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Bifurcations in a Leslie-Gower Type Predator-Prey Model with a Rational Non-Monotonic Functional Response

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Abstract. A Leslie-Gower type predator-prey model including group defense formation is analyzed. This phenomenon, described by a non-monotonic function originates interesting dynamics; positiveness, boundedness, permanence of solutions, and existence of up to three positive equilibria are established. The solutions are highly sensitive to initial conditions since there exists a separatrix curve dividing their behavior. Two near trajectories can have far omega-limit sets. The weakness of a singularity is established showing two limit cycles can exist. Numerical simulations endorse the analytical outcomes.

Keywords: limit cycles, stability, separatrix, predator-prey model, functional response.

AMS Subject Classification: 92D25; 34C23; 58F14; 58F21.

1 Introduction

The development of the ecological theory has had an increasing growth in the last decades. This is due to the intensive use of mathematical models describing the interaction between species, particularly those described by nonlinear ordinary differential equation systems (ODEs). Therefore, carrying out an adequate analysis of simple theoretical models and using numerical simulations, more realistic and complex food chains can be studied.

The most popular framework for modeling predator with its prey (resource-consumer models) are the autonomous Gause-type predator-prey models. These were formulated by the Russian biologist Georgii F. Gause at 1934 [10], based on the *mass action law transference of mass principle.*

Nevertheless, the new proposed systems have more complicated dynamics [11, 34]. This happens in the class of predator-prey models here analyzed, in which the following important aspects are considered: 1) the predator's growth function is of logistic type; 2) the functional response or predator consumption rate is a rational non-monotonic Holling type IV.

The first aspect characterizes the predator-prey model proposed by the English ecologist Patrick F. Leslie in 1948 [18], called *logistic predator-prey model* [3, 21, 29] or *Leslie-Gower model* [19, 20], proposed as an alternative to the Gause models.

One important aspect of this type of models is the assumption that the predator's environmental carrying capacity K_y is proportional to the prey population size x, i.e., it depends on the available resources.

In this work, it is also assumed $K_y = nx$, as it is considered in the May-Holling-Tanner model [26, 29], partially studied in [3]. Nonetheless, in the case of severe scarcity, some predator species can switch over to other available food, if their favorite food is not available in abundance [2].

This ability is modelled adding a positive constant c to the environmental carrying capacity for predators, which is described by $K(x) = nx + c$. So, the model is represented by a *Leslie-Gower scheme* or a *modified Leslie-Gower model* [2]; if $x = 0$, then $K(0) = c$, concluding that the predators are *generalist* since they search an alternative food source, avoiding its extinction [29].

1.1 The functional response

One of the main elements of the predator-prey relationship is the *predator functional response* or *consumption function.* It refers to the change in attacked prey density per unit of time per predator when the prey density changes [7,21]. Prey-dependent functional responses are classified into four categories. Three of them were proposed in an original work by the Canadian biologist Crawford S. Holling in 1959 [13]. He based the classification on laboratory experments, all of them being monotonic increasing and saturated functions. They are called Holling Type I, II, and III [29], and they were expressed dependent only on prey population (prey-dependent) [21, 29].

Later in 1984, Robert J. Taylor [28] included a fourth type prey dependent, described by the function $h_m(x) = qx/(x^2 + a^2)$, calling it Holling type IV or dome-shaped functional response, which is non-monotonic; this has been used in different previous works [20, 24, 25, 34]. It must highlight the Holling type I is a piecewise-continuous function [27].

In most predator-prey models considered in the ecological literature, the functional response is assumed increasing monotonically with respect to prey density, as the linear [18], the hyperbolic [2] or the sigmoid [12]. This is an inherent assumption, meaning that the more prey animals there are in the environment, the better off the predator [34].

In this work, the effect of the predation is represented by a non-monotonic functional response or Holling type IV or Monod-Haldane, which is described by the function $H(x) = qx/(x^2 + bx + a)$ with $q > 0$, $a > 0$, and $b \in \mathbb{R}$. As the functional response $H(x)$ must be positive; then $x^2 + bx + a > 0$. Thus, $b^2 - 4a < 0$, so that $-2\sqrt{a} < b$ [35, 36].

It is easy to prove that $H(x)$ tends to zero as the prey population tends to infinity and attains the maximum value when $x = \sqrt{a}$, as shown in the following Figure 1, i.e., the quantity of prey needed for which depredation effect is maximum. The maximum value of $H(x)$ is $H(x_{\max}) = \frac{q\sqrt{a}}{2a+b\sqrt{a}}$, which represents the maximal per capita consumption rate, that is, the maximum number of prey that can be eaten by a predator in each time unit.

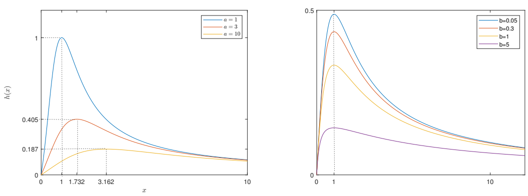

Figure 1. Graph of the generalized Holling type IV functional response $H(x)$. i) In the left panel for different values of the parameter a, with $q = 1$, and $b = 1$ fixed. The values are: $a = 1$ (blue), $a = 3$ (red), $a = 10$ (sienna). ii) In the right panel, different values of the parameter b, are considered for $q = 1$, and $a = 1$ fixed. The values are: $b = 0.05$ (blue), $b = 0.3$ (red), $b = 1$ (orange), $b = 5$ (sienna).

Remark 1. The differences between the graphs of the generalized non-monotonic functional response $H(x)$ for different values of the parameter a, implies that if a is small, few preys are exposed to intensive predation; meanwhile, when a is bigger, small numbers of prey are necessary to avoid predation. For different values of the parameter b, it has a distinct situation; if b is small, predation is more intensive; while, when b is bigger, the predation is minor; in both cases, few preys are necessary to avoid predation.

The function $H(x)$ has been used to study the dynamics of the Gause type predator-prey models in [35, 36]. This function generalizes the hyperbolic functional response given by $h(x) = qx/(x^2 + a^2)$ [1, 11, 20, 24], which describes an antipredator behavior (APB) called *group defense formation* [8, 28, 33, 34].

Examples of this phenomenon are described in [8]. Lone musk ox can be successfully attacked by wolves. Small herds of musk ox (2-6 animals) are attacked but with rare success. No successful attacks have been observed in larger herds. A second example involves certain insect populations. Large swarms of the insects make individual identification difficult for their predators.

Another manifestations of APB, in which a non-monotonic functional response can be used for its description are the following phenomena: a) *aggregation*, which is a social behavior of prey, in which prey congregate on a fine scale relative to the predator; so that the predators hunting is not spatially homogeneous [28, 33], similar to what happens with miles-long schools of certain classes of fishes; b) *inhibition*, a behavior of the predators that occur at the microbial level where evidence indicates that when faced with an overabundance of nutrients (the prey), the effectiveness of the consumers decline [8, 34, 35, 36]. This is often seen when micro-organisms are used for waste decomposition or for water purification [8, 33].

A similar to Holling type III functional response described by $G(x) = qx^2/(x^2 + bx + a)$ was considered in [14] for the case $b < 0$, which is also non-monotonic. Then, an interesting comparative analysis could arise between the models, considering the three functional responses $H(x)$, $h(x)$ and $G(x)$.

Another collective APB is the called prey *herd behavior* [30, 31]. This is a social conduct to avoid predation, when the individuals realizing a senseless reaction equal to that carried out by the majority of the other members of the group [31]. This phenomenon has been modeled by the monotonic function $g_1(x) = q\sqrt{x}/(a + \sqrt{x})$, but can also be described by the generalized monotonic function $g_\alpha(x) = qx^\alpha/(a + x^\alpha)$, with $0 < \alpha < 1$ [31]. Both are Holling type II functional response and non-differentiable in $x = 0$. The obtained ODE system is non-Lipschitzian; it has two solutions for each point on the vertical axis.

Some authors have tried to homologate the way to model this phenomenon with the defense group formation [30]. Although both are social interactions among prey, we are do not completely agree with this version of similarity [31]. We believe those phenomena should be considered different because of the distinct dynamics originated in each system when both kinds of functions are incorporated.

