Global bifurcations of limit cycles in the Leslie–Gover model with the Allee effect *

Valery A. Gaiko

National Academy of Sciences of Belarus, United Institute of Informatics Problems, Minsk 220012, Belarus

Jean-Marc Ginoux

Université de Toulon, Laboratoire des Sciences de l'Information et des Systèmes, 83957 La Garde Cedex, France

Cornelis Vuik

Delft University of Technology, Institute of Applied Mathematics, 2600 GA Delft, The Netherlands

Abstract

In this paper, we complete the global qualitative analysis of the Leslie–Gover system with the Allee effect which models the dynamics of the populations of predators and their prey in a given ecological or biomedical system. In particular, studying global bifurcations, we prove that such a system can have at most two limit cycles surrounding one singular point. We also conduct some numerical experiments to illustrate the obtained results.

Keywords: Leslie-Gover model; Allee effect; field rotation parameter; bifurcation; singular point; limit cycle; Wintner-Perko termination principle

^{*} The first author was supported by the Netherlands Organization for Scientific Research (NWO) and the Institute of Advanced Scientific Studies (IHÉS, France). Email address: valery.gaiko@gmail.com (Valery A. Gaiko).

1 Introduction

In this paper, we complete the global qualitative analysis of a predator-prey system derived from the Leslie–Gower type model, where the most common mathematical form to express the Allee effect in the prey growth function is considered; see [24]. The basis for analyzing the dynamics of such complex ecological or biomedical systems is the interactions between two species, particularly the dynamical relationship between predators and their prey [27]. From the classical Lotka–Volterra model, several alternatives for modeling continuous time consumer-resource interactions have been proposed [30]. In our paper, a predator-prey model described by an autonomous two-dimensional differential system is analyzed considering the following aspects: 1) the prey population is affected by the Allee effect [4], [9]; 2) the functional response is linear [29]; 3) the equation for predator is a logistic-type growth function as in the Leslie–Gower model [1].

The main objective of the study in [24] was to describe the model behavior and to establish the number of limit cycles for the system under consideration. Such results are quite significant for the analysis of most applied mathematical models, thus facilitating the understanding of many real world oscillatory phenomena in nature. The problem of determining conditions which guarantee the uniqueness of a limit cycle or the global stability of the unique positive equilibrium in predator-prey systems has been extensively studied over the last decades. This question starts with the work [7] where it was proved for the first time the uniqueness of a limit cycle for a specific predator-prey system with a Holling type II functional response using the symmetry of prey isocline. It is well-known that if a unique unstable positive equilibrium exists in a compact region, then, according to the Poincaré-Bendixon theorem, at least one limit cycle must exist. On the other hand, if the unique positive equilibrium of a predator-prey system is locally stable but not hyperbolic, there might be more than one limit cycle created via multiple Hopf bifurcations [8] and the number of limit cycles must be established. The studied system is defined in an open positive invariant region and the Poincaré-Bendixon theorem does not apply. Due to the existence of an heteroclinic curve determined by the equilibrium point associated to the strong Allee effect, a subregion in the phase plane is determined where two limit cycles exist for certain parameter values, the innermost stable and the outermost unstable. Such result has not been reported in previous papers and represents a significant difference with the Gause-type predation models [23]. In [24], it was proved also the existence of parameter subsets for which the system can have: a cusp point (Bogdanov-Takens bifurcation), homoclinic curves (homoclinic bifurcation), Hopf bifurcation and the existence of two limit cycles, the innermost stable and the outermost unstable, in inverse stability as they usually appear in the Gause-type models. However, the qualitative analysis of [24] was incomplete, since the global bifurcations of limit cycles could not be studied properly by means of the methods and techniques which were used earlier in the qualitative theory of dynamical systems. Applying to the system new bifurcation methods and geometric approaches developed in [6], [10]–[22], we complete this qualitative analysis. We also conduct some numerical experiments to illustrate the obtained results [31]. In Section 2, we present several predator-prey models which we considered earlier in [6], [20], [21] and will consider in this paper. In Section 3, we give some basic facts on singular points and limit cycles of planar dynamical systems. In Section 4, we complete the global qualitative analysis of a quartic dynamical system corresponding to the Leslie–Gover system with the Allee effect which models the dynamics of the populations of predators and their prey in a given ecological or biomedical system.

