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Stability and Hopf Bifurcation in Three-Dimensional Predator-Prey Models with Allee Effect

İlknur Kuşbeyzi Aybar [*1]

Abstract

In this study, we perform the stability and Hopf bifurcation analysis for two population models with Allee effect. The population models within the scope of this study are the one prey-two predator model with Allee growth in the prey and the two prey-one predator model with Allee growth in the preys. Our procedure for investigating each model is as follows. First, we investigate the singular points where the system is stable. We provide the necessary parameter conditions for the system to be stable at the singular points. Then, we look for Hopf bifurcation at each singular point where a family of limit cycles cycle or oscillate. We provide the parameter conditions for Hopf bifurcation to occur. We apply the algebraic invariants method to fully examine the system. We investigate the algebraic properties of the system by finding all algebraic invariants of degree two and three. We give the conditions for the system to have a first integral.

Keywords: predator-prey model, stability, Hopf bifurcation, algebraic invariants

1. INTRODUCTION

Various generalized predator-prey models that involve quadratic functions which exhibit logistic behaviour [1-3], cubic functions which show different rates of reproduction[4,5], Holling type II functions which state constant consumption[6,7] and Beddington-DeAngelis functions which indicate mutual interference and extinction[8,9] have been shown to overcome some of the biological problems of the original Lotka-Volterra model[10,11]. Population carrying capacities are introduced into these generalizations by adding the proposed functions to the self-interaction and the coupling terms [12]. Applications of these generalizations have been studied in comparison in order to find suitable functional responses for modeling predation [13].

One of these generalizations include Allee effect which presents a positive relationship between the population size and the individual fitness particularly for invading species [14] and at low population [15-17]. The individual fitness is defined as the per capita population growth rate.

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Behaviours such as cooperative predation, cooperative defense and environmental and seasonal changes may result in the Allee effect. W. C. Allee first proposed the Allee effect to describe the relationship between the population and the mean of the individual population with the following cubic model [18].

$$\frac{dx}{dt} = ax(1-x)(x-\alpha)$$

Here, x denotes the population density, a denotes the population growth rate and α is the carrying capacity.

Allee effect is defined as a positive correlation between the individual fitness and the population density [19]. Populations with low densities are shown to be more likely to extinct [20] in the population models with the Allee effect. The carrying capacity of the populations may decrease below a critical density threshold in the presence of the Allee effect. In the models representing the spread of the invading organisms, the threshold exposed by the Allee effect may increase the invasion rate [21]. Population models with the Allee effect have various applications in plants and animals, hence it is important to understand the density thresholds to understand the underlying mechanisms of the propagation and extinction of these models. In 2008, Courchamp et.al suggested that Allee effect may even occur at high population levels for some species [22].

The Allee effect can be induced into the system in the prey's growth function. Hence there are two possible versions of inducing Allee effect into a three-dimensional predator-prey system. The differences in the dynamical properties of the two possible three-dimensional predator-prey generalizations with Allee effect have been given in this work. In section 2, we investigate the one prey-two predator system with Allee growth in the prey. In section 3, we investigate the two prey-one predator system with Allee growth in the preys.

2. THE ONE PREY-TWO PREDATOR SYSTEM WITH ALLEE GROWTH IN THE PREY

The one prey- two predator model with Allee growth in the prey is given by the following set of differential equations.

$$\frac{dx}{dt} = ax(1-x)(x-\alpha) - bxy - cxz \qquad (1)$$

$$\frac{dy}{dt} = -dy + exy \qquad (1)$$

$$\frac{dz}{dt} = -fz + gxz$$

Here x denotes the population density of the prey and y and z denote the population densities of the predators. The parameter a denotes the population growth rate and α is the carrying capacity. b and c are the consumption rates of the predators y and z over the prey. On the other hand, e and g are the growth rates of the predators from the consumption. d and f are the natural death rates of the predators. All parameters are positive since they represent physical values.

Theorem 1. System (1) has at least one stable singular point.

The Jacobian matrix of system (1) is

$$\begin{pmatrix} J_{11} & -bx & -cx \\ ey & ex-d & 0 \\ gz & 0 & gx-f \end{pmatrix},$$

$$J_{11} = a(x(2-3x) + \alpha(2x-1) - by - cz.$$

Singular points and corresponding eigenvalues of the Jacobian matrix of system (1) are given in Table 1.