Recently, it has been suggested that even though the shape of some functional responses can be similar, the dynamic of the systems including that functions, could change qualitatively [15]. This phenomenon is called *structural sensitivity* [15]. An interesting question would be to verify whether there exist equivalences of the dynamical behaviors on the systems incorporating different non-monotonic functional responses. One of the aim of this paper is to study dynamical behaviors of a system performing a qualitative and bifurcation analysis in the phase plane $\left(\mathbb{R}_0^+\right)^2$ of the proposed model depending on the parameter values.

The rest of the paper is organized as follows: In the Section 2, the modified Leslie-Gower predator.prey model is presented. In Section 3, the main properties of model are proven. Some numerical simulations are shown in the Section 4, and in Section 5 we explain the ecological meanings of the obtained analytical outcomes.

2 The model

2.1 Model formulation

The Leslie-Gower predation model [19] to be analyzed, is described by the autonomous ordinary differential equation system of Kolmogorov type [7]:

$$X_\mu(x, y) : \begin{cases} \frac{dx}{dt} &= \left(r\left(1 - \frac{x}{K}\right) - \frac{qy}{x^2+bx+a}\right) x, \\ \frac{dy}{dt} &= s\left(1 - \frac{y}{n\,x}\right) y, \end{cases} \tag{2.1}$$

where $x(t)$ and $y(t)$ denote the prey and predator population sizes respectively, measured as biomass or densities by unit of area or volume, for all $t \geq 0$. The parameters are positives, i.e., $\mu = (r, K, q, a, b, s, n) \in \mathbb{R}^7_+$, having the following ecological meanings: r represents the intrinsic growth rate of the prey, K is the prey's environmental carrying capacity, q is the per capita attack rate of predators, a and b are the fitting parameters [17], s represents the intrinsic growth rate of the predators, n is an energy quality measure provided by the prey as food for predators.

System (2.1) or the vector field $X_\mu(x, y)$ is defined in the first quadrant except for $x = 0$, i.e., in the set $\Omega = \left\{(x, y) \in \mathbb{R}^2 / x > 0, y \geq 0\right\}$. The equilibrium point of the system (2.1) or singularities of the vector field $X_\mu(x, y)$ are: $P_K = (K, 0)$ and $P_e = (x_e, y_e)$ the positive equilibria, that satisfies the equations of the isoclines $y = nx$, and $y = \frac{r}{q}\left(1 - \frac{x}{K}\right)\left(x^2 + bx + a\right)$. Then, the abscissa x_e of the positive equilibrium points is a solution of the third degree polynomial equation:

$$p(x) = \frac{r}{Kq}x^3 - \left(\frac{r}{q} - \frac{br}{Kq}\right)x^2 + \left(\frac{ar}{Kq} - \frac{br}{q} + n\right)x - \frac{a}{q}r = 0.$$

2.2 Positive invariance, boundedness and permanence

For system (2.1) or vector field $X_\mu(x, y)$, the following results can be obtained:

Lemma 1 [Existence of a positively invariant region]. *The set* $\Gamma = \left\{(x, y) \in \mathbb{R}^2 / 0 < x \leq K,\ y \geq 0\right\}$ *is a positively invariant region.*

Proof. As system (2.1) is of Kolmogorov type, then, the coordinates axis are invariant set [5]. Let $x = K$; we have that $\frac{dx}{dt} = -\frac{qyx}{K^2 + bK + a} \leq 0$. Whatever the sign of $\frac{dy}{dt} = s\left(1 - \frac{y}{n\,x}\right)y$, the trajectories of the system get into the region Γ. □

Proposition 1 [Boundedness of trajectories]. *All solutions are uniformly bounded.*

Proof. From the first equation of (2.1), the following condition is obtained $\frac{dx}{dt} < rx\left(1 - x/K\right)$, with initial condition $x(0) = x_0 > 0$. This shows that the solutions of defined system must satisfy the condition $x(t) \leq K, \forall t > 0$.

Now, consider a function $w(t)$ such that $w(t) = x(t) + y(t)$, then

$$\begin{aligned} \frac{dw}{dt} &= \frac{dx}{dt} + \frac{dy}{dt} = rx\left(1 - \frac{x}{K}\right) - \frac{qyx}{x^2 + bx + a} + sy - \frac{y^2}{n\,x} \\ &< rx\left(1 - x/K\right) + sy - y^2/nK. \end{aligned}$$

Let $L > 0$ and rewriting the above equations, we have

$$\begin{aligned} \frac{dw}{dt} + Lw &\leq -\frac{r}{K}\left(x^2 - Kx\right) - \frac{1}{nK}\left(y^2 - snKy\right) + Lx + Ly \\ &\leq -\frac{r}{K}\left(x^2 - \frac{(r + L)K}{r}x\right) - \frac{1}{nK}\left(y^2 - (s + L)nKy\right) \end{aligned}$$

and a further simplification gives

$$\frac{dw}{dt} + Lw \leq -\frac{r}{K}\left(x - \frac{(r+L)K}{2r}\right)^2 - \frac{1}{nK}\left(y \; - \frac{(s+L)nK}{2}\right)^2 + \frac{K(r+L)^2}{4r} + \frac{nK(s+L)^2}{4} \leq \frac{K(r+L)^2}{4r} + \frac{nK(s+L)^2}{4}.$$

Denoting $N = K(r+L)^2/4r + nK(s+L)^2/4$, we have

$$0 \leq \frac{dw}{dt} + Lw \leq N.$$

Applying a comparison theorem for differential inequalities, we obtain

$$w(t) \leq N/L + (w(0) - N)e^{-Lt}, \quad 0 < \limsup_{t\to\infty} w(t) \leq N/L.$$

Thus, there is a region R such that $R = \left\{(x, y) \in \Omega/0 < x+y \leq \frac{N}{L} + \epsilon, \forall \epsilon > 0\right\}$. This proves that all solutions are bounded. □

Remark 2. A dynamical system is said to be *dissipative* if all positive trajectories eventually lie in a bounded set. This is to ensure that all solutions exist for all positive time. The last lemma assures this property for the system (2.1).

DEFINITION 1. A system is said to be permanent if there is a possibility of getting some positive constants k_1, k_2 and K_1, K_2 such that each positive solution of system with some initial condition $(x_0, y_0) \in \mathbb{R}^2_+$ satisfies:

$$k_1 \leq \liminf_{t\to\infty} x(t.x_0, y_0) \leq \limsup_{t\to\infty} x(t.x_0, y_0) \leq K_1,$$
$$k_2 \leq \liminf_{t\to\infty} y(t.x_0, y_0) \leq \limsup_{t\to\infty} y(t.x_0, y_0) \leq K_2.$$

Proposition 2 [Permanence of solutions]. *The system (2.1) with initial condition $(x_0, y_0) \in \Omega$ is permanent if and only if $K_2 < ra/q$.*

Proof. From the first equation of (2.1), we get:

$$\frac{dx}{dt} < rx\left(1 - \frac{x}{K}\right).$$

This implies

$$\limsup_{t\to\infty} x(t) \leq \max\{x_0, K\} = K \equiv K_1.$$

From the second equation of system (2.1), we see that

$$\frac{dy}{dt} \leq \; sy\left(1 \; - \frac{y}{n\,K}\right).$$

Thus,

$$\limsup_{t\to\infty} y(t) \leq \max\{y_0, nK\} \equiv K_2.$$

On the other hand, it is easy to see that, if $K_2 < ra/q$ holds, from the first equation of (2.1)

$$\frac{dx}{dt} = x\left(r\left(1-\frac{x}{K}\right) - \frac{qy}{x^2+bx+a}\right) \geq x\left(r\left(1-\frac{x}{K}\right) - \frac{qy}{a}\right)$$
$$\geq rx\left(1-\frac{qK_2}{ra}-\frac{x}{K}\right).$$

