

## Stability and bifurcation in two species predator–prey models

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### ABSTRACT

Changes in the number and stability of equilibrium points in the Lotka–Volterra model as well as some of its generalizations that lead to qualitative changes in the behavior of the system as a function of some of its parameters are studied by bifurcation analysis. A generalization involving a cubic interaction as proposed by Nutku is shown to change the stability properties in a simple way and in particular cases introduce additional stability. Numerical methods and the approach provided by approximate techniques near equilibrium points are used in the analysis.

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### 1. Introduction

The predator–prey problem attempts to model the relationship in the populations of different species that share the same environment where some of the species (predators) prey on the others. The prey is assumed to exhibit linear growth given by a positive parameter. Predator species consume preys with a nonlinear interaction with another set of parameters that determine the rate of competition between predators. The natural death rate of the predator is assumed to be linear and given by a negative parameter. One of the earliest implementations, the Lotka–Volterra model serves as a starting point of more advanced models in the analysis of population dynamics. Because of its unrealistic stability characteristics [1], stability analysis of the model and its generalizations have recently gained much attention. To understand the behavior of a nonlinear system one can analyze the existence and stability of equilibrium points. As parameters are varied changes in the number and stability of equilibrium points lead to bifurcation. Numerical methods are usually employed to perform this analysis [2]. Approximate techniques near equilibrium points, such as the normal form method [3] provides a complementary approach for our study. The well-known generalizations of the Lotka–Volterra model include the addition of polynomial interactions [4], non-monotonic response functions [5], time delayed [6] and diffusion effected, time delayed [7] non-monotonic interactions. Nutku has proposed a generalization where an additional cubic rather than a quadratic interaction is involved. In this work, bifurcation properties of quadratic and cubic local and monotonic interactions are studied. The Nutku generalization is shown to introduce additional stability in a simple way.

### 2. The classic Lotka–Volterra model and normal forms

The classic mathematical model of predator–prey systems was first developed [8] by Alfred Lotka and Vito Volterra to model the cyclic changes in the populations of predatory and prey fish in the Adriatic Sea during World War I and also to

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describe chemical reactions in which chemical concentrations oscillate. This model also serves as a first approximation to more complex models of physical systems such as resonantly coupled laser models [8,9]. The classic Lotka–Volterra model is given by the following system of differential equations, where dots denote time derivatives.

$$\begin{aligned}\dot{x} &= ax - bxy, \\ \dot{y} &= -cy + dxy.\end{aligned}\quad (1)$$

Here  $a, b, c, d > 0$  are parameters characterizing the predator–prey environment,  $x(t)$  and  $y(t)$  are the prey and predator populations respectively. The equilibrium points are  $(0, 0)$  and  $(\frac{c}{d}, \frac{a}{b})$ . Linearized eigenvalues about the first equilibrium point (henceforth to be referred to as “eigenvalues for” for brevity)  $(0, 0)$  are  $\{a, -c\}$ ; they do not ordinarily satisfy resonance conditions and the origin is a saddle point. On the other hand the eigenvalues for the equilibrium point  $(\frac{c}{d}, \frac{a}{b})$  are  $\{\pm i\sqrt{ac}\}$ ; these purely imaginary values satisfy the resonance conditions and the system can be expanded into a resonant normal form. Moving this equilibrium point to the origin gives the following system [5–7]:

$$\begin{aligned}\dot{x} &= -\frac{bc}{d}y - bxy, \\ \dot{y} &= \frac{ad}{b}x + dxy.\end{aligned}\quad (2)$$

We can diagonalize the linear part using the transformation  $x = -i\frac{b}{d}\sqrt{\frac{c}{a}}(x_1 - x_2)$  and  $y = x_1 + x_2$ . This gives the following system, where the replacement  $x_1 \rightarrow x, x_2 \rightarrow y$  has been done following the substitution;

$$\begin{aligned}\dot{x} &= -i\sqrt{ac}x - \frac{b}{2}\left(1 + i\sqrt{\frac{c}{a}}\right)(x^2 - y^2), \\ \dot{y} &= i\sqrt{ac}y + \frac{b}{2}\left(1 - i\sqrt{\frac{c}{a}}\right)(x^2 - y^2).\end{aligned}\quad (3)$$

These last two steps will not be henceforth shown for brevity.

If we consider  $x$  and  $y$  as the complex conjugates of one another, this can be rewritten as:

$$\dot{z} = -i\sqrt{ac}z - \frac{b}{2}\left(1 + i\sqrt{\frac{c}{a}}\right)(z^2 - \bar{z}^2)\quad (4)$$

and its complex conjugate.

