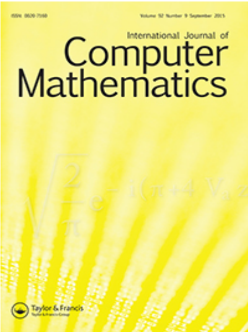

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A Leslie–Gower-type predator–prey model with sigmoid functional response

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In this work, a continuous-time predator–prey model of Leslie–Gower type considering a sigmoid functional response is analysed. Using the MatLab package some simulations of the dynamics are shown. Conditions for the existence of equilibrium points, their nature and the existence of at least one limit cycle in phase plane are established. The existence of a separatrix curve dividing the behaviour of trajectories is proved. Thus, two closed trajectories can have different ω-*limits* being highly sensitive to initial conditions. Moreover, for a subset of parameter values, it can be possible to prove that the point (0,0) can be globally asymptotically stable. So, both populations can go to extinction, but simulations show that this situation is very difficult. According to our knowledge no previous work exists analysing the model presented here. A comparison of the model here studied with the May–Holling–Tanner model shows a difference on the quantity of limit cycles.

Keywords: predator–prey model; functional response; bifurcation; separatrix curve; heteroclinic orbit; stability

2000 AMS Subject Classifications: 92D25; 34C23; 58F14; 58F21

1. Introduction

This work deals with a class of continuous-time predator–prey model, considering two important aspects for describing the interaction:

(1) The functional response or predator consumption rate is a Holling type III, sigmoid or S-shaped [18,25].
(2) The predators growth function is of logistic type [18,26].

The second aspect characterize the Leslie-type predator–prey models [18] also known as logistic predator–prey model [26] or Leslie–Gower model [1,3,13]. In this type of model, the conventional environmental carrying capacity for predators K_y is a function of the available prey quantity [1,3,12,13].

A particular case is the Holling–Tanner (or May–Holling–Tanner) model [2,23,26], in which K_y is also proportional to prey abundance $x = x(t)$, that is, $K_y = K(x) = nx$ and the functional response is hyperbolic [4,18]. An interesting comparison arose between both models, the May–Holling and the model proposed here.

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These types of models can lead to anomalies in their predictions [26], because they predict that even at very low prey density when the consumption rate by an individual predator is essentially zero, predator population can nevertheless increase, if predator–prey ratio is very small [26]. However, these models are recently employed in Population Dynamics [26].

Also, other description for K_y can be given in [3,16], obtaining the so-called *modified* Leslie–Gower models.

On the other hand, 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 three decades [15], starting with the work by Cheng [5] who was the first to prove the uniqueness of a limit cycle for a specific predator–prey model with a Holling type II functional response, using the symmetry of the prey isocline.

This problem is related to Hilbert's well-known 16th Problem for polynomial systems [9], and it is a question that has remained unanswered for the predation model. This question was 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, in which the degree of each polynomial must be equal to $m \in \mathbb{N}$.

However, it is not an easy task to study the quantity of limit cycles that can be generated throughout the bifurcation of a centre focus [9], existing various forms to establish this number as the Lyapunov number method [6].

This paper is organized as follows: in the next subsection, the sigmoid functional response is presented. In Section 2, the modified Leslie–Gower model is presented; in Section 3, the main properties of the model are showed; and in the last section, we make a discussion of the results.

1.1 *Sigmoid functional response*

The predator functional response or consumption function refers to the change in attacked prey density per unit of time per predator when the prey density changes [8,18].

In most predator–prey models considered in the ecological literature, the predator response to the prey density is assumed to be increasingly monotonic; an inherent assumption meaning that the more prey animals there are in the environment, the better off the predator [22].

We will considered that the predator functional response is expressed by the function $h(x) = qx^2/(x^2 + a^2)$ as in [11,21]. Here, the parameter a is a measure of abruptness [10] of the functional response. If $a \to 0$, the curve grows quickly, while if $a \to K$, the curve grows slowly, that is, a bigger amount of prey is needed to obtain $q/2$ (Figure 1).

Ecologically a sigmoid functional response explains the fact that in low densities of prey population the effect of predation is low [17], but if the population size increases, the predation is more intensive [26]. This phenomenon appears in varied interactions of the real world and in this case it is said that the predator is a generalist, due to which, if the prey population size is low, it seeks other food alternatives [26].

A Holling type III functional response can be generated in nature, for example, by prey switching on the part of the predator [24]. However, it is crucial to assess predation in a field setting in order to correctly interpret the importance of a defense mechanism [24], and it is also possible to think of describing the use of prey refuge to avoid the predation [11]. This phenomenon can be observed in a number of interactions in the real world [19].

Many marine mammals appear to be generalist predators, and theory would predict that they have a Holling type III functional response tending to stabilize prey populations [26]. These predictions were tested in [19], where it is shown that the abundance of seals in a river was directly related to the abundance of returning salmon. Dietary data supported the Holling type III functional response to changes in salmonid abundance, providing empirical support for the use

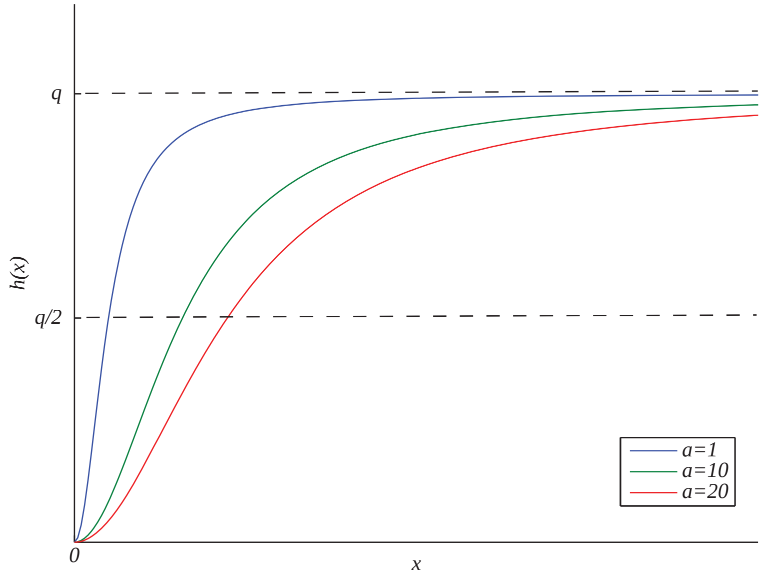

Figure 1. Graphic of the sigmoid functional response $h(x) = qx^2/(x^2 + a^2)$, for $q = 1$ and different values of a. When $a \to 0$, the curve is more abrupt.

of the Holling type III response in modelling studies, which has historically been associated with switching predators [19].