Denoting $m = 1 - qK_2/(ra) > 0$, the following can be concluded

$$\liminf_{t\to\infty} x(t) \geq \min\{x_0, mK\} \equiv k_1.$$

Now, from the second equation of system (2.1) we have

$$\frac{dy}{dt} = sy\left(1 - \frac{y}{nx}\right) \geq sy\left(1 - \frac{y}{nk_1}\right),$$

which yields that

$$\liminf_{t\to\infty} y(t) \geq \min\{y_0, nk_1\} \equiv k_2.$$

Therefore, the system is permanent. □

3 Main results

3.1 Topologically equivalent system

In order to carry out an adequate description of behavior of system (2.1) and to simplify the calculations, we follow the methodology used in [25, 26], doing a change of variables and a time re-scaling given by the function: $\varphi : \bar{\Omega} \times \mathbb{R} \to \Omega \times \mathbb{R}$ such as,

$$\varphi(u,v,\tau) = \left(Ku, Knv, \frac{u\left(u^2+\frac{b}{K}u+\frac{a}{K^2}\right)\tau}{r}\right) = (x,y,t)$$

with $\bar{\Omega} = \{(u,v) \in \mathbb{R}^2/\ u \geq 0,\ v \geq 0\} = \mathbb{R}_0^+ \times \mathbb{R}_0^+$. As

$$D\varphi(u,v,\tau) = \begin{pmatrix} K & 0 & 0 \\ 0 & Kn & 0 \\ \frac{1}{K^2 r}\tau\left(3K^2u^2+2bKu+a\right) & 0 & \frac{u\left(u^2+\frac{b}{K}u+\frac{a}{K^2}\right)}{r} \end{pmatrix}.$$

Then,

$$\det D\varphi(u,v,\tau) = \frac{1}{r}\left(nK^2u^3 + bnKu^2 + anu\right) > 0,$$

that is, φ is a diffeomorphism preserving the time orientation [5, 6], for which the vector field $X_\mu(x,y)$ in the new system of coordinates, is topologically equivalent to the vector field, with $Y_\eta(u,v) = \varphi \circ X_\mu(x,y)$; it takes the form $Y_\eta = P(u,v)\frac{\partial}{\partial u} + Q(u,v)\frac{\partial}{\partial v}$ [6] and the associated polynomial differential equation system of fifth order is given by

$$Y_\eta(u,v) : \begin{cases} \frac{du}{d\tau} &= \left((1-u)\left(u^2+Bu+A\right) - Qv\right)u^2, \\ \frac{dv}{d\tau} &= S(u-v)\left(u^2+Bu+A\right)v, \end{cases} \tag{3.1}$$

with $A = a/K^2$, $B = b/k$, $Q = qn/(rk^2)$ and $S = s/rk$, where $\eta = (A, B, Q, S) \in \mathbb{R}^4_+$. System (3.1) is defined at $\bar{\Omega}$.

Remark 3. The set $\bar{\Gamma}_0 = \left\{(u, v) \in \mathbb{R}^2 / 0 \leq u \leq 1,\ 0 \leq v \leq u\right\} \subset \bar{\Omega}$ is a positively invariant region of system (3.1).

3.2 Existence of equilibrium points

As system (2.1) is not defined at the point $(0, 0)$, system (3.1) is topologically equivalent to a continuous extension of the system (2.1) at the point $(0, 0)$.

The equilibrium point of the system (3.1) or singularities of vector field $Y_\eta(u, v)$ are: $(0, 0)$, $(1, 0)$ and $P_e = (u_e, v_e)$ determined by the intersection of the isoclines

$$v = u, \text{ and } v = \frac{1}{Q}(1 - u)\left(u^2 + Bu + A\right).$$

Then, the abscissa u_e of the positive equilibrium points is a solution of the third degree polynomial equation:

$$P(u) = u^3 - (1 - B)u^2 + (A - B + Q)u - A = 0. \tag{3.2}$$

According to Descartes' Rule of signs, the polynomial $P(u)$ might have:

1) A unique positive root, if and only if, $1 - B \leq 0$ and $A + Q - B > 0$, or
2) Three different positive roots, if and only if, $1 - B > 0$ and $A + Q - B > 0$,
3) A unique positive root, if and only if, $1 - B > 0$ and $A - B + Q \leq 0$.

Substituting u by $-u$ the following polynomial is obtained

$$P(-u) = -u^3 - (1 - B)u^2 - (A - B + Q)u - A = 0.$$

Based on Descartes' Rule of signs, the polynomial $P(-u)$

4) Does not change sign if and only if $1 - B \geq 0$ y $A + Q - B > 0$; therefore, $P(u)$ would not have negative real roots.

5) It might have up two negative real roots or none, if and only if, $1 - B < 0$ and $A + Q - B > 0$.

Let $u_e = H$ be, the positive real root that always exists for Equation (3.2). We assume that $P_e = (H, H)$ lies at $\mathbb{R}^2_+$.
Performing the division among the polynomial $P(u)$ and the binomial $(u - H)$, the following quadratic polynomial is obtained

$$P_1(u) = u^2 - (1 - H - B)u + A - B + Q - H(1 - H - B) = 0. \tag{3.3}$$

As the polynomial $P_1(u)$ is a factor of $P(u)$, the rest of the division is

$$R(H) = H^3 - (1 - B)H^2 + (A - B + Q)H - A = 0.$$

Then, a parameter can be isolated, for instance $Q = (1-H)\left(A+BH+H^2\right)/H$. As $Q > 0$, it must fulfill that $H < 1$.

Let Δ the discriminant of the quadratic equation associated (3.3), i.e.,

$$\Delta = (1 - H - B)^2 - 4\left(A - B + Q - H(1 - H - B)\right).$$

Replacing the value of Q, it has $\Delta = (1 - H - B)^2 - 4A/H$.

Lemma 2 [Number of real roots and equilibrium points]. *1. For Equation (3.2) we have:*

1a) There is one positive real root, if and only if, $\Delta < 0$.

1b) Three different real positive roots, if and only if, $\Delta > 0$.

1c) Two real positive roots, one of them having multiplicity two, if and only if, $\Delta = 0$*; they are* $u_{e1} = H$ *and* $u_{e*} = (1 - H - B)/2$.

2. For system (3.1) or vector field $Y_\eta(u, v)$*, we have:*

2a) If $\Delta<0$*, there is a unique equilibrium point* (H, H) *at the interior of* $\bar{\Omega}$.

2b) If $\Delta = 0$*, two equilibrium points exist at the interior of* $\bar{\Omega}$*, which are* (H, H) *and* $(1 - H - B/2, 1 - H - B/2)$.

2c) If $\Delta > 0$*, three equilibrium points exist at the interior of* $\bar{\Omega}$*, which are* (H, H)*,* (u_2, u_2) *and* (u_3, u_3)*, where* $u_2 = (1 - H - B - \sqrt{\Delta})/2$ *and* $u_3 = (1 - H - B + \sqrt{\Delta})/2$*, with* $u_2 < u_3$.

Proof. 1. Replacing Q in $P_1(u)$ and simplifying it, we have $P_1(u) = u^2 - (1 - H - B)\,u + A/H$. Then, the roots of $P_1(u)$ when $1 - H - B > 0$ are: $u_2 = (1 - H - B - \sqrt{\Delta})/2$ and $u_3 = (1 - H - B + \sqrt{\Delta})/2$.

(a) $P_1(u)$ has no real root, if and only if, $\Delta < 0$. Then, $P(u)$ has an unique positive real root.

(b) There are three different real positive roots, if and only if, $\Delta > 0$. The roots are H, u_2 and u_3; clearly, $u_2 < u_3$.

(c) $P_1(u)$ has one positive root of multiplicity two, if and only if, $\Delta = 0$, given by $u^* = (1 - H - B)/2$.

Then, $P(u)$ has two positive roots.

2. The second part of the lemma is immediate. □

Therefore, the number of positive equilibrium points, and the different cases obtained are displayed in the following Table 1.

Table 1. Number of positive real roots of Equation (3.2).

