

ARTICLE TYPE

Influence of the Rosenzweig functional response on the dynamics of the Leslie-Gower model

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Summary

After the well-known classification formulated by Crawford S. Holling in 1959 of the functional responses dependent only of the prey populations, various other have been proposed.

In this work a simple Leslie-Gower type predator-prey model is analyzed, incorporating the Rosenzweig functional response described by $h(x) = qx^\alpha$, with $0 < \alpha < 1$.

This function does not conform to the types proposed by Holling, since is not bounded. Although this functional response is non-differentiable for $x = 0$, it is proved that the obtained system is Lipschitzian.

However, the existence of a separatrix curve Σ in the phase plane it is proven, which divides the phase plane en two complementary sectors. According to the relative position of the initial conditions respect to the curve Σ , the trajectories can have different ω -limit, which can be the equilibrium $(0, 0)$, or else, a positive equilibrium point, or a limit cycle or a heteroclinic curve.

These properties show the great difference of this model with the original and well-known Leslie-Gower model (when $\alpha = 1$), since this last has only a unique positive equilibrium, which is globally asymptotically stable.

Then, it can concluded that

- i) a small change in the mathematical expression for the functional response, it produces a strong change on the dynamics of model.
- ii) a slightest deviation in the initial population sizes, respect to the curve Σ , it can signify the coexistence of populations or the extinction of both.

Numerical simulations are given to endorse our analytical results.

KEYWORDS:

Bifurcation, stability, limit cycle, separatrix curve, predator-prey model, functional response

1 | INTRODUCTION

The description of predator-prey models is frequently made by non-linear bidimensional autonomous ordinary differential equations systems (ODES)¹⁴, which can have interesting and rich dynamics.

However, the properties arising of the analysis can be independent of the interaction, and they could not be in correlation with the ecological phenomenon in study; for this reason it is necessary an adequate and rigorous mathematical study of this systems, particularly when some modifications are incorporated in the model.

One of the characterizations of the predation interactions is the action of the predator consuming the prey, called *functional response* or *consumption rate*^{5,39}, which can be represented by different functions in the basic models.

In this work, this consumption is described by a functional response proposed by the american ecologist Michael L. Rosenzweig at 1971³⁵; it is represented by the function $h(x) = qx^\alpha$, with $0 < \alpha < 1$,^{3,8,33,37}, where $x = x(t)$ is the prey population size. It is called *Rosenzweig* or *ath power functional responses*³⁵ or *power law*¹², being its main feature that is non-differentiable when $x = 0$ ³⁷.

This functional response appears also proposed in the bioeconomic literature¹¹ and denominated as *compensatory power functional response*, and is a particular case of a more general function called *Cobb-Douglas type production function*¹². As we will show, this function has a strong implication on the dynamics of the system, which it may lead to unexpected behavior, such as happens in the Volterra model³⁹.

Above papers show that this particular Gause model, it can be proved that the system is non-Lipschitzian^{8,37}, since for each point in the vertical axis pass two trajectories.

Other interesting property in the Volterra model with Rosenzweig functional response is the existence of a separatrix curve Σ determined by the stable manifold of the non-hyperbolic equilibrium $(0, 0)$. Trajectories with initial conditions over the curve Σ attain in finite time to the vertical axis³⁷.

According to Myerscough and al (1996)²⁹, this function is unsuitable for modelling a interaction described by a Gause type predation model, where the predator is approaching satiety²⁹. It also has some other problems²⁹, since when is incorporated into the basic Volterra model³⁹, these do not satisfy the conditions of the Kolmogorov Theorem²⁶.

In that model could produce a situation where there are neither nonzero stable populations nor stable oscillations but where one or both species becomes extinct^{8,21,29,37}, situation for which could not have an example in the real world.

A special case of the Rosenzweig functional response is given the function by $h(x) = qx^{\frac{1}{2}}$, considering the value $\alpha = \frac{1}{2}$, proposed by Georgii F. Gause in 1934¹⁷, called *root square functional response*^{27,40} and used to describe an antipredator behavior (APB) named as *prey herd behavior*^{1,42}.

A prey species exhibits this more elaborated collective social conduct, when "the individuals of one population gather together in herds, to wander about in search of food sources and for defensive purposes"¹.

This APB has received increasing attention of the modellers after to the work of Ajraldi et al¹, but its consequences have been analyzed only in Gause-type predator-prey models^{9,42}

We postulate that the mentioned APB can be described using any value of the parameter $\alpha \neq \frac{1}{2}$ ⁴².

On the other hand, to describe the interplay among the two species we will use the Leslie-Gower model²⁴ which has two essential properties:

- i) the growth for predators is assumed as a logistic-like equation^{26,39},
- ii) the functional response is linear, as in the classic Lotka-Volterra⁵ or in the Volterra model³⁹.

The model proposed by the British biologist Patrick Holt Leslie (b1900-d1972)⁴ on 1948²⁴ incorporates the dependence on the quotient between the population sizes of predators and prey as fundamental element to express the interaction³¹, assuming that the predator's carrying capacity is dependent on quantity of available resources³⁹.

Of this way, Leslie established a great difference with the compartmentalized Gause-type models^{15,41,42}, so called after the russian ecologist Georgii F. Gause¹⁷ (1910-1986), and based in the mass action principle⁶.

In the Leslie model is assumed that the conventional environmental carrying capacity for predators K_y is proportional to the prey population size $x = x(t)$, that is $K_y = K(x) = nx$ ^{26,39}.

The model proposed by Leslie does not fit to the Lotka-Volterra framework³⁹ and it is not defined in $x = 0$. For this fact, it has been strongly criticized, because it predicts that even in very low prey population density, when the consumption rate per predator is almost zero, predator population might increase, if the predator/prey ratio is very small³⁹, constituting anomalies in their predictions.

It is well-known that for the original Leslie-Gower model^{18,26,39} there exists a wide set of parameter values for which the unique positive equilibrium point is globally asymptotically stable^{10,14}, i.e., it is a global attractor; this property is proved constructing a suitable Lyapunov function²².

In the modified Leslie-Gower model here studied, we establish conditions on the parameter values for which there exists at least a limit cycle and for other parameter sets there exists a heteroclinic curve joining the equilibrium points $(0, 0)$ and $(1, 0)$, i.e., there exist oscillations of the population sizes.

The outcome of the analysis shows that novel properties arise, impossible in simple Leslie-Gower model (a quadratic systems)^{26,39}, in which there no exists periodic trajectories nor separatrix curve.

Although some of these results could also be obtained introducing other nonlinear functional response or different prey growth functions¹⁹, the Rosenzweig functional response make here that render the system interesting. It shows that the observed oscillations in the field for predator-prey interaction may be due to factors distinct than those assumed for example, in the hyperbolic functional responses¹.

The model proposed by Leslie assumes implicitly that the predators are *specialist*. However, some predator species can switch over to other available food in the case of severe scarcity of their favorite prey; thus, it says that the predators are *generalists*. In this situation the variable carrying capacity of predators is described by $K_y = K(x) = nx + c$ being c a positive constant expressing the population size of other available food^{33,34,38}. If $x = 0$, then $K(0) = c$ and the equation for the predators is now defined.

