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Rosenzweig-MacArthur model with variable disappearance rate

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Abstract

In this article, we consider a modified Rosenzweig -MacArthur model in which we take into account a general variable disappearance rate of the predator, in addition to its natural constant death rate. We show that the conditions of existence of a positive equilibrium are the same as for the Rosenzweig -MacArthur model, but those of stability are not. We define an arc of the ascending branch of the prey isocline out of which a positive equilibrium can be locally exponentially stable, and the ends of which can correspond to Hopf bifurcations. We apply our geometrical interpretation to the Bazykin's model for which the disappearance rate depends only on the predator density, and to the Variable-Territory model for which the disappearance rate depends on both densities. Theoretical predictions are illustrated by numerical simulations.

Keywords

Rosenzweig -MacArthur model; General disappearance rate; Bazykin's model; Variable-territory model.

I INTRODUCTION

The aim of this work is to extend the well-known results of the Rosenzweig -MacArthur model (RMA) to the modified RMA model (MRMA) where a general disappearance term is added in the the equation of the prey. What is notable with this modification that already appeared in the literature for specific disappearance terms (see for example [2, 3, 5]), is that one can have one or more positive attractive equilibria even on the ascending branch of the prey isocline. This never occurs for the RMA model. Indeed, recall that the RMA model [4, 8] takes the form

$$\begin{cases} \dot{x} = rx \left(1 - \frac{x}{K}\right) - \frac{axy}{c+x}, \\ \dot{y} = \left(e \frac{ax}{c+x} - m\right) y, \end{cases} \quad (1)$$

where $x(t)$ and $y(t)$ are the density of prey and predator species respectively, at time t and the dot represents the derivative with respect of time : $\dot{x} = \frac{dx}{dt}$, $\dot{y} = \frac{dy}{dt}$. The parameters r , K , a , c , e and m are all positive biological parameters. It is well known that the solutions of (1), with non-negative initial conditions, are non-negative and bounded. Moreover, besides the boundary equilibria $E_1 = (0, 0)$ and $E_2 = (K, 0)$ that always exist, the system (1) can have a positive equilibrium $E^* = (x^*, y^*)$, where $x^* = x_1$ and $y^* = h(x^*)$, where x_1 and h are given by

$$x_1 = \frac{mc}{ea-m}, \quad h(x) := \frac{r}{aK}(K-x)(c+x). \quad (2)$$

The positive equilibrium E^* exists if and only if $0 < x_1 < K$. Note that the curve $y = h(x)$, together with the semi axis $x = 0$, constitute the prey isocline and the vertical line $x = x_1$, together with the semi axis $y = 0$, constitute the predator isocline. Hence, E^* is at the intersection of the isoclines $x = x_1$ and $y = h(x)$, while E_1 is at the intersection of the isoclines $x = 0$ and $y = 0$ and E_2 is at the intersection of the isoclines $y = 0$ and $y = h(x)$. Finally, we recall the main result on the stability of the equilibria : E_1 is a saddle point, E_2 is locally exponentially stable (LES) if and only if $x^* > K$, and it is a saddle point if $x^* < K$. If $0 < x^* < K$, then E^* exists and it is LES if and only if $h'(x^*) < 0$, i.e. $x^* > \hat{x}$, where

$$\hat{x} := \frac{K-c}{2} \quad (3)$$

is the abscissa of the maximum of the function h . Therefore, if E^* lies in the ascending part of the prey isocline $y = h(x)$, then it is unstable. If it lies in the descending part of the prey isocline $y = h(x)$, then it is LES. Our contribution is mainly to define, for the MRMA model, an arc of the ascending part of the prey isocline out of which eventual positive equilibria can be asymptotically stable and to get a geometrical reading of the stability properties of such equilibria. Further results will be developed in a forthcoming paper. The article is organized as follows : in Section II, we make sure that the MRMA is biologically well-posed (Proposition 1) and we give the local stability properties of the equilibria (Theorem 2 and Proposition 2). We then apply our results for specific choices of $d(x, y)$, by considering Bazykin's and Variable-Territory models in Section III. A conclusion is given in Section IV. Finally, we illustrate our theoretical predictions with numerical simulations in Appendices A and B.