$1 - B$	$A - B + Q$	Δ	Positive real roots
+	+	+	3
+	+	0	2
+	+	−	1
+	0		1
+	−		1
0	+		1
0	−		1
0	0		1
−	+		1
−	−		1
−	0		1

3.3 Nature of boundary equilibria

In order to determine the nature of the hyperbolic equilibria of system (3.1), the Jacobian matrix is required, which is

$$DY_{\eta}(u,v) = \begin{pmatrix} DY_{\eta}(u,v)_{11} & -Qu^2 \\ Sv\left(A+2Bu-Bv-2uv+3u^2\right) & S(u-2v)\left(u^2+Bu+A\right) \end{pmatrix},$$

with

$$DY_{\eta}(u,v)_{11} = -\,u^2\left(A-B-2u+2Bu+3u^2\right) + 2u\left((1-u)\left(u^2+Bu+A\right) - Qv\right).$$

Lemma 3 [Nature of $(1,0)$]. *The singularity $(1,0)$ is a hyperbolic saddle point for all $\eta = (A,B,Q,S)$.*

Proof. Evaluating the Jacobian matrix at equilibrium point $(1,0)$.

$$DY_{\eta}(1,0) = \begin{pmatrix} -(A+B+1) & -Q \\ 0 & S(A+B+1) \end{pmatrix}.$$

Clearly, $\det DY_{\eta}(1,0) = -S(A+B+1)^2 < 0$; thus, the point $(1,0)$ is a hyperbolic saddle point. □

Lemma 4 [Nature of $(0,0)$]. *The point $(0,0)$ has a hyperbolic sector and a parabolic sector.*

Proof. Evaluating the Jacobian matrix at the point $(0,0)$ we have that:

$$DY_{\eta}(0,0) = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}.$$

Thus, the origin is a non-hyperbolic singularity [5,23]. To desingularize the origin, we use the directional blowing-up method [6]. We consider a function given by $\Theta(p,q) = (p,pq) = (u,v)$; we have that $\frac{dp}{d\tau} = \frac{du}{d\tau}$ and $\frac{dq}{d\tau} = \frac{1}{p}\left(\frac{dv}{d\tau} - q\frac{dp}{d\tau}\right)$. Rescaling the time by $T = p\tau$, it becomes,

$$\overline{Y}_{\eta}(p,q) : \begin{cases} \frac{dp}{dT} &= p\left(A - Bp^2 - Ap + Bp + p^2 - p^3 - Qpq\right) \\ \frac{dq}{dT} &= -q\begin{pmatrix} A - Bp^2 - Sp^2 - AS - Ap + Bp + p^2 - p^3 \\ +Sp^2q + ASq - BSp - Qpq + BSpq \end{pmatrix}. \end{cases}$$

If $p = 0$, then

$$\frac{dp}{dT} = 0, \quad \frac{dq}{dT} = -q\left(A - AS + ASq\right).$$

Thus the singularities are: $(0,0)$ and $(0,(S-1)/S)$. This last point is positive, if and only if, $S > 1$. The Jaccobian matrix of vector field $\overline{Y}_{\eta}(p,q)$ is

$$D\overline{Y}_{\eta}(p,q) = \begin{pmatrix} \overline{Y}_{\eta}(p,q)_{11} & -Qp^2 \\ \overline{Y}_{\eta}(p,q)_{21} & \overline{Y}_{\eta}(p,q)_{22} \end{pmatrix}$$

with

$$\overline{Y}_\eta(p,q)_{11} = A - 3Bp^2 - 2Ap + 2Bp + 3p^2 - 4p^3 - 2Qpq,$$
$$\overline{Y}_\eta(p,q)_{21} = q\left(A - B - 2p + BS + 2Bp + Qq + 2Sp + 3p^2 - BSq - 2Spq\right),$$
$$\overline{Y}_\eta(p,q)_{22} = Bp^2 - A + Sp^2 + AS + Ap - Bp - p^2 + p^3 - 2Sp^2q - 2ASq + BSp + 2Qpq - 2BSpq.$$

a) When $p = 0$, it has

$$\overline{Y}_\eta(0,q)_{21} = q\left(A - B + BS + Qq - BSq\right),$$
$$\overline{Y}_\eta(0,q)_{22} = -A + AS - 2ASq.$$

Evaluating on the equilibrium $(0,0)$ it has

$$D\overline{Y}_\eta(0,0) = \begin{pmatrix} A & 0 \\ 0 & A(S-1) \end{pmatrix}.$$

Thus,

a1. $\det D\overline{Y}_\eta(0,0) = A^2(S-1) < 0$, if and only if, $S < 1$. Then the singularity $(0,0)$ is a saddle point.

a2. $\det D\overline{Y}_\eta(0,0) = A^2(S-1) > 0$, if and only if, $S > 1$. Then the singularity $(0,0)$ depends on the sign of the $\operatorname{tr} D\overline{Y}_\eta(0,0) = A + A(S-1) > 0$.

Then, the singularity $(0,0)$ is a repeller.

b) When $q = (S-1)/S$, with $S > 1$

$$\overline{Y}_\eta(0,(S-1)/S)_{21} = (S-1)(-Q + AS + QS)/S^2,$$
$$\overline{Y}_\eta(0,(S-1)/S)_{22} = -A(S-1).$$

Evaluating on the equilibrium $(0,(S-1)/S)$, it obtains

$$D\overline{Y}_\eta\left(0, \frac{S-1}{S}\right) = \begin{pmatrix} A & 0 \\ \frac{(S-1)(AS-Q+QS)}{S^2} & -A(S-1) \end{pmatrix}$$

with, $\det D\overline{Y}_\eta(0,(S-1)/S) = -A^2(S-1) < 0$. Then, the point $\left(0, \frac{S-1}{S}\right)$ is a saddle point, attractor on the vertical axis and repeller on the horizontal axis.

Then, by blowing down, the point $(0,0)$ is a non-hyperbolic saddle or a non-hyperbolic repeller in the system (3.1). We notice that when $S < 1$, the point $(0,(S-1)/S)$ is out of the first quadrant, but in that case is a repeller. □

3.4 Model with a unique positive equilibrium

In the following, we analyzed only one case assuming the existence of a unique positive equilibrium point; the other cases must be studied in future research to complete the description of the model properties described by system (3.1) or vector field $Y_\eta(u,v)$.

Remark 4. We notice that the vector field Y_η has up to three positive equilibrium points at the interior of the first quadrant, the model has the same quantity of equilibrium points as the Gause type model studied in [17] and the Leslie-Gower type models studied in [11, 20] and [14], respectively.

Theorem 1 [Existence of a heteroclinic curve].

Let $W^s(0,0)$ *and* $W^u(1,0)$ *be the stable and unstable manifolds of* $(0,0)$ *and* $(1,0)$*; then, a subset of parameters exist for which the intersection of* $W^s(0,0)$ *and* $W^u(1,0)$ *is not empty, i.e.,* $W^s(0,0) \cap W^u(1,0) \neq \phi$*, giving rise to a heteroclinic curve joining the points* $(0,0)$ *and* $(1,0)$.

Proof. By Lemma 4, the point $(0,0)$ has a separatrix with an inclination of $v = u\left(\frac{S-1}{S}\right)$ and by Lemma 3, the equilibrium $(1,0)$ is a saddle point.

Let $W^s(0,0) = \bar{\Sigma}$ and $W^u(1,0)$ be the stable and unstable manifolds of $(0,0)$ and $(1,0)$. It is clear that $\alpha-$ *limit* of $W^s(0,0)$ and the $\omega -$ *limit* of $W^u(1,0)$ are not at infinity on the direction of $v - axis$; then there are points $(u^*, v^s) \in W^s(0,0)$ and $(u^*, v^u) \in W^u(1,0)$ where v^s and v^u are functions of the parameters A, B, Q and S.

It is clear that if $0 < u << 1$, then, $v^s < v^u$ and if $0 << u < 1$, then $v^s > v^u$. Since the vector field Y_η is continuous with respect to the parameter values, then the stable manifold $W^s(0,0) = \bar{\Sigma}$ intersects with the unstable manifold $W^u(1,0)$; then there exist $(u^*, v^*) \in \bar{\Gamma}$, such as $v^s = v^u = v^*$. This equation defines a surface in the parameter space for which the heteroclinic curve exists. □

Figure 2 shows the relative positions of stable and unstable manifolds of $(0,0)$ and $(1,0)$.

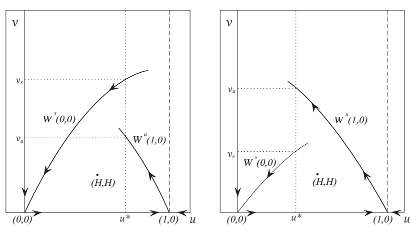

Figure 2. The intersection of $W^s(0,0)$ and $W^u(1,0)$ is not empty, giving rise to the heteroclinic curve joining the points $(0,0)$ and $(1,0)$.

The separatrix curve $\bar{\Sigma}$, the straight line $u = 1$ and the $u-axis$ determines a subregion $\bar{\Gamma}$, which is closed and bounded, that is,

$$\bar{\Psi} = \left\{(u,v) \in (\mathbb{R}_+)^2 / 0 \leq u \leq 1,\ 0 \leq v \leq v^s \text{ and } (u,\ v^s) \in \bar{\Sigma}\right\}$$

is a compact region, where it is possible to apply the Poincaré-Bendixon theorem. By the diffeomorphim φ a separatrix Σ and a subregion Ψ exist, where the Poincaré-Bendixon theorem applies, in system (2.1) (see Figure 3).