Table 1. Singular points and corresponding eigenvalues of the one prey-two predator system with Allee growth in the prey

	Singular point	Corresponding eigenvalue
E_0	(0,0,0)	$\{-a\alpha, -d, -f\}$
E_1	(1,0,0)	$\{a(\alpha-1), \alpha e-d, \alpha g-f\}$
E_2	(α,0,0)	$\{-a\alpha(\alpha-1), \alpha e-d, \alpha g-f\}$
E_3	$(\frac{d}{c}, \frac{a(e-d)(d-\alpha e)}{be^2}, 0)$	$\{\frac{dg}{e}-f, \lambda_{3\pm}\}$
E_4	$(\frac{f}{g}, 0, \frac{a(g-f)(f-\alpha g)}{cg^2})$	$\{\frac{ef}{g}-d, \lambda_{41,42}\}$

where

$$\lambda_{3\pm} = \frac{ad(e(1+\alpha)-2d) \pm \sqrt{ad(4e^2(d-e)(d-\alpha e)+ad(e(1+\alpha)-2d)^2)}}{2e^2}$$

and

$$\lambda_{4\pm} = \frac{af(g(1+\alpha)-2f) \pm \sqrt{af(4g^2(f-g)(f-\alpha g)+af(g(1+\alpha)-2f)^2)}}{2g^2}$$

The eigenvalues of the Jacobian matrix of system (1) at E_0 are all negative which shows that system (1) is always stable at the origin.

According to the eigenvalues of the Jacobian matrix, E_1 is a stable singular point when $e < d$, $g < f$ and $\alpha < 1$ are satisfied together.

According to the eigenvalues of the Jacobian matrix, system (1) is stable at E_2 when $e < d$ and one of the following cases is satisfied.

i. $g \le \frac{ef}{d}$ and $1 < \alpha < \frac{d}{e}$
ii. $\frac{ef}{d} < g < f$ and $1 < \alpha < \frac{f}{g}$

System (1) is stable at E_3 if $e < 2d$, $g < \frac{ef}{d}$ and $\alpha < \frac{2d}{e} - 1$.

E_4 is a stable singular point of system (1) when $e < 2d, \frac{ef}{d} < g < 2f$ and $\alpha < \frac{2f}{g} - 1$.

Therefore, system (1) is guaranteed to have at least one stable singular point which is at the origin.

Theorem 2. Hopf bifurcation occurs in system (1) if one of the following conditions is satisfied.

i. $e < d$
ii. $d < e < 2d$
iii. $g < f$
iv. $f < g < 2f$

According to the eigenvalues of the Jacobian matrix at E_3, system (1) shows Hopf bifurcation if $\alpha = \frac{2d}{e} - 1$ and one of the cases i or ii is satisfied.

Furthermore, system (1) has Hopf bifurcation at E_4 if $\alpha = \frac{2f}{g} - 1$ and one of the cases iii or iv is satisfied.

Remark 1. The Hopf bifurcation at E_3 is stable if $g < \frac{ef}{d}$ additionally.

Remark 2. The Hopf bifurcation at E_4 is stable if one of the following cases is satisfied additionally.

i. $e < d$ and $\frac{ef}{d} < g < f$
ii. $f < g < 2f$
iii. $d \le e < 2d$ and $\frac{ef}{d} < g < 2f$

Theorem 3. System (1) has a first integral if one of the following conditions is satisfied.

i. $a = d = f = 0$
ii. $a = b = f = 0$
iii. $a = c = d = 0$
iv. $a = b = c = 0$
v. $d = e = 0$
vi. $e + g = d + f = 0$
vii. $f = g = 0$

Proof. System (1) has the first integral

$$I_i = 1 + x + \frac{b}{e}y + \frac{c}{g}z + \frac{e}{2b}x^2 + xy + \frac{b}{2e}y^2 + \frac{ce}{bg}xz + \frac{c}{g}yz + \frac{c^2a}{2bg^2}z^2$$

when case i holds. System (1) has the first integrals $I_{ii_1} = 1 + y$, $I_{ii_2} = 1 + z$ and

$$I_{ii_3} = 1 + x + \frac{g}{2c}x^2 + \frac{c}{g}z + xz + \frac{c}{2g}z^2$$

when case ii is satisfied. For case iii, system has the first integral

$$I_{iii} = 1 + x + \frac{e}{2b}x^2 + \frac{b}{e}y + xy + \frac{b}{2e}y^2.$$

The first integrals of the system is

$I_{iv} = 1 + x + x^2$ for case iv and $I_v = 1 + y + y^2$ for case v. System has the first integral $I_{vi} = 1 + yz$ for case vi and $I_{vii} = 1 + z + z^2$ for case vii.

