory of monotone dynamical systems developed by Smith [14] to determine global stability.

Future research may also include a deeper discussion and analytic results on the various bifurcation scenarios. Another direction would be the study of systems with the Allee effect [9].

From the biological perspective, we have established all the possible scenarios of the dynamics of both host and parasitoid. We have shown that under no circumstances would both host and parasitoid go to extinction. However, it is possible that parasitization of the host would fail. Moreover, we have established ecological conditions under which both host and parasitoid tend to a stable equilibrium state.

Now outside the stability region in the parameter space (Figure 14), the three bifurcation scenarios indicate the possible dynamics of both host and parasitoid. Crossing the saddle-node bifurcation line ($0 < \mu < 1$ and $0 < r < 2$), the parasitoid will go to extinction. Moreover, crossing the period-doubling bifurcation line, both populations will undergo periodic fluctuation in this sizes which may lead to erratic and chaotic fluctuations. However, crossing the Neimark-Sacker bifurcation line, the populations will spiral and tend towards a closed invariant curve. The
oscillation is caused by having a pair of complex conjugate eigenvalues of the Jacobian of our plane maps.

In conclusion, parasitization succeeds and both species persist under most ecological conditions.

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