To study the nature of the equilibrium point (H,H) with $H < 1$, we will use the relation obtained above: $Q = (1-H)\left(H^2 + BH + A\right)/H$, then, the vector field Y_η or system (3.1) takes the form:

$$Y_\theta : \begin{cases} \frac{du}{d\tau} &= \left((1-u)\left(u^2 + Bu + A\right) - \frac{(1-H)\left(H^2+BH+A\right)}{H} v \right) u^2, \\ \frac{dv}{d\tau} &= S\,(u - v)\left(u^2 + Bu + A\right) v \end{cases} \tag{3.4}$$

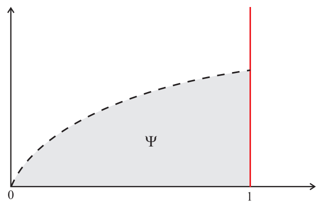

Figure 3. Subregion in the phase plane where it is possible to apply the Poincaré-Bendixson theorem.

with $\theta = (A, B, H, S)$. The Jacobian matrix is now:

$$DY_\theta(H,H) = \begin{pmatrix} -H^2\left(A - B - 2H + 2BH + 3H^2\right) & -H(1-H)\left(A + BH + H^2\right) \\ HS\left(A + BH + H^2\right) & -HS\left(A + BH + H^2\right) \end{pmatrix}$$

with $\det DY_\theta(H,H) = H^2 S\left(A + BH + H^2\right)\left(A + H^2(B + 2H - 1)\right).$

It has that $\det DY_\theta(H,H) > 0$, if and only if, $A + H^2(B + 2H - 1) > 0$, that is, if and only if, $A > H^2(1 - B - 2H)$. The trace is given by:

$$\mathrm{tr} DY_\theta(H,H) = -H^2\left(A - B - 2H + 2BH + 3H^2\right) - HS\left(H^2 + BH + A\right).$$

If $\mathrm{tr} DY_\theta(H,H) = 0$, then $S = -H\left(A{-}B{-}2H{+}2BH{+}3H^2\right)/(H^2{+}BH{+}A)$. Then, as $S > 0$, $A - B - 2H + 2BH + 3H^2 > 0$, if and only if, $A > B + H(2 - 2B - 3H)$. We remember that in this case, $\Delta = (1 - H - B)^2 - 4\frac{A}{H} = 0$. Then, $A = 4H(1 - H - B)^2$.

Replacing Q, Equation (3.2) can be rewritten as

$$P(u) = u^3 - (1-B)u^2 + (4(1-B) - 3H)(1-H-B)u - 4H(1-H-B)^2 = 0,$$

since $Q = (1-H)\left(-7B - 7H + 8BH + 4B^2 + 4H^2 + 4\right)$. Let us

$$P = \left(\mathrm{tr} DY_\theta(H,H)\right)^2 - 4\det DY_\theta(H,H).$$

For the system (3.4) we have

Theorem 2 [Nature of the positive equilibrium].

Let us $(u^*, v^s) \in W^s(0,0)$ and $(u^*, v^u) \in W^u(1,0)$. Assuming $0 < H < 1$, the equilibrium point (H,H) is in the interior of the first quadrant.

1. Assuming $v^s > v^u$, it has that (H,H) is

(a) an attractor, if and only if, $S > \frac{-H\left(A-B-2H+2BH+3H^2\right)}{H^2+BH+A}$. Moreover, assuming the last inequality

i. an attractor node, if and only if, $P > 0$ (see Figure 4), and

ii. an attractor focus, if and only if, $P < 0$ (see Figure 5),

(b) a repeller, if and only if, $S < \frac{-H\left(A-B-2H+2BH+3H^2\right)}{H^2+BH+A}$. Moreover, assuming the last inequality

i. a repeller node, if and only if, $P > 0$ *and*

ii. a repeller focus, which is surrounded by a limit cycle, if and only if, $P < 0$ *(see Figure 6),*

(c) a weak focus, if and only if, $S = \frac{-H\left(A-B-2H+2BH+3H^2\right)}{H^2+BH+A}$.

2. Assuming $v^s < v^u$*, it has that* (H, H) *is a repeller (node or focus).*

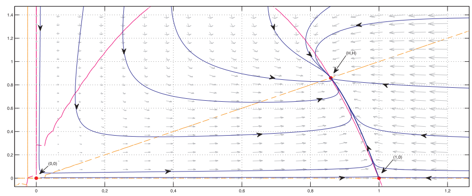

Figure 4. For $A = 0.1$, $B = 4$, $S = 0.15$ and $Q = 0.7$. The positive equilibrium point is an attractor node and $(1, 0)$ is a hyperbolic saddle.

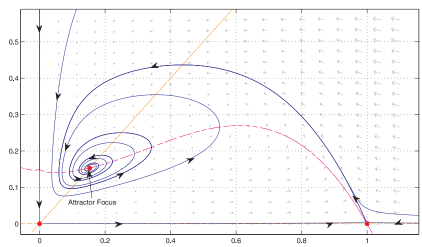

Figure 5. Considering $A = 0.1$, $B = 0.02$, $S = 0.3$ and $Q = 0.7$, the unique positive equilibrium point is an attractor focus and $(1, 0)$ is a hyperbolic saddle.

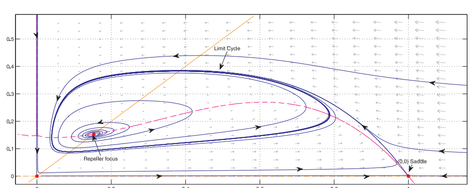

Figure 6. For $A = 0.1$, $B = 0.02$, $S = 0.15$ and $S = 0.7$, the unique positive equilibrium is a repeller focus surrounded by a stable limit cycle and $(1, 0)$ is a hyperbolic saddle.

Proof. 1. Immediate, considering the sign of $\mathrm{tr} DY_\theta(H, H)$ and P.

When $P < 0$, then, the point is a repeller focus; by the Poincaré-Bendixon Theorem [3, 5] in the subregion $\bar{\Gamma}$ determined by the straight line $u = 1$, the $u-axis$ and the stable manifold $W^s(0,0) = \bar{\Sigma}$, the point (H, H) is surrounded by at least one limit cycle.

2. Assuming that $v^s > v^u$, then the stable manifold $W^s(0,0)$ lies under the unstable $W^u(1,0)$ and the equilibrium point (H,H) is a repeller node or focus. The trajectories have the origin as their $\omega - limit$. □

Corollary 1. A Hopf bifurcation occurs at equilibrium point (H,H) for the bifurcation value $S = -H\left(A - B - 2H + 2BH + 3H^2\right)/(H^2 + BH + A)$.

Proof. It follows from the theorem described above since $\det DY_\theta(H,H)$ is positive and $\mathrm{tr}DY_\theta(H,H)$ changes sign. Moreover, the transversality condition is verified since

$$\frac{\partial}{\partial S}\left(\mathrm{tr}DY_\theta(H,H)\right) = -H\left(H^2 + BH + A\right) < 0.$$

□

Remark 5. 1. When $v^s > v^u$ in the theorem described above, the point $(0,0)$ is almost globally asymptotically stable [22], since the equilibrium (H,H) is the unique solution not attaining that point. Thus, all the trajectories in the neighborhood of the point (H,H) go to the equilibrium $(0,0)$.

2. When the parameters change, the limit cycle generated by the Hopf bifurcation expands and hits the heteroclinic curve, which is then broken and disappears.

