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A Discrete Predator-prey Model with Allee and Refuge Effect

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Abstract. We consider a predator-prey model, where some prey are completely free from predation within a temporal or spacial refuge and the predator population is subject to Allee effect. We study the effect of the presence of refuge and Allee effect on the stability and bifurcation of the system. We investigate the existence and stability of the model as well as the stability region. We also obtain the invariant manifolds of the system.

2020 Mathematics Subject Classifications: 37N25, 37D10, 39A28, 39A30, 39A60

Key Words and Phrases: Allee Effect, Refuge Effect, Invariant Manifolds

1. Introduction

In this paper, we investigate a predator-prey model, where some prey are completely free from predation within a temporal or spacial refuge and predator are subject to Allee effect. The most common type of spacial refuge, that we investigate here, takes the form where a constant proportion of the prey population is protected. Some of studies have investigated the influence of prey refuge and concluded that the refuge used by the prey has a stabilizing effect on the predator-prey interaction and also that the prey species can be prevented well from extinction. Some studies on refuge effect can be found in [3, 12, 13].

The Allee effect is characterized by a positive correlation between population size and the mean individual fitness of a population. When the population density is low, the population will experience a reduced overall growth rate, and may increase the risk of extinction. If there are more individuals, population grows more rapidly, and the aggregation can improve the survival rate of individuals. Recently, many studies have been done on predator-prey models with Allee effect. Livadiotis, Assas, Elaydi, Kwessi, Dennis [11] investigated the impact of the Allee effect on the global dynamics of Beddington model. Some other predator-prey studies with/without Allee effect were conducted in [5–7]/[1, 9].

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Maynard Smith [17] proposed the following predator-prey model:

$$X_{t+1} = RX_t - \frac{R-1}{X_E}X_t^2 - CX_tY_t, \\ Y_{t+1} = \frac{r}{X_E}X_tY_t, \tag{1}$$

where X_t and Y_t represent the prey and predator population in year t, respectively. X_E is the equilibrium value of X_t in the absence of predator. R and r are maximum reproductive rates of prey and predator, respectively.

In [14], Murakami investigates the stability and bifurcation, including Neimark-Sacker bifurcation, of model (1).

In this paper, we study model (1) with prey and predator subject to a refuge and Allee effect, respectively. Regarding the refuge effect, we assume the presence of spacial heterogeneity. The refuge model is due to Hassel [3]. In the absence of predator, the growth of the prey population is logistic. The following model is proposed:

$$X_{t+1} = R(1-b)X_t - \frac{R-1}{X_E}(1-b)^2X_t^2 + RbX_t - \frac{(R-1)b^2}{X_E}X_t^2 - CbX_tY_t, \\ Y_{t+1} = \frac{rb}{X_E}X_tY_t\frac{Y_t}{A+Y_t}. \tag{2}$$

In equation (2), the expression $(1-b)X_t$ is the number of the prey in a protective refuge at time t, $0 < b < 1$, which has logistic growth represented by the expression $R(1-b)X_t - \frac{R-1}{X_E}(1-b)^2X_t^2$. The rest of the prey, bX_t, is affected by the predator. The expression $RbX_t - \frac{(R-1)b^2}{X_E}X_t^2 - CbX_tY_t$ gives this interaction. We provide support for the stabilizing power of physical refuge. We show that with refuge present, the host and parasitoid can, apparently, persist together indefinitely. The expression $\frac{Y_t}{A+Y_t}$ is a mate-finding Allee effect on predator.

Simplifying equation (2), we obtain the following system:

$$X_{t+1} = RX_t - \frac{R-1}{X_E}(2b^2-2b+1)X_t^2 - CbX_tY_t, \\ Y_{t+1} = \frac{rb}{X_E}X_tY_t\frac{Y_t}{A+Y_t}. \tag{3}$$

Note that, in equation (3), when $b = 1$ and $A = 0$, there is no prey in a protective refuge and no Allee effect. Hence we obtain equation (1) for this particular case. When $b = 0$, all the prey population is protected and has logistic growth while the predator population extincts in the next generation.