2 Predator-prey models

In [20], [21], we considered a quartic family of planar vector fields corresponding to a rational Holling-type dynamical system which models the dynamics of the populations of predators and their prey in a system which is a variation on the classical Lotka-Volterra one. For the latter system the change of the prey density per unit of time per predator called the response function is proportional to the prey density. This means that there is no saturation of the predator when the amount of available prey is large. However, it is more realistic to consider a nonlinear and bounded response function, and in fact different response functions have been used in the literature to model the predator response; see [3]-[6], [25], [26], [32].

For instance, in [32], the following predator—prey model has been studied:

$$\dot{x} = x(a - \lambda x) - yp(x)$$
 (prey),
 $\dot{y} = -\delta y + yq(x)$ (predator). (1.1)

The variables x > 0 and y > 0 denote the density of the prey and predator populations respectively, while p(x) is a non-monotonic response function given by

$$p(x) = \frac{mx}{\alpha x^2 + \beta x + 1},\tag{1.2}$$

where α , m are positive and where $\beta > -2\sqrt{\alpha}$. Observe that in the absence of predators, the number of prey increases according to a logistic growth law. The coefficient a represents the intrinsic growth rate of the prey, while $\lambda > 0$ is the rate of competition or resource limitation of prey. The natural death rate of the predator is given by $\delta > 0$. In Gause's model the function q(x) is

given by q(x) = cp(x), where c > 0 is the rate of conversion between prey and predator [32].

In [5], [6], the following family has been investigated:

$$\dot{x} = x \left(1 - \lambda x - \frac{y}{\alpha x^2 + \beta x + 1} \right),$$

$$\dot{y} = -y \left(\delta + \mu y - \frac{x}{\alpha x^2 + \beta x + 1} \right),$$
(1.3)

where $\alpha \geq 0$, $\beta > -2\sqrt{\alpha}$, $\delta > 0$, $\lambda > 0$, and $\mu \geq 0$ are parameters. Note that (1.3) is obtained from (1.1) by adding the term $-\mu y^2$ to the second equation and after scaling x and y, as well as the parameters and the time t. In this way, it has been taken into account competition between predators for resources other than prey. The non-negative coefficient μ is the rate of competition amongst predators. Systems (1.1)–(1.3) represent predator–prey models with a generalized Holling response functions of type IV.

In [26], it has been considered the following generalized Gause predator—prey system

$$\dot{x} = rx(1 - x/k) - yp(x),$$

$$\dot{y} = y(-d + cp(x))$$
(1.4)

with a generalized Holling response function of type III:

$$p(x) = \frac{mx^2}{ax^2 + bx + 1}. (1.5)$$

This system, where x > 0 and y > 0, has seven parameters: the parameters a, c, d, k, m, r are positive and the parameter b can be negative or nonnegative. The parameters a, b, and m fitting parameters of response function. The parameter d is the death rate of the predator while c is the efficiency of the predator to convert prey into predators. The prey follows a logistic growth with a rate r in the absence of predator. The environment has a prey capacity determined by k.

The case $b \geq 0$ has been studied earlier; see the references in [26]. The case b < 0 is more interesting: it provides a model for a functional response with limited group defence. In opposition to the generalized Holling function of type IV studied in [5], [6], [32], where the response function tends to zero as the prey population tends to infinity, the generalized function of type III tends to a non-zero value as the prey population tends to infinity. The functional response of type III with b < 0 has a maximum at some point; see [26]. When studying the case b < 0, one can find also a Bogdanov-Takens bifurcation of

codimension 3 which is an organizing center for the bifurcation diagram of system (1.4)–(1.5) [26].

After scaling x and y, as well as the parameters and the time t, this system can be reduced to a system with only four parameters $(\alpha, \beta, \delta, \rho)$ [26]:

$$\dot{x} = \rho x(1-x) - yp(x),$$

$$\dot{y} = y(-\delta + p(x)),$$
(1.6)

where

$$p(x) = \frac{x^2}{\alpha x^2 + \beta x + 1}. (1.7)$$

In [20], [21], we studied the system

$$\dot{x} = x \left(1 - \lambda x - \frac{xy}{\alpha x^2 + \beta x + 1} \right),$$

$$\dot{y} = -y \left(\delta + \mu y - \frac{x^2}{\alpha x^2 + \beta x + 1} \right),$$
(1.8)

where x > 0 and y > 0; $\alpha \ge 0$, $-\infty < \beta < +\infty$, $\delta > 0$, $\lambda > 0$, and $\mu \ge 0$ are parameters.