This paper is organized as follow: In the next section, the modified Leslie-Gower model is presented; in Section 3, the main properties of model are presented and proved; in Section 4 some numerical simulations are shown to reinforced the analytical results, and in the last section we discuss the obtained results, giving the ecological meanings of them.

2 | THE MODEL

The modified Leslie-Gower model is described by the system:

$$X_\mu(x, y) : \begin{cases} \frac{dx}{dt} = r \left(1 - \frac{x}{K}\right) x - qx^\alpha y \\ \frac{dy}{dt} = s \left(1 - \frac{y}{nx}\right) y \end{cases} \quad (1)$$

where $x = x(t)$ and $y = y(t)$, indicate the prey and predators population sizes, respectively, for $t \geq 0$, measured as density per unit area or volume, or biomass.

The parameters are all positives, i.e., $\mu = (r, K, q, s, n, \alpha) \in \mathbb{R}_+^5 \times]0, 1[$ and have the ecological meanings^{26,39} described in the following table:

Table 1 Parameters and Meanings in system (1)

parameters	meanings
r	intrinsic prey growth rate
K	prey environmental carrying capacity
q	consuming rate per capita of the predators
s	intrinsic predator growth rate
n	measure of the quality of food
α	measure of the aggregation of prey

The parameter n also indicates how the predators turn eaten prey into new predator births and α describes the slope of the functional response near the origin.

From a bioeconomic point of view, C. W. Clark¹¹, assure that the parameter α , called the *catchability exponent*¹², is a measure of aggregation of the resources, which is reinforced in⁴⁰ affirming that represents a kind of aggregation efficiency.

In system (1) is assumed that the carrying capacity of the population of predators K_y is variable and dependent on the quantity of prey available at each time $t \geq 0$ ²⁶.

As the model (1) is not a Kolmogorov system¹⁵, there is no guarantee that stable limit cycles will exist when the positive equilibrium becomes unstable²⁹.

The equilibrium points of system (1) or singularities of vector field $X_\mu(x, y)$ are $(K, 0)$ and (u_e, v_e) over the isoclines $y = nx$ and $y = \frac{r}{q} \left(1 - \frac{x}{K}\right) x^{1-\alpha}$.

As the functional response $h(x) = qx^\alpha$, with $0 < \alpha < 1$, and system (1) are non-differentiable in $x = 0$, it is required a non usual analysis to established all properties of the proposed model.

To simplify the calculations, we make a change of coordinates and a time rescaling, described by the function $\varphi : \mathbb{R}^2 \times \mathbb{R}_0^+ \rightarrow \mathbb{R}^2 \times \mathbb{R}_0^+$, such that

$$\varphi \left(Ku, nKv, \frac{u}{r} \tau \right) = (x, y, t)$$

The following result is obtained:

Proposition 1. Topologically equivalence

The vector field $X_\mu(x, y)$ or system (1) is topologically equivalent to the system

$$Y_\eta(u, v) : \begin{cases} \frac{du}{d\tau} = ((1-u)u - Qu^\alpha v)u \\ \frac{dv}{d\tau} = S(u-v)v, \end{cases} \quad (2)$$

with $\eta = (Q, S, \alpha) \in \mathbb{R}^2 \times]0, 1[$, where $Q = \frac{qK^\alpha n}{r}$ and $S = \frac{s}{r}$.

Proof. Let $x = Ku$ and $y = nKv$; replacing it has

$$U_\mu(u, v) : \begin{cases} K \frac{du}{dt} = r(1-u)Ku - q(Ku)^\alpha nKv \\ nK \frac{dv}{dt} = s \left(1 - \frac{nKv}{nKu}\right) nKv. \end{cases}$$

Simplifying and factoring it obtains

$$U_\mu(u, v) : \begin{cases} \frac{du}{dt} = r \left((1-u)u - \frac{qK^\alpha n}{r} u^\alpha v \right) \\ \frac{dv}{dt} = s \left(1 - \frac{v}{u} \right) v. \end{cases}$$

By means of a time rescaling given by $\tau = \frac{r}{u}t$, and applying the Chain Rule we have

$$\frac{dx}{dt} = \frac{dx}{d\tau} \frac{d\tau}{dt} = \frac{dx}{d\tau} \frac{r}{u}; \text{ analogously, } \frac{dy}{dt} = \frac{r}{u} \frac{dy}{d\tau}.$$

Replacing and simplifying it is obtained

$$V_\mu(u, v) : \begin{cases} \frac{du}{d\tau} = \left((1-u)u - \frac{qK^\alpha n}{r} u^\alpha v \right) u \\ \frac{dv}{d\tau} = \frac{s}{r} (u-v)v. \end{cases}$$

Defining the new parameter by $Q = \frac{qK^\alpha n}{r}$ and $S = \frac{s}{r}$, the new system (2) is obtained. \square

Remark 1. The Jacobian matrix of φ is

$$D\varphi(u, v, \tau) = \begin{pmatrix} K & 0 & 0 \\ 0 & nK & 0 \\ \frac{1}{r} & 0 & \frac{u}{r} \end{pmatrix},$$

then, $\det D\varphi(u, v, \tau) = \frac{nK^2u}{r} > 0$.

Furthermore,

$$\varphi^{-1}(r, K, q, s, n, \alpha) = \left(\frac{qK^\alpha n}{r}, \frac{s}{r}, \alpha \right) = (Q, S, \alpha),$$

i.e., φ is a smooth change of variables with a rescaling of the time preserving the time orientation.

System (2) or vector field $Y_\eta(u, v)$ is defined in

$$\bar{\Omega} = \{(u, v) \in \mathbb{R}^2 : 0 \leq u, 0 \leq v\},$$

i.e., defined in the first quadrant.

Hence, from system (1) we obtained a qualitatively (topologically) equivalent vector field $Y_\eta = \varphi \circ X_\mu$, which has the form $Y_\eta = P_1(u, v) \frac{\partial}{\partial u} + P_2(u, v) \frac{\partial}{\partial v}$ ¹⁴, where $P(u, v)$ and $Q(u, v)$ are the equations of the right side of system (2).

Clearly, the associated second order differential equation system (2) is a polynomial Kolmogorov type system¹⁵. Moreover, is topologically equivalent to a continuous extension of system (1), defined in $x = 0$.

The equilibrium points of system (2) are $(0, 0)$, $(1, 0)$ and (H, H) where H satisfies the equation of the null isoclines

$$v = \frac{1}{Qu^\alpha}(1-u)u \text{ and } v = u.$$

Then, the abscissas H of that equilibrium points satisfies the trascendental equation:

$$p(u) = 1 - u - Qu^\alpha = 0 \quad (3)$$

Proposition 2. Number of positive equilibrium points

system (2) has a unique positive equilibrium point in the open interval $]0, 1[$.

Proof. In the equation (3), we consider the functions

$$g_1(u) = 1 - u \text{ and } g_2(u) = Qu^\alpha, \text{ with } 0 < \alpha < 1.$$

Clearly, $p(u) = g_1(u) - g_2(u)$. The solutions of equation (3) correspond to the intersection of the curves $g_1(u)$ and $g_2(u)$.

Graphically, $g_1(u)$ is a decreasing slanted straight line passing by the points $(0, 1)$ and $(1, 0)$. Meanwhile, $g_2(u)$ is a increasing power function with $0 < \alpha < 1$, wich pass by the points $(0, 0)$ and $(1, Q)$, for all $Q \in \mathbb{R}_+$.