**Definition 1.** The definition and the notation used for normal forms of  $2 \times 2$  autonomous systems are summarized below. Let the system of differential equation  $\dot{\underline{x}} = \underline{F}(\underline{x})$  be given where  $\underline{x} \in \mathbb{R}^2$  and  $\underline{F} \in \mathbb{R}^2 \rightarrow \mathbb{R}^2$ . To consider the system near its equilibrium point  $\underline{x} = \underline{x}_0$  such that  $\underline{F}(\underline{x}_0) = 0$ , this point is moved to the origin by  $\underline{x} = \underline{x} - \underline{x}_0$ . Taylor expansion near  $\underline{x} = 0$  gives

$$\dot{\underline{x}} = \underline{A}\underline{x} + \underline{F}_2(\underline{x}, \underline{y}) + \dots\quad (5)$$

Diagonalizing  $\underline{A}$  or bringing it to the Jordan canonical form by a linear transformation produces

$$\dot{\underline{x}} = \underline{J}\underline{x} + \tilde{\underline{F}}_2(\underline{x}, \underline{y}) + \dots\quad (6)$$

Then a sequence of near identity transformation of the form

$$\underline{x} = \underline{u} + \underline{E}_2(\underline{u}) + \dots\quad (7)$$

are applied to simplify the system.

In the rest of this work,  $u$  and  $v$  will refer to the variables in the near identity transformation.

Eigenvalues of the linearized matrix of coefficients around this equilibrium point make the system resonant in every odd order of the normal form expansion starting from the third order and also yield a Hopf bifurcation. For example,

$$\begin{aligned}\dot{u} &= i\sqrt{ac}u \left( -1 + \frac{b^2}{6a} \left( \frac{1}{c} + \frac{1}{a} \right) uv + \frac{17b^4}{432a^2} \left( \frac{1}{c} + \frac{1}{a} \right)^2 (uv)^2 \right) + \dots \\ \dot{v} &= i\sqrt{ac}v \left( 1 - \frac{b^2}{6a} \left( \frac{1}{c} + \frac{1}{a} \right) uv - \frac{17b^4}{432a^2} \left( \frac{1}{c} + \frac{1}{a} \right)^2 (uv)^2 \right) + \dots\end{aligned}\quad (8)$$

is the fifth order normal form.

These equations have the first integral  $uv = \text{constant}$  and both parameters have periodic solutions that can be generalized to all orders. Furthermore all the solutions are periodic, causing the predator and prey populations to cycle

and oscillate around this equilibrium. This model is popular as a simple predator–prey system since it shows cycling of predator–prey populations [10]. However, the model inappropriately describes realistic predator and prey populations which typically reach characteristic steady state values. Since it does not exhibit structural stability, the simulated values for the population cycle endlessly without settling down [5–7,11]. Thus, it fails to describe realistic predator and prey populations which typically reach characteristic steady state values. Realistic models should predict a single closed orbit, or perhaps finitely many, but not a continuous family of neutrally stable cycles. For this reason, several generalizations of the model has been proposed by adding additional information that offer more realistic descriptions [12–14].

The integrability of the simple Lotka–Volterra model has been shown [11,15] where elimination of the time gives

$$\frac{dx}{dy} = \frac{(a - yb)x}{(-c + xd)y}. \tag{9}$$

The integral is  $x d + y b - c \log x - a \log y = \text{constant}$ .

### 3. Generalized quadratic Lotka–Volterra model with polynomial interaction

The simplest polynomial generalization involves the addition of a quadratic self-coupling suggested by the Verhulst model. The relative coefficient between the linear and quadratic term can be set to one without any loss of generality by rescaling the variables, and if necessary, the parameters. In all cases, the quadratic self-coupling does not possess structural stability, as in the ordinary Lotka–Volterra model. This generalization can introduce one or two stable equilibrium points in the linearized approximation for appropriate values of the parameters.

There are four different versions of the quadratic self-interaction model, that depends on the relative sign between the linear and quadratic terms in each equation. By changing the signs of variables and the coefficient of the coupling term, one can transform the unphysical region of one version to the physical region of another one. Since each form has different bifurcation properties, we will examine each form and clearly indicate the transformation leading to it from the basic form given below.

#### 3.1. The case of a supercritical and a subcritical transcritical bifurcation

The basic form is

$$\begin{aligned} \dot{x} &= ax(1 - x) - bxy, \\ \dot{y} &= -cy(1 - y) + dxy. \end{aligned} \tag{10}$$

The equilibrium points are  $(0, 0)$ ,  $(1, 0)$ ,  $(\frac{(a-b)c}{ac-bd}, \frac{a(c-d)}{ac-bd})$  and  $(0, 1)$  which have the eigenvalues  $\{a, -c\}$ ,  $\{-a, -c + d\}$ ,  $\{\frac{ac(a-b-c+d) \pm \sqrt{\Delta}}{2(-ac+bd)}\}$  and  $\{a - b, c\}$  in that order where

$$\Delta = ac(ac(a - b - c + d)^2 + 4(a - b)(c - d)(ac - bd)).$$

The change to a quadratic self-interaction leaves the equilibrium point at the origin unchanged. We no longer have an unconditional Hopf bifurcation point. This is to be expected since the self-interaction has a form characteristic of transcritical rather than Hopf bifurcation. The point  $(\frac{(a-b)c}{ac-bd}, \frac{a(c-d)}{ac-bd})$  gives Hopf bifurcation under the condition,  $a < b$  and  $c < d$ . The system has a stable equilibrium point within physical values if  $d < c$  [12].