Theorem 3 [Existence of two limit cycles]. *The equilibrium point (H,H) is a second order weak focus.*

Proof. We use the calculations of the Lyapunov quantities [16] and consider the change of variables,

$$Su = U + H, \quad v = V + H, \text{ so, } \frac{du}{d\tau} = \frac{dU}{d\tau}; \frac{dv}{d\tau} = \frac{dV}{d\tau}.$$

Then, the new system translated to the origin is:

$$A_\eta(U,V): \begin{cases} \frac{dU}{d\tau} = \begin{pmatrix} (1-U-H)\left((U+H)^2 + B(U+H) + A\right) \\ -\frac{1}{H}(1-H)\left(A + BH + H^2\right)(V+H) \end{pmatrix}(U+H)^2, \\ \frac{dV}{d\tau} = S(V+H)\ (U-V)((U+H)^2 + B(U+H) + A). \end{cases}$$

A normal form [3] for this system is obtained by making an adequate change of coordinates. For this, we use the Jordan matrix [3] associated to vector field $A_\eta(U,V)$:

$$J = \begin{pmatrix} 0 & -W \\ W & 0 \end{pmatrix}$$

with, $W^2 = \det DA_\eta(0,0) = H^2 S\left(A + BH + H^2\right)\left(A + BH^2 - H^2 + 2H^3\right)$. The first Lyapunov quantity is $\eta_1 = \mathrm{tr}DA_\eta(H,H) = 0$. The matrix for the change of coordinates is:

$$M=\begin{pmatrix} HS\left(A+BH+H^2\right) & -W \\ HS\left(A+BH+H^2\right) & 0 \end{pmatrix}.$$

Considering the change of variables given by

$$\begin{pmatrix} U \\ V \end{pmatrix}=\begin{pmatrix} HS\left(A+BH+H^2\right) & -W \\ HS\left(A+BH+H^2\right) & 0 \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix},$$

that is, $U = HS\left(A+BH+H^2\right)x - Wy$ and $V = HS\left(A+BH+H^2\right)x$. Then,

$$\begin{pmatrix} x \\ y \end{pmatrix}=\begin{pmatrix} 0 & \frac{1}{HS(A+BH+H^2)} \\ -\frac{1}{W} & \frac{1}{W} \end{pmatrix}\begin{pmatrix} U \\ V \end{pmatrix}$$

with, $x=\frac{1}{HS(A+BH+H^2)}V$ and $y=-\frac{1}{W}U+\frac{1}{W}V$. After long algebraic calculations and by means of time rescaling, we obtain the normal form:

$$\bar{Z}_\eta=\left(\frac{dx}{d\tau},\ \frac{dy}{d\tau}\right):$$

where

$$\begin{aligned}
\frac{dx}{d\tau} &= -y - S\left(A+2BH+3H^2\right)xy+\frac{W\left(B+2H\right)}{A+BH+H^2}y^2 - HS^2\left(B+3H\right)\\
&\quad\times\left(A+BH+H^2\right)x^2y+SW\left(B+4H\right)xy^2-\frac{W^2}{A+BH+H^2}y^3\\
&\quad- S^3H^2\left(A{+}BH{+}H^2\right)^2x^3y+2S^2HW\left(A{+}BH{+}H^2\right)x^2y^2-SW^2xy^3;\\
\frac{dy}{d\tau} &= x+\frac{1}{W^2}H^2S^2\left(2A+3BH^2-3H^2+7H^3\right)\left(A+BH+H^2\right)^2x^2\\
&\quad+\frac{1}{W}HS\left(A+BH+H^2\right)\big((-2A-8BH^2{-}3H^2S{-}2AH{+}2BH{-}AS{+}8H^2\\
&\quad-16H^3-2BHS\big)xy+H\left(2A-2B-5H+5BH+BS+2HS+9H^2\right)y^2\\
&\quad+\frac{1}{W}H^2S^3\left(A+3BH^2-3H^2+9H^3\right)\left(A+BH+H^2\right)^3x^3\frac{1}{W}+HS^2\\
&\quad\times\left(A+BH+H^2\right)^2\big(-2A-10BH^2-3H^2S-AH+BH+10H^2-28H^3\\
&\quad-BHS\big)x^2y+S\left(A+BH+H^2\right)\big(A+11BH^2+4H^2S+2AH-2BH\\
&\quad-11H^2+29H^3+BHS\big)xy^2-W\left(A-B-4H+4BH+HS+10H^2\right)y^3\\
&\quad+\frac{1}{W^2}H^4S^4\left(B{+}5H{-}1\right)\left(A{+}BH{+}H^2\right)^4x^4-\frac{1}{W}H^3S^3\left(A{+}BH{+}H^2\right)^3\\
&\quad\times\left(4B{+}20H{+}S{-}4\right)x^3y{+}2H^2S^2W\left(A{+}BH{+}H^2\right)\left(3B{+}15H{+}S{-}3\right)x^2y^2\\
&\quad-HSW\left(A+BH+H^2\right)\left(4B+20H+S-4\right)xy^3+W^2\left(B+5H-1\right)y^4\\
&\quad+\frac{1}{W^2}H^5S^5\left(A+BH+H^2\right)^5x^5-\frac{1}{W}5H^4S^4\left(A+BH+H^2\right)^4x^4y\\
&\quad+10H^3S^3\left(A+BH+H^2\right)^3x^3y^2-10H^2S^2W\left(A+BH+H^2\right)^2x^2y^3\\
&\quad+5HSW^2\left(A+BH+H^2\right)xy^4+W^3y^5.
\end{aligned}$$

Using the Mathematica package [32], the second Liapunov quantity [5] is obtained, being given by:

$$\eta_2\left(A,B,H\right)=AHf\left(A,B,H\right)/\left(B\left(A+H^3\right)^2\right),$$

where

$$\begin{aligned}f\left(A,B,H\right)&=17A^8-56A^8B-15A^8B^2+38A^8H+51A^8B^2H+51A^8B^2H\\&-39A^8B^3H-27A^7H^2-19A^8H^2+79A^2BH^2-22A^8B^2H^3+25A^6B^2H^3\\&-56A^7H^3-9A^6B^2H^3-23A^8B^2H^3+17A^6B^2H^3+35A^5H^4-41A^6H^4\\&-A^4BH^4+42A^6B^2H^4-63A^4B^3H^4+29A^6B^2H^4-31A^5BH^5+67A^6H^5\\&-53A^4BH^5+11A^6B^2H^5+15A^4B^2H^7+18A^3H^6-21A^2BH^6-24A^2B^2H^6\\&+12A^4B^2H^7+12A^3B^2H^6+13A^4B^3H^6+47A^3H^7+196A^5H^7-214A^3B^3H^7\\&+72A^4B^3H^7+45A^2B^3H^8-5A^3H^8+96A^3B^3H^8-31A^2B^3H^6\\&+46BH^9+32A^4H^9+37B^3H^9+41A^2B^2H^9+18B^2H^9+35ABH^{10}\\&-91B^2H^{10}-5B^2H^{10}+13BH^{11}-7BH^{11}.\end{aligned}$$

Clearly, the sign of η_2 depends on $f\left(A,B,H\right)$. Taking into account that $A=\frac{1}{4}H\left(1-B-H\right)^2$ by Lemma 3, and after some simplifications and algebraic calculations, it has that:

$$\begin{aligned}f\left(B,H\right)&=96BH^7+\left(312B^2-1296B-888\right)H^6+\left(20B^4+280B^3-2784B^2\right.\\&\left.+1360B+2148\right)H^5+\left(20B^5+44B^4-1810B^3+4442B^2-442B-2878\right)H^4\\&+\left(5B^6+6B^5-349B^4+2612B^3-4453B^2-1242B+2333\right)H^3\\&+\left(3B^6-38B^5+508B^4-2422B^3+1789B^2+1292B-1212\right)H^2\\&+\left(42B^5-5B^6-473B^4+806B^3-297B^2-512B+391\right)H\\&+\left(88B^4-30B^5-3B^6-114B^3+19B^2+96B-56\right).\end{aligned}$$

Numerically, it can show that $f\left(B,H\right)$ changes its sign. For instance: i) choosing $H=0.1$, it has

$$\begin{aligned}f\left(B,0.1\right)=&-3.465B^6-26.172B^5+45.436B^4-55.186B^3\\&+3.1537B^2+56.446B-26.954.\end{aligned}$$

Evaluating for $B=0.6$ and $B=0.7$ we obtain, $f\left(0.6,0.1\right)=-0.179\,54$ and $f\left(0.7,0.1\right)=1.277\,5$; thus a value B^* exists in $B\in\left]0.6,0.7\right[$, for which $f\left(B^*,0.1\right)=0$. Next: ii) analogously, choosing $H=0.5$, it has

$$f\left(B,0.5\right)=3.12B-16.5B^5-61.75B^4-94.37B^3-43.38B^2-4.125B^6+1.5.$$

Evaluating for $B=0.1$ and $B=0.3$ we obtain, $f\left(0.1,0.5\right)=1.277\,5$ and $f\left(0.3,0.5\right)=-4.559\,5$; therefore a value B^{**} exists in $B\in\left]0.1,0.3\right[$, for which $f\left(B^{**},0.5\right)=0$. Then, $f\left(B,H\right)$ and $f\left(A,B,H\right)$ change of sign. Thus, values of A,B and H exist such that $\eta_2\left(A,B,H\right)=0$. Therefore, at least two limit cycles can exist (see Figure 7). This complete the proof. □

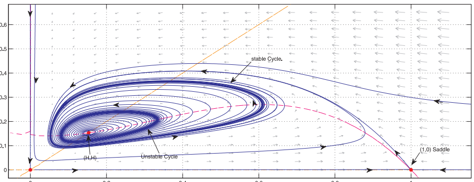

Figure 7. For $A = 0.1$, $B = 0.02$, $S = 0.01$ and $Q = 0.7$, the positive equilibrium point is a weak focus of order two, surrounded by two limit cycles, the innermost unstable and the outermost stable and $(1, 0)$ is a hyperbolic saddle.