We apply $y_t = CbY_t$ and $x_t = \frac{rb}{X_E}X_t$ with $\alpha = R$, $\beta = \frac{2b^2-2b+1}{rb}$, and $\gamma = ACb$. Hence we obtain the following system:

$$\begin{aligned} x_{t+1} &= x_t(\alpha - \beta(\alpha-1)x_t) - x_t y_t, \\ y_{t+1} &= \frac{x_t y_t^2}{\gamma + y_t}, \end{aligned} \tag{4}$$

where $\alpha, \beta > 0$ and $\gamma > 0$.

2. Existence of the Fixed Points

In this section, we analyse the existence of fixed points of discrete system (4). Firstly, we focus on the following isocline equations:

$$\begin{aligned} x &= x(\alpha - \beta(\alpha-1)x) - xy, \\ y &= \frac{xy^2}{\gamma + y}. \end{aligned} \tag{5}$$

2.1. Extinction and Exclusion Fixed Points

In equation (5), if $x = 0$, we have the extinction fixed point $P_0 = (0,0)$ for any parameter values. If $x \neq 0$ and $y = 0$, we obtain the exclusion fixed point $P_1 = (\frac{1}{\beta}, 0)$.

2.2. Coexistence Fixed Points

If $x \neq 0$ and $y \neq 0$, the isoclines become

$$\begin{aligned} y &= -\beta(\alpha-1)x + \alpha - 1, \\ y &= \frac{\gamma}{x-1}. \end{aligned} \tag{6}$$

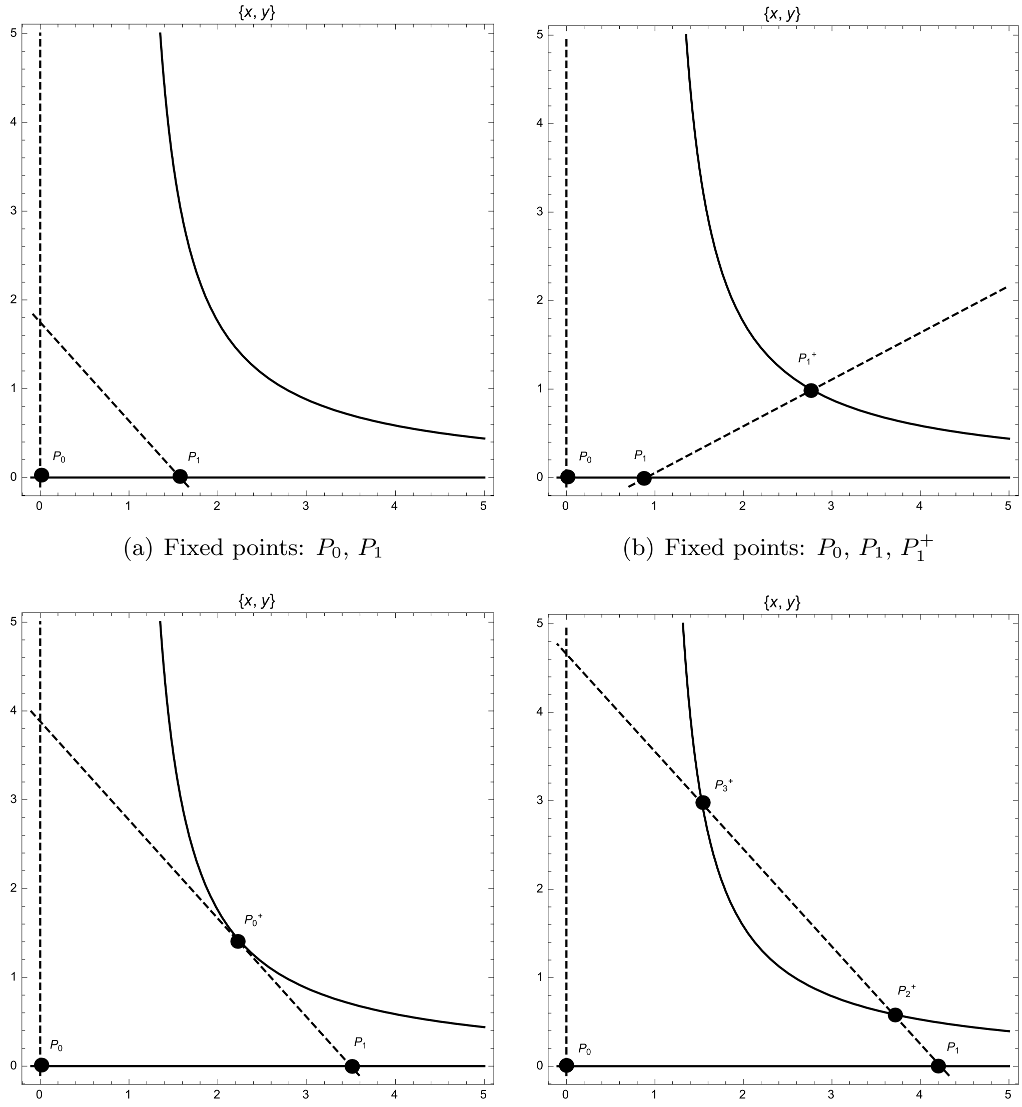
The intersection points of the isoclines in equation (6) give us the candidates for coexistence fixed points which can be found by solving the following quadratic equation:

$$\beta(\alpha-1)x^2 - (\alpha-1)(\beta+1)x + (\alpha+\gamma-1) = 0. \tag{7}$$

Note that in order to have a positive fixed point, by the second equation of system (6), it is necessary that x-component of the fixed point is bigger than 1. Therefore, we have a coexistence fixed point if and only if x^* is a real root of equation (7) and $x^* > 1$. The possible roots of the equation (7) are the following:

$$x_{1,2}^* = \frac{(\alpha-1)(\beta+1) \pm \sqrt{\Delta}}{2\beta(\alpha-1)}, \tag{8}$$

where $\Delta = (\alpha-1)^2(\beta-1)^2 - 4\beta(\alpha-1)\gamma$. In order to have positive fixed points, we must have $\Delta \geq 0$ and $x_i^* > 1$ for some $i \in \{1,2\}$. Under the condition $\Delta > 0$, we obtain two different scenario: (a) there exist two coexistence fixed points if $\alpha > 1$ and $\beta < 1$. (b) there exists one coexistence fixed point if $\alpha < 1$. For the case when $\Delta = 0$, the condition that a coexistence fixed point exists is $\beta < 1$. We obtain the following theorem for the condition of existence and the corresponding fixed points of system (4).



(a) Fixed points: P_0, P_1

(b) Fixed points: P_0, P_1, P_1^+

(c) Fixed points: P_0, P_1, P_0^+

(d) Fixed points: P_0, P_1, P_2^+, P_3^+

Figure 1: Four possible cases for existence of the fixed points. The dashed line is the isocline $x = x(\alpha - \beta(\alpha - 1)x) - xy$ whereas the solid graph is the isocline $y = \frac{xy^2}{\gamma+y}$.

Theorem 1. *The following table gives the existence condition for the fixed points of system (4).*

Fixed Point	Condition for Existence
$P_0 = (0,0)$	*Always exists*
$P_1 = \left(\frac{1}{\beta}, 0\right)$	*Always exists*
$P_0^+ = \left(\frac{\beta+1}{2\beta}, \frac{2\gamma\beta}{1-\beta}\right)$	$\beta < 1$ *and* $(\beta-1)^2 = \frac{4\beta\gamma}{\alpha-1}$
$P_1^+ = \left(\frac{(\alpha-1)(\beta+1)-\sqrt{\Delta}}{2\beta(\alpha-1)}, \frac{-(\alpha-1)(\beta-1)+\sqrt{\Delta}}{2}\right)$	$\alpha < 1$
$P_2^+ = \left(\frac{(\alpha-1)(\beta+1)+\sqrt{\Delta}}{2\beta(\alpha-1)}, \frac{-(\alpha-1)(\beta-1)-\sqrt{\Delta}}{2}\right)$	$\beta < 1,\ \alpha > 1,$ *and* $(\beta-1)^2 > \frac{4\beta\gamma}{\alpha-1}$
$P_3^+ = \left(\frac{(\alpha-1)(\beta+1)-\sqrt{\Delta}}{2\beta(\alpha-1)}, \frac{-(\alpha-1)(\beta-1)+\sqrt{\Delta}}{2}\right)$	$\beta < 1,\ \alpha > 1,$ *and* $(\beta-1)^2 > \frac{4\beta\gamma}{\alpha-1}$