The system possesses an algebraic integral of the form

$$x^{c_1}y^{c_2}(1 + c_3x + c_4y) \tag{11}$$

where  $c_1, c_2, c_3, c_4$  are given expressions involving the equation parameters and provided that  $ac \neq bd$  and

$$\frac{ac(a - b - c + d)}{bd - ac} = 0.$$

#### 3.2. Special case

Using  $a = c = 1$  and  $b = d = 2$  gives:

$$\begin{aligned} \dot{x} &= x(1 - x) - 2xy, \\ \dot{y} &= -y(1 - y) + 2xy. \end{aligned} \tag{12}$$

This system has four equilibrium points  $(0, 0)$ ,  $(1, 0)$ ,  $(\frac{1}{3}, \frac{1}{3})$  and  $(0, 1)$  with the corresponding eigenvalues  $\{\pm 1\}$ ,  $\{\pm 1\}$ ,  $\{\pm \frac{i}{\sqrt{3}}\}$  and  $\{\pm 1\}$ . The bifurcation diagram is shown in Fig. 1. The first two and the last equilibrium points are saddle points and they are unstable. Nevertheless the third equilibrium point has pure imaginary eigenvalues satisfying the resonance condition,

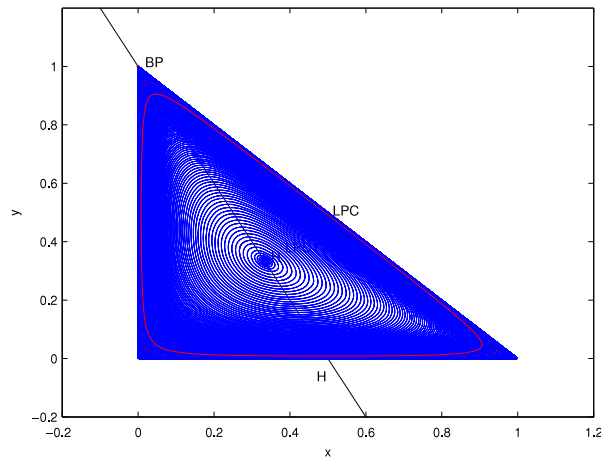


Fig. 1. Family of limit cycles for system (12).

the system can be expanded into a resonant normal form. Moving the third equilibrium point to the origin and transforming the new system into complex form, one has:

$$\dot{z} = i\frac{z}{\sqrt{3}} - i\sqrt{3}z^2 \tag{13}$$

and its complex conjugate.

Normal form expansion to the fifth order gives:

$$\begin{aligned} \dot{u} &= \frac{i u}{\sqrt{3}}(1 - 6uv - 24(uv)^2), \\ \dot{v} &= \frac{i v}{\sqrt{3}}(-1 + 6uv + 24(uv)^2). \end{aligned} \tag{14}$$

Except for the difference in coefficients this normal form is exactly the same as that for the ordinary Lotka–Volterra case and possesses the identical integral  $uv = \text{constant}$  [12–14].

When each of the parameters is allowed to become variable one by one, and a bifurcation analysis is carried out, the system exhibits a subcritical, a supercritical Hopf bifurcation and a transcritical bifurcation for each parameter. The supercritical Hopf bifurcation point  $(\frac{1}{3}, \frac{1}{3})$  has the eigenvalues  $\{\pm \frac{i}{\sqrt{3}}\}$  and leads to a limit point cycle with double characteristic exponents  $\mu = 1$  and nonzero normal form coefficients, hence intermittency is observed. A family of limit cycles surround the supercritical Hopf equilibrium point  $(\frac{1}{3}, \frac{1}{3})$ ; their period and extent continues to grow until the transcritical bifurcation point at  $(0, 1)$  is reached. All of the limit cycles lie within a right triangle whose vertices are the equilibrium points  $(0, 0)$ ,  $(1, 0)$  and the transcritical bifurcation point. The median between the equilibrium points that do not show transcritical bifurcation leads to the subcritical Hopf point at  $(0.5, 0)$ .

This system admits as a special case of (11), the first integral  $xy(-1 + x + y) = \text{constant}$  and the triangle that forms the boundary consists of the lines  $x = 0$ ,  $y = 0$  and  $x + y = -1$  that forms the degenerate cases of the first integral with the constant set to zero [13,14,11].