3. THE TWO PREY-ONE PREDATOR SYSTEM WITH ALLEE GROWTH IN THE PREYS

The two prey-one predator system with Allee effect in the preys' growth functions' is given by the following set of equations where *x* and *y* denote the population densities of the prey species and *z* denotes the population density of the predator species.

$$\frac{dx}{dt} = ax(1-x)(x-\alpha) - bxy \qquad (2)$$

$$\frac{dy}{dt} = -dy(1-y)(y-\beta) - eyz$$

$$\frac{dz}{dt} = -fz + gxz + hyz$$

The parameters a and d denote the population growth rates and α and β are the carrying capacities of the prey population densities. b and e are the consumption rates of the predator z over the preys. On the other hand, g and h are the growth rates of the predator from the consumption. f is the natural death rate of the predator. All parameters are positive since they represent physical values.

Theorem 4. System (2) can be stable at given singular points.

Proof. The Jacobian matrix of system (2) is

$$\begin{pmatrix} J_{11} & 0 & -bx \\ 0 & dy(2-3y) + \beta d(2y-1) - ez & -ey \\ gz & hz & hy - f \end{pmatrix},$$

$$J_{11} = a(x(2-3x) + \alpha(2x-1) - bz.$$

The singular points and corresponding eigenvalues of the Jacobian matrix of system (2) is given in Table 2.

Table 2. Singular points and corresponding eigenvalues of the two prey-one predator system with Allee growth in the preys

	Singular point	Corresponding eigenvalue
E_0	(0,0,0)	$\{-a\alpha, -d\beta, -f\}$
E_1	(1,0,0)	$\{a(\alpha-1), -d\beta, g-f\}$
E_2	(0,1,0)	$\{-a\alpha, d(\beta-1), h-f\}$
E_3	(1,1,0)	$\{a(\alpha-1), d(\beta-1), g+h-f\}$
E_4	$(\alpha,0,0)$	$\{a\alpha(1-\alpha), -d\beta, g\alpha-f\}$
E_5	$(\alpha,1,0)$	$\{a\alpha(1-\alpha), d(\beta-1), g\alpha+h-f\}$
E_6	$(0,\beta,0)$	$\{-a\alpha, d\beta(1-\beta), h\beta-f\}$
E_7	$(1,\beta,0)$	$\{a(\alpha-1), d\beta(1-\beta), g+h\beta-f\}$
E_8	$(\alpha,\beta,0)$	$\{a\alpha(1-\alpha), d\beta(1-\beta), g\alpha+h\beta-f\}$
E_9	$(\frac{f}{g}, 0, \frac{a(g-f)(f-\alpha g)}{bg^2})$	$\{\frac{ae(f-g)(f-g\alpha)}{bg^2} - d\beta, \lambda_{9\pm}\}$
E_{10}	$(\frac{f}{g}, 0, \frac{a(g-f)(f-\alpha g)}{bg^2})$	$\{\frac{bd(f-h)(f-h\beta)}{eh^2} - a\alpha, \lambda_{10\pm}\}$
E_{11}	(x_{11}, y_{11}, z_{11})	$(\{A, B \pm iC\}$
E_{12}	$(\bar{x}_{11}, \bar{y}_{11}, \bar{z}_{11})$	$\{A, B \pm iC\}$

where

$$\lambda_{9\pm} = \frac{1}{2g^2}(af(g(1+\alpha)-2f) \pm \sqrt{af(4g^2(f-g)(f-g\alpha) + af(g(1+\alpha)-2f)^2)})$$

$$\lambda_{10\pm} = \frac{1}{2h^2}(df(h(1+\beta)-2f) \pm \sqrt{df(4h^2(f-h)(f-h\beta) + df(h(1+\beta)-2f)^2)})$$

$$x_{11} = \frac{1}{2(bdg^2 - aeh^2)}\left(bdg\left(2f - h(1+\beta)\right) - aeh^2(1+\alpha) - \sqrt{\Delta_1}\right),$$

$$y_{11} = \frac{1}{2h(bdg^2 - aeh^2)}\Big(h\big(bdg^2(1+\beta) + aeh(g(1+\alpha) - 2f) + g\sqrt{\Delta_1}\big)$$

$$z_{11} = \frac{ad}{2(bdg^2 - aeh^2)^2}\Big(bdg^2\Big(2(g-f)(f - \alpha g) - h\big(1+\beta(g(1+\alpha)-2f) - h^2(1+\beta^2)\big)\Big) - g(g(1+\alpha) + h(1+\beta) - 2f)\sqrt{\Delta_2} + aeh^2(2f(g(1+\alpha) + h(1+\beta) - 2f^2 - g^2(1+\alpha^2) - gh(1+\alpha)(1+\beta) - 2\beta h^2)$$

$$\Delta_1 = \big(aeh^2(1+\alpha) + bdg(h(1+\beta) - 2f)\big)^2 - 4(bdg^2 - aeh^2)(bd(f-h)(f-\beta h) - \alpha a e h^2),$$

$$\Delta_2 = h^2(bd(bdg^2(\beta-1)^2 + 4ae(f-g)(f-\alpha g) - 2abdeh(1+\beta)\big(2f - g(1\alpha)\big) + ae(4b\beta d + aeh^2(\alpha-1)^2))$$