The main goal of this work is to describe the behaviour by means of a bifurcation diagram [4], depending on the parameter values and to classify the different resulting dynamics. Moreover, the obtained results will be compared with those obtained in the analysis of similar models, as are the May–Holling–Tanner [23] and the Leslie–Gower models, considering the Allee effect [13].

2. The model

The predator–prey model is described by the autonomous bidimensional differential equations system of the Kolmogorov type [8] given by

$$X_\mu : \begin{cases} \dfrac{\mathrm{d}x}{\mathrm{d}t} = \left(r\left(1 - \dfrac{x}{K}\right) - \dfrac{qxy}{x^2 + a^2}\right)x, \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = s\left(1 - \dfrac{y}{nx}\right)y, \end{cases} \tag{1}$$

where $x(t)$ and $y(t)$ denote the prey and predator population size, respectively, of densities as functions of time, and all the parameters are positives; $\mu = (r, a, s, K, n, q) \in \mathbb{R}^6_+$, having the following biological meanings:

- r represents the intrinsic prey growth rate,
- K represents the prey environmental carrying capacity,
- q represents the consuming maximum rate per capita of the predators (satiation rate),
- a represents the amount of prey needed to achieve one-half of q (that is, it is half the saturation rate), s represents the intrinsic growth rate of predators, and
- n represents a measure of the quality of food and it indicates how the predators turn eaten prey into new predator births.

System (1) is defined in the first quadrant except for $x = 0$, that is, the y-axis; then, the definition set is

$$\Omega = \left\{ (x, y) \in \frac{\mathbb{R}^2}{x} > 0,\ y \geq 0 \right\}.$$

The equilibrium points of the system (1) or singularities of vector field X_μ are $(K, 0)$ and (x_e, y_e), satisfying the equations of the isoclines

$$y = nx \quad \text{and} \quad y = \frac{r}{qx}\left(1 - \frac{x}{K}\right)(x^2 + a^2).$$

We note that

(i) system (1) is not defined in point $(0, 0)$; however, this point has a strong influence on the behaviour of the system as will be seen in this work;
(ii) the point (x_e, y_e) can lie in the interior of the first quadrant, if and only if, $x_e < K$ and is a positive equilibrium point;
(iii) the point (x_e, y_e) can lie in the fourth quadrant, if and only if, $x_e > K$; then the unique equilibrium is point $(K, 0)$.

In order to make an adequate description of the behaviour of the system (1) and to simplify the calculus, we follow the methodology used in [11–13,21,23], making a change in variables and in the time rescaling given in the following proposition.

Proposition 2.1 *System* (1) *is topologically equivalent to*

$$Y_\eta : \begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}\tau}((1-u)(u^2 + A^2) - Quv)u^2, \\ \dfrac{\mathrm{d}v}{\mathrm{d}\tau}B(u-v)(u^2 + A^2)v, \end{cases} \tag{2}$$

where $\eta = (A; Q; B) \in]0, 1[\times \mathbb{R}_+^2$ *with* $A^2 = a^2/K^2$, $Q = qn/r$, $B = s/r$.

Proof Let $x = Ku$ and $y = nKv$. Substituting in vector field X_μ, we have

$$U_\mu : \begin{cases} K\dfrac{\mathrm{d}u}{\mathrm{d}t} = \left(r(1-u) - \dfrac{qKunKv}{(Ku)^2 + a^2}\right)Ku, \\ nK\dfrac{\mathrm{d}v}{\mathrm{d}t} = s\left(1 - \dfrac{nKv}{nKu}\right)nKv. \end{cases}$$

Simplifying and factoring, we obtain

$$U_\mu : \begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}t} = r\left(1 - u - \dfrac{qn}{r}\dfrac{uv}{u^2 + (a/K)^2}\right)u, \\ \dfrac{\mathrm{d}v}{\mathrm{d}t} = s\left(1 - \dfrac{v}{u}\right)v. \end{cases}$$

Now, Let $\tau = (r/u(u^2 + (a/K)^2))t$; substituting and simplifying, we have

$$V_\mu : \begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}\tau} = \left((1-u)\left(u^2 + \left(\dfrac{a}{K}\right)^2\right) - \dfrac{qn}{r}uv\right)u^2, \\ \dfrac{\mathrm{d}v}{\mathrm{d}\tau} = \dfrac{s}{r}(u-v)\left(u^2 + \left(\dfrac{a}{K}\right)^2\right)v. \end{cases}$$

Making the substitutions $A^2 = a^2/K^2$, $Q = qn/r$, $B = s/r$, the system (2) is obtained. ■

Clearly, system (2) is defined in

$$\bar{\Omega} = \left\{ (u, v) \in \frac{\mathbb{R}^2}{u} \geq 0,\ v \geq 0 \right\}.$$

Remark 1 We have constructed a diffeomorphism $\varphi : \bar{\Omega} \times \mathbb{R} \to \Omega \times \mathbb{R}$, such that

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

The Jacobian matrix of φ is

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

and $\det D\varphi(u, v, \tau) = (nK^2 u/r)(u^2 + (a/K)^2) > 0$.

So, φ is a diffeomorphism preserving the time orientation [6,7], for which vector field X_μ in the new system of coordinates is topologically equivalent to vector field $Y_\eta = \varphi \circ X_\mu$. Hence, Y_η it take the form $Y_\eta = P(u, v)(\partial/\partial u) + Q(u, v)(\partial/\partial v)$ and the associated differential equations is given by a fifth-order polynomial system (2).