### 3.3. The case of two supercritical transcritical bifurcations

Unphysical regions of the model given by [16] can be mapped to physical regions of two models where either the predator or prey self-coupling acquires the positive sign. This will impose the same asymptotic behavior for both self-couplings. However the modified systems lose Hopf bifurcation property in the physical region.

Changing the signs of  $y$  and  $b$  yields the system

$$\begin{aligned} \dot{x} &= ax(1 - x) - bxy, \\ \dot{y} &= -cy(1 + y) + dxy. \end{aligned} \tag{15}$$

The equilibrium points are  $(0, 0)$ ,  $(1, 0)$ ,  $(\frac{(a+b)c}{ac+bd}, \frac{a(-c+d)}{ac+bd})$  and  $(0, -1)$ . Eigenvalues associated with the equilibrium point  $(0, 0)$  are  $\{a, -c\}$  so that this is a saddle node. Eigenvalues associated with the equilibrium point  $(1, 0)$  are  $\{-a, d - c\}$ . If  $d > c$  this equilibrium is a saddle node, otherwise it is stable. The eigenvalues associated with the equilibrium point  $(\frac{c(a+b)}{ac+bd}, \frac{a(d-c)}{ac+bd})$  form a complex conjugate pair and the corresponding eigenvectors are complex conjugates of one another. If  $\frac{ac(a+b-c+d)}{-2(ac+bd)} < 0$  then this equilibrium is stable. Eigenvalues associated with the equilibrium point  $(0, -1)$  are  $\{a + b, c\}$ .

This equilibrium is unstable. Since the stability of the equilibrium points can change with the parameter values, bifurcation may, in principle, occur [8,15–17].

**Lemma 1.** For the system (15), the condition for the existence of an algebraic integral in the form  $xy(-1+x+y) = \text{constant}$  coincides with the Hopf bifurcation condition.

**Proof.** The required condition for Hopf bifurcation to occur is  $ac(a+b-c+d) = 0$ . The system possesses an algebraic integral of the form  $x^{c_1}y^{c_2}(1+c_3x+c_4y)$  provided that  $ac \neq -bd$  and

$$\frac{ac(-a-b+c-d)}{ac+bd} = 0$$

which coincides with the required condition for the third equilibrium point to give Hopf bifurcation. Otherwise only transcritical bifurcation is observed in the physical region.  $\square$

### 3.4. The case of two subcritical transcritical bifurcations

On the other hand changing the signs of  $x$  and the parameter  $d$  yields the system

$$\begin{aligned}\dot{x} &= ax(1+x) - bxy, \\ \dot{y} &= -cy(1-y) + dxy\end{aligned}\tag{16}$$

where this time there is a stable equilibrium point at  $(-1, 0)$  with the eigenvalues  $\{-a, -c-d\}$ . The origin is again a saddle point with the persistent eigenvalues  $\{a, -c\}$ . The remaining two equilibrium points are  $(\frac{c(b-a)}{ac+bd}, \frac{a(c+d)}{ac+bd})$  and  $(0, 1)$  which have the eigenvalues  $\{\frac{ac(a-b-c-d)\pm\sqrt{\Delta}}{2(-ac-bd)}\}$  and  $\{a-b, c\}$  respectively where

$$\Delta = ac(ac(-a+b+c+d)^2 + 4(a-b)(c+d)(ac+bd)).$$

Although the third equilibrium point seems to promise a Hopf bifurcation, the required condition  $\frac{c(c+d)(b+c+d)}{b+c} < 0$  indicates that this is impossible for physical parameter values [8,15–17].

### 3.5. The case of a subcritical and a supercritical transcritical bifurcation

Combining both transformations (changing the signs of  $x, y, b$  and  $d$ ) yields the system

$$\begin{aligned}\dot{x} &= ax(1+x) - bxy, \\ \dot{y} &= -cy(1+y) + dxy\end{aligned}\tag{17}$$

which has an identical stability analysis with a slight modification in the denominator of the eigenvalue of the third equilibrium point and in the eigenvalues of the last equilibrium point as compared to the previous system. The condition for Hopf bifurcation is also different, namely,  $\frac{c(c+d)(c-b+d)}{c-b} < 0$ . It can occur for physically acceptable values of the parameters [15–17].

## 4. Cubic model with $x^k y$ interaction

Nutku has suggested a model that includes a cubic rather than quadratic self-interaction. Unlike the classical Lotka–Volterra system or the system with quadratic coupling [8,15–17], the cubic self-coupling can lead to a structurally stable system if the cubic terms have the negative sign [18–20]. If one insists on structural semi-stability, the interaction coupling should be of the form  $xy$  in both equations or  $x^k y$  in the prey and  $xy^k$  in the predator equation where  $k$  is a positive integer and  $k \leq 2$ . A cubic interaction of this form has not been studied before. The possibility of  $xy^2$  in the prey and  $x^2 y$  can be reduced to the quadratic coupling case with the transformation  $u = x^2, v = y^2$ .