II MODIFIED ROSENZWEIG -MACARTHUR MODEL

Contrary to the system (1) where the mortality rate of predators m is considered as a constant, we consider a prey-predator model in which, we take into account, in addition to the natural mortality, the disappearance of predator caused by competition or intraspecific interaction of the predators. The model is given by

$$\begin{cases} \dot{x} = rx \left(1 - \frac{x}{K}\right) - \frac{axy}{c+x}, \\ \dot{y} = \left(e \frac{ax}{c+x} - d(x, y) - m\right) y, \end{cases} \quad (4)$$

with the assumptions

$$d(x, y) \geq 0, \quad d(x, 0) = 0, \quad d_y(x, y) \geq 0, \quad d_x(x, y) \leq 0. \quad (5)$$

2.1 Positivity and boundedness of the solutions, isoclines and equilibria

The next result deals with the positiveness and the boundedness of the solutions of (4).

Proposition 1:

The solutions of (4) with nonnegative initial conditions are nonnegative and bounded.

Proof. The axes $x = 0$ and $y = 0$ being invariant for the model (4), the positive cone is invariant. We put $\sigma := x + \frac{y}{e}$ and we calculate the derivative

$$\dot{\sigma} = rx \left(1 - \frac{x}{K}\right) - \frac{m+d(x,y)}{e} y = \left[r \left(1 - \frac{x}{K}\right) + m\right] x - m\sigma - \frac{d(x,y)}{e} y.$$

The maximum of $\left[r \left(1 - \frac{x}{K}\right) + m\right] x$ is $M := \frac{(r+m)^2 K}{4r}$. Then, we obtain $\dot{\sigma} + m\sigma \leq M$. Using the comparison lemma, we can prove that

$$\limsup_{t \rightarrow +\infty} \sigma(t) \leq M.$$

Therefore, $x(t)$ and $y(t)$ are uniformly bounded. \square

As for the RMA model, the prey isocline $\dot{x} = 0$ is the union of the semi axis $x = 0$ and the curve $y = h(x)$ where h is given in (2). For the MRMA model, the predator isocline $\dot{y} = 0$ is the union of the semi axis $y = 0$ and the curve $x = \psi(y)$ of equation

$$e \frac{a\psi(y)}{c+\psi(y)} - d(\psi(y), y) - m = 0. \quad (6)$$

Using the implicit function theorem, we deduce that

$$\psi'(y) = \frac{d_y(\psi(y), y)(c + \psi(y))^2}{eac - d_x(\psi(y), y)(c + \psi(y))^2} \quad (7)$$

From assumptions (5), $\psi'(y) \geq 0, \forall y \geq 0$. Therefore, ψ is a non-decreasing function. Replacing y by 0 in (6) and using assumptions (5), we obtain that $\psi(0) = x_1$, where x_1 is given in (2). Hence, ψ is a non-negative function such that

$$\forall y \geq 0, \psi(y) \geq x_1. \quad (8)$$

Therefore, besides the boundary equilibria $E_1 = (0, 0)$ and $E_2 = (K, 0)$ that always exist, the system (4) can have positive equilibria $E^* = (x^*, y^*)$ as an intersection of the curves $y = h(x)$ and $x = \psi(y)$, that is $x = x^*$ is a solution of $x = \psi(h(x))$ and $y^* = h(x^*)$. The following theorem gives indeed a necessary and sufficient condition for the existence of a positive equilibrium, which is the same condition as for the RMA model.

Theorem 1:

Suppose that assumptions (5) are satisfied. A positive equilibrium $E^*(x^*, y^*)$ of (4) exists if and only if $0 < x_1 < K$ where $x_1 = mc/(ea - m)$.