So, always there exists a unique intersection H between both curves in the interval $]0, 1[$. Then, system (2) has a unique positive equilibrium point (H, H) . \square

To determine the nature of the equilibrium points of system (2), the Jacobian matrix is required, which is

$$DY_\eta(u, v) = \begin{pmatrix} 2u - 3u^2 - (\alpha + 1)Qu^\alpha v & -Qu^{\alpha+1} \\ Sv & S(u - 2v) \end{pmatrix}$$

We note that $DY_\eta(u, v)$ is defined for $u = 0$.

3 | MAIN RESULTS

For system (2) or vector field $Y_\eta(u, v)$, we have the following properties:

Lemma 1. Existence of a region of invariance

The set $\bar{\Gamma} = \{(u, v) \in \bar{\Omega} : 0 \leq u \leq 1, v \geq 0\}$ is a positively invariant region.

Proof. Clearly, the axis $u = 0$ and $v = 0$ are invariant set, since the system (2) is one of Kolmogorov type.

Considering $u = 1$, we obtain

$$Y_\eta(1, v) : \begin{cases} \frac{du}{d\tau} = -Qv \\ \frac{dv}{d\tau} = S(1 - v)v, \end{cases}$$

Hence, the orbits with initial condition outside of the set $\bar{\Gamma}$ will cross toward inside of this set, any be the direction of the component $\frac{dv}{d\tau}$ of vector field $Y_\eta(1, v)$. \square

We note that the subregion

$$\bar{\Gamma}_0 = \{(u, v) \in \bar{\Omega} : 0 \leq u \leq 1, 0 \leq v \leq u\}$$

is also positively invariant.

Moreover, in system (1) the set

$$\Gamma_0 = \{(x, y) \in \Omega : 0 < x \leq K, 0 \leq y \leq nx\}$$

is a positively invariant region.

Lemma 2. Boundedness of solutions

The solutions are bounded.

Proof. From the first equation of system (2) we becomes

$$\frac{du}{d\tau} \leq (1 - u)u^2, \quad \forall v \in \mathbb{R}_+.$$

We have that

$$u(\tau) \rightarrow 1, \text{ when } \tau \rightarrow \infty \text{ and } u < 1.$$

Furthermore,

$$u(\tau) \rightarrow 1, \text{ when } \tau \rightarrow \infty \text{ and } u > 1.$$

Considering $L = \max\{u(0), 1\}$, we have

$$u(\tau) \leq L, \quad \forall \tau, v \geq 0.$$

Besides, $0 \leq v \leq u$.

Let $W(\tau) = u(\tau) + \frac{1}{S}v(\tau)$. Clearly $0 < W(\tau)$, $\forall \tau \geq 0$.

Now, we consider the sum $\frac{dW(\tau)}{d\tau} + W(\tau)$.

$$\begin{aligned} \frac{dW(\tau)}{d\tau} + W(\tau) &= \frac{du}{d\tau} + \frac{1}{S} \frac{dv}{d\tau} + \left(u + \frac{1}{S}v\right) \\ &= u^2 - u^3 - Qu^{\alpha+1}v + uv - v^2 + u + \frac{1}{S}v \\ &\leq u^2 + uv + u + \frac{1}{S}v \end{aligned}$$

$$\begin{aligned}
&\leq u^2 + uv + u + \frac{1}{S}v \\
&\leq u^2 + uv + \frac{v^2}{4} - \frac{v^2}{4} + u + \frac{1}{S}v \\
&\leq \left(u + \frac{v}{2}\right)^2 - \frac{v^2}{4} + u + \frac{1}{S}v \\
&\leq (u+v)^2 - \left(\frac{1}{S^2} - \frac{1}{S}v + \frac{v^2}{4}\right) + u \\
&\leq (u+v)^2 - \left(\frac{1}{S^2} - \frac{v}{2}\right)^2 + u + \frac{1}{S^2} \\
&\leq (u+v)^2 + u + \frac{1}{S^2} \\
&\leq (1+v)^2 + 1 + \frac{1}{S^2} = R
\end{aligned}$$

Then,

$$0 \leq \frac{dW(\tau)}{d\tau} + W(\tau) \leq R$$

being a first-order linear inequality.

Applying the theorem of Comparison Theorem for differential inequality (Page 30 in ⁷), we obtain

$$W(\tau)e^\tau \leq Re^\tau + C.$$

When $\tau = 0$

$$\begin{aligned}
W(0) &\leq R + C \\
W(0) - R &\leq C
\end{aligned}$$

There exists $n \in \mathbb{N}$ such that $C \leq n(W(0) - R)$, then

$$\begin{aligned}
W(\tau)e^\tau &\leq e^\tau R + n(W(0) - R) \\
W(\tau) &\leq R + e^{-\tau}n(W(0) - R).
\end{aligned}$$

Clearly, when $\tau \rightarrow \infty$ then $W(\tau) \leq R$. □

Remark 2. The result above assures that there exists a set

$$B = \{(u, v) \in \bar{\Omega} : W(u, v) \leq R + \epsilon, \forall \epsilon > 0\}$$

which is the region where all the solutions of system (2) with initial conditions in $\bar{\Omega}$ are confined. This property assures that the model is well-posed, i.e., it is no possible the existence of many predators and a little prey population size, which would be a counterintuitive situation, not sustainable ecologically.

Theorem 1. Uniqueness of solutions

The system is Lipschitzian in $\bar{\Omega}$.

Proof. Let us $P_1(u; v)$ and $P_2(u; v)$ as before, i.e.,

$$P_1(u; v) = ((1-u)u - Qu^\alpha v)u \text{ and } P_2(u; v) = S(u-v)v,$$

with $(u_1; v_1)$ and $(u_2; v_2)$ in $\bar{\Omega}$.

We will consider the differences

$$D_1 = |P_1(u_1; v_1) - P_1(u_2; v_2)| \text{ and } D_2 = |P_2(u_1; v_1) - P_2(u_2; v_2)|$$

$$\begin{aligned}
\text{i) } D_1 &= |P_1(u_1; v_1) - P_1(u_2; v_2)| \\
&= |(1-u_1)u_1 - Qu_1^\alpha v_1)u_1 - ((1-u_2)u_2 - Qu_2^\alpha v_2)u_2| \\
&= |(1-u_1)u_1^2 - (1-u_2)u_2^2 - Qu_1^{1+\alpha}v_1 + Qu_2^{1+\alpha}v_2| \\
&\leq |(1-u_1)u_1^2 - (1-u_2)u_2^2| + Q|u_2^{1+\alpha}v_2 - u_1^{1+\alpha}v_1|
\end{aligned}$$

Let us $F_1(u) = (1-u)u^2$ and $F_2(u) = u^{1+\alpha}v$.

Clearly $F_1 \in C^\infty(\mathbb{R})$ and $F_2 \in C^1(\mathbb{R})$.

