A predator-prey model with ratio-dependent functional response and Strong Allee effect on prey

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Abstract: A ratio-dependent predator-prey model with strong Allee effect on prey is analyzed by making a parametric analysis of stability properties of dynamics on the system in which the functional response is a function of the ratio of prey to predator. It is shown that incorporating of Allee effect on prey equation significantly modifies the dynamics of the original system, as the modified model involves other non-topological equivalent behaviors. We prove the existence of a parameter subsets for which the system can have a Hopf bifurcation, a Bogdanov-Takens bifurcation, and showing the existence of separatrix curves in the phase plane determining that the long-term dynamics of the system is high sensitivity to initial conditions.

Key–Words: Predator-prey, Ratio-dependent, Allee effect.

1 Introduction

In this work we study a predator-prey model with ratio-dependent Holling type II functional response where we have incorporated Allee effect [20, 21] into the growth function for prey.

The ratio-dependent concept can be simply stated as the per capita predator growth rate should be a function of the ratio of the prey to predator abundance. The concept of ratio-dependent has been studied on predator prey models presenting solid arguments to justify that in some cases [19], especially when predators have to search (share and/or compete) for food, a more suitable predator-prey model should be based in the ratio-dependent theory [1, 13, 17]. An analysis given in [15] shows that the ratio-dependence models are capable of producing richer and more realistic dynamics than models considering only prey-dependent functional response.

The ratio-dependent predator-prey models are of particular mathematical interest because the functional response is undefined at the origin. The origin is studied using bowing up techniques [4, 5, 9, 16]. Ratio-dependent predator-prey models can display atypical and original dynamics properties which are not observed before in simple two-dimensional predator-prey models [3]. It has been shown that the origin is a non-hyperbolic node which is simultaneously attractive and saddle (repulsive), giving new inside to ecological extinction and coexistence, especially in the context of biological control [2].

We extend the study of the classical form of the ratio-dependent predator prey model [4, 16, 23] incorporating the Allee effect on the growth function of the prey. The modified model with Allee effect on the prey equation provides an interesting dynamics, since it presents up to five equilibrium points, a separatrix curve, a cusp point and so on.

Basic details on the implementation of the models are given in section 2. The results are presented in section 3, and a discussion of our finding in section 4.

2 The model

The classical form of the ratio-dependent predator-prey model has been studied in [1, 4]. The dimensionless system of equations is written as

$$\frac{dx}{dt} = x(1 - x)(x - m) - \alpha \frac{xy}{x + y}$$
$$\frac{dy}{dt} = \beta \frac{xy}{x + y} - \gamma y$$

(1)

The parameter \(\gamma\) represents the death rate of the re-defined predator \(y\). The new parameters \(\alpha\) is the maximum (asymptotic) prey death rate due to predation for an infinite number of predators, it is known as the consumption ability. The parameters \(\beta\) is the maximum (asymptotic) predator growth rate for an infinite number of prey, it is called the predator growing ability.
System (1) is analytical at all points in the \((x, y)\)-plane except at the axes \(x = 0\) and \(y = 0\), but the origin is a removable singularity. Extending the domain to the first quadrant \(x \geq 0\) and \(y \geq 0\) and then applying the time rescaling \(dt \to (x+y)dt\) we obtain the system
\[
\frac{dx}{dt} = x(x-m)(1-x)(x+y) - \alpha xy \\
\frac{dy}{dt} = \beta xy - \gamma y(x+y)
\] (2)

We propose to study the system (2) and describe its qualitative behavior over the first quadrant of the \((x, y)\)-plane, and its dependance on the positive parameters \(\alpha, \beta, \gamma, \text{and } m\).

For system (2) the prey isoclines are: \(y \sim \frac{x(x-1)(x-m)}{\alpha + mx - m + x^2}\) and the curve \(x; y\) not intersect the isocline prey curve. Therefore by analyzing the prey and predator isoclines we have that the origin \(y_2(x) = \left(\frac{\beta}{\gamma} - 1\right)x\).