The Leslie-Gower predator-prey model incorporating the Allee effect phenomenon on prey is described by the Kolmogorov-type rational dynamical system [24]:

$$\dot{x} = x \left(r \left(1 - \frac{x}{K} \right) (x - m) - qy \right)$$
 (prey),

$$\dot{y} = sy \left(1 - \frac{y}{nx} \right)$$
 (predator),

where the parameters have the following biological meanings: r and s represent the intrinsic prey and predator growth rates, respectively; K is the prey environment carrying capacity; m is the Allee threshold or minimum of viable population; q is the maximal per capita consumption rate, i. e., the maximum number of prey that can be eaten by a predator in each time unit; n is a measure of food quality that the prey provides for conversion into predator births.

System (1.9) can be written in the form of a quartic dynamical system [24]:

$$\dot{x} = x^2((1-x)(x-m) - \alpha y) \equiv P,$$

$$\dot{y} = y (\beta x - \gamma y) \equiv Q.$$
(1.10)

Together with (1.10), we will also consider an auxiliary system (see [2], [28])

$$\dot{x} = P - \delta Q, \qquad \dot{y} = Q + \delta P, \tag{1.11}$$

applying to these systems new bifurcation methods and geometric approaches developed in [6], [10]–[22] and completing the qualitative analysis of (1.9).

3 Basic facts on singular points and limit cycles

The study of singular points of system (1.9) (or (1.10) and (1.11)) will use two index theorems by H. Poincaré; see [2]. But first let us define the singular point and its Poincaré index [2].

Definition 3.1. A singular point of the dynamical system

$$\dot{x} = P(x, y), \quad \dot{y} = Q(x, y),$$
 (3.1)

where P(x, y) and Q(x, y) are continuous functions (for example, polynomials), is a point at which the right-hand sides of (3.1) simultaneously vanish.

Definition 3.2. Let S be a simple closed curve in the phase plane not passing through a singular point of system (3.1) and M be some point on S. If the point M goes around the curve S in positive direction (counterclockwise) one time, then the vector coinciding with the direction of a tangent to the trajectory passing through the point M is rotated through the angle $2\pi j$ $(j=0,\pm 1,\pm 2,\ldots)$. The integer j is called the *Poincaré index* of the closed curve S relative to the vector field of system (3.1) and has the expression

$$j = \frac{1}{2\pi} \oint_{S} \frac{P \ dQ - Q \ dP}{P^2 + Q^2}.$$

According to this definition, the index of a node or a focus, or a center is equal to +1 and the index of a saddle is -1.

Theorem 3.1 (First Poincaré Index Theorem). If N, N_f , N_c , and C are respectively the number of nodes, foci, centers, and saddles in a finite part of the phase plane and N' and C' are the number of nodes and saddles at infinity, then it is valid the formula

$$N + N_f + N_c + N' = C + C' + 1.$$

Theorem 3.2 (Second Poincaré Index Theorem). If all singular points are simple, then along an isocline without multiple points lying in a Poincaré hemisphere which is obtained by a stereographic projection of the phase plane, the singular points are distributed so that a saddle is followed by a node or a focus, or a center and vice versa. If two points are separated by the equator of the Poincaré sphere, then a saddle will be followed by a saddle again and a node or a focus, or a center will be followed by a node or a focus, or a center.

Consider polynomial system (3.1) in the vector form

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x}, \boldsymbol{\mu}), \tag{3.2}$$

where $x \in \mathbb{R}^2$; $\mu \in \mathbb{R}^n$; $f \in \mathbb{R}^2$ (f is a polynomial vector function).

Let us recall some basic facts concerning limit cycles of (3.2). But first of all, let us state two fundamental theorems from theory of analytic functions [10].