As system (1) is not defined at $(0, 0)$, system (2) is topologically (qualitatively) equivalent to a continuous extension to system (1), in point $(0, 0)$.

The equilibrium point of system (2) or singularities of vector field Y_η are: $(0, 0)$, $(1, 0)$ and (u_e, v_e), determined by the intersection of isoclines

$$v = u \quad \text{and} \quad v = \frac{1}{Qu}(1 - u)(u^2 + A^2).$$

Then, the abscissa u is a solution of the third-degree equation:

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

Moreover, the Jacobian matrix of vector field Y_η is

$$DY_\eta(u, v) = \begin{pmatrix} DY_\eta(u, v)_{11} & -Qu^3 \\ Bv(3u^2 - 2uv + A^2) & B(u^2 + A^2)(u - 2v) \end{pmatrix}, \tag{4}$$

where $DY_\eta(u, v)_{11} = -u(5u^3 - 4u^2 + (3A^2 + 3Qv)u - 2A^2 t)$.

3. Main results

For system (2) or vector field Y_η, we have the following results.

Lemma 3.1 *The set* $\bar{\Gamma} = \{(u, v) \in \mathbb{R}^2 : 0 \leq u \leq 1, v \geq 0\} \subset \bar{\Omega}$ *is an invariant region.*

Proof As system (2) is of the Kolmogorov type [8], the coordinate axes are invariant sets [6].

Replacing $u = 1$ in Equation (2), we obtain $\mathrm{d}u/\mathrm{d}v = -Qv < 0$ and $\mathrm{d}v/\mathrm{d}\tau = B(u - v)(A^2 + u^2)v$, which can be positive or negative. Therefore, let $\mathrm{d}v/\mathrm{d}\tau$ be the trajectory point inside $\bar{\Gamma}$. ■

LEMMA 3.2 *The solutions are bounded.*

Proof Using the Poincaré compactification [6,20], let $X = u/v$ and $Y = 1/v$; then,

$$\frac{\mathrm{d}X}{\mathrm{d}\tau} = \frac{1}{v^2}\left(v\frac{\mathrm{d}u}{\mathrm{d}\tau} - u\frac{\mathrm{d}v}{\mathrm{d}\tau}\right) \Longrightarrow \frac{\mathrm{d}u}{\mathrm{d}\tau} = v\frac{\mathrm{d}X}{\mathrm{d}t} + \frac{u}{v}\frac{\mathrm{d}v}{\mathrm{d}\tau},$$
$$\frac{\mathrm{d}Y}{\mathrm{d}\tau} = -\frac{1}{v^2}\frac{\mathrm{d}v}{\mathrm{d}\tau} \Longrightarrow \frac{\mathrm{d}v}{\mathrm{d}\tau} = -v^2\frac{\mathrm{d}Y}{\mathrm{d}\tau}.$$

Then, the system takes the form:

$$v\frac{\mathrm{d}X}{\mathrm{d}\tau} + \frac{u}{v}\frac{\mathrm{d}v}{\mathrm{d}\tau} = \left(\left(1 - \frac{X}{Y}\right)\left(\frac{X^2}{Y^2} + A^2\right) - Q\frac{X}{Y}\frac{1}{Y}\right)\frac{X^2}{Y^2}$$
$$-v^2\frac{\mathrm{d}Y}{\mathrm{d}\tau} = B\left(\frac{X}{Y} - \frac{1}{Y}\right)\left(\frac{X^2}{Y^2} + A^2\right)\frac{1}{Y}.$$

$$\bar{Y}_\eta : \begin{cases} \dfrac{\mathrm{d}X}{\mathrm{d}\tau} &= -\dfrac{1}{Y^4}(-X^4Y + X^5 + A^2X^3Y^2 - BX^3Y + BX^4Y \\ & \quad +QX^3Y - A^2BXY^3 - A^2X^2Y^3 + A^2BX^2Y^3), \\ \dfrac{\mathrm{d}Y}{\mathrm{d}\tau} &= -B(X-1)\dfrac{A^2Y^2 + X^2}{Y^2}. \end{cases}$$

Making a time rescaling given by $T = (1/Y^4)\tau$, then

$$\tilde{Y}_\eta : \begin{cases} \dfrac{\mathrm{d}X}{\mathrm{d}T} &= -(X^4Y + X^5 + A^2X^3Y^2 - BX^3Y + BX^4Y + QX^3Y - A^2BXY^3 \\ & \quad -A^2X^2Y^3 + A^2BX^2Y^3), \\ \dfrac{\mathrm{d}X}{\mathrm{d}T} &= -Y^2B(X-1)(A^2Y^2 + X^2). \end{cases}$$

So, we construct the function $\Phi : \hat{\Omega} \times \mathbb{R} \longrightarrow \bar{\Omega} \times \mathbb{R}$ defined by $\Phi(X, Y, T) = (X/Y, 1/Y, Y^4T) = (u, v, \tau)$. Then, the conjugated vector field $\Phi(Y_\eta)$ is $\tilde{Y}_\eta$.

Evaluating the Jacobian matrix of $\tilde{Y}_\eta$, we have

$$D\tilde{Y}_\eta(0,0) = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}.$$

In order to desingularize the origin of vector field $\tilde{Y}_\eta$, we consider the blowing-up directional method [7], making the change of variables $X = r$ and $Y = r^2s$, obtaining

$$V_\eta : \begin{cases} \dfrac{\mathrm{d}r}{\mathrm{d}T} = \dfrac{\mathrm{d}r}{\mathrm{d}T}, \\ \dfrac{\mathrm{d}s}{\mathrm{d}T} = \dfrac{1}{r^2}\left(\dfrac{\mathrm{d}Y}{\mathrm{d}T} - 2rs\dfrac{\mathrm{d}r}{\mathrm{d}T}\right). \end{cases}$$