Therefore, there exists constants K_1 and K_2 such as:

$$D_1 \leq K_1 |u_1 - u_2| + K_2 |u_1 - u_2 + v_1 - v_2|$$

$$D_1 \leq (K_1 + K_2) |u_1 - u_2| + K_2 |v_1 - v_2|$$

$$D_1 \leq K |u_1 - u_2| + K |v_1 - v_2|$$

$$D_1 \leq K \left\| (u_1; v_1) - (u_2; v_2) \right\|$$

with $K = \max \{K_1 + K_2, K_2\}$.

Thus, $P_1(u; v)$ is Lipschitzian.

ii) Analogously considering $D_2 = \left| P_2(u_1; v_1) - P_2(u_2; v_2) \right|$ we proof the existence of a constant K' such that

$$D_2 \leq K' \left\| (u_1; v_1) - (u_2; v_2) \right\|$$

Thus, $P_2(u; v)$ is Lipschitzian.

From i) and ii) the system (2) is Lipschitzian. □

3.1 | Nature of equilibria over the axis

Lemma 3. Nature of the point $(1, 0)$.

The equilibrium $(1, 0)$ is a saddle for all parameter values.

Proof. The Jacobian matrix $DY_\eta(u, v)$ evaluated in $(1, 0)$ is:

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

As $\det DY_\eta(1, 0) = -S < 0$.

The result follows from the Hartman and Grobman Theorem. □

Theorem 2. Nature of the point $(0, 0)$

The non-hyperbolic equilibrium point $(0, 0)$ has a hyperbolic and a parabolic sector³⁰ determined by the stable manifold $W^s(0, 0) = \tilde{\Sigma}$. Moreover, there exists a unstable manifold $W^u(0, 0)$ in the parabolic sector.

Proof. We note that in system (2), when $v = 0$, the derivative $\frac{du}{d\tau}$ is positive for all $0 < u < 1$. Moreover, (2) is differentiable at the origin.

Nonetheless, the Jacobian matrix evaluated in the the origin is the null matrix.

To desingularize the point $(0, 0)$ the horizontal blowing-up method^{14,37} is applied, defining the variables r and p by means of the change of variables given by $u = r$, $v = rp$.

Then, $\frac{du}{d\tau} = \frac{dr}{d\tau}$, $\frac{dv}{d\tau} = p \frac{dr}{d\tau} + r \frac{dp}{d\tau}$. Thus, $\frac{dr}{d\tau} = \frac{du}{d\tau}$ and $\frac{dp}{d\tau} = \frac{1}{r} \frac{dv}{d\tau} - \frac{p}{r} \frac{dr}{d\tau}$.

Replacing and factoring we have

$$\begin{aligned} \frac{du}{d\tau}(r, p) &= (1 - r - Qr^\alpha p) r^2 \\ \frac{dp}{d\tau}(r, p) &= S(1 - p)r^2 p, \end{aligned}$$

Therefore, the vector field is

$$Z_\eta(r, p) : \begin{cases} \frac{dr}{d\tau} = (1 - r - Qr^\alpha p) r^2 \\ \frac{dp}{d\tau} = S(1 - p)rp - (1 - r - Qr^\alpha p)rp, \end{cases}$$

Rescaling the time by $T = r\tau$, we have $\frac{dr}{dT} = \frac{dr}{d\tau} \frac{d\tau}{dT}$ and $\frac{dp}{dT} = \frac{dp}{d\tau} \frac{d\tau}{dT}$ and becomes

$$\bar{Z}_\eta(r, p) : \begin{cases} \frac{dr}{dT} = (1 - r - Qr^\alpha p) r \\ \frac{dp}{dT} = (S(1 - p) - (1 - r - Qr^\alpha p)) p, \end{cases}$$

When $r = 0$, from the second equation de \bar{Z}_η it has

$$\frac{dp}{dT} = (S(1 - p) - 1)p = 0.$$

Then, $p = 0$ and $p = \frac{S-1}{S}$. Thus, the equilibrium point od vector field \bar{Z}_η are $(0, 0)$ and $\left(0, \frac{S-1}{S}\right)$.

The Jacobian matrix of vector field $\bar{Z}_\eta(r, p)$ is

$$D\bar{Z}_\eta(r, p) = \begin{pmatrix} 1 - 2r - Qpr^\alpha(\alpha + 1) & -Qr^{\alpha+1} \\ p(Qpr^{\alpha-1}\alpha + 1) & S + r - 2Sp + 2Qpr^\alpha - 1 \end{pmatrix}$$

Evaluating in the equilibrium points $(0, 0)$ and $\left(0, \frac{S-1}{S}\right)$ we have

$$\text{i) } D\bar{Z}_\eta(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & S - 1 \end{pmatrix}$$

$$\text{ii) } D\bar{Z}_\eta\left(0, \frac{S-1}{S}\right) = \begin{pmatrix} 1 & 0 \\ \frac{S-1}{S} & -(S-1) \end{pmatrix}$$

Thus, assuming $S > 1$ in $\bar{Z}_\eta(r, p)$ we have

- a) the equilibrium $(0, 0)$ is a hyperbolic repeller, and
- b) the equilibrium $\left(0, \frac{S-1}{S}\right)$ is a hyperbolic saddle point.

Assuming $S < 1$ in $\bar{Z}_\eta(r, p)$ we have

c) the equilibrium $(0, 0)$ is a hyperbolic saddle point, and

d) the equilibrium $(0, \frac{S-1}{S})$ is a hyperbolic repeller, but it lies in the fourth quadrant.

Then, in Z_η we have a non-hyperbolic repeller and saddle.

By the blowing-down, $(0, 0)$ and $(0, \frac{S-1}{S})$ are non-hyperbolic equilibrium in $Y_\eta(u, v)$.

When $S > 1$, the non-hyperbolic saddle point $(0, \frac{S-1}{S})$ determines the separatrix curve $\bar{\Sigma}$, determined by the stable manifold $W^s(0, 0)$.

When $S < 1$, the non-hyperbolic saddle point $(0, 0)$ determines the separatrix curve $\bar{\Sigma}$. \square

Remark 3. Let us $W^u(1, 0)$ the unstable manifold of the hyperbolic saddle point $(1, 0)$ and $\bar{\Sigma} = W^s(0, 0)$ the stable manifold of the non-hyperbolic saddle point $(0, 0)$, in system (2). (See figure 1). The relative position of both manifold determines a heteroclinic curve, when $W^u(1, 0) \cap \bar{\Sigma} \neq \emptyset$.

Notice that the unique positive equilibrium (H, H) is in the region

$$\bar{\Lambda} = \{(u, v) \in \bar{\Gamma} / 0 \leq u, 0 \leq v \leq v_\Sigma, \text{ such that } (u, v_\Sigma) \in \bar{\Sigma}\}$$

and its nature depends of the relation between v_u and v_s .