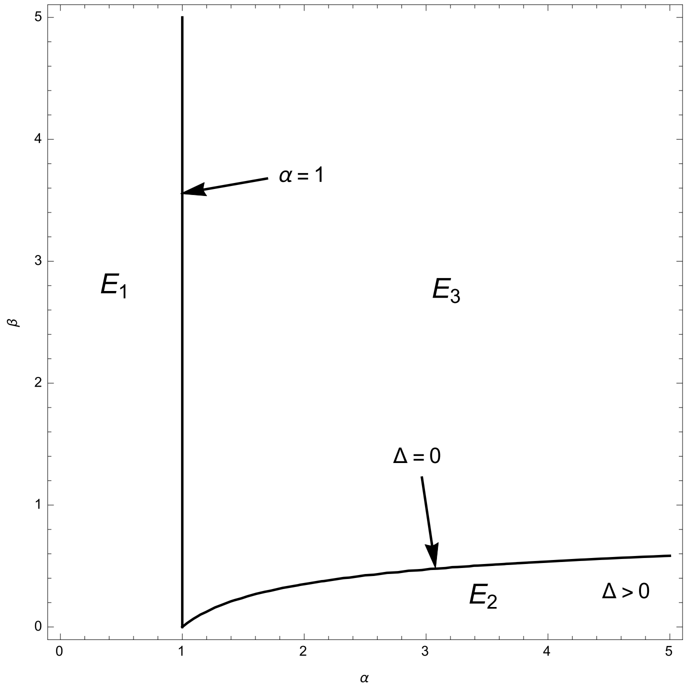


Figure 2: Existence regions for system (4) in α-β plane.

Figure 2 represents the existence regions for fixed points in α-β plane. By Theorem 1, extinction fixed point P_0 and exclusion fixed point P_1 exist for any parameter values. P_0^+ exists only on the borderline of E_2 and E_3. This is the curve where $\Delta = 0$. Region E_1 is the region for existence of P_1^+. E_2 is the region where $\Delta > 0$ and we have two distinct positive fixed points $P_{2,3}^+$.

3. Stability Analysis of System (4)

In this section, we analyse the stability of system (4). The Jacobian matrix of the system is

$$J(x,y) = \begin{pmatrix} \alpha - 2\beta(\alpha-1)x - y & -x \\ \frac{y^2}{\gamma+y} & \frac{xy(2\gamma+y)}{(\gamma+y)^2} \end{pmatrix}.$$

3.1. Stability of the Extinction Fixed Point

For the extinction fixed point $P_0 = (0,0)$, the Jacobian matrix J is given by

$$J_0 = \begin{pmatrix} \alpha & 0 \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues of the matrix are $\lambda_1 = \alpha$ and $\lambda_2 = 0$. Hence the fixed point P_0 is locally asymptotically stable if $\alpha < 1$.

3.2. Stability of the Exclusion Fixed Point

For the exclusion fixed point $P_1 = \left(\frac{1}{\beta}, 0\right)$, we have the following Jacobian matrix:

$$J_1 = \begin{pmatrix} 2-\alpha & -\frac{1}{\beta} \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues of the Jacobian matrix are $\lambda_1 = 2-\alpha$ and $\lambda_2 = 0$. Hence the fixed point P_1 is locally asymptotically stable if $1 < \alpha < 3$.

3.3. Stability of the Coexistence Fixed Points

By Theorem 1, the coexistence fixed points exist if $\Delta \geq 0$. We start with the following case:

3.3.1. Stability of P_1^+, P_2^+, and P_3^+: if $\Delta > 0$

For the case when $\Delta > 0$, we investigate three possible fixed points P_1^+, P_2^+, P_3^+. Trace and determinant of the Jacobian matrices J_1^+, J_2^+, J_3^+, respectively, at these fixed points are given by

$$tr(J_{1,2,3}^+) = \frac{1}{2}\left(\frac{\beta\gamma + \gamma \pm \sqrt{\Delta}}{\alpha+\gamma-1} - \alpha(\beta+1) \pm \sqrt{\Delta} + 6\right),$$

$$\det(J_{1,2,3}^+) = \frac{1}{2}\left(\frac{\beta\gamma + \gamma \pm \sqrt{\Delta}}{\alpha+\gamma-1} - \alpha(\beta+1) \pm 3\sqrt{\Delta} + 4\right),$$

where $\Delta = (\alpha-1)^2(\beta-1)^2 - 4\beta(\alpha-1)\gamma$.