So,

$$V_\eta : \begin{cases} \dfrac{\mathrm{d}r}{\mathrm{d}T} = r^5(Bs - Qs + rs - A^2r^2s^2 + A^2r^3s^3 - Brs + A^2Br^2s^3 - A^2Br^3s^3 - 1), \\ \dfrac{\mathrm{d}s}{\mathrm{d}T} = r^4s(-2rs^3 - Bs + 2Qs + 2A^2r^2s^2 - 2A^2r^3s^3 + Brs - A^2Br^2s^3 + A^2Br^3s^3 + 2). \end{cases}$$

Additionally, with a time rescaling given by $\lambda = r^4 T$, a new rescaled vector field is obtained.

$$\bar{V}_\eta : \begin{cases} \dfrac{\mathrm{d}r}{\mathrm{d}\lambda} = r(Bs - Qs + rs - A^2r^2s^2 + A^2r^3s^3 - Brs + A^2Br^2s^3 - A^2Br^3s^3 - 1), \\ \dfrac{\mathrm{d}s}{\mathrm{d}\lambda} = s(-2rs^3 - Bs + 2Qs + 2A^2r^2s^2 - 2A^2r^3s^3 + Brs - A^2Br^2s^3 + A^2Br^3s^3 + 2). \end{cases}$$

Evaluating the Jacobian matrix of $\bar{V}_\eta$ in $(0,0)$, we obtain

$$D\bar{V}_\eta(0,0) = \begin{pmatrix} -1 & 0 \\ 0 & 2 \end{pmatrix}.$$

Thus $(0,0)$ is an hyperbolic saddle point of vector field $\bar{V}_\eta$ since $\det D\bar{V}_\eta(0,0) < 0$; so, $(0,0)$ is a non-hyperbolic saddle point of vector field $\tilde{Y}_\eta$ and $\bar{Y}_\eta$, which is repelling over the positive s-axis; hence, $(0,t)$ is a non-hyperbolic saddle point of vector field Y_η, repelling negatively over the v-axis. Therefore, the solutions of system (2) are bounded. ∎

Lemma 3.3 *Equation* (3) *has a unique real positive root.*

Proof According to Descartes sign rule, the polynomial $P(u)$ can have

(i) a unique positive root, if and only if, $1 - Q \leq 0$, or
(ii) three different possible positive roots, if and only if, $1 - Q > 0$.

Substituting u by $-u$ is obtained $P(-u) = -u^3 - (1-Q)u^2 - A^2u - A^2$.

(i) $P(-u)$ is not a changed sign, if and only, if $1 - Q \geq 0$; therefore, Equation (3) have no negative real roots,
(ii) $P(-u)$ has two negative real roots, if and only if, $1 - Q < 0$.

Let $u_e = H < 1$, the positive real root that always exists for Equation (3) and (H, H), the equilibrium point that always exists in Ω for system (2).
Dividing the polynomial $P(u)$ by $(u - H)$ the polynomial is obtained as follows:

$$P_1(u) = u^2 - (1 - Q - H)u + (A^2 - H(1 - Q - H)).$$

$P_1(u)$ is a factor of $P(u)$ and the rest is

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

Then,

$$Q = \frac{1}{H^2}(1-H)(A^2 + H^2).$$

Substituting the second coefficient of $P_1(u)$, we have the factor

$$1 - Q - H = 1 - \frac{1}{H^2}(1-H)(A^2+H^2) - H = -A^2\frac{1-H}{H^2},$$

obtaining that

$$P_1(u) = u^2 + A^2\frac{1-H}{H^2}u + \frac{A^2}{H}.$$

As the coefficients of $P_1(u)$ are positives, then $P_1(u)$ have no positive real roots.

Moreover, the discriminant $(A^2((1-H)/H^2))^2 - 4(A^2/H)$ must be negative; then, $(1-H)^2A^2 - 4H^3 < 0$, obtaining the condition $A^2 < 4H^3/(1-H)^2$. ∎

Lemma 3.4 *The singularity* $(1,0)$ *is a saddle point.*

Proof Evaluating the Jacobian matrix (4) at the equilibrium point $(1,0)$, we have

$$DY_\eta(1,0) = \begin{pmatrix} -(A^2+1) & -Q \\ 0 & B(A^2+1) \end{pmatrix}.$$

Clearly, $\det DY_\eta(1,0) < 0$ and the point $(1,0)$ is a hyperbolic saddle point. ∎

Lemma 3.5 *The point* $(0,0)$ *is a non-hyperbolic singularity of vector field* Y_η *having a hyperbolic and a parabolic sector* [20].

Proof Evaluating the Jacobian matrix (4) in this equilibrium point, we have the null matrix, that is:

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

So, the origin is a non-hyperbolic singularity. For desingularizing the origin, we consider the polar blowing-up method [7,20]. Let $\Phi : S^1 \times \mathbb{R}_0^+ \to \mathbb{R}^2$ such as

$$\begin{aligned} \Phi : S^1 \times \mathbb{R}_0^+ &\to \mathbb{R}^2 \\ (r,\theta) &\rightsquigarrow (r\cos\theta, r\sin\theta) \end{aligned}$$

then, $\Phi_*(Y) = (D\Phi)^{-1}Y\phi = \tilde{Y}$, where, $\tilde{Y} = r\bar{Y} : S^1 \times \mathbb{R}_0^+ \to T(S^1 \times \mathbb{R}_0^+)$ with, $\bar{Y}(r,\theta) = rf(r,\theta)(\partial/\partial r) + g(r,\theta)(\partial/\partial\theta)$, where

$$\begin{aligned} f(\theta,r) = &-A^2\sin\theta\cos^2\theta - r^2\sin\theta\cos^4\theta + A^2r\sin\theta\cos^3\theta \\ &+ r^3\sin\theta\cos^5\theta + r^2Q\cos^3\theta\sin^2\theta + BA^2\sin\theta\cos^2\theta \\ &+ Br^2\sin\theta\cos^4\theta - BA^2\cos\theta\sin^2\theta - Br^2\sin^2\theta\cos^3\theta \end{aligned}$$

and

$$\begin{aligned} g(\theta,r) = &A^2\cos^3\theta + r^2\cos^5\theta - A^2r\cos^4\theta - r^3\cos^6\theta - r^2Q\cos^4\theta\sin\theta \\ &+ BA^2\sin^2\theta\cos\theta + Br^2\sin^2\theta\cos^3\theta - BA^2\sin^3\theta - Br^2\sin^3\theta\cos^2\theta. \end{aligned}$$