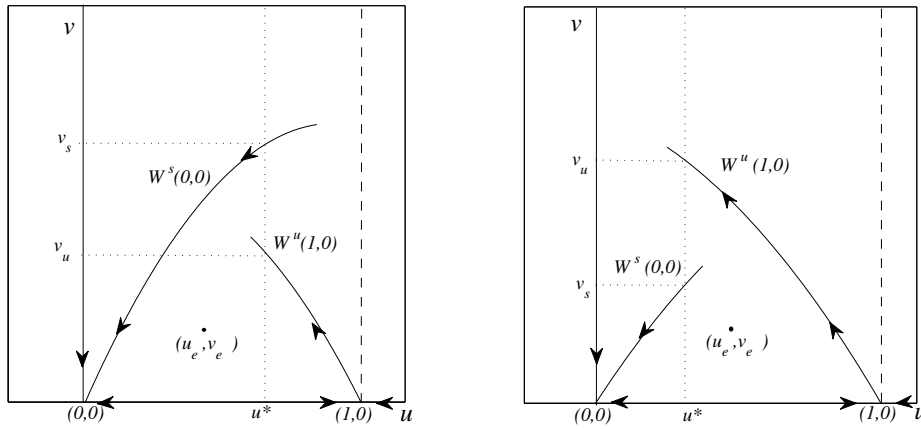


FIGURE 1 Relative position of the stable manifold $\bar{\Sigma} = W^s(0, 0)$ and the unstable manifold $W^u(1, 0)$, in the region $\bar{\Lambda}$ of system (2).

Theorem 3. Existence of a heteroclinic curve

Let us $W^u(1, 0)$ the unstable manifold of the hyperbolic saddle point $(1, 0)$ and $\bar{\Sigma} = W^s(0, 0)$ the stable manifold of the non-hyperbolic saddle point $(0, 0)$. Then, a subset of parameter values exists, for which $W^u(1, 0) \cap \bar{\Sigma} \neq \emptyset$, giving rise to a heteroclinic curve Υ_{01} , joining the saddle points $(1, 0)$ and $(0, 0)$.

Proof. Let us $(u^*, v^s) \in \bar{\Sigma} = W^s(0, 0)$ and $(u^*, v^u) \in W^u(1, 0)$, with v^s and v^u dependent on the parameters, i.e. $v^s = F_1(Q, S, \alpha)$ and $v^u = F_2(Q, S, \alpha)$.

i) Assuming $v^u < v^s$, then the stable manifold $\bar{\Sigma} = W^s(0, 0)$ is above the unstable manifold $W^u(1, 0)$, for all $0 < u^* < 1$.

Moreover, the ω -limit of the $W^u(1, 0)$ can be the point (H, H) or a limit cycle surrounding that point, since this manifold cannot cross the manifold $\bar{\Sigma}$.

Meanwhile, the α -limit of $\bar{\Sigma}$ cannot at infinity in the direction of the v -axis, since the solutions are bounded.

ii) Assuming $v^u > v^s$, then the stable manifold $\bar{\Sigma} = W^s(0, 0)$ is below the unstable manifold $W^u(1, 0)$, for all $0 < u^* < 1$.

Furthermore, the ω -limit of the $W^u(1, 0)$ cannot at infinity in the direction of the v -axis.

Therefore, $W^u(1, 0) \cap \bar{\Sigma} \neq \emptyset$, by continuity of the system (2) with respect to the parameter values. Furthermore, by uniqueness of solutions of the systems, this intersection must occur along a trajectory joining the saddle points $(1, 0)$ and $(0, 0)$.

Thus, the equation $F_1(Q, S, \alpha) = F_2(Q, S, \alpha)$ defines a subset in the parameter space, for which the heteroclinic curve Y_{01} exists. \square

Remark 4. In system (1) there is a separatrix curve Σ associated with the point $(0, 0)$, although the system is not defined there. We define the set

$$\Lambda = \{(x, y) \in \Gamma / 0 \leq x, 0 \leq y \leq y_\Sigma, \text{ such that } (x, y_\Sigma) \in \Sigma\},$$

and the phase plane is divided in the set Λ and $\Psi = \Gamma - \Lambda$.

Moreover, there exists a heteroclinic curve γ_{0K} , joining the saddle points $(K, 0)$ and $(0, 0)$.

In the following figure we show the sectors determined by the curve separatrix Σ in system (1).

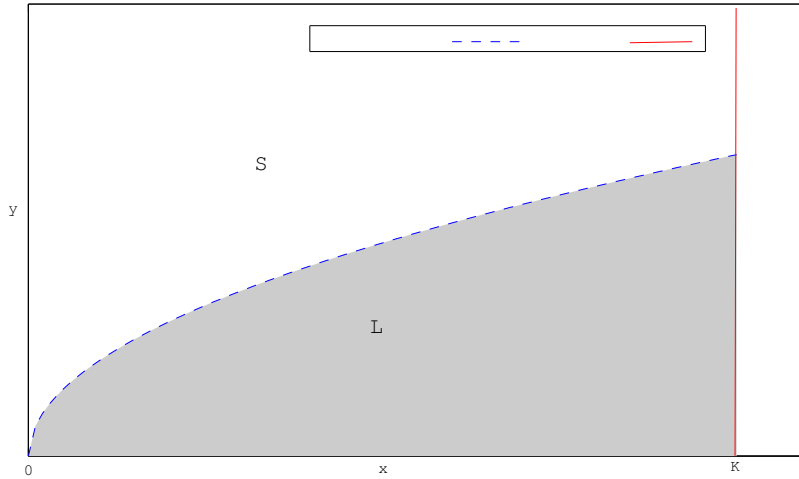


FIGURE 2 In the phase plane of the system (1)

are shown the sets Λ and $\Psi = \Gamma - \Lambda$, determined by the separatrix curve Σ , associated to the point $(0, 0)$, with $0 < x < K$.

Theorem 4. Existence of a homoclinic loop

Let us $W^u(0, 0)$ the unstable manifold, $\bar{\Sigma} = W^s(0, 0)$ the stable manifold of the non-hyperbolic saddle point $(0, 0)$, respectively, and $(u^0, v_{u0}) \in W^u(0, 0)$ and $(u^0, v_{s0}) \in \bar{\Sigma}$, with $v_{u0} < v_{s0}$. Then, a subset of parameter values exists, for which $W^u(0, 0) \cap \bar{\Sigma} \neq \emptyset$, determining a homoclinic loop.

Proof. As $v_{u0} < v_{s0}$, the stable manifold $\bar{\Sigma} = W^s(0, 0)$ is above the unstable manifold $W^u(0, 0)$, for all $0 < u^{**} < 1$.

Moreover, the ω -limit of the $W^u(0, 0)$ can be the point (H, H) or a unstable limit cycle surrounding that point, since this manifold cannot cross the manifold $W^u(1, 0)$, when $v^u < v^s$, with $(u^{**}, v^s) \in \bar{\Sigma} = W^s(0, 0)$ and $(u^{**}, v^u) \in W^u(1, 0)$.

Assuming $v^u > v^s$, it has $v_{u0} < v_{s0} < v^u$; then, the ω -limit of the $W^u(0, 0)$ is the stable manifold $\bar{\Sigma} = W^s(0, 0)$, for all $0 < u^{**} < 1$.

Thus, a subset of parameter values exists, for which $W^u(0, 0) \cap \bar{\Sigma} \neq \emptyset$ (The graph is similar to Figure 7). \square

3.2 | Nature of positive equilibrium point

For study of the equilibrium (H, H) , let us make a change of parameters in the system (2), given by:

$$Q = \frac{1 - H}{H^\alpha},$$

with $H \in]0, 1[$, getting the system

$$X_v(u, v) : \begin{cases} \frac{du}{d\tau} = \left((1 - u)u - \frac{1-H}{H^\alpha} u^\alpha v \right) u \\ \frac{dv}{d\tau} = S(u - v)v, \end{cases} \quad (4)$$

with $v = (S, H, \alpha) \in \bar{\Pi} = \mathbb{R}^2 \times]0, 1[$. The vector field X_v or system (4) has an equilibrium (H, H) and it is topologically equivalent to the (2) in $\bar{\Omega}$.