The equilibria of system (2) are; the singular equilibrium \(\mathcal{O}(0, 0)\), the Allee threshold equilibrium \(E_{m}(m, 0)\), the carrying capacity equilibrium \(E_{1}(1, 0)\), and two equilibria in the first quadrant \(E_{2}(x_2, y_2)\), with
\[
x_2 = \frac{\beta(m+1) - \sqrt{\beta(4\alpha \gamma + \beta((m-1)^2 - 4\alpha))}}{2\beta} \\
y_2 = \frac{\beta(\beta(m+1) - \sqrt{\beta(4\alpha \gamma + \beta((m-1)^2 - 4\alpha))})}{2\beta \gamma}
\]
and \(E_{3}(x_3, y_3)\), with
\[
x_3 = \frac{\beta(m+1) + \sqrt{\beta(4\alpha \gamma + \beta((m-1)^2 - 4\alpha))}}{2\beta} \\
y_3 = \frac{\beta(\beta(m+1) + \sqrt{\beta(4\alpha \gamma + \beta((m-1)^2 - 4\alpha))})}{2\beta \gamma}
\]
The points \(E_2\) and \(E_3\) collide when the line \(y = \left(\frac{\beta}{\gamma} - 1\right)x\) is tangent to the prey isocline curve in which case \(x_2 = x_3\) and \(y_2 = y_3\). Moreover, both equilibrium points cease to exist when the line does not intersect the isocline prey curve. Therefore by analyzing the prey and predator isoclines we have that the system (2) has at least three equilibria and at most five equilibria.

3 Results

Lemma 1 (1) The equilibria \(\mathcal{O}, E_{m}\) and \(E_{1}\) exit for all parameter values. (2) For suitable choice of parameters there exist at most two interior equilibria of system (2) in the first quadrant.

Lemma 2 Let \(\beta > \gamma\) and \(\Delta = \beta((1-m)^2 - 4\alpha) + 4\alpha\gamma\). The number of equilibria in the interior of the first quadrant are:

(i) two interior equilibria \(E_{2}\) and \(E_{3}\), if \(\Delta > 0\),

(ii) a unique interior point when \(E_{2}\) and \(E_{3}\) collide, if \(\Delta = 0\), and

(iii) there is no interior equilibria for the system, if \(\Delta < 0\).

3.1 Stability

3.1.1 The origin \(\mathcal{O}(0, 0)\).

System (2) can be written in the form
\[
\frac{dx}{dt} = P(x, y) + P^*(x, y) \\
\frac{dy}{dt} = Q(x, y) + Q^*(x, y)
\] (3)

where \(P(x, y) = -x^2m - xy(\alpha + m)\) and \(Q(x, y) = xy(\beta - \gamma) - \gamma y^2\), are homogeneous polynomials of second order, and \(P^*(x, y) = -x^4 + x^2(1 + m) - y + x^2y(1 + m)\) the polynomial which contains the terms of order higher than two, which will be depleted, \(P^*(x, y) = \mathcal{O}((|x, y|)^3)\), and \(Q^*(x, y) = 0\) in this particular case. Our analysis is reduced to the following homogeneous system
\[
\frac{dx}{dt} = -x^2m - xy(\alpha + m) = P(x, y) \\
\frac{dy}{dt} = xy(\beta - \gamma) - \gamma y^2 = Q(x, y)
\] (4)

To further analyze the singular equilibrium \(\mathcal{O}(0, 0)\) we proceed with the blowing up method for the system (3) [9, 16]. This technique consist in expanding it on a whole axis by studying the transformed systems \((x/y, y)\) and \((x, y/x)\).

By using the change of variables \(x = x, y = ux\) on system (3) [16] and by rescaling the time variable \(dt \to xdt\) which transforms in a non-degenerated first quadrant of the \((x, y)\)-plane, except \(x = 0\), into the first quadrant of the \((x, u)\)-plane and blows up the origin \((0, 0)\) into the \(u\)-axis. We obtain the system
\[
\frac{dx}{dt} = -x(m + u(m + \alpha)) \\
\frac{du}{dt} = u(\beta + m - \gamma + u(\alpha + m - \gamma))
\] (5)

System (5) has two equilibria, both on the \(u\)-axis \((0, 0)\) and \(U(0, u^*)\) with \(u^* = -\frac{\beta + m - \gamma}{\alpha + m - \gamma}\).