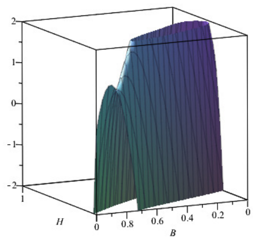

Figure 8. The factor $f\,(B, H)$ in the Theorem 3 that presents changes of sign.

Figure 8 shows graph of the factor $f\,(B, H)$ of the Theorem 3, which changes its sign.

Remark 6. As it's well-known, the existence of limit cycles is relevant to the existence, stability and bifurcation of a positive equilibrium. They are important in the study of the oscillations of the populational sizes. Thus, the order of a weak focus plays a key role to determine the number of limit cycles for the predator-prey models, which is an open problem in Populational Dynamic.

Following the methodology described in [9], where studying global bifurcations of limit cycles and applying the Wintner-Perko termination principle [23], it could be shown that the system has at most two concentric limit cycles surrounding one positive equilibrium point, as we have verified in Figure 7.

4 Numerical simulations

Some simulations that agree with the mathematical results are shown related with the behavior of the positive equilibrium point (H, H). Here, we can appreciate different situations for the system when parameters values change.

We show two cases considering the number of positive equilibrium points, at the phase plane. In all simulations, it can appreciate that the stable manifold $W^s\,(0, 0)$ has a great slope, and it almost coincides with the vertical axis.

Case 1. Existence of one positive equilibrium point. In Figures 4 to 7, the main dynamics of the system (3.1) are shown, which have been proved in the text.

Case 2. Existence of three positive equilibrium points. In Figures 9 and 10, we show complex dynamic behaviors of the system (3.1) not described in the proven properties.

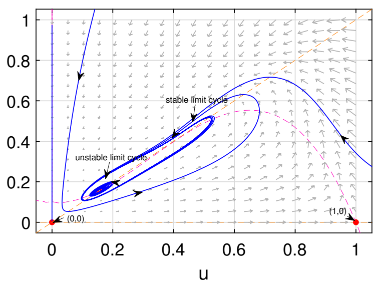

Figure 9. For $A = 0.0275$, $B = 0.0075$, $S = 0.65$ and $Q = 0.2875$, there exists a non-infinitesimal limit cycle surrounded three positive equilibrium points, one of them (u_{e1}, u_{e1}) to the left, is an attractor focus encircled by a unstable cycle. The point $(0, 0)$ is a non-hyperbolic saddle and $(1, 0)$ is a hyperbolic saddle.

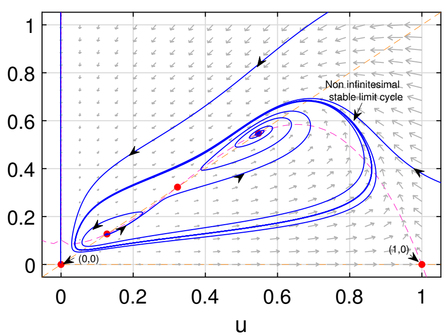

Figure 10. For $A = 0.0245$, $B = 0.001$, $S = 0.01$ and $Q = 0.2675$, there exists a non-infinitesimal limit cycle surrounded three positive equilibrium points, one of them (u_{e1}, u_{e1}) to the left, is a repeller node, (u_{e2}, u_{e2}) to the right is an attractor focus. The point $(0, 0)$ is a non-hyperbolic saddle and $(1, 0)$ is a hyperbolic saddle.

5 Discussion

In this work, a Leslie-Gower type predator prey model, described by a bidimensional continuous-time differential equations system, is analyzed, considering a rational functional response of Holling type IV. By means of both a reparametrization and a time rescaling, the original system was transformed into a polynomial system topologically equivalent, in order to reduce the calculations and to carry out an adequate study of the model.

First, we established the quantity of singularities of the vector field, showing that the system can have up three positive equilibria. Nevertheless, we focused the attention on the case in which a unique positive equilibrium exists.

We have shown the importance of the point $(0,0)$ in the modified Leslie-Gower model, although system (2.1) is not defined there. The singularity $(0,0)$ is a point with a complex nature since it possesses parabolic and hyperbolic sectors on the phase plane. Using the blowing up method [6], we demonstrated the existence of a separatrix curve $\bar{\Sigma}$, determined by the stable manifold of non-hyperbolic singularity $(0,0)$. This curve divides the behavior of trajectories; very near solutions, but to different sides with respect to this curve have distinct $\omega-$ *limit*; then, solutions are highly sensitive to initial conditions.

The existence of a heteroclinic curve joining the equilibrium $(1,0)$ and the singularity $(0,0)$ is also proven, which is generated by the stable manifold of non-hyperbolic equilibrium $(0,0)$ and the unstable manifold of the $(1,0)$.

Also, we proved the boundedness of solutions of system (3.1), using the compactification of Poincaré method [23], showing that the modified Leslie-Gower model is well-posed. Furthermore, we proved the existence of parameter constraints for which the positive equilibrium point is an attractor or is a repeller surrounded by a unique limit cycle.

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 is an interesting problem. This problem is related to the unsolved problem proposed by the mathematician David Hilbert in 1900 and refers to finding the maximum number of limit cycles of a bidimensional polynomial differential equation system, whose degree must be less than or equal to $n \in N$.

In Population Dynamics, this issue has been extensively studied over the last three decades starting with the work by Kuo-Shung Cheng in 1981 [4]. Using the symmetry of the prey isocline, he was the first scientist to prove the uniqueness of a limit cycle for a specific predator-prey model with a Holling type II functional response.

By using the Lyapunov quantities method [16] we demonstrate that the model has a two-order weak focus, that is, the unique positive equilibrium point is an attractor focus surrounded two limit cycles, the innermost unstable and the outhermost stable.

As the systems (2.1) and (3.1) are topologically equivalent, it is possible affirm that the main characteristic of the model (2.1) is that both species can coexist or else, the predators can go extinct, for the same parameter values, according to the relation between their initial population sizes.

Simulations considering three positive equilibrium points in system (3.1) show that the stable manifold $W^s(0,0)$ of the equilibrium point $(0,0)$ is also very near to the vertical axis. This result implies in system (2.1) that both populations cannot be driven into extinction, simultaneously.

Some prospective studies can be considered to analyze, such as:

i) the cases in which two or three positive equilibria exist. Moreover, the some model considering alternative food for predator, i.e, assuming the variable environmental carrying capacity of predators described by $K(x) = nx + c$, with $c > 0$.

ii) The Leslie-Gower type predator-prey model considering the generalized non-monotonic functional response $h(x) = \frac{qx^m}{x^n + a}$, with n, $m \in \mathbb{N}$ and $n > m \geq 1$. Simple cases have been analyzed in [11, 20], assuming $m = 1$ and $n = 2$.

iii) The Allee effect [9] can also be included in the above models. Some particular cases have been studied in [1, 9].

iv) Likewise, the influence of the shape of non-monotonic functional responses may also be a topic to be developed.

Therefore, the comparison among these models arises naturally; in particular, the showdown about the number of positive equilibria and their nature, as well as the number of limit cycles around of a positive equilibrium point generated by Hopf bifurcation, or else, the existence of non-infinitesimal limit cycle originated by homoclinic or heteroclinic bifurcations.

References

[1] P. Aguirre, E. González-Olivares and E. Sáez. Three limit cycles in a LeslieGower predator-prey model with additive Allee effect. *SIAM Journal on Applied Mathematics*, **69**(5):1244–1262, 2009. https://doi.org/10.1137/070705210.