Theorem 3.3 (Weierstrass Preparation Theorem). Let F(w, z) be an analytic in the neighborhood of the point (0,0) function satisfying the following conditions

$$F(0,0) = \frac{\partial F(0,0)}{\partial w} = \dots = \frac{\partial^{k-1} F(0,0)}{\partial^{k-1} w} = 0; \frac{\partial^k F(0,0)}{\partial^k w} \neq 0.$$

Then in some neighborhood $|w| < \varepsilon$, $|z| < \delta$ of the points (0,0) the function F(w,z) can be represented as

$$F(w,z) = (w^{k} + A_{1}(z)w^{k-1} + \ldots + A_{k-1}(z)w + A_{k}(z))\Phi(w,z),$$

where $\Phi(w,z)$ is an analytic function not equal to zero in the chosen neighborhood and $A_1(z), \ldots, A_k(z)$ are analytic functions for $|z| < \delta$.

From this theorem it follows that the equation F(w, z) = 0 in a sufficiently small neighborhood of the point (0,0) is equivalent to the equation

$$w^{k} + A_{1}(z)w^{k-1} + \ldots + A_{k-1}(z)w + A_{k}(z) = 0,$$

which left-hand side is a polynomial with respect to w. Thus, the Weierstrass preparation theorem reduces the local study of the general case of implicit function w(z), defined by the equation F(w,z) = 0, to the case of implicit function, defined by the algebraic equation with respect to w.

Theorem 3.4 (Implicit Function Theorem). Let F(w, z) be an analytic function in the neighborhood of the point (0,0) and F(0,0)=0, $F'_w(0,0)\neq 0$.

Then there exist $\delta > 0$ and $\varepsilon > 0$ such that for any z satisfying the condition $|z| < \delta$ the equation F(w,z) = 0 has the only solution w = f(z) satisfying the condition $|f(z)| < \varepsilon$. The function f(z) is expanded into the series on positive integer powers of z which converges for $|z| < \delta$, i. e., it is a single-valued analytic function of z which vanishes at z = 0.

Assume that system (3.2) has a limit cycle

$$L_0: \boldsymbol{x} = \boldsymbol{\varphi}_0(t)$$

of minimal period T_0 at some parameter value $\mu = \mu_0 \in \mathbb{R}^n$; see Fig. 1 [10].

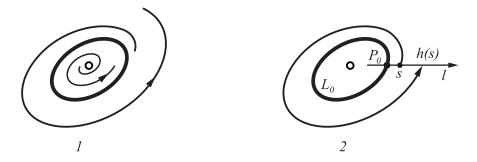


Figure 1. The Poincaré return map in the neighborhood of a multiple limit cycle.

Let l be the straight line normal to L_0 at the point $\mathbf{p}_0 = \boldsymbol{\varphi}_0(0)$ and s be the coordinate along l with s positive exterior of L_0 . It then follows from the implicit function theorem that there is a $\delta > 0$ such that the Poincaré map $h(s, \boldsymbol{\mu})$ is defined and analytic for $|s| < \delta$ and $\|\boldsymbol{\mu} - \boldsymbol{\mu}_0\| < \delta$. Besides, the displacement function for system (3.2) along the normal line l to L_0 is defined as the function

$$d(s, \boldsymbol{\mu}) = h(s, \boldsymbol{\mu}) - s.$$

In terms of the displacement function, a multiple limit cycle can be defined as follows [10].

Definition 3.3. A limit cycle L_0 of (3.2) is a multiple limit cycle iff $d(0, \mu_0) = d_r(0, \mu_0) = 0$ and it is a simple limit cycle (or hyperbolic limit cycle) if it is not a multiple limit cycle; furthermore, L_0 is a limit cycle of multiplicity m iff

$$d(0, \boldsymbol{\mu}_0) = d_r(0, \boldsymbol{\mu}_0) = \dots = d_r^{(m-1)}(0, \boldsymbol{\mu}_0) = 0,$$

$$d_r^{(m)}(0, \boldsymbol{\mu}_0) \neq 0.$$

Note that the multiplicity of L_0 is independent of the point $p_0 \in L_0$ through which we take the normal line l.