The Jacobian matrix \(J(x, u)\) of system (5) is given as follows
\[
\begin{pmatrix}
-(m + u(\alpha + m)) & -x(m + \alpha) \\
0 & m + \beta - \gamma + 2u(\alpha + m - \gamma)
\end{pmatrix}
\]
The eigenvalues of the Jacobian matrix $J(0,0)$ are $\lambda_1 = -m$, and $\lambda_2 = \beta + m - \gamma$, and the eigenvalues of $J(0,w^*)$ are $\lambda_1 = \frac{\beta(\alpha + m) - \alpha m}{\alpha + m - \gamma}$, and $\lambda_2 = -(\beta + m - \gamma)$. The point $w^* = -\frac{\alpha + m - \gamma}{\beta + m - \gamma}$ must be positive to be of interest, that is, $\beta + m - \gamma$ and $\alpha + m - \gamma$ must have different signs. We summarize these results in the following lemma;

**Lemma 3** Depending on the parameters $\alpha$, $\beta$, $\gamma$, and $m$, we have the following cases for the system (5) in the first quadrant of the $(x,y)$ - plane.

1. If $\beta + m - \gamma > 0$, $\alpha + m - \gamma < 0$, then $O$ is a saddle and $U$ is asymptotically stable node.

2. If $\beta + m - \gamma < 0$, $\alpha + m - \gamma > 0$, then $O$ is asymptotically stable node and $U$ is a saddle point.

We now repeat the procedure to study the behavior of the system (3) near the $y - axis$. We use the change of variables $y = y$, $x = yw$, and $dt \to ydt$ which transforms in a non-degenerated the first quadrant of the $(x,y)$-plane, except $y = 0$, into the first quadrant of the $(w,y)$-plane and blows up the origin $O(0,0)$ into the $w$-axis.

We obtain the system

$$
\begin{align*}
\frac{dw}{dt} &= w((\alpha + m - \gamma) - w(\beta + m - \gamma)) \\
\frac{dy}{dt} &= y(-\gamma + w(\beta - \gamma))
\end{align*}
$$

(6)

System (6) has two equilibria on the $w - axis$, $O(0,0)$ and $W(w^*,0)$ with $w^* = -\frac{\alpha + m - \gamma}{\beta + m - \gamma}$. The point $W$ correspond to the point $U (w^* = 1/u^*)$, and it does not need to be analyzed again.

The Jacobian matrix $J(w,y)$ of system (6) is

$$
\begin{pmatrix}
-(\alpha + m - \gamma) - 2w(\beta + m - \gamma) & 0 \\
0 & y(\beta - \gamma) - w(\beta - \gamma)
\end{pmatrix}
$$

The Jacobian evaluated at the origin $O(0,0)$ has the following eigenvalues $\lambda_1 = -(\alpha + m - \gamma)$, and $\lambda_2 = -\gamma$.

Since $\gamma > 0$ then the stability of the origin $O(0,0)$ depends only on the sign of the term $(\alpha + m - \gamma)$ which is summarized in the following lemma.

**Lemma 4** Depending on the parameters $\alpha$, $\beta$, $\gamma$, and $m$, we have the following cases for the system (6) in the first quadrant of the $(w,y)$ - plane.

1. If $\alpha + m - \gamma < 0$, then $O$ is a saddle point.

2. If $\alpha + m - \gamma > 0$, then $O$ is an asymptotically stable node.

Assembling together the results from lemmas 3 and 4 and expressing them into the initial variables $(x,y)$, we obtain different topological structures of the origin $O(0,0)$ in the first quadrant of the $(x,y)$ - plane depending on the system parameters.

**Theorem 5** The origin in system (2) posses a parabolic and a hyperbolic sector [18] in the first quadrant determined by the line $y = -(\beta + m - \gamma)/(\alpha + m - \gamma)$. That is, there exists a separatrix curve in the phase plane which divides the behavior’s trajectories; the origin is an attractor point for certain trajectories and a saddle point for others.