Theorem 5. Nature of the positive equilibrium

Let us

$$\bar{\Lambda}_K = \{(u, v) \in \bar{\Gamma} / 0 \leq u \leq K, 0 \leq v \leq v_\Sigma, \text{ such that } (u, v_\Sigma) \in \bar{\Sigma}\} \subset \bar{\Lambda}.$$

- a) Assuming $v_u < v_s$, for (u^*, v_u) and $(u^*, v_u) \in \bar{\Lambda}_K$. Then, the positive equilibrium (H, H) is
- i) an attractor, if and only if, $S > 1 - \alpha - 2H + \alpha H$.
 - ii) a repeller, if and only if, $S < 1 - \alpha - 2H + \alpha H$.
 - iii) a weak (fine) focus, if and only if, $S = 1 - \alpha - 2H + \alpha H$.
- b) Assuming $v_u > v_s$, for (u^*, v_u) and $(u^*, v_u) \in \bar{\Lambda}_K$. Then, the positive equilibrium (H, H) is a repeller (focus or node), and $(0, 0)$ is an almost global stable point^{28,32}.

Proof. The Jacobian matrix evaluated the equilibrium (H, H) is

$$DX_v(H, H) = \begin{pmatrix} 2H - 3H^2 - (\alpha + 1)(1 - H)H & -(1 - H)H \\ SH & -SH \end{pmatrix}.$$

Then,

$$\det DX_v(H, H) = SH^2(\alpha + H(1 - \alpha)) > 0 \text{ and}$$

$$\text{tr} DX_v(H, H) = H(1 - \alpha - 2H + \alpha H - S).$$

Hence, the nature of the equilibrium (H, H) , depends on the sign of trace, which at once depends on the sign of the factor

$$T(S, H, \alpha) = 1 - \alpha - 2H + \alpha H - S.$$

a) Assuming $v_u < v_s$.

i) If $S > 1 - \alpha - 2H + \alpha H$, the equilibrium (H, H) is a hyperbolic attractor of system (4) for all trajectories with initial conditions in $\bar{\Lambda}$.

ii) If $S < 1 - \alpha - 2H + \alpha H$, the equilibrium (H, H) is a hyperbolic repeller.

Clearly, $\bar{\Lambda}_K$ is a compact region; then the Poincaré-Bendixson Theorem applies in $\bar{\Lambda}_K$ and there exist at least a limit cycle in system (4).

Therefore, all trajectories with initial conditions in $\bar{\Lambda}$ have a this limit cycle as their ω -limit.

iii) If $S = 1 - \alpha - 2H + \alpha H$, the equilibrium (H, H) is a weak focus.

b) Assuming $v_u > v_s$, (H, H) is a hyperbolic repeller (focus or node).

By the Existence and Uniqueness Theorem, the trajectories born in the neighborhoods of $(0, 0)$ not cross the unstable manifold $W^u(1, 0)$ of equilibrium $(1, 0)$, and they have the point $(0, 0)$ as their ω -limit. \square

Remark 5. The set

$$\Lambda_K = \{(x, y) \in \Gamma / 0 \leq x \leq K, 0 \leq y \leq y_\Sigma, \text{ such that } (x, y_\Sigma) \in \Sigma\}$$

is a compact region in system (1).

Corollary 1. Transversality condition

If $S = 1 - \alpha - 2H + \alpha H$, there exists at least limit cycle generated by Hopf bifurcation surrounding the positive equilibrium point (H, H) .

Proof. Applying the transversality Theorem³⁰.

Deriving $\text{Tr} DX_v(H, H) = H(1 - \alpha - 2H + \alpha H - S)$, respect to the parameter S it has,

$$\frac{\partial \text{Tr} DX_v(H, H)}{\partial S} = -H \neq 0. \quad \square$$

Remark 6. Uniqueness of the limit cycle

We conjecture the limit cycle generated by Hopf bifurcation^{16,23} surrounding the positive equilibrium point (H, H) is unique.

Due to the difficulty applying the method of Lyapunov quantities^{10,23} due to the exponent $\alpha \in]0, 1[$, the determination of the weakness of the equilibrium point (H, H) have not been proved.

4 | SOME SIMULATIONS AND BIFURCATION DIAGRAMS

To reinforced the analytical results we show some numerical simulations. The figures 3 to 7 show the dynamic of system (2) proved in the above section.

1. Existence of two local attractors

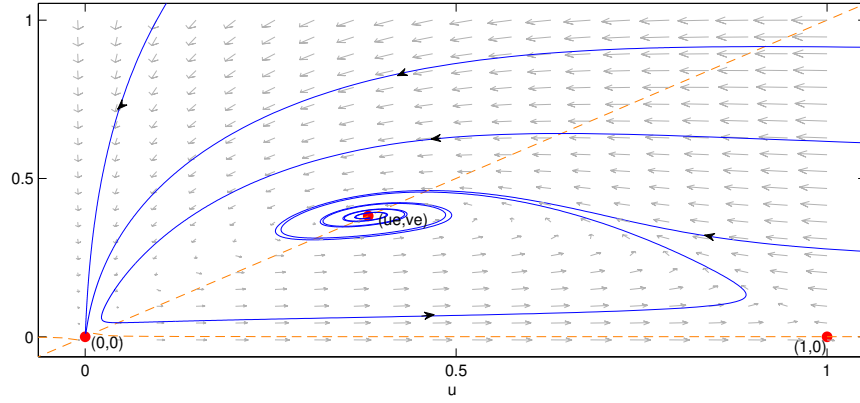


FIGURE 3 For $\alpha = 0.2$, $Q = 0.75$ and $S = 0.175$, system (1) has two local attractors, $(0, 0)$ and (u_e, u_e) .

2. Existence of limit cycle and $(0, 0)$ local attractor

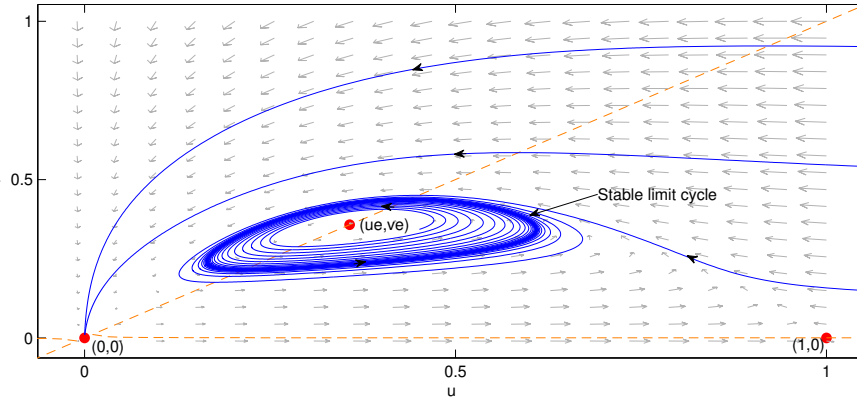


FIGURE 4 For $\alpha = 0.15$, $Q = 0.75$ and $S = 0.175$, there exists a limit cycle surrounding the repeller positive equilibrium point (u_e, u_e) .