As $r > 0$, the dynamics in $S^1 \times \mathbb{R}_0^+$ of $\tilde{Y}$ and $\bar{Y}$ are qualitatively equivalent and

$$\begin{aligned} \bar{Y}(0,\theta) &= -A^2\sin\theta\cos^2\theta + BA^2\sin\theta\cos^2\theta - BA^2\cos\theta\sin^2\theta \\ &= (\sin\theta\cos\theta)A^2(-\cos\theta + B\cos\theta - B\sin\theta) = 0. \end{aligned}$$

Then the possible singularities of $\bar{Y}$ in the first quadrant of S^1 are

$$(0,0), \left(0, \frac{\pi}{2}\right), \left(0, \arctan\left(\frac{B-1}{B}\right)\right)$$

and the Jacobian matrix of $\bar{Y}$ at singularities $D\bar{Y}(0,\theta)$ depends on the value of θ, with $\theta \in \{0, \pi/2, \arctan((B-1)/B)\}$.

If $\theta = 0$, the Jacobian matrix of $\bar{Y}$ at $(0, 0)$ is

$$D\bar{Y}(0,0) = \begin{pmatrix} A^2 & 0 \\ 0 & -A^2 + BA^2 \end{pmatrix},$$

then the equilibrium point nature depends on parameter B. If $B < 1$, then, we have a saddle point, as $\det D\bar{Y}(0, 0) = -A^4(1 + B) < 0$ and if $B \geq 1$, the point $(0, 0)$ is an attractor.

If $\theta = \pi/2$, the Jacobian matrix of $\bar{Y}$ at $(0, \pi/2)$ is

$$D\bar{Y}\left(0, \frac{\pi}{2}\right) = \begin{pmatrix} -BA^2 & 0 \\ 0 & BA^2 \end{pmatrix},$$

then $\det D\bar{Y}(0, \theta) = -B^2A^4 \leq 0$ and the singularity is a hyperbolic saddle.

If $\theta = \arctan((B - 1)/B)$, the Jacobian matrix of $\bar{Y}$ at $(0, \pi/2)$ is

$$D\bar{Y}(0,\theta) = \frac{A^2}{B((1/B^2)(2B^2 - 2B + 1))^{3/2}} \begin{pmatrix} \dfrac{2B^2 - 2B + 1}{B} & 0 \\ (B-1)^2 & \dfrac{(B-1)(2B^2 - 2B + 1)}{B} \end{pmatrix}.$$

Now, using the blowing down [7], we can determine the behaviour of system (3) at the origin, using the following transformation $\Phi^{-1} : \mathbb{R}^2 \to \mathbb{R}^2$,where

$$\Phi^{-1} : \mathbb{R}^2 \to \mathbb{R}^2$$
$$(r\cos\theta, r\sin\theta) \rightsquigarrow (u, v)$$

under this transformation, we obtain the following:

$$\Phi^{-1} : (r, 0) \rightsquigarrow (u, 0), \quad \Phi^{-1} : (r, \pi/2) \rightsquigarrow (0, v),$$

and

$$\Phi^{-1} : \left(r, \arctan\left(\frac{B-1}{B}\right)\right) \rightsquigarrow \left((u^2 + v^2)^{1/2}, \arctan\frac{v}{u}\right).$$

So, we have that, the line $v = ((B - 1)/B)u$ in system (2) is tangent to a separatrix curve Σ in the phase plane [7]. ■

Remark 2 By Lemma 3.5, the point $(0; 0)$ is a non-hyperbolic saddle point with a hyperbolic sector; the stable manifold $W^s(0; 0)$ determined by the separatrix curve Σ, divides the behaviour of trajectories in the phase plane; any solution above the manifold $W^s(0; 0)$ have $(0; 0)$ as its *ω-limit*.

Those trajectories with initial conditions below the separatrix curve Σ, can have different *ω-limits*.

According to the relative position between $W^s(0; 0)$ and the unstable manifold $W^u(1; 0)$, the point $(0; 0)$ will be global or local attractor.

LEMMA 3.6 *Let $W^s(0, 0)$ and $W^u(1, 0)$ be the stable and unstable manifolds of singularities $(0, 0)$ and $(1, 0)$, respectively; then, there exists a subset of parameters for which the intersection of $W^s(0, 0)$ and $W^u(1, 0)$ is not empty, giving rise to a heteroclinic curve γ_{10} joining point $(0, 1)$ and $(0, 0)$.*

Proof By Lemma 3.5, the point $(0,0)$ has a separatrix curve Σ with an inclination given by the straight line $v = ((B-1)/B)u$ in the neighbourhood of this point; by Lemma 3.4, the point $(1,0)$ is a saddle.

Let $W^s(0,0)$ and $W^u(1,0)$ be the stable and unstable manifolds of $(0,0)$ and $(1,0)$, it is clear that the α-*limit* of $W^s(0,0)$ and the ω-*limit* of $W^u(1,0)$ are not at infinity in the direction of the v-*axis*.

There are points $(u, v^s) \in W^s(0,0)$ and $(u, v^u) \in W^s(1,0)$, where v^s and v^u are functions of the parameters A, B, and Q; that is, $v^s = f_1(A;B;Q)$ and $v^u = f_2(A;B;Q)$.

It is clear that if $0 < u \ll 1$ then, $v^s < v^u$ and if $0 \ll u < 1$ then $v^s > v^u$.

Since vector field Y_η is continuous with respect to the parameter values, the unstable manifold $W^s(0,0)$ intersects the unstable manifold $W^u(1,0)$. Then, there are $(u^*; v^{*s})$ and $(u^*; v^{*u}) \in \bar{\Gamma}$, such that $v^{*s} = v^{*u}$and the equation $f_1(A,B,Q) = f_2(A,B,Q)$ defines a surface in the parameter space for which the heteroclinic curve exists (Figure 2). ■

Remark 3 The separatrix curve Σ, the straight line $u = 1$ and the u-*axis* determines a subregion $\bar{\Lambda}$ (see left poster in Figure 2), which is closed and bounded, i.e.

$$\bar{\Lambda} = \left\{ (u,v) \in \frac{\bar{\Gamma}}{0} \le v \le v_\Sigma, \text{ with } (u_\Sigma, v_\Sigma) \in \Sigma \right\}$$

is a compact region and the Poincaré–Bendixson theorem applies there (Figure 3).