### 3.1.2 The equilibria on the x-axis

The Jacobian matrix for system (2) is

$$
J(x,y) = \begin{pmatrix}
J_{11}(x,y) & x(1-x)(x-m) - x\alpha \\
y(\beta - \gamma) & x\beta - (x + 2y)\gamma
\end{pmatrix}
$$

where $J_{11}(x,y) = -4x^3 - 3x^2(y - 1) + 2xy + m(-y + x(3x + 2y - 2)) - y\alpha$.

**Lemma 6** The stability of the equilibrium $E_m$ for $0 < m < 1$ is as follows; (1) an unstable node if $\beta > \gamma$, or (2) a saddle point if $\beta < \gamma$.

**Proof** The Jacobian matrix $J(x,y)$ evaluated at the Allee threshold equilibrium $E_m(m,0)$, has eigenvalues $\lambda_1(E_m) = m^2(1-m)$, and $\lambda_2(E_m) = m(\beta - \gamma)$.

1. Since in our model is assume $0 < m < 1$ then $\lambda_1(E_m) > 0$, and the sign of $\lambda_2(E_m)$ depends on the inequality between $\beta$ and $\gamma$. That is, if $\beta > \gamma$ then $\lambda_2(E_m) > 0$. The equilibrium $E_m$ is an unstable node.

2. If $\beta < \gamma$, we have that $\lambda_2(E_m) < 0$, hence the equilibrium $E_m$ is a saddle point. The predator isocline intersects the prey isocline in the fourth quadrant, therefore there no nontrivial equilibria in the positive quadrant. But this property indeed changes the stability of the equilibrium $E_m$. □

**Lemma 7** The stability of the equilibrium $E_1$ for $0 < m < 1$ is as follows; (1) a saddle point if $\beta > \gamma$, or an stable node if $\beta < \gamma$.

**Proof** The Jacobian matrix $J(x,y)$ evaluated at the carrying capacity equilibrium $E_1(1,0)$ has eigenvalues $\lambda_1(E_1) = m - 1$, and $\lambda_2(E_1) = \beta - \gamma$.

1. Since $0 < m < 1$, $\lambda_1(E_1) < 0$ and in this case we are assuming $\beta > \gamma$, then $\lambda_2(E_1) > 0$, and the result follows.
2. Since \(0 < m < 1\) is the condition on the model, \(\lambda_1(E_1) < 0\), and in this case we are assuming \(\beta < \gamma\), therefore \(\lambda_1(E_2) < 0\). Hence \(E_1(1,0)\) is an stable node. Same as in the previous lemma in this case also there are no nontrivial equilibria in the first quadrant. \(\square\)

3.1.3 The interior equilibria

The existence of equilibria interior to the first quadrant depend the sufficient condition on the slope of the predator isoline be positive, that is, \(\beta > \gamma\), and on whether the predator and prey isolines intersect, which determined by the sign of the discriminant

\[
\Delta = \beta((1 - m)^2 - 4\alpha) + 4\alpha \gamma
\]

**Theorem 8** Let \(\Delta = \beta((1 - m)^2 - 4\alpha) + 4\alpha \gamma\). Assume the system (2) has two interior points in the first quadrant, the sufficient condition, \(\beta > \gamma\), is satisfies and \(\Delta > 0\), then we have the following results;

(a) The equilibrium \(E_2\) is a saddle point for all the parameter values for which it exits, that is, when \(\beta > \gamma\).

(b) The equilibrium \(E_3\) is:

1. asymptotically stable node if

\[
\beta \sqrt{\Delta} \left[ (1 + m) \sqrt{\beta - \sqrt{\Delta}} \right] < 2\gamma (\beta - \gamma)(\beta - \alpha),
\]

2. unstable node if

\[
\beta \sqrt{\Delta} \left[ (1 + m) \sqrt{\beta - \sqrt{\Delta}} \right] > 2\gamma (\beta - \gamma)(\beta - \alpha).
\]

**Indicating the occurrence of a Hopf bifurcation.**

**Proof** (a) For the equilibrium \(E_2\) the determinant of the jacobian matrix is reduced to

\[
Det(E_2) = \frac{\beta - \gamma}{8\beta \gamma} \sqrt{\Delta} \left[ \sqrt{\Delta} - (1 + m) \sqrt{\beta} \right]^3
\]

Assuming all parameter positives, the expression enclosed by the square brackets has been proved to be negative when the condition \(\beta > \gamma\) holds, the result follows.