E_0 is a stable singular point of system (2) when one of the following set of conditions are satisfied in addition to $\beta < \frac{2f}{h} - 1$.

i. $h < f, \alpha \leq \frac{bdf(f-h)}{aeh^2}$ and $\frac{f}{h} - \frac{a\alpha h^2}{bdh(f-h)} < \beta$
ii. $h < f$ and $\alpha > \frac{bdf(f-h)}{aeh^2}$
iii. $f \leq h < 2f$

System (2) is stable at E_1 when $g < f$ and $\alpha < 1$ both hold.

At E_2 system (2) is stable when $< f$, $h < f - g$, $1 < \alpha < \frac{f-h}{g}$ and $\beta < 1$ hold.

E_3 is a stable singular point if $g < f$, $h < f - g$, $\alpha < 1$ and $\beta < 1$ hold.

E_4 is a stable singular point if $g < f$ and $1 < \alpha < \frac{f}{g}$ hold.

System (2) is stable at E_5 when $< f$, $h < f - g$, $1 < \alpha < \frac{f-h}{g}$ and $\beta < 1$ hold.

The singular point E_6 is stable when $h < f$ and $\beta < 1$ hold.

E_7 is a stable singular point when $g < f, h < f - g$, $\alpha < 1$ and $1 < \beta < \frac{f-g}{h}$ hold.

System (2) is stable at E_8 when $g < f$, $h < f - g$, $1 < \alpha < \frac{f-h}{g}$ and $1 < \beta < \frac{f-\alpha g}{h}$ are satisfied.

System (2) is stable at E_9 when one of the following cases holds.

i. $g < f$, $\alpha \leq \frac{f}{g}$ and $$\beta > \frac{aef(f-g) - \alpha a e g(f+g)}{bdg^2}$$
ii. $g < f$ and $\frac{f}{g} < \alpha < \frac{2f}{g} - 1$
iii. $f \leq g < 2f$ and $\alpha < \frac{2f}{g} - 1$

System (2) is stable at E_{10} when $h < f$ and $1 < \beta < \frac{f}{h}$ hold.

Since the expressions of system (2) at E_{11} and E_{12} are complex, it is not possible to calculate the eigenvalues of the Jacobian matrix at these singular points. In order to analyse the system at these points, the method of algebraic invariants can be applied.[23,24]

Theorem 5. Hopf bifurcation at E_0 is stable if it exists.

Proof. System (2) has Hopf bifurcation at E_0 when $\beta = \frac{2f}{h} - 1$ and one of the following conditions is satisfied.

i. $h < f$
ii. $f < h < 2f$

These conditions coincide with the stability of Hopf bifurcation.

Theorem 6. System (2) has a first integral when one of the following holds.

i. $a = d = f = 0$
ii. $a = f = h = 0$
iii. $d = f = g = 0$
iv. $f = g = h = 0$

Proof. For case i, system (2) has the first integral $I_i = 1 + \frac{g}{b}x + \frac{h}{e}y + z$.

The first integral of system (2) for case ii is $I_{ii} = 1 + x + \frac{b}{g}z$.

System (2) has the first integral $I_{iii} = 1 + y + \frac{e}{h}z$ for case iii. When case iv holds, the first integral of system (2) is $I_{iv} = 1 + z$.

Theorem 7. System (2) has an algebraic invariant when $b = 0$ or $e = 0$ holds.

Proof. We look for an algebraic invariant of the form

$$L = a_0 + a_1x + a_2y + a_3z$$

with the corresponding cofactor

$$k = s_0 + s_1x + s_2y + s_3z + s_4x^2 + s_5y^2 + s_6z^2 + s_7xy + s_8xz + s_9yz$$

When $b = 0$ holds, system (2) has the algebraic invariants $l_1 = 1 - x$ with the cofactor $k_1 = a\alpha x - ax^2$ and $l_2 = 1 - \frac{x}{\alpha}$ with the cofactor $k_2 = ax - ax^2$. When $e = 0$, The algebraic invariants of system (2) are $l_1 = 1 - y$ with the cofactor $k_1 = \beta dy - dy^2$ and $l_2 = 1 - \frac{y}{\beta}$ with the cofactor $k_2 = dy - dy^2$.

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