Proof. We have that $h(x) > 0$ if and only if $0 < x < K$. According to equation (8), we have $\psi(h(x^*)) = x^* \geq x_1$. Then, for the existence of a positive equilibrium, it is necessary that $0 < x_1 < K$ in which case $x_1 < x^* < K$. To show that such an x^* exists in $[x_1, K)$, we can apply the Intermediate Value Theorem to the continuous function $A(x) := x - \psi(h(x))$: on one hand, according to equation (8), we have $A(x_1) = x_1 - \psi(h(x_1)) \leq 0$. On the other hand, $A(K) = K - \psi(h(K)) = K - \psi(0) = K - x_1 > 0$. \square

Note that, if $A(x_1) = 0$, then $x^* = x_1$. It is the case for RMA model. If $d_y \neq 0$, the predator isocline $x = \psi(y)$ can also be given as the graph of the function $y = \varphi(x)$ which verifies

$$\frac{eax}{c+x} - d(x, \varphi(x)) - m = 0. \quad (9)$$

Model	d	Predator isocline
RMA	$d(x, y) = 0$	$x = x_1$
Bazykin	$d(x, y) = \alpha y$	$\varphi(x) = \frac{1}{\alpha} \frac{(ea-m)x-mc}{c+x}$, for $x \geq x_1$
V-T	$d(x, y) = \frac{\alpha y}{\delta+x}$	$\varphi(x) = \frac{\delta+x}{\alpha} \frac{(ea-m)x-mc}{c+x}$, for $x \geq x_1$

Table 1: The predator isocline of RMA, Bazykin and V-T models, where $x_1 = \frac{mc}{ea-m}$.

2.2 Stability of equilibria

In the next theorem, we give the conditions of stability of the boundary and positive equilibria.

Theorem 2:

Suppose that assumptions (5) are satisfied. Then $E_1(0, 0)$ is a saddle point and $E_2(K, 0)$ is LES if and only if $x_1 > K$, and it is a saddle point if $x_1 < K$. If a positive equilibrium E^* exists and $d_y \neq 0$, then E^* is LES if and only if

$$h'(x^*) < \varphi(x^*) \quad \text{and} \quad H(x^*) < G(x^*), \quad (10)$$

where $h(x)$ is defined by equation (2), $\varphi(x)$ is the solution of (9), and $H(x)$ and $G(x)$ are given by

$$H(x) := \frac{ax}{c+x} \frac{h'(x)}{h(x)} = \frac{ax(K-c-2x)}{(K-x)(c+x)^2}, \quad G(x) = d_y(x, h(x)). \quad (11)$$

For the RMA model, for which $d_y = 0$, E^* is LES if and only if $h'(x^*) < 0$, or equivalently, $x^* > \hat{x}$, where \hat{x} is defined by (3).

Proof. The Jacobian matrix of (4) is given by

$$\mathcal{J}(x, y) = \begin{pmatrix} r \left(1 - \frac{2x}{K}\right) - \frac{ac}{(c+x)^2} y & \frac{-ax}{c+x} \\ \left(\frac{eac}{(c+x)^2} - d_x(x, y)\right) y & \frac{eax}{c+x} - d(x, y) - m - d_y(x, y)y \end{pmatrix}.$$

For $E_1 = (0, 0)$, and according to (5), we obtain the Jacobian matrix

$$\mathcal{J}(0, 0) = \begin{pmatrix} r & 0 \\ 0 & -m \end{pmatrix},$$

the eigenvalues of which are r and $-m$. Hence, E_1 is a saddle point. According to (5), the Jacobian matrix at E_2 is given by

$$\mathcal{J}(K, 0) = \begin{pmatrix} -r & \frac{-aK}{c+K} \\ 0 & \frac{eak}{c+K} - m \end{pmatrix},$$

the eigenvalues of which are $-r$ and $\frac{eak}{c+K} - m$. Hence, E_2 is LES if and only if $\frac{eak}{c+K} < m$, i.e. $x_1 > K$, where x_1 is given in (2). If $x_1 < K$, then it is a saddle point. Since $E^*(x^*, y^*)$ verifies