(b) For the equilibrium \(E_3\) the determinant of the jacobian matrix is reduced to

\[
Det(E_3) = \frac{\beta - \gamma}{8\beta \gamma} \sqrt{\Delta} \left[ \sqrt{\Delta} + (1 + m) \sqrt{\beta} \right]^3
\]

which is positive if \(\beta > \gamma\). Therefore, computing the Trace of the Jacobian matrix evaluated at \(E_3\) we obtain the formula

\[
Tr(E_3) = \frac{\left[(1 + m)\sqrt{\beta - \sqrt{\Delta}}\right]}{4\beta^{3/2} \gamma}
\]

\[
(\beta \sqrt{\Delta} \left[ (1 + m) \sqrt{\beta - \sqrt{\Delta}} \right] - 2\gamma (\beta - \gamma)(\beta - \alpha)).
\]

The expression inside the square brackets is positive for \(\beta > \gamma\). Therefore, the sign of \(Tr(E_3)\) depends on the sign of the expression,

\[
\beta \sqrt{\Delta} \left[ (1 + m) \sqrt{\beta - \sqrt{\Delta}} \right] - 2\gamma (\beta - \gamma)(\beta - \alpha).
\]

Since it has been assumed \(\Delta > 0\), the stability of \(E_3\) follows:

1. if \(\beta \sqrt{\Delta} \left[ (1 + m) \sqrt{\beta - \sqrt{\Delta}} \right] - 2\gamma (\beta - \gamma)(\beta - \alpha) < 0\), then \(Tr(E_3) < 0\) and \(E_3\) is asymptotically stable node, and

2. if \(\beta \sqrt{\Delta} \left[ (1 + m) \sqrt{\beta - \sqrt{\Delta}} \right] - 2\gamma (\beta - \gamma)(\beta - \alpha) > 0\), then \(Tr(E_3) > 0\) and the equilibrium \(E_3\) as an unstable node. \(\square\)

**Theorem 9** Let \(\beta > \gamma\) and \(\Delta = \beta((1 - m)^2 - 4\alpha) + 4\alpha \gamma = 0\), then there exits a unique equilibriun point at the interior of the first quadrant, obtained by collapsing the equilibria \(E_2\) and \(E_3\). This unique point \(E(e_1, e_2)\) has coordinates \(e_1 = \frac{m+1}{2}\) and \(e_2 = \frac{(\beta - \gamma)}{\gamma} \left(\frac{m+1}{2}\right)\) is:

(i) a nonhyperbolic attractor node, if and only if, \(\alpha < \beta\),

(ii) a nonhyperbolic repellor node, if and only if, \(\alpha > \beta\).

(iii) a cusp point, if and only if, \(\alpha = \beta\).

**Proof** The condition \(\Delta = 0\) implies \(\gamma = \beta(4\alpha - (m-1)^2)\). Therefore the Jacobian matrix \(J(E(e_1, e_2))\) is given as follows,

\[
\begin{pmatrix}
\frac{\beta}{8\alpha} \frac{(m-1)^2(m+1)}{(m+1)(\beta - (m-1)^2 - 4\alpha)} & \frac{\beta}{8\alpha} \frac{8\alpha((m+1)(\alpha-\beta))}{(m-1)^2 - 4\beta} \\
\end{pmatrix}
\]

Hence, we have that \(det(E(e_1, e_2)) = 0\), and \(Tr(E(e_1, e_2)) = \frac{(m-1)^2(m+1)(\alpha-\beta)}{8\alpha}\), and then since \(0 < m \ll 1\) we have the results (i) and (ii).

Moreover, \(Tr(E(e_1, e_2)) = 0\) if and only \(\alpha = \beta\).