It is always possible to set the relative coefficient in the self-coupling term to 1 by rescaling the variables and to change the relative sign between the linear and cubic term in either equation. Details will be given in Lemma 4 for the  $xy$  coupling, other couplings can also be treated in a similar way.

The suggested system is:

$$\begin{aligned}\dot{x} &= ax(1-x^2) - bx^k y, \\ \dot{y} &= -cy(1+y^2) + dxy^k.\end{aligned}\tag{18}$$

Its generalization would involve self-couplings of the form  $ax(1 \pm x^2)$  and  $-cy(1 \mp y^2)$ . To find the equilibrium points, we need to solve the equations  $x(a(1 \pm x^2) - bx^{k-1}y) = 0$  and  $y(c(1 \mp y^2) - dxy^{k-1}) = 0$ .

**Lemma 2.** From the factorization of the equations above, it is clear that for all appropriate values of  $k$ , five of the roots are of the form  $(0, 0)$ ,  $(0 \pm 1)$  or  $(0, \pm i)$ ,  $(\pm 1, 0)$  or  $(\pm i, 0)$ .

**Proof.** Setting the factor  $x = 0$  into each of the two factors in the  $y$  equation and the factor  $y = 0$  into each of the two factors in the  $x$  equation. The remaining roots are obtained by solving the two nonzero factors simultaneously:  $a(1 \pm x^2) = bx^{k-1}y$  and  $c(1 \mp y^2) = bxy^{k-1}$ . In spite of the fact that these equations depend on  $k$ , it will be seen that for  $k \leq 2$ , the solution will involve a quartic equation in a single variable, so that there will be nine equilibrium points.  $\square$

Returning to system (18), the Jacobian matrix is

$$\begin{bmatrix} a - 3ax^2 - bkyx^{k-1} & -bx^k \\ dy^k & -c - 3cy^2 + dkxy^{k-1} \end{bmatrix}.$$

The simple equilibrium points are  $(0, 0)$ ,  $(0, \pm i)$ ,  $(\pm 1, 0)$ . If  $k = 1$ , the eigenvalues are  $\{-a, -c\}$ ,  $\{a \pm ib, 2c\}$  and  $\{-2a, -c \pm d\}$  and if  $k = 2$ , eigenvalues are  $\{-a, -c\}$ ,  $\{a, 2c\}$  and  $\{-2a, -c\}$  in the given order.

The remaining roots for  $k = 1$  and  $k = 2$  will now be analyzed. The quartic equation for the remaining four equilibrium points for  $k = 1$  is

$$(1 - x^2)^2 = \frac{b^2}{a^2} \left( \frac{xd}{c} - 1 \right) \quad (19)$$

which leads to the following cases.

**Lemma 3.** *The quartic equation above can have two or zero positive real roots.*

**Proof.** Since the left-hand side is  $(1 - x^2)^2$ , its intersection with the right-hand side  $\frac{b^2}{a^2} \left( \frac{xd}{c} - 1 \right)$  cannot lead to negative roots for physical values of the parameters. Hence, two of the roots are complex. As far as the remaining roots are concerned, the equation can be rewritten as:

$$x^4 - 2x^2 - \frac{b^2}{a^2} \frac{xd}{c} + \frac{b^2}{a^2} + 1 = 0 \quad (20)$$

and we have the following cases:

- i. two real and positive roots if  $c < d$ ,
- ii. two complex roots if  $d < c$ ,
- iii. If  $c = d$ , the equation is

$$(1 - x^2)^2 = \frac{b^2}{a^2} (x - 1)$$

and this gives a degenerate case and a root of 1.  $\square$

We turn to the system for  $k = 2$ . The equilibrium points are  $(0, 0)$ ,  $(0, \pm i)$ ,  $(\pm 1, 0)$  and four nontrivial points. The remaining four equilibrium points satisfy the following quadratic equation for  $t = x^2$ .

$$\frac{bc}{ad}t + \frac{ca}{bd}(1 - t^2) = t(1 - t). \quad (21)$$

The roots of this equation are

$$x_{1,2} = \pm \sqrt{\frac{-c + 2a^2c + abd - \sqrt{c^2 - 4(ac)^2 - 2abcd + (abd)^2}}{2a(ac + bd)}}$$

$$x_{3,4} = \pm \sqrt{\frac{-c + 2a^2c + abd + \sqrt{c^2 - 4(ac)^2 - 2abcd + (abd)^2}}{2a(ac + bd)}}.$$

The cubic self-coupling is of interest since the system undergoes pitchfork bifurcation rather than transcritical bifurcation [17–19] irrespective of the interaction coupling. Although further self-couplings retain similar results in the linearized eigenvalue expansions they are not of interest for structural stability reasons.

We now give examples of the cases mentioned in Lemma 3.