We obtained the stability conditions applying the Tr-Det Formula

$$|tr(J)| - 1 < \det(J) < 1.$$

Theorem 2. *For system (4),*

i. P_1^+ *is unstable.*

ii. P_2^+ *is unstable.*

iii. P_3^+ *is locally asymptotically stable if*

$$2 + 3\sqrt{\Delta} < \alpha(\alpha+\beta) - K < 6 + 2\sqrt{\Delta},$$

where $K = \frac{\beta\gamma+\gamma-\sqrt{\Delta}}{\alpha+\gamma-1}$ *and* $\Delta = (\alpha-1)^2(\beta-1)^2 - 4\beta(\alpha-1)\gamma$.

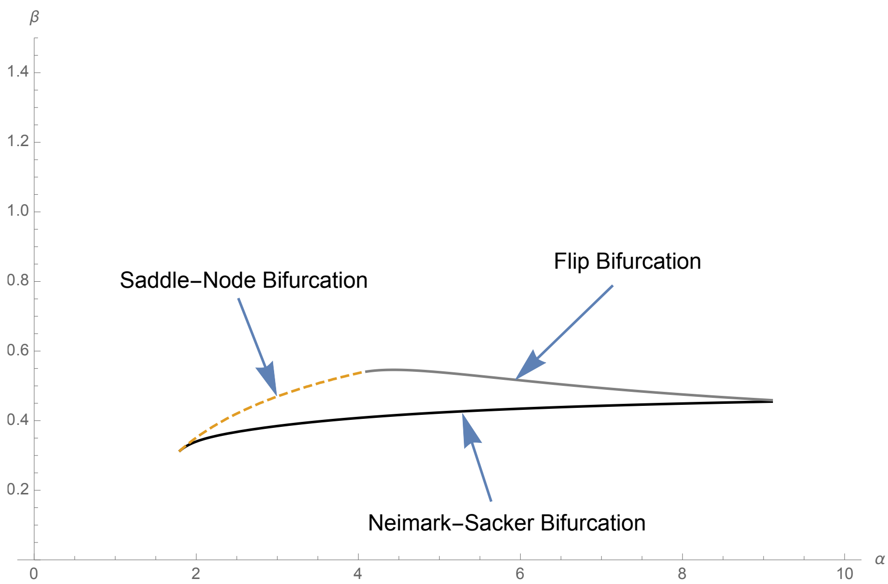
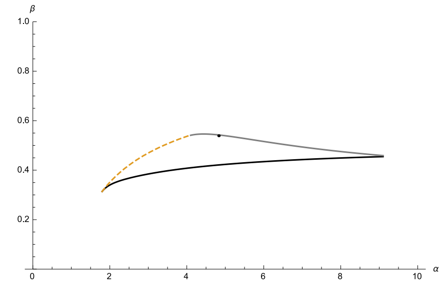
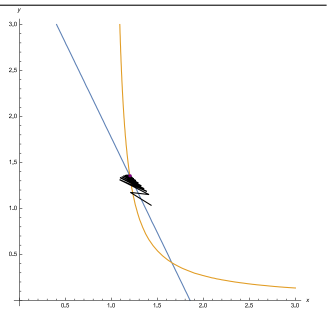
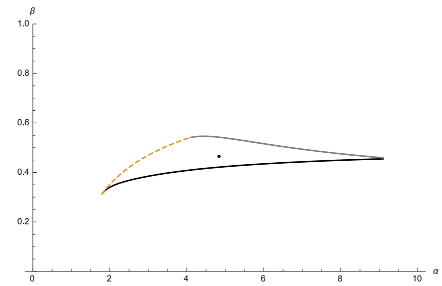
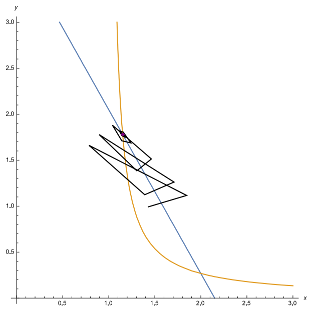
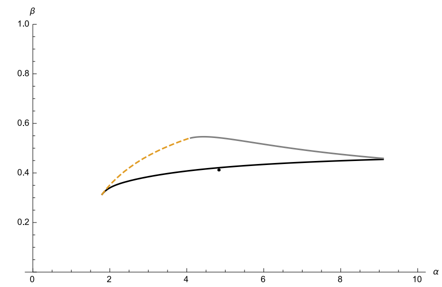
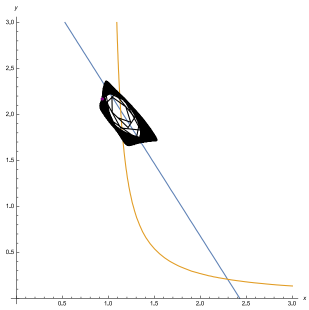