Let us write down also the following formulas which have already become classical ones and determine the derivatives of the displacement function in terms of integrals of the vector field \mathbf{f} along the periodic orbit $\boldsymbol{\varphi}_0(t)$ [10]:

$$d_s(0, \boldsymbol{\mu}_0) = \exp \int_0^{T_0} \nabla \cdot \boldsymbol{f}(\boldsymbol{\varphi}_0(t), \boldsymbol{\mu}_0) dt - 1$$

and

$$d_{\mu_j}(0, \boldsymbol{\mu}_0) = \frac{-\omega_0}{\|\boldsymbol{f}(\boldsymbol{\varphi}_0(0), \boldsymbol{\mu}_0)\|} \times \int_0^{T_0} \exp\left(-\int_0^t \boldsymbol{\nabla} \cdot \boldsymbol{f}(\boldsymbol{\varphi}_0(\tau), \boldsymbol{\mu}_0) \, \mathrm{d}\tau\right) \times \boldsymbol{f} \wedge \boldsymbol{f}_{\mu_j}(\boldsymbol{\varphi}_0(t), \boldsymbol{\mu}_0) \, \mathrm{d}t$$

for j = 1, ..., n, where $\omega_0 = \pm 1$ according to whether L_0 is positively or negatively oriented, respectively, and where the wedge product of two vectors $\mathbf{x} = (x_1, x_2)$ and $\mathbf{y} = (y_1, y_2)$ in \mathbf{R}^2 is defined as

$$\boldsymbol{x} \wedge \boldsymbol{y} = x_1 y_2 - x_2 y_1.$$

Similar formulas for $d_{ss}(0, \boldsymbol{\mu}_0)$ and $d_{s\mu_j}(0, \boldsymbol{\mu}_0)$ can be derived in terms of integrals of the vector field \boldsymbol{f} and its first and second partial derivatives along $\boldsymbol{\varphi}_0(t)$.

Now we can formulate the Wintner-Perko termination principle [28] for polynomial system (3.2).

Theorem 3.5 (Wintner-Perko Termination Principle). Any one-parameter family of multiplicity-m limit cycles of relatively prime polynomial system (3.2) can be extended in a unique way to a maximal one-parameter family of multiplicity-m limit cycles of (3.2) which is either open or cyclic.

If it is open, then it terminates either as the parameter or the limit cycles become unbounded; or, the family terminates either at a singular point of (3.2), which is typically a fine focus of multiplicity m, or on a (compound) separatrix cycle of (3.2) which is also typically of multiplicity m.

The proof of this principle for general polynomial system (3.2) with a vector parameter $\boldsymbol{\mu} \in \mathbf{R}^n$ parallels the proof of the planar termination principle for the system

$$\dot{x} = P(x, y, \lambda), \quad \dot{y} = Q(x, y, \lambda)$$
 (3.3)

with a single parameter $\lambda \in \mathbf{R}$ (see [10], [28]), since there is no loss of generality in assuming that system (3.2) is parameterized by a single parameter λ ; i. e., we can assume that there exists an analytic mapping $\mu(\lambda)$ of \mathbf{R} into \mathbf{R}^n such that (3.2) can be written as (3.3) and then we can repeat everything, what

had been done for system (3.3) in [28]. In particular, if λ is a field rotation parameter of (3.3), the following Perko's theorem on monotonic families of limit cycles is valid; see [28].

Theorem 3.6. If L_0 is a nonsingular multiple limit cycle of (3.3) for $\lambda = \lambda_0$, then L_0 belongs to a one-parameter family of limit cycles of (3.3); furthermore:

- 1) if the multiplicity of L_0 is odd, then the family either expands or contracts monotonically as λ increases through λ_0 ;
- 2) if the multiplicity of L_0 is even, then L_0 bifurcates into a stable and an unstable limit cycle as λ varies from λ_0 in one sense and L_0 disappears as λ varies from λ_0 in the opposite sense; i. e., there is a fold bifurcation at λ_0 .

4 Global bifurcation analysis

Consider system (1.10). This system has two invariant straight lines: x = 0 (double) and y = 0. Its finite singularities are determined by the algebraic system

$$x^{2}((1-x)(x-m) - \alpha y) = 0,$$

 $y(\beta x - \gamma y) = 0.$ (4.1)

From (4.1), we have got: three singular points (0,0), (m,0), (1,0) (suppose that m < 1) and at most two points defined by the system

$$(1-x)(x-m) - \alpha y = 0,$$

$$\beta x - \gamma y = 0.$$
(4.2)

In according to the second Poincaré index theorem (Theorem 3.2), the point (0,0) is a double (saddle-node), (m,0) is a node, and (1,0) is a saddle (for m < 1); see also [24]. In addition, a double singular point (saddle-node) may appear in the first quadrant and bifurcate into two singular points. If there exist exactly two simple singular points in the open first quadrant, then the singular point on the left with respect to the x-axis is a saddle and the singular point on the right is an anti-saddle [24]. If a singular point is not in the first quadrant, in consequence, it has no biological significance.