To study the nature of the equilibrium point (H,H) with $H < 1$, by Lemma 3.3, we have that

$$Q = \frac{1}{H^2}(1-H)(H^2+A^2).$$

Then, vector field Y_η becomes

$$Y_\theta : \begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}\tau} = ((1-u)(A^2+u^2) - \dfrac{1}{H}(1-H)(A^2+H^2)uv)u, \\ \dfrac{\mathrm{d}v}{\mathrm{d}\tau} = B(u-v)(A^2+u^2)v, \end{cases} \tag{5}$$

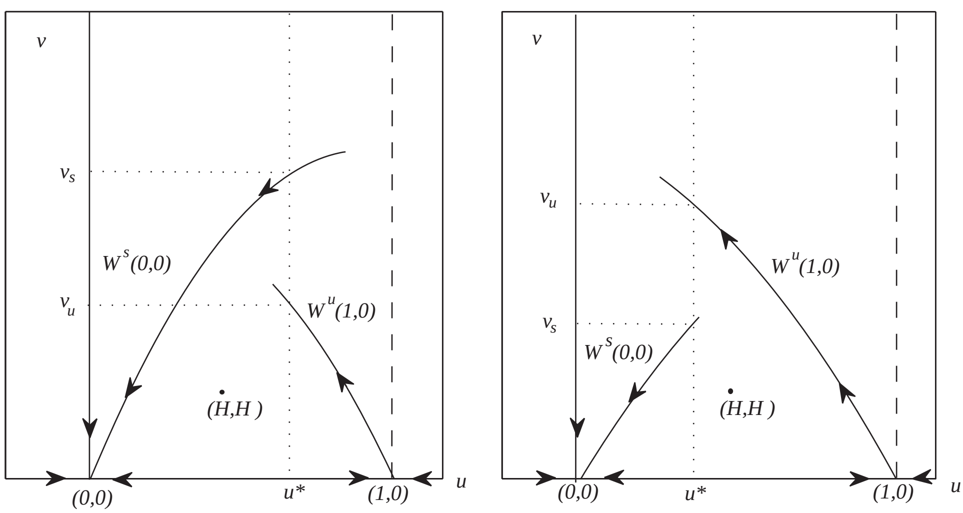

Figure 2. For $0 < H < 1$, the two possible relative positions between the stable manifold $W^s(0,0)$ of singularity $(0,0)$ and the unstable manifold $W^u(1;0)$ of saddle point $(1,0)$ are shown.

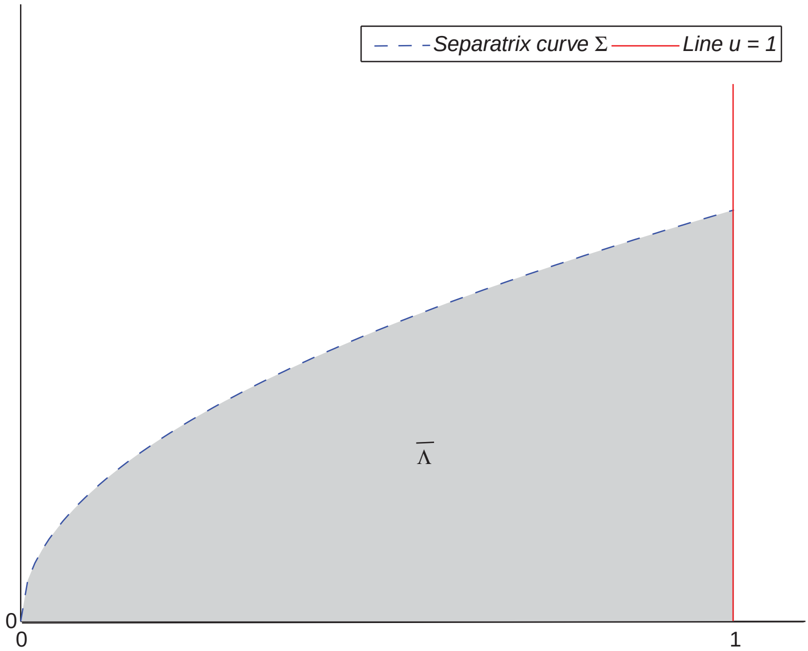

Figure 3. The region $\bar{\Lambda}$ where is possible to apply, the Poincaré–Bendixson theorem.

with $\theta = (A, H, B) \in (]0, 1[)^2 \times \mathbb{R}$. The Jacobian matrix is

$$DY_\theta(H;H) = \begin{pmatrix} -H(A^2 - H^2(1-2H)) & -H(1-H)(A^2+H^2) \\ BH(A^2+H^2) & -BH(A^2+H^2) \end{pmatrix},$$

with

$$\det DY_\theta(H;H) = BH^2((2-H)A^2 + H^3)(A^2+H^2) > 0$$

and

$$\operatorname{tr} DY_\theta(H;H) = -H(B(A^2+H^2) + A^2 + H^2(2H-1)).$$

Let

$$\begin{aligned} M &= (\operatorname{tr} DY_\theta(H;H))^2 - 4\det DY_\theta(H;H) \\ &= H^2((A^2+H^2)^2B^2 + 2(2A^2H - 3A^2 - H^2)(A^2+H^2)B + (H^2(2H-1)+A^2)^2). \end{aligned}$$

THEOREM 3.7 *Nature of the positive equilibrium point.*
Let $(u^*, v_s) \in W^s(0,0)$ and $(u^*, v_u) \in W^u(1,0)$ and assuming $0 < H < 1$, the equilibrium point (H, H) is in the interior of the first quadrant.