Figure 3: ($\gamma = 0.26$) Stability region of coexistence fixed point P_3^+

Figure 3 represents the stability region of the coexistence fixed point P_3^+ *in the parameter plane* α-β. *Types of bifurcations are also given. In Table 1 and 2, we give several parameter values and corresponding phase diagrams. One can see in the table that the system also exhibits Neimark-Sacker bifurcation (see [4, 8, 10, 15, 16]) for some values of parameters. This is the case when* $\det(J_3^+) = 1$ *and* $|tr(J_3^+)| < 2$. *When the parameter point is in the stability region and close to the Neimark-Sacker borderline, the orbit is spiraling and just after the parameter point* (α, β) *crosses the N-S curve, orbits converge to a closed invariant curve in the phase diagram.*

Table 1: ($\gamma = 0.26$) Stability of the coexistence fixed point.

α-β **Plane**	**Phase Diagram**
	
	
	

3.3.2. Stability of P_0^+: Non-hyperbolic case or the case $\Delta = 0$

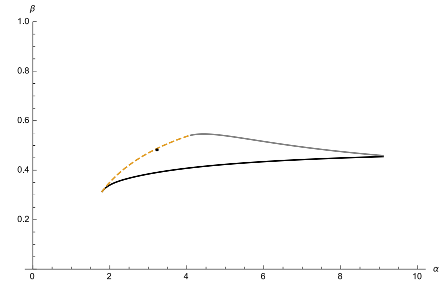
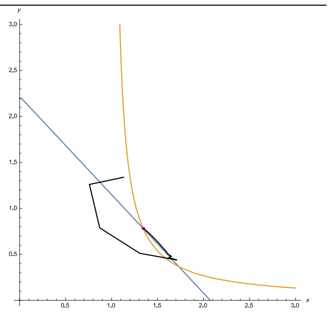
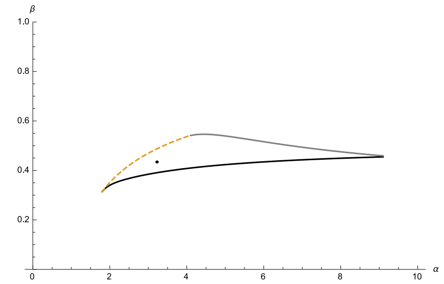
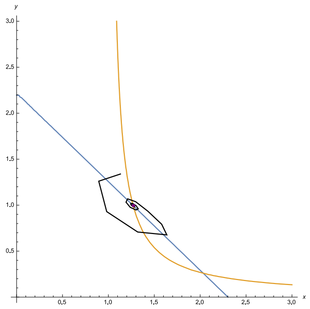
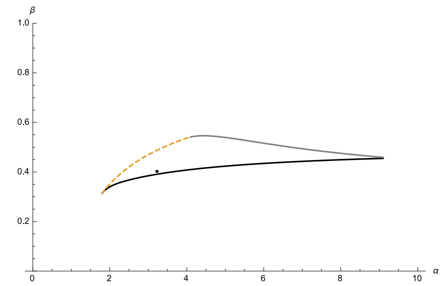
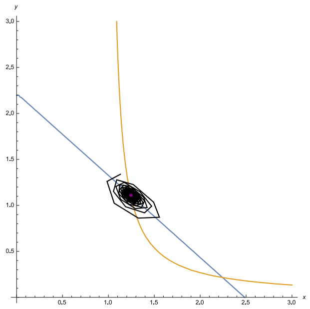
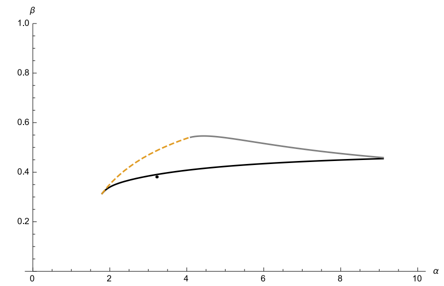
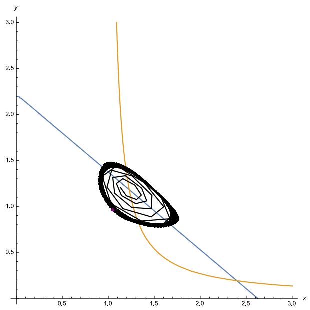
There is only one positive fixed point when $\Delta = 0$ and $\beta < 1$ by Theorem 1: $P_0^+ = \left(\frac{\beta+1}{2\beta}, \frac{2\gamma\beta}{1-\beta}\right)$. Applying this point to Jacobian matrix and eliminating γ using the equation $\Delta = 0$, we obtain