#### 4.1. Case I

According to the choice of the parameters in the predator equation the generalized cubic system has two real roots one between zero and one, the other greater than one.

In this case the generalized Lotka–Volterra system has additionally two complex equilibrium points.

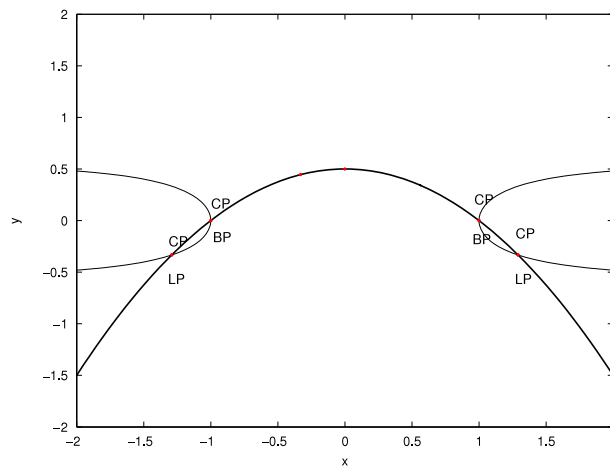


Fig. 2. Bifurcation diagram for system (22).

**Example.** As an example, we use  $a = c = 0.5$  and  $b = d = 1$  so that we have the system

$$\begin{aligned} \dot{x} &= 0.5x(1 - x^2) - xy, \\ \dot{y} &= -0.5y(1 + y^2) + xy \end{aligned} \tag{22}$$

which has nine equilibrium points  $(0, 0)$ ,  $(0, \pm i)$ ,  $(\pm 1, 0)$ ,  $(-1.35 \pm 1.52i, 0.73 \pm 2.06i)$  and the two real positive roots  $(0.55, 0.34)$ ,  $(2.15, -1.81)$ , the quartic has four complex roots. Varying the predator’s growth rate gives the bifurcation diagram in Fig. 2. There are two pitchfork bifurcation points (BP) each of which bifurcate one new branch. In addition the main bifurcation curve gives rise to two saddle node bifurcation points (LP). Each branch of the bifurcation point with  $x \neq y$  illustrates the phenomenon of symmetry breaking. Where each of the two branches meet, four cusp bifurcation points (CP) are observed signaled by a zero eigenvalue and vanishing quadratic coefficient for the saddle node bifurcation [15,17–19].

#### 4.2. Case II

Using,  $a = c = 1.5$  and  $b = d = 1$  we have the system

$$\begin{aligned} \dot{x} &= 1.5x(1 - x^2) - xy, \\ \dot{y} &= -1.5y(1 + y^2) + xy \end{aligned} \tag{23}$$

which has nine equilibrium points  $(\pm 1, 0)$ ,  $(0, 0)$ ,  $(0, \pm i)$ ,  $(-1.049 \pm 0.415i, 0.106 \pm 1.308i)$ ,  $(1.049 \pm 0.177i, -0.105 \mp 0.558i)$ . A local bifurcation analysis around these equilibrium points gives no bifurcation points but only a closed orbit.

#### 4.3. Case III (degenerate case)

This is the degenerate case where  $x = 1$  [21].

$$\begin{aligned} \dot{x} &= x(1 - x^2) - xy, \\ \dot{y} &= -y(1 + y^2) + xy. \end{aligned} \tag{24}$$

Equilibrium points are  $(0, 0)$ ,  $(0, \pm i)$ ,  $(\pm 1, 0)$ ,  $(1, 0)$ ,  $(1.205, -0.453)$ ,  $(-1.102 + 0.665i, 0.226 + 1.467i)$ ,  $(-1.102 - 0.665i, 0.226 - 1.467i)$ . A local bifurcation analysis similar to Case I is obtained for the equilibrium point  $(1.205, -0.453)$ .

### 5. The generalized cubic Lotka–Volterra model with simple polynomial interaction

**Lemma 4.** The following systems of generalized cubic Lotka–Volterra models with simple polynomial interaction can be transformed into each other.

**Proof.** Let us consider the system

$$\begin{aligned} \dot{x} &= ax(1 - x^2) - bxy, \\ \dot{y} &= -cy(1 + y^2) + dxy. \end{aligned} \tag{25}$$

Using the transformation  $x = ix$  and  $d = -id$  and dividing the first equation by  $i$  gives the first varied version of the system

$$\begin{aligned}\dot{x} &= ax(1 + x^2) - bxy, \\ \dot{y} &= -cy(1 + y^2) + dxy.\end{aligned}\quad (26)$$

Using the transformation of  $y = iy$  and  $b = -ib$  and dividing the second equation by  $i$  we have the second varied version which is

$$\begin{aligned}\dot{x} &= ax(1 - x^2) - bxy, \\ \dot{y} &= -cy(1 - y^2) + dxy.\end{aligned}\quad (27)$$