To study singular points of (1.10) at infinity, consider the corresponding differential equation

$$\frac{dy}{dx} = \frac{y(\beta x - \gamma y)}{x^2((1-x)(x-m) - \alpha y)}.$$
(4.3)

Dividing the numerator and denominator of the right-hand side of (4.3) by x^4 ($x \neq 0$) and denoting y/x by u (as well as dy/dx), we will get the equation

$$u = 0$$
, where $u = y/x$, (4.4)

for all infinite singularities of (4.3) except when x = 0 (the "ends" of the y-axis); see [2], [10]. For this special case we can divide the numerator and denominator of the right-hand side of (4.3) by y^4 ($y \neq 0$) denoting x/y by y^4 (as well as dx/dy) and consider the equation

$$v^4 = 0$$
, where $v = x/y$. (4.5)

In according to the Poincaré index theorems (Theorem 3.1 and Theorem 3.2), the equations (4.4) and (4.5) give two singular points at infinity for (4.3): a simple node on the "ends" of the x-axis and a quartic saddle-node on the "ends" of the y-axis.

Using the obtained information on singular points and applying a geometric approach developed in [6], [10]–[22], we can study the limit cycle bifurcations of system (1.10). This study will use some results obtained in [24]: in particular, the results on the cyclicity of a singular point of (1.10). However, it is surely not enough to have only these results to prove the main theorem of this paper concerning the maximum number of limit cycles of system (1.10).

Applying the definition of a field rotation parameter [2], [10], [28], i.e., a parameter which rotates the field in one direction, to system (1.10), let us calculate the corresponding determinants for the parameters α , β , and γ , respectively:

$$\Delta_{\alpha} = PQ'_{\alpha} - QP'_{\alpha} = x^2 y^2 (\beta x - \gamma y), \tag{4.6}$$

$$\Delta_{\beta} = PQ'_{\beta} - QP'_{\beta} = x^{3}y((1-x)(x-m) - \alpha y), \tag{4.7}$$

$$\Delta_{\gamma} = PQ_{\gamma}' - QP_{\gamma}' = -x^2 y^2 ((1 - x)(x - m) - \alpha y). \tag{4.8}$$

It follows from (4.6) that in the first quadrant the sign of Δ_{α} depends on the sign of $\beta x - \gamma y$ and from (4.7) and (4.8) that the sign of Δ_{β} or Δ_{γ} depends on the sign of $(1-x)(x-m) - \alpha y$ on increasing (or decreasing) the parameters α , β , and γ , respectively.

Therefore, to study limit cycle bifurcations of system (1.10), it makes sense together with (1.10) to consider also an auxiliary system (1.11) with a field rotation parameter δ :

$$\Delta_{\delta} = P^2 + Q^2 \ge 0. \tag{4.9}$$

Using system (1.11) and applying Perko's results, we will prove the following theorem.

Theorem 4.1. The Leslie–Gover system with the Allee effect (1.10) can have at most two limit cycles surrounding one singular point.

Proof. In [24], it was proved that system (1.10) can have at least two limit cycles. Let us prove now that this system has at most two limit cycles. The proof is carried out by contradiction applying Catastrophe Theory; see [10], [28].

Consider system (1.11) with four parameters: α , β , γ , and δ (we can fix the parameter m fixing the position of the node on the x-axis). Suppose that system (1.11) with two finite singularities in the first quadrant, a saddle S and an anti-saddle A, has three limit cycles surrounding A. Then we get into some domain of the parameters α , β , γ , and δ bounded by two fold bifurcation surfaces forming a cusp bifurcation surface of multiplicity-three limit cycles in the space of the parameters α , β , γ , and δ ; see Fig. 2 [10].