3. Existence of heteroclinic curve

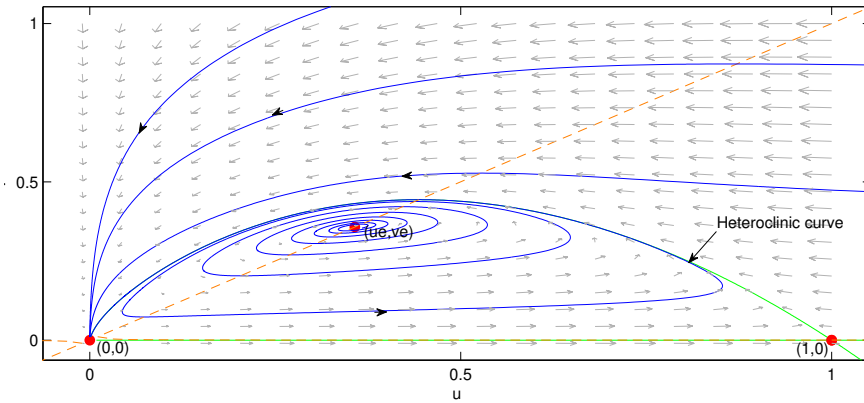


FIGURE 5 For $\alpha = 0.15$, $Q = 0.75$ and $S = 0.1515$, there exists a heteroclinic curve joining the points $(1, 0)$ and $(0, 0)$. The equilibrium point (u_e, v_e) is a repeller focus and $(0, 0)$ is a nearly global attractor^{28,32}.

4. Existence of an almost global attractor^{28,32}

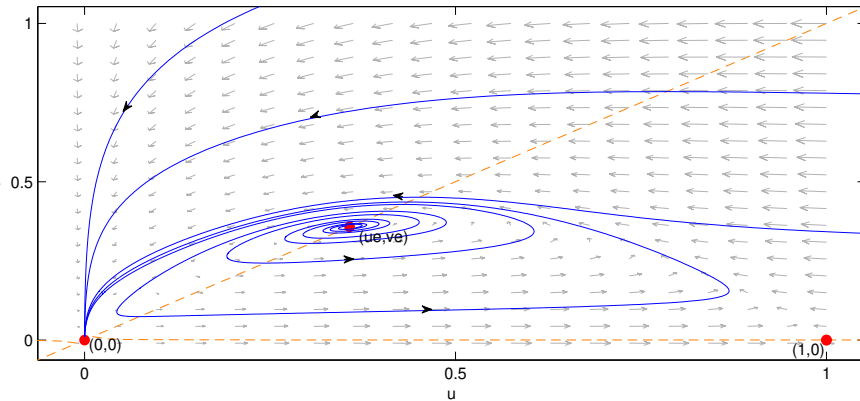


FIGURE 6 For $\alpha = 0.15$, $Q = 0.75$ and $S = 0.125$, the positive equilibrium point (u_e, v_e) is a repeller focus and $(0, 0)$ is an almost global attractor^{28,32}.

5. Existence of an elliptic sector³⁰

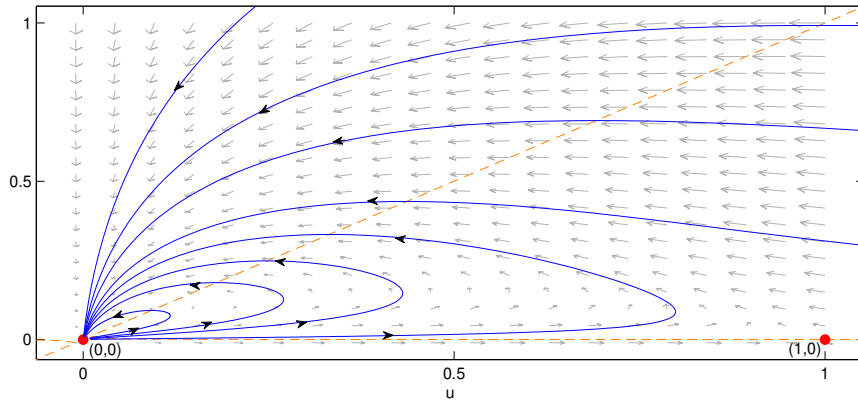


FIGURE 7 For $\alpha = 0.15$, $Q = 1.9$ and $S = 0.75$, there exists an elliptic sector, generated by the stable and unstable manifolds of the non-hyperbolic equilibrium $(0, 0)$, $\tilde{S} = W^s(0, 0)$ and $W^u(0, 0)$, respectively.

4.1 | Bifurcation diagrams

To get the bifurcation diagrams we use the numerical bifurcation package MATCONT¹³, following the realized in²; we will distinguish three cases considering the bifurcation curves obtained from Theorem 14 and Corollary 16

1. When the bifurcation curves divide the (α, S) parameter space into three parts. If the parameters α, S are located in Region I (red area), the equilibrium point (H, H) is stable, while in Region II (blue area) the equilibrium point is unstable surrounded by a stable limit cycle.

Moreover, when the parameters α, S are located in Region III (grey area), the equilibrium point (H, H) is unstable. Additionally, we can observe that the modification of the parameter S changes the stability of the positive equilibrium point (H, H) of system (2), while the other equilibrium points $(0, 0)$ and $(1, 0)$ do not change their behaviour.

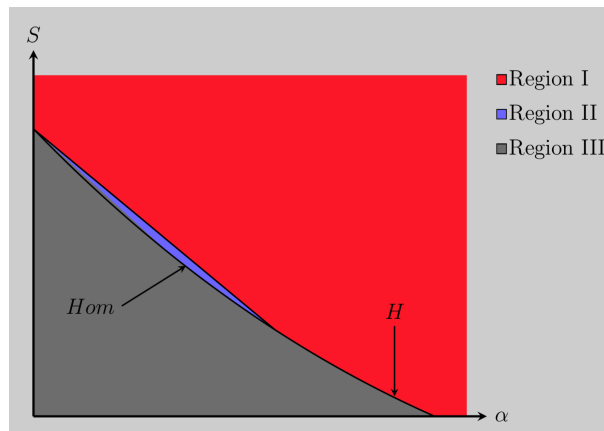


FIGURE 8 The bifurcation diagram of system (2) for $Q = 0.75$ fixed and created with the numerical bifurcation package MATCONT¹³. The curve H represents the Hopf curve and Hom represents the homoclinic curve.

2. When the bifurcation curves divide the (Q, S) parameter space into three parts. If the parameters Q, S are located in Region I (red area), the equilibrium point (H, H) is stable, while in Region II (blue area) the equilibrium point is unstable surrounded by a stable limit cycle.

Furthermore, when the parameters Q, S are located in Region III (grey area), the equilibrium point (H, H) is unstable. Additionally, we can observe that the modification of the parameter S changes the stability of the positive equilibrium point (H, H) of system (2), while the other equilibrium points $(0, 0)$ and $(1, 0)$ do not change their behaviour.