$$J_0^+ = \begin{pmatrix} \frac{1}{2}(\beta - \alpha(\beta+1) + 3) & -\frac{\beta+1}{2\beta} \\ -\frac{(\alpha-1)(\beta-1)\beta}{\beta+1} & \frac{2}{\beta+1} \end{pmatrix}.$$

The eigenvalues of the Jacobian matrix are $\lambda_1 = 1$ and $\lambda_2 = \frac{-\alpha(\beta+1)^2+\beta^2+2\beta+5}{2(\beta+1)}$. The fixed point P_0^+ is non-hyperbolic. If $|\lambda_2| > 1$, then it is unstable. If $|\lambda_2| < 1$, we have to apply the center manifold theory [2].

It is more convenient to make a change of variables in system (4) so we can have a shift from the point P_0^+ to $(0,0)$. Let $u = x - \frac{\beta+1}{2\beta}$ and $v = y - \frac{2\gamma\beta}{1-\beta}$. Then the new system

Table 2: ($\gamma = 0.26$) Stability of the coexistence fixed point.

α-β **Plane**	**Phase Diagram**
	
	
	
	

is

$$u_{t+1} = \left(\frac{\beta+1}{2\beta} + u_t\right)\left(\alpha - (\alpha-1)\beta\left(\frac{\beta+1}{2\beta} + u_t\right)\right) - \left(\frac{\beta+1}{2\beta} + u_t\right)\left(\frac{2\beta\gamma}{1-\beta} + v_t\right) - \frac{\beta+1}{2\beta},$$

$$v_{t+1} = \frac{\left(\frac{\beta+1}{2\beta} + u_t\right)\left(\frac{2\beta\gamma}{1-\beta} + v_t\right)^2}{\left(\frac{2\beta\gamma}{1-\beta} + v_t\right) + \gamma} - \frac{2\beta\gamma}{1-\beta}. \tag{9}$$

The Jacobian matrix of the system (9) at $(0,0)$ *is*

$$\tilde{J}_0^+ = \begin{pmatrix} A & B \\ C & D \end{pmatrix} = \begin{pmatrix} \frac{1}{2}(\beta - \alpha(\beta+1)+3) & -\frac{\beta+1}{2\beta} \\ -\frac{(\alpha-1)(\beta-1)\beta}{\beta+1} & \frac{2}{\beta+1} \end{pmatrix}.$$

Now we can write the equations in system (9) as

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

where $\tilde{f}(u_t, v_t)$ *and* $\tilde{g}(u_t, v_t)$ *are the rest of the expressions.*

Let us assume that the map h*, which represents a center manifold, takes the form*

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

Now we have to compute the constants a *and* b*. The function* h *must satisfy the center manifold equation*

$$h(Au + Bh(u) + \tilde{f}(u, h(u))) - Cu - Dh(u) - \tilde{g}(u, h(u)) = 0. \tag{11}$$

The Taylor series expansions, at the point $u = 0$*, are evaluated for the equation above. Equating the coefficients of the series and using the equation* $\Delta = 0$*, after some manipulations, we obtain*

$$a = -\frac{4(\alpha-1)\beta^2}{\alpha(\beta+1)^2 - \beta^2 - 3}$$

$$b = \frac{16\beta^3\left(\alpha^3(\beta+1)^3 - \alpha^2(\beta+1)(3\beta(\beta+1)+4) + \alpha\left(3\beta\left(\beta^2+\beta+1\right)+7\right) - \beta^3 + \beta - 4\right)}{\left(\alpha(\beta+1)^2 - \beta^2 - 3\right)^3}.$$