The third varied version is obtained by carrying out both transformations and divisions mentioned above.

$$\begin{aligned}\dot{x} &= ax(1 - x^2) - bxy, \\ \dot{y} &= -cy(1 - y^2) + dxy.\end{aligned}\quad (28)$$

The original system and its three varied forms mentioned above cover all possibilities. Finally it is possible to change the equilibrium points by using the transformations  $x = xk$ ,  $y = yk$ ,  $b = \frac{b}{k}$ ,  $d = \frac{d}{k}$  and dividing both equations by  $k$

$$\begin{aligned}\dot{x} &= ax(1 - (kx)^2) - bxy, \\ \dot{y} &= -cy(1 + (ky)^2) + dxy.\end{aligned}\quad (29)$$

Hence the unstable systems can be transformed into stable systems via variable transformations [13,14,21].  $\square$

Nevertheless we will investigate each system in its own physical region and give the associated bifurcation schemes.

### 5.1. The case of two supercritical pitchfork bifurcations

We use the system given by

$$\begin{aligned}\dot{x} &= ax(1 - x^2) - bxy, \\ \dot{y} &= -cy(1 + y^2) + dxy.\end{aligned}\quad (30)$$

The equilibrium point  $(0, 0)$  has the eigenvalues  $\{a, -c\}$  and again it is a saddle point. The equilibrium points  $(0, -i)$  and  $(0, i)$  have the eigenvalues  $\{a + bi, 2c\}$  and  $\{a - bi, 2c\}$  respectively and they are both unstable equilibrium points. The equilibrium points  $(1, 0)$  and  $(-1, 0)$  have the eigenvalues  $\{-2a, -c - d\}$  and  $\{-2a, -c + d\}$  respectively where one of them is a stable equilibrium point and the other one is a stable equilibrium point under the condition  $d < c$  which falls into case II. Considering these equilibrium points we can conclude that for positive parameter values a resonant normal form does not exist around the stable equilibrium points. With the help of the Lyapunov function  $V(x, y) = x^2 + y^2$  we have  $\dot{V} = 2ax^2 - 2ax^4 - 2bx^2y - 2cy^2 - 2cy^4 + 2dxy^2$  so the system is shown to be stable and structurally stable for  $a > 0$  and  $c > 0$ . This is obvious if one considers that the dominant terms are

$$\begin{aligned}\dot{x} &= -ax^3, \\ \dot{y} &= -cy^3\end{aligned}\quad (31)$$

with the obvious solution  $x^2(t) = \frac{x^2(t=0)}{1+2ax^2(t=0)}$  and  $y^2(t) = \frac{y^2(t=0)}{1+2cy^2(t=0)}$ .

### 5.2. The case of two subcritical pitchfork bifurcations

We use the system given by

$$\begin{aligned}\dot{x} &= ax(1 + x^2) - bxy, \\ \dot{y} &= -cy(1 - y^2) + dxy.\end{aligned}\quad (32)$$

The equilibrium points are  $(0, 0)$ ,  $(0, 1)$ ,  $(0, -1)$  and six nontrivial points. The origin is hyperbolic saddle.  $(0, 1)$  may be either saddle or unstable point.  $(0, -1)$  is an unstable point.

### 5.3. The case of a subcritical and a supercritical pitchfork bifurcation

We use the system given by

$$\begin{aligned}\dot{x} &= ax(1 + x^2) - bxy, \\ \dot{y} &= -cy(1 + y^2) + dxy.\end{aligned}\quad (33)$$

The equilibrium points are  $(0, 0)$ ,  $(0, \pm i)$ ,  $(\pm i, 0)$  and four nontrivial points. In this case locally stable equilibrium in the parameter plane is guaranteed.



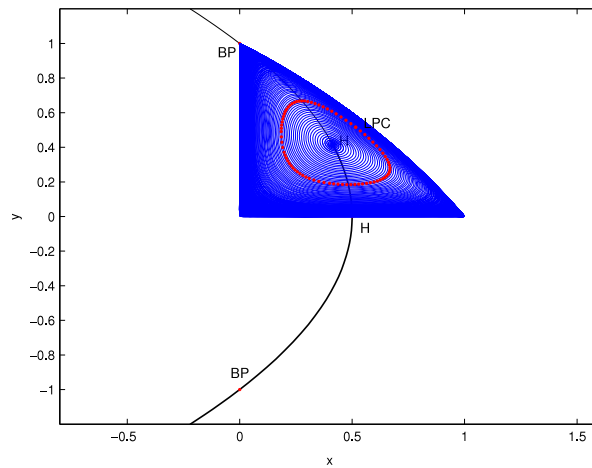


Fig. 3. Bifurcation diagram showing the family of limit cycles around the Hopf point of system (35).