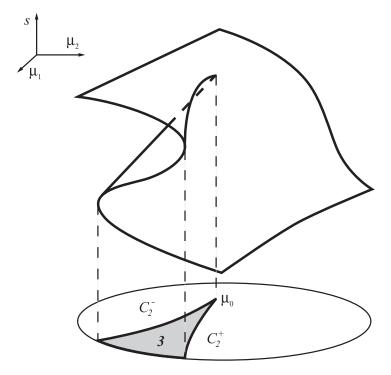


Figure 2. The cusp bifurcation surface.

The corresponding maximal one-parameter family of multiplicity-three limit cycles cannot be cyclic, otherwise there will be at least one point corresponding to the limit cycle of multiplicity four (or even higher) in the parameter space; see Fig. 3 [10].

Extending the bifurcation curve of multiplicity-four limit cycles through this point and parameterizing the corresponding maximal one-parameter family of multiplicity-four limit cycles by the field rotation parameter δ , according to Theorem 3.6, we will obtain again two monotonic curves of multiplicity-

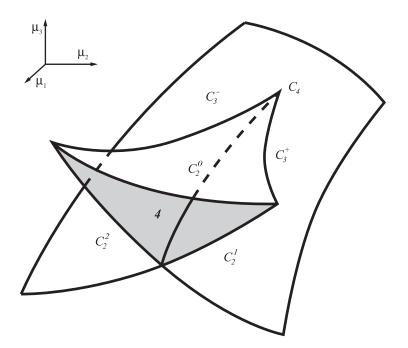


Figure 3. The swallow-tail bifurcation surface.

three and one, respectively, which, by the Wintner-Perko termination principle (Theorem 3.5), terminate either at the point A or on a separatrix loop surrounding this point. Since we know at least the cyclicity of the singular point which is equal to two (see [24]), we have got a contradiction with the termination principle (Theorem 3.5); see Fig. 4 [10].

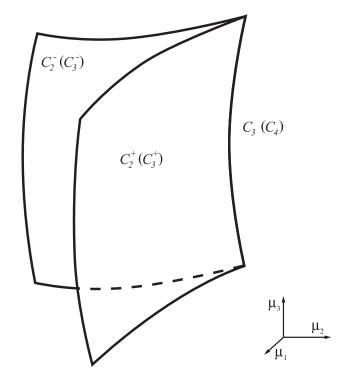


Figure 4. The bifurcation curve (one-parameter family) of multiple limit cycles.

If the maximal one-parameter family of multiplicity-three limit cycles is not cyclic, using the same principle, this again contradicts the cyclicity of A (see [24]) not admitting the multiplicity of limit cycles higher than two. Moreover, it also follows from the termination principle that a separatrix loop cannot have the multiplicity (cyclicity) higher than two in this case.

Thus, we conclude that system (1.11) (and system (1.10) as well) cannot have either a multiplicity-three limit cycle or more than two limit cycles surrounding a singular point which proves the theorem.

References

- [1] M.A. Aziz-Alaoui, M. Daher Okiye, Boundedness and global stability for a predator-prey model with modified Leslie–Gower and Holling-type II schemes, *Appl. Math. Lett.* **16** (2003), 1069–1075.
- [2] N.N. Bautin, E.A. Leontovich, Methods and Ways of the Qualitative Analysis of Dynamical Systems in a Plane, Nauka, Moscow, 1990 (in Russian).
- [3] A.D. Bazykin, Nonlinear Dynamics of Interacting Populations, World Scientific, New Jersey, 1998.
- [4] L. Berec, E. Angulo, F. Courchamp, Multiple Allee effects and population management, *Trends Ecol. Evol.* **22** (2007), 185–191.
- [5] H.W. Broer, V. Naudot, R. Roussarie, K. Saleh, Dynamics of a predator-prey model with non-monotonic response function, *Discrete Contin. Dyn. Syst. Ser. A* 18 (2007), 221–251.
- [6] H.W. Broer, V.A. Gaiko, Global qualitative analysis of a quartic ecological model, *Nonlinear Anal.* **72** (2010), 628–634.
- [7] K.S. Cheng, Uniqueness of a limit cycle for a predator-prey system, SIAM J. Math. Anal. 12 (1981), 541–548.
- [8] C. Chicone, Ordinary Differential Equations with Applications, Springer, New york, 2006.
- [9] F. Courchamp, T. Clutton-Brock, B. Grenfell, Inverse density dependence and the Allee effect, *Trends Ecol. Evol.* **14** (1999), 405–410.
- [10] V.A. Gaiko, Global Bifurcation Theory and Hilbert's Sixteenth Problem, Kluwer, Boston, 2003.
- [11] V.A. Gaiko, Limit cycles of quadratic systems, Nonlinear Anal. 69 (2008), 2150– 2157.
- [12] V.A. Gaiko, On the geometry of polynomial dynamical systems, *J. Math. Sci.* **157** (2009), 400–412.