Thus on the center manifold $v = h(u)$ *we find the map* $P(u)$*. Because of the lengthy expressions we omit it here. Calculations show that* $P'(0) = 1$*. Since* $0 < \beta < 1$ *and* $|\lambda_2| < 1$*, we have* $\alpha > 1$ *and* $\alpha(\beta+1)^2 > \beta^2 + 3$*. Therefore,*

$$P''(0) = \frac{4(\alpha-1)\beta(\beta+1)}{\alpha(\beta+1)^2 - \beta^2 - 3} > 0.$$

Hence, for the map P*, the origin is semistable from the left.*

Now, we are going to find the stable manifold, which exists when $|\lambda_2| < 1$ *or*

$$-\alpha(\beta+1)^2 + \beta^2 + 2\beta + 5 < 2(\beta+1).$$

Since the stable manifold is tangent to the eigenvector at the point, let us take

$$h(u) = \frac{2(\beta-1)\beta}{(\beta+1)^2}u + au^2 + bu^3 + O(u^4), \quad a, b \in \mathbb{R}.$$

This map must satisfy the centre manifold equation (11). We calculate map Q on the stable manifold and found that

$$Q'(0) = \frac{-\alpha(\beta+1)^2 + \beta^2 + 2\beta + 5}{2(\beta+1)}.$$

Because of the long output of the computations we omit them here.

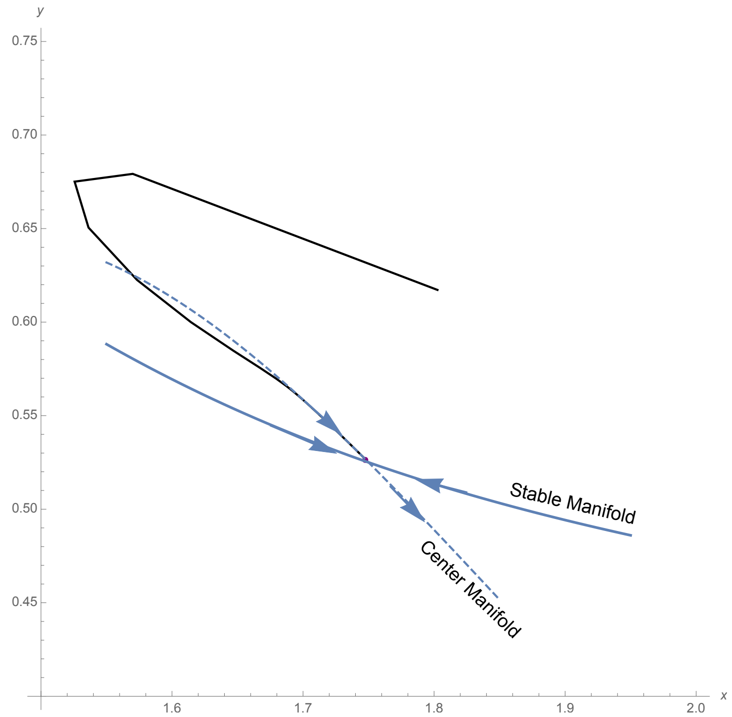


Figure 4: ($\alpha = 2.75$ and $\beta = 0.4$) Phase Diagram of system (4) with the invariant manifolds.

Stable and centre manifolds are given in the phase diagram in Figure 4 for the case $\Delta = 0$. *The dashed curve is the centre manifold for which the fixed point is semi-stable. The solid curve is the stable manifold. An orbit approaching the fixed point is also shown.*

4. Conclusions

In this paper, we investigated the stability of a predator-prey model with refuge and Allee effect. We showed that the presence of a safe refuge, where a portion of the host is in a safe refuge from predation has a stabilizing effect on the model. The conditions *for the existence of the fixed points are found. We also obtained the invariant manifolds for the positive fixed point P_0^+. Furthermore, we obtained the stability region for the coexistence fixed point P_3^+. By numerical computations, we confirm our analytic results. The Mathematica codes displaying phase diagram can be found in [18].*

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