(1) *Supposing $v_s > v_u$, the singularity (H, H) is*
  (a) *a hyperbolic local attractor, if and only if, $B > (H^2(1-2H) - A^2)/(A^2+H^2)$; moreover*
    (a1) *an attractor node, if and only if, $M > 0$.*
    (a2) *an attractor focus, if and only if, $M < 0$,*
  (b) *a hyperbolic repeller, if and only if, $B < (H^2(1-2H) - A^2)/(A^2+H^2)$; moreover*
    (b1) *a repeller focus surrounded by at least a limit cycle, if and only if, $M < 0$,*
    (b2) *a repeller node, if and only if, $M > 0$,*
  (c) *a weak focus, if and only if, $B = (H^2(1-2H) - A^2)/(A^2+H^2)$.*

(2) *Supposing* $v_s < v_u$*, the singularity* (H, H) *is a repeller node or focus. In this case, the equilibrium point* $(0, 0)$ *is the* ω*-limit for all trajectories of system.*

Proof When, $0 < H < 1$, then, the nature of (H, H) depends on the relative position on v_S and v_u, and the sign of $\operatorname{tr} DY_\eta(H, H)$, which depends on the factor $T_1 = B(H^2 + A^2) + (A^2 - H^2(1 - 2H))$.

(1) Supposing $v_s > v_u$, the singularity (H, H) is
  (a) $B > (H^2(1 - 2H) - A^2)/(A^2 + H^2)$, if and only if, $\operatorname{tr} DY_\eta(H, H) < 0$ and (H, H) is an attractor. Moreover,
    (a1) if $M < 0$, then, the point is an attractor focus,
    (a2) if $M > 0$, then, the point is an attractor node.
  (b) $B < (H^2(1 - 2H) - A^2)/(A^2 + H^2)$, if and only if, $\operatorname{tr} DY_\eta(H, H) > 0$ and (H, H) is a repeller. Moreover,
    (b1) if $M < 0$, then, the point is a repeller focus; in the invariant subregion $\bar{\Lambda}$, the point (H, H) is surrounded by at least one limit cycle, by the Poincaré–Bendixon theorem [6,14,20].
    (b2) (H, H) is *a repeller node, if and only if,* $M > 0$.
  (c) If $B = (H^2(1 - 2H) - A^2)/(A^2 + H^2)$, the equilibrium (H, H) is a weak focus,
(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 equilibrium points $(0, 0)$ and $(1, 0)$ are saddle points. The trajectories have the origin as their ω*-limit*. This equilibrium point is globally asymptotically stable. ■

Remark 4 The limit cycle determined by the Poincaré–Bendixon theorem increases until it collapses with the heteroclinic cycle determined by separatrix curve Σ and the unstable manifold $W^u(1, 0)$, when $v_s = v_u$.

LEMMA 3.8 *A Hopf bifurcation occurs at equilibrium point* (H, H) *for the bifurcation value* $B = (H^2(1 - 2H) - A^2)/(H^2 + A^2)$.

Proof The proof follows from Theorem 3.7 since the $\det DY_\eta(H, H)$ is always positive and the $\operatorname{tr} DY_\eta(H, H)$ changes sign.

Moreover, verifying the transversality condition [14], we have $\partial(\operatorname{tr} DY_\theta(H; H))/\partial A = -AH(B + 1) < 0$. ■

In Figures 4–7, some simulations are shown to reinforce the obtained results.

4. Discussion

In this work, a bidimensional continuous-time differential equations system was analysed which is derived from a Leslie–Gower-type predator–prey model by considering a functional response Holling type III. We made a reparameterization and a time rescaling to obtain a topologically equivalent polynomial system in order to facilitate calculus. We have shown the importance of point $(0, 0)$ in the original Leslie–Gower model, although system (1) is not defined there.

In the dimensionless system (2), we have shown that the singularity $(0, 0)$ is a point with a complex nature since it possess parabolic and hyperbolic sectors [20] on the phase plane. Using the method of blowing up, we demonstrate the existence of a separatrix curve Σ, determined by the stable manifold of non-hyperbolic singularity $(0, 0)$, dividing the behaviour of trajectories, which can have different ω*-limit*s.

Then, some solutions are highly sensitive to initial conditions. Those trajectories over the separatrix curves have the point $(0;0)$ as their ω-*limit*, meanwhile, those under this curve can have a point or a limit cycles as their ω-*limit*, implying that two solutions with very close initial conditions can have final conditions very different from one another.

Also, we proved the boundness of solutions of system (2), using the extended real line to apply the compactification of Poincaré [7,20], showing that the modified Leslie–Gower model is well-posed. Furthermore, we prove the existence of parameter constraints for which the unique positive equilibrium point is an attractor (Figures 4 and 5) or is a repeller (Figures 6 and 7) surrounded by at least one limit cycle and, there exists a heteroclinic curve joining the equilibrium $(1,0)$ and the singularity $(0,0)$.

All properties of system (1) are similar to system (2), because we construct a diffeomorphism φ assuring a topological equivalence behaviour between systems.

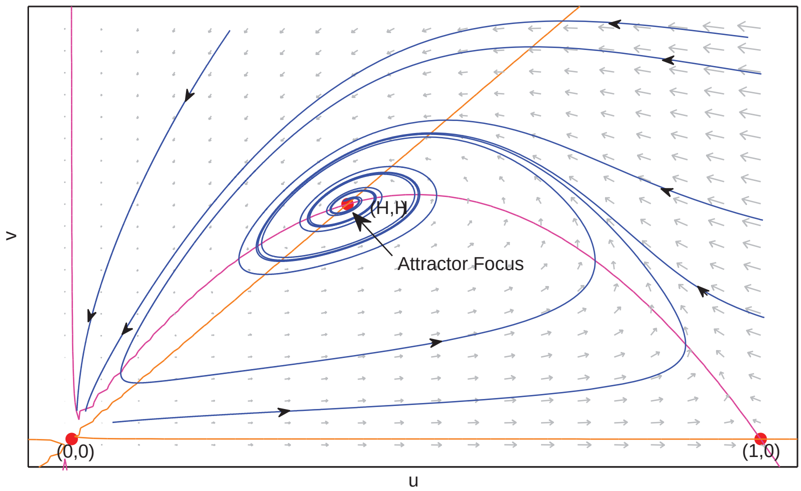

Figure 4. For $A = 0.01$, $Q = 0.6$ and $B = 0.29$, the equilibrium (H, H) is an attractor focus. The separatrix curve generated by the stable manifold of $(0,0)$ is shown and this singularity is also a local attractor.