- [13] V.A. Gaiko, A quadratic system with two parallel straight-line-isoclines, Nonlinear Anal. 71 (2009), 5860–5865.
- [14] V.A. Gaiko, Multiple limit cycle bifurcations of the FitzHugh–Nagumo neuronal model, *Nonlinear Anal.* **74** (2011), 7532–7542.
- [15] V.A. Gaiko, On limit cycles surrounding a singular point, *Differ. Equ. Dyn. Syst.* **20** (2012), 329–337.
- [16] V.A. Gaiko, The applied geometry of a general Liénard polynomial system, *Appl. Math. Letters* **25** (2012), 2327–2331.
- [17] V.A. Gaiko, Limit cycle bifurcations of a general Liénard system with polynomial restoring and damping functions, *Int. J. Dyn. Syst. Differ. Equ.* 4 (2012), 242–254.
- [18] V.A. Gaiko, Limit cycle bifurcations of a special Liénard polynomial system, Adv. Dyn. Syst. Appl. 9 (2014), 109–123.
- [19] V.A. Gaiko, Maximum number and distribution of limit cycles in the general Liénard polynomial system, Adv. Dyn. Syst. Appl. 10 (2015), 177–188.
- [20] V.A. Gaiko, Global qualitative analysis of a Holling-type system, *Int. J. Dyn. Syst. Differ. Equ.* **6** (2016), 161–172.
- [21] V. A. Gaiko, Global bifurcation analysis of a rational Holling system, *Comp. Res. Model.* **9** (2017), 537–545 (in Russian).
- [22] V. A. Gaiko, J.-M. Ginoux, C. Vuik, The termination principle of multiple limit cycles for the Kukles cubic system, *Cyber. Phys.* **6** (2017), 195–200.
- [23] E. González-Olivares, B. González-Yañez, E. Sáez, I. Szántó, On the number of limit cycles in a predator-prey model with non-monotonic functional response, *Discrete Contin. Dynam. Syst. Ser. B* **6** (2006), 525–534.
- [24] E. González-Olivares, J. Mena-Lorca, A. Rojas-Palma, J.D. Flores, Dynamical complexities in the Leslie-Gower predator-prey model as consequences of the Allee effect on prey, Appl. Math. Model. 35 (2011), 366–381.
- [25] C.S. Holling, The functional response of predators to prey density and its role in mimicry and population regulation, *Mem. Entomol. Soc. Can.* **45** (1965), 3–60.
- [26] Y. Lamontagne, C. Coutu, C. Rousseau, Bifurcation analysis of a predator–prey system with generalized Holling type III functional response, *J. Dyn. Diff. Equat.* **20** (2008), 535–571.
- [27] Y. Li, D. Xiao, Bifurcations of a predator-prey system of Holling and Leslie types, *Chaos Solitons Fract.* **34** (2007), 8606–8620.
- [28] L. Perko, Differential Equations and Dynamical Systems, Springer, New York, 2002.

- [29] G. Seo, M. Kot, A comparison of two predator-prey models with Holling's type I functional response, *Math. Biosci.* **212** (2008), 161–179.
- [30] P. Turchin, Complex Population Dynamics. A Theoretical/Empirical Synthesis, Princeton University Press, Princeton, 2003.
- [31] C. Vuik, F.J. Vermolen, M.B. van Gijzen, M.J. Vuik, Numerical Methods for Ordinary Differential Equations, Delft Academic Press, Delft, 2015.
- [32] H. Zhu, S.A. Campbell, G.S.K. Wolkowicz, Bifurcation analysis of a predator—prey system with nonmonotonic functional response, *SIAM J. Appl. Math.* **63** (2002), 636–682.