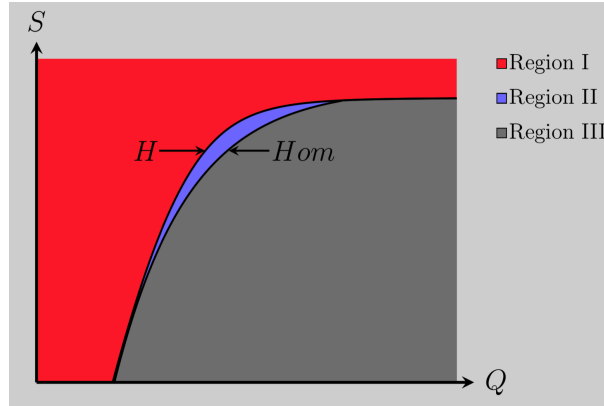


FIGURE 9 The bifurcation diagram of system (2) for $\alpha = 0, 1652335$ fixed and created with the numerical bifurcation package MATCONT¹³. The curve H represents the Hopf curve and Hom represents the homoclinic curve.

3. When the bifurcation curves divide the (α, S) parameter space into three parts, see left panel of Figure 8, in red. If the parameters α, S are located in Region I (red area), the equilibrium point (H, H) is stable, while in Region II (blue area) the equilibrium point is unstable surrounded by a stable limit cycle.

Moreover, when the parameters α, S are located in Region III (grey area), the equilibrium point (H, H) is unstable. Additionally, we can observe that the modification of the parameter S changes the stability of the positive equilibrium point (H, H) of system (2), while the other equilibrium points $(0, 0)$ and $(1, 0)$ do not change their behaviour.

Note that changing the parameter Q the bifurcation diagram (right panel of Figure 8 in red) has the same qualitative effect in the stability of the equilibrium point (H, H) .

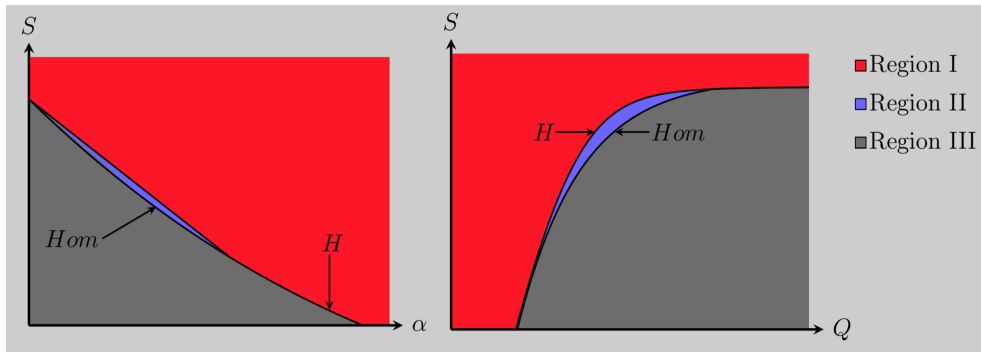


FIGURE 10 The bifurcation diagram of system (2) created with the numerical bifurcation package MATCONT¹³. In the left panel $Q = 0.75$ fixed and varying α and S and in the right panel $\alpha = 0, 1652335$ fixed and varying Q and S . The curve H represents the Hopf curve and Hom represents the homoclinic curve.

5 | CONCLUSIONS

In this work, the dynamics of a class of modified Leslie-Gower type predation models^{24,26,39} has been studied, in which was incorporating the non-differentiable functional response proposed by Michael L- Rosenzweig³⁵, described by the mathematical form $h(x) = qx^\alpha$, with $0 < \alpha < 1$. This function is a generalisation of an expression used by G. F. Gause in 1934¹⁷, and the obtained system (1) is not of the Kolmogorov type¹⁵.

We have shown that this function has a strong influence on the dynamics of the system because new properties appear that do not occur in the original model formulated by Leslie in 1948.

In order to simplify the calculations, a reparameterization and a time rescaling were made, obtaining the topologically equivalent system (2), which is the Kolmogorov type¹⁵.

It was established that the system can have up to 3 singularities, two of them are hyperbolic and the origin is non-hyperbolic. This last equilibrium has a complicated behavior.

Using the directional blowing-up method to determine the nature of this point, we comprobe that there exists a separatrix curve $\tilde{\Sigma}$ determined by the stable manifold of the non-hyperbolic equilibrium point $(0, 0)$ (a separatrix curve Σ in the original system).

An important results is the new system obtained (2) is differentiable at the origin (Lemma 3.1), unlike the original (1), showing also that the solutions of the system are bounded (Lemma 3.2).

We show that the only positive equilibrium point (H, H) is locally asymptotically stable for certain parameter conditions; for other conditions in the parameter space, there is at least one limit cycle, a fact that establishes a clear difference with the dynamics of the Leslie-Gower model proposed in 1948²⁴.

Due to the existence of the separatrix curve $\tilde{\Sigma}$, we can conclude that both population can go extinction, since there are many trajectories have the point $(0, 0)$ as their ω -limit.

Furthermore, the both populations becomes extinction, when the stable manifold $\tilde{\Sigma} = W^s(0, 0)$ of the origin is under the unstable manifold $W^u(1, 0)$ of the point free of predators, being the ratio prey/predator relatively great (many prey and few predators).

We have demonstrated the existence of at least one limit cycle via Hopf bifurcation^{16,23}. We conjecture that it is unique, according to the simulations performed and because in the case $\alpha = 1$ (Leslie's model²⁴), there is no limit cycle.

Therefore, in the model (1) there is a subset of parameter values for which stable oscillations exist. In this case, populations may not tend to these attractor oscillations, but instead may go to extinction²⁹, specially when the ratio prey/predator is small.

Although in the system there exists a separatrix curve $\tilde{\Sigma}$ of the trajectories in the phase plane, there are no trajectories that attain at the vertical axis in finite time³, as it happens with the Volterra model³⁹ (a Gause type predation model) using the same functional response^{3,37}.

Moreover, it was shown that the system is Lipschitzian¹⁰, differentiating it from the Gause type model considering the same Rosenzweig functional response and other modified Leslie-Gower model considering alternative food for predators²⁰.

We reiterate that the particular case $\alpha = \frac{1}{2}$ has been used to represent the called *prey herd behavior*^{1,27,42}; we estimate that any value $\alpha \in]0, 1[$ can be employed to describe this behavior, since the properties here shown are valid for that special case.

On the other hand, in the case of severe scarcity, some predator species can switch over to other foods, i.e., the predators have an alternative food since they are generalist. This situation can be modelled by adding a positive constant c in the carrying capacity $K_y(x)$, which is now described by $K(x) = nx + c$,³⁸ being a function of the prey population size and the other available food^{33,34,38}.

We will assume this function in a future work, where an adequate comparison among the two models will be made, because there exist significative differences on the dynamic of both systems²⁰. According to the numerical simulations already carried out, it is verified that the new modified Leslie-Gower model has trajectories that in finite time reach the vertical axis and possibly be non-Lipschitzian on that axis.

We conclude that, in general, a small change in the mathematical expression for the functional response, it can produce a strong change on the dynamics of a model. For this reason, modellers must have great care with the use of a more complicated functional response, since non-usual mathematical properties can emerge, which could have not an adequate interpretation in specific interactions of the real world.

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