[2] C. Arancibia-Ibarra and E. González-Olivares. The Holling-Tanner model considering an alternative food for predator. In J. Vigo-Aguiar(Ed.), *Proceedings of the 2015 International Conference on Computational and Mathematical Methods in Science and Engineering CMMSE 2015*, pp. 130–141. CMMSE, 2015.

[3] D. Arrowsmith and C.M. Place. *Dynamical Systems: Differential Equations, Maps, and Chaotic Behaviour*. Chapman Hall/CRC Mathematics Series. Taylor & Francis, 1992. ISBN 9780412390807.

[4] K.-S. Cheng. Uniqueness of a limit cycle for a predator-prey system. *SIAM Journal on Mathematical Analysis*, **12**(4):541–548, 1981. https://doi.org/10.1137/0512047.

[5] C. Chicone. *Ordinary Differential Equations with Applications*. Texts in Applied Mathematics. Springer, New York, 2008.

[6] F. Dumortier, J. Llibre and J.C. Artés. *Qualitative Theory of Planar Differential Systems*. Universitext. Springer, Berlin, Heidelberg, 2006.

[7] H.I. Freedman. *Deterministic Mathematical Models in Population Ecology*. Monographs and textbooks in pure and applied mathematics. Dekker, New York, 1980.

[8] H.I. Freedman and G.S.K. Wolkowicz. Predator-prey systems with group defence: The paradox of enrichment revisited. *Bulletin of Mathematical Biology*, **48**(5):493–508, 1986. https://doi.org/10.1016/S0092-8240(86)90004-2.

[9] V.A. Gaiko and C. Vuik. Global dynamics in the LeslieGower model with the allee effect. *International Journal of Bifurcation and Chaos*, **28**(12):1850151, 2018. https://doi.org/10.1142/S0218127418501511.

[10] G.F. Gause. *The Struggle for Existence*. The Struggle for Existence. The Williams & Wilkins company, Baltimore, 1934. ISBN 9780598976703. https://doi.org/10.5962/bhl.title.4489.

[11] B. González-Yañez, E. González-Olivares and J. Mena-Lorca. Multistability on a Leslie-Gower type predator prey model with nomonotonic functional response. In R. Mondaini and R. Dilao(Eds.), *International Symposium on Mathematical and Computational, Biology, Biomat 2006*, pp. 359–384. World Scientific Co., 2007. https://doi.org/10.1142/9789812708779_0023.

[12] E. Gonzlez-Olivares, P. Tintinago-Ruiz and A. Rojas-Palma. A LeslieGower-type predatorprey model with sigmoid functional response. *International Journal of Computer Mathematics*, **92**(9):1895–1909, 2015. https://doi.org/10.1080/00207160.2014.889818.

[13] C.S. Holling. The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. *The Canadian Entomologist*, **91**(5):293–320, 1959. https://doi.org/10.4039/Ent91293-5.

[14] J. Huang, S. Ruan and J. Song. Bifurcations in a predatorprey system of Leslie type with generalized Holling type III functional response. *Journal of Differential Equations*, **257**(6):1721–1752, 2014. https://doi.org/10.1016/j.jde.2014.04.024.

[15] M.C. Köhnke, I. Siekmann, H. Seno and H. Malchow. A type IV functional response with different shapes in a predatorprey model. *Journal of Theoretical Biology*, **505**:110419, 2020. https://doi.org/10.1016/j.jtbi.2020.110419.

[16] Y. Kuznetsov. *Elements of Applied Bifurcation Theory*. Applied Mathematical Sciences. Springer, New York, 2013. https://doi.org/10.1007/978-1-4757-3978-7.

[17] Y. Lamontagne, C. Coutu and C. Rousseau. Bifurcation analysis of a predatorprey system with generalised Holling type III functional response. *Journal of Dynamics and Differential Equations*, **20**(3):535–571, 2008. https://doi.org/10.1007/s10884-008-9102-9.

[18] P.H. Leslie. Some further notes on the use of matrices in population mathematics. *Biometrika*, **35**(3-4):213–245, 12 1948. https://doi.org/10.1093/biomet/35.3-4.213.

[19] P.H. Leslie and J.C. Gower. The properties of a stochastic model for the predator-prey type of interaction between two species. *Biometrika*, **47**(3-4):219–234, 12 1960. https://doi.org/10.1093/biomet/47.3-4.219.

[20] Y. Li and D. Xiao. Bifurcations of a predator-prey system of Holling and Leslie types. *Chaos, Solitons & Fractals*, **34**(2):606–620, 2007. https://doi.org/10.1016/j.chaos.2006.03.068.

[21] R.M. May. *Stability and Complexity in Model Ecosystems*. Princeton Landmarks in Biology. Princeton University Press, 2019. https://doi.org/10.2307/j.ctvs32rq4.

[22] P. Monzón. Almost global attraction in planar systems. *Systems & Control Letters*, **54**(8):753–758, 2005. ISSN 0167-6911. https://doi.org/10.1016/j.sysconle.2004.11.014.

[23] L. Perko. *Differential Equations and Dynamical Systems*. Texts in Applied Mathematics. Springer, New York, 2012. https://doi.org/10.1007/978-1-4613-0003-8.

[24] L. Puchuri, E. González-Olivares and A. Rojas-Palma. Multistability in a Leslie-Gowertype predation model with a rational nonmonotonic functional response and generalist predators. *Computational and Mathematical Methods*, **2**(2):e1070, 2020. https://doi.org/10.1002/cmm4.1070.

[25] A. Rojas-Palma, E. González-Olivares and B. González-Yañez. Metastability in a Gause type predator-prey models with sigmoid functional response and multiplicative Allee effect on prey. In R. Mondaini(Ed.), *Proceedings of the 2006 International Brazilian Symposium on Mathematical and Computational Biology*, pp. 295–321. E-Papers Serviços Editoriais, Ltda., 2007.

[26] E. Sáez and E. González-Olivares. Dynamics of a predator-prey model. *SIAM Journal on Applied Mathematics*, **59**(5):1867–1878, 1999. https://doi.org/10.1137/S0036139997318457.

[27] G. Seo and D.L. DeAngelis. A predator-prey model with a Holling type I functional response including a predator mutual interference. *Journal of Nonlinear Science*, **21**(6):811–833, 2011. https://doi.org/10.1007/s00332-011-9101-6.

[28] R.J. Taylor. *Predation.* Population and Community Biology. Springer, Netherlands, 2013.

[29] P. Turchin. *Complex Population Dynamics: A Theoretical/Empirical Synthesis.* Monographs in Population Biology. Princeton University Press, 2013. https://doi.org/10.1515/9781400847280.

[30] E. Venturino and S. Petrovskii. Spatiotemporal behavior of a preypredator system with a group defense for prey. *Ecological Complexity*, **14**:37–47, 2013. https://doi.org/10.1016/j.ecocom.2013.01.004. Special Issue on the occasion of Horst Malchow's 60th birthday.

[31] K. Vilches, E. González-Olivares and A. Rojas-Palma. Prey herd behavior modeled by a generic non-differentiable functional response. *Mathematical Modelling of Natural Phenomena*, **13**(3):26, 2018. https://doi.org/10.1051/mmnp/2018038.

[32] Inc Wolfram Research. *Mathematica: A System for Doing Mathematics by Computer.* Wolfram Research, Incorporated, 1992.

[33] G.S.K. Wolkowicz. Bifurcation analysis of a predator-prey system involving group defence. *SIAM Journal on Applied Mathematics*, **48**(3):592–606, 1988. https://doi.org/10.1137/0148033.

[34] D. Xiao and S. Ruan. Global analysis in a predator-prey system with nonmonotonic functional response. *SIAM Journal on Applied Mathematics*, **61**(4):1445–1472, 2001. https://doi.org/10.1137/S0036139999361896.

[35] D. Xiao and H. Zhu. Multiple focus and hopf bifurcations in a predator-prey system with nonmonotonic functional response. *SIAM Journal on Applied Mathematics*, **66**(3):802–819, 2006. https://doi.org/10.1137/050623449.

[36] H. Zhu, S.A. Campbell and G.S.K. Wolkowicz. Bifurcation analysis of a predator-prey system with nonmonotonic functional response. *SIAM Journal on Applied Mathematics*, **63**(2):636–682, 2003. https://doi.org/10.1137/S0036139901397285.