In this case we obtain the Jacobian matrix \(J(E(e_1, e_2)) = \begin{pmatrix}
\frac{\beta}{8\alpha} \frac{(m-1)^2(m+1)}{(m+1)(\beta - (m-1)^2 - 4\alpha)} & \frac{\beta}{8\alpha} \frac{8\alpha((m+1)(\alpha-\beta))}{(m-1)^2 - 4\beta} \\
\end{pmatrix}\)

which has associated Jordan matrix

\[
J_E = \begin{pmatrix}
0 & 1 \\
0 & 0 \\
\end{pmatrix}
\]

The singularity \(E(e_1, e_2)\) is a cusp point, since it is a point of codimension two we have a Bogdanov-Takens bifurcation [18]. \(\square\)
Figure 1: The Cusp point for the system (2). $\alpha = 0.3$, $\beta = 0.2$, $\gamma = 0.065$, and $m = 0.1$. The origin is a global attractor except for those orbits starting on the heteroclinic curve joining $E_m$ and $E$.

Figure 2: System (2) with $\beta < \gamma$ and no interior equilibrium points to the first quadrant. The stable manifold $W^s(E_m)$ serves as a separatrix for the orbits on the first quadrant.

4 Conclusion

The local stability, global stability, and bifurcation behavior of the model with ratio-dependent functional response and strong Allee effect have been shown. We have analyzed the system mathematically and described some of its biological applications as well.

Since the ratio-dependent model always has difficult dynamics in the neighborhood of the point $(0, 0)$ [24, 4, 16] and system (1) thus cannot be linearized there; the analytical behavior of the system closed to origin is studied using the equivalent system (2), which is continuous extension of system (1).

The new system (2) is well defined at $(0, 0)$ and can be linearized at this point, but being the Jacobian matrix at the origin a zero matrix. Using the directional blowing-up method we proved the existence of a separatrix curve dividing the behavior of trajectories in system (2) which is determined by the unstable manifold of non-hyperbolic equilibrium point $(0, 0)$ [9]; this point possess parabolic and hyperbolic sectors [18] on the phase plane, being a local attractor for a wide set of solutions. Figure 1.

Then, there are trajectories nearby this separatrix, which can have different $\omega-limit$ for the same set of parameter values, showing they are highly sensitive to initial conditions Figure 2. So, for a fixed set of parameters, the following may happen: the extinction of two populations, the coexistence for determined population sizes or the oscillation of both populations.

Extinction of one or both populations in predator-prey systems has occupied the most of the predator-prey literature since the classical experiments of Georgii Gause in 1932 [10], who endeavored to reproduce in the laboratory the cycles predicted by the Kolmogorov Theorem for predator-prey model. However, instead of the desired coexistence, the most frequent result was that the populations went extinct either immediately or after a couple of oscillations.

Also, extinction is a frequent outcome in simple laboratory predator-prey interactions as happened with experiment by Leo Luckinbill with Didinium and Paramecium in 1973 [14] and biologists had modified conditions in order to obtain a cyclic coexistence. As predator-prey interactions are inherently prone to oscillations [22], it is therefore obvious investigate the ratio-dependent functional response as a potential mechanism for the creation of population cycles.

Since traditional predator-prey models predict cyclic dynamics, extinction has been explained as the result of stochasticity occurring when the trajectories come close to the axes [13]. We have shown that for some region in the parameter space of the ratio-dependent model, multiple attractors can appear, one of them being the origin $(0, 0)$, which is undefined in system (1). Hence, extinction can be explained as a simple deterministic process in the predator-prey model with ratio-dependent functional response [13]. In this case, both the populations are driven to extinction deterministically, an outcome that our model is able to reproduce same as the classical ratio-dependent model in which the Allee effect is absent. Then, trajectories of system (1) are undoubtedly highly sensitive to disturbances and requires careful management when it is applied in contexts of conservation [13] and fisheries [7, 11].

In support of our analytical findings, numerical
simulations have been done using arbitrary data in our nondimensionalized system (2).

Acknowledgements: Authors thank to the members of the Mathematics Ecology Group from the Mathematics Institute at Pontificia Universidad Católica de Valparaíso for their valuable comments and suggestions. JDF has been partially supported by grants from the National Science Foundation (NSF Grant DMPS-0838704), the National Security Agency (NSA Grant H98230-09-1-0104), the Alfred P. Sloan Foundation and the Office of the Provost of Arizona State University.

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