5.4. The case of a supercritical and a subcritical pitchfork bifurcation

The generic form describing the case of supercritical and subcritical bifurcation is given by the following system

$$\begin{aligned} \dot{x} &= ax(1 - x^2) - bxy, \\ \dot{y} &= -cy(1 - y^2) + dxy. \end{aligned} \tag{34}$$

For convenience we study the following special case of the system

$$\begin{aligned} \dot{x} &= x(1 - x^2) - 2xy, \\ \dot{y} &= -y(1 - y^2) + 2xy. \end{aligned} \tag{35}$$

The system has the equilibrium points (0, 0), (0, 1), (1, 0) and  $(-1 - \sqrt{2}, -1 - \sqrt{2})$  as hyperbolic saddles, (0, -1) as an unstable point with the eigenvalues {2, 3}, two complex conjugate points with cross conjugate eigenvalues, a stable point at  $(-1, 0)$  with the eigenvalues  $\{-2, -3\}$  and the point  $(\sqrt{2} - 1, \sqrt{2} - 1)$  with a pair of purely imaginary eigenvalues as a Hopf point. The third order normal form about this equilibrium point is, as expected

$$\begin{aligned} \dot{u} &= iu(-27.8611918118930381uv + 313.2622478846395944) \\ \dot{v} &= iv(27.8611918118930381uv - 313.2622478846395944) \end{aligned}$$

higher order terms are omitted for brevity. The reason for the coefficients with large absolute values is the fact that a small denominator  $5\sqrt{2} - 7$  appears. Since the exact expressions are very complicated the expressions are given to sixteen places of decimals. This gives supercritical Hopf bifurcation. There is also observed a subcritical Hopf bifurcation at (0.5, 0) and two symmetric pitchfork bifurcation points at (0, 1) and (0, -1). The bifurcation diagram is shown in Fig. 3. The Hopf point leads to intermittency [8,15–17,22,23].

6. Cubic model with  $x^2y$  interaction

The equilibrium points and bifurcation scenarios for this interaction are summarized below.

6.1. The case of two supercritical pitchfork bifurcations

We use the system given by

$$\begin{aligned} \dot{x} &= ax(1 - x^2) - bx^2y, \\ \dot{y} &= -cy(1 + y^2) + dxy^2. \end{aligned} \tag{36}$$

The equilibrium points are (0, 0), (0, ±i), (±1, 0) and four nontrivial points.

6.2. The case of two subcritical pitchfork bifurcations

We use the system given by

$$\begin{aligned} \dot{x} &= ax(1 + x^2) - bx^2y, \\ \dot{y} &= -cy(1 - y^2) + dxy^2. \end{aligned} \tag{37}$$

The equilibrium points are (0, 0), (0, ±1), (±i, 0) and four nontrivial points.

### 6.3. The case of a subcritical and a supercritical pitchfork bifurcation

We use the system given by

$$\begin{aligned}\dot{x} &= ax(1 + x^2) - bx^2y, \\ \dot{y} &= -cy(1 + y^2) + dxy^2.\end{aligned}\tag{38}$$

The equilibrium points are  $(0, 0)$ ,  $(0, \pm i)$ ,  $(\pm i, 0)$  and four nontrivial points.

### 6.4. The case of a supercritical and a subcritical pitchfork bifurcation

We use the system given by

$$\begin{aligned}\dot{x} &= ax(1 - x^2) - bx^2y, \\ \dot{y} &= -cy(1 - y^2) + dxy^2.\end{aligned}\tag{39}$$

The equilibrium points are  $(0, 0)$ ,  $(0, \pm 1)$ ,  $(\pm 1, 0)$  and four nontrivial points.

In all cases the eigenvalues are  $\{a, 2c\}$  for simple equilibrium points except the origin which is saddle [22,23].

Due to the problems of stability we do not go further than the interaction  $x^2y$ .

## 7. Conclusion

In this work, the stability and bifurcation properties of two species Lotka–Volterra systems were studied. Both the regular Lotka–Volterra model and its generalization via a quadratic self-coupling show transcritical and Hopf bifurcation. In both cases, bounded orbits exist under appropriate conditions but the system is not stable in the Lyapunov sense [8,15,17,22].

Although approaches such as non-polynomial or time delay couplings have been used, an alternative way to overcome the inherent instability of the two dimensional Lotka–Volterra system with a quadratic self-interaction is simply replacing the quadratic self-coupling by a cubic one as suggested by Nutku. A further generalization involving couplings of the form  $x^k y$  in the prey and  $xy^k$  has also been considered. Normal form expansions near equilibrium points leading to Hopf bifurcation were given. In spite of its simplicity [8,15–17], the Nutku generalization provides a rich spectrum of equilibrium points leading to Hopf, pitchfork, saddle node and cusp bifurcations. These systems are Lyapunov stable for proper choice of the sign of the cubic term. Thus, the simplicity of the Nutku suggestion that keeps the interaction at a simple yet stable form is demonstrated [20,22,24,23].

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