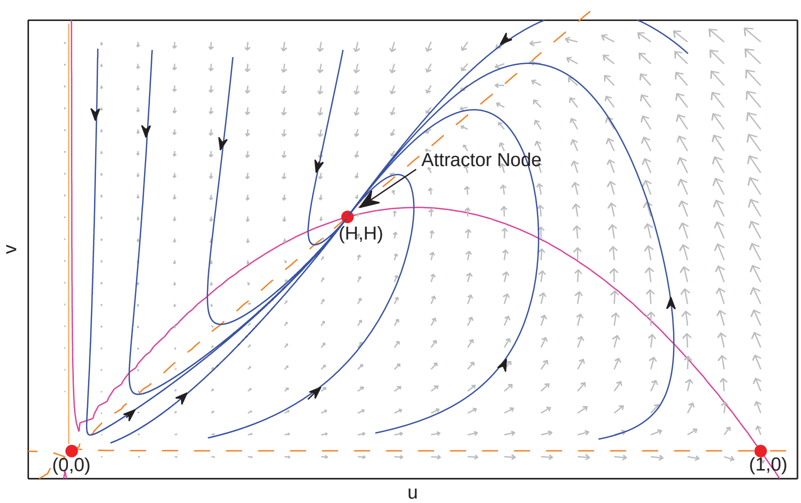

Figure 5. For $A = 0.01$, $Q = 0.6$ and $B = 2$, the equilibrium (H, H) is an attractor node. In this case, the positive equilibrium is a global attractor.

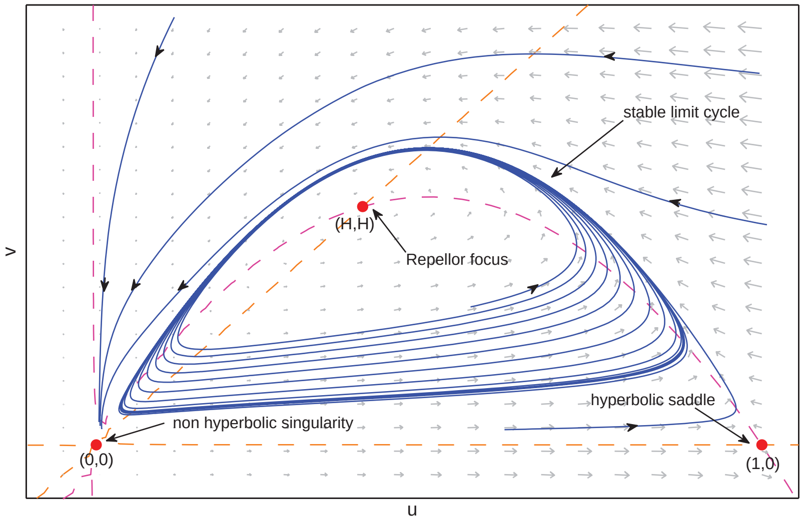

Figure 6. For $A = 0.01$, $Q = 0.6$ and $B = 0.1$, The equilibrium (H, H) is a repeller focus surrounded by a stable limit cycle and the equilibrium $(0, 0)$ is an attractor node.

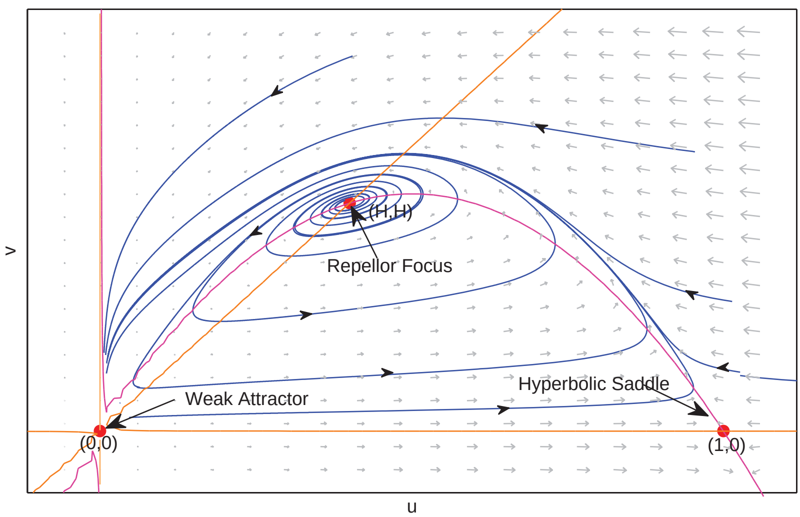

Figure 7. For $A = 0.005$, $Q = 0.6$ and $B = 0.1$, the equilibrium (H, H) is a repeller focus. The point $(0, 0)$ s a global attractor.

Therefore, for the same parameter values, populations can become extinct or there is coexistence, according to the relation between their initial populations sizes. However, simulations show that the point $(0, 0)$ is a 'weak' attractor, since trajectories going to this ω-*limit* are attracted very slowly. This dynamical behaviour allows the recovery of the populations, reaffirming the claim that a sigmoid functional response has a stabilizing effect on the interaction [25,26].

The model studied here has a unique limit cycle. Comparing with the May–Holling–Tanner model studied in [23], we can see a difference on the quantity of limit cycles, since this last model has two limit cycles surrounding the unique positive equilibrium point.

As was said above, in model (2) studied here, by computer simulations we observe that the approach of paths to point $(0; 0)$ is very slow, which does not happen with the Holling–Tanner model. We conjecture the existence of a numerical conditioning problem in system (2), due to be topologically equivalent to the original system which is not defined at point $(0; 0)$, which has not been studied in the present work.

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