$$\frac{eax^*}{c+x^*} - d(x^*, y^*) - m = 0,$$

where $y^* = h(x^*)$, and $h(x)$ is defined in (2), and noting that

$$\begin{aligned} r \left(1 - \frac{2x^*}{K}\right) - \frac{ac}{(c+x^*)^2} h(x^*) &= r \left(1 - \frac{2x^*}{K}\right) - \frac{cr}{K(c+x^*)} (K-x^*) \\ &= \frac{ax^*}{c+x^*} \left[\frac{r}{aK} (K-c-2x^*) \right] = \frac{ax^*}{c+x^*} h'(x^*), \end{aligned}$$

the Jacobian matrix at E^* can be written

$$\mathcal{J}(x^*, y^*) = \begin{pmatrix} \frac{ax^*}{c+x^*} h'(x^*) & \frac{-ax^*}{c+x^*} \\ \left(\frac{eac}{(c+x^*)^2} - d_x(x^*, h(x^*)) \right) h(x^*) & -d_y(x^*, h(x^*)) h(x^*) \end{pmatrix}.$$

Therefore, the determinant is given by

$$\det \mathcal{J}(x^*, y^*) = \frac{ax^*}{c+x^*} h(x^*) \left(\frac{eac}{(c+x^*)^2} - d_x(x^*, h(x^*)) - h'(x^*) d_y(x^*, h(x^*)) \right).$$

If $d = 0$ (the RMA model), then the determinant is $\det \mathcal{J}(x^*, y^*) = \frac{ax^*}{c+x^*} h(x^*) \frac{eac}{(c+x^*)^2}$, which is always positive. If, in assumptions (5), $d_y \neq 0$, then the derivative with respect to x of equation (9), satisfied by the predator isocline $y = \varphi(x)$, gives

$$\frac{eac}{(c+x)^2} - d_x(x, \varphi(x)) - d_y(x, \varphi(x)) \varphi'(x) = 0.$$

Since x^* satisfies $\varphi(x^*) = h(x^*)$, we have

$$\varphi'(x^*) = \frac{\frac{eac}{(c+x^*)^2} - d_x(x^*, h(x^*))}{d_y(x^*, h(x^*))}.$$

Therefore, the determinant can be written

$$\det \mathcal{J}(x^*, y^*) = \frac{ax^*}{c+x^*} h(x^*) d_y(x^*, h(x^*)) (\varphi'(x^*) - h'(x^*)).$$

From assumptions (5), $\det \mathcal{J}(x^*, y^*) > 0$ if and only if $\varphi'(x^*) > h'(x^*)$. The trace is given by

$$\text{tr} \mathcal{J}(x^*, y^*) = \frac{ax^*}{c+x^*} h'(x^*) - d_y(x^*, h(x^*)) h(x^*) = h(x^*) (H(x^*) - G(x^*)),$$

where $H(x)$ and $G(x)$ are defined by (11). Consequently, $\text{tr} \mathcal{J}(x^*, y^*) < 0$ if and only if $H(x^*) < G(x^*)$. Hence, if and only if the two conditions of (11) hold, then the eigenvalues have negative real parts, hence E^* is LES. For the RMA model, we have $G(x) = 0$. This second condition reduces to $H(x^*) < 0$, that is to say $h'(x^*) < 0$, or equivalently, $x^* > \hat{x}$, where \hat{x} is defined by (3). \square

Let us denote by

$$\mathcal{A} = \{(x, h(x)), H(x) \geq G(x)\},$$

the subset of the ascending branch of the prey isocline $y = h(x)$, such that if E^* is in the interior of \mathcal{A} , then E^* is unstable. Therefore, the positive equilibrium E^* is LES if and only if $E^* \notin \mathcal{A}$ and, in addition, the slope of h at E^* is smaller than the slope of φ , which is the condition $h'(x^*) < \varphi'(x^*)$ in Theorem 2. As a consequence of Theorem 2 we obtain the following geometrical description of the stability of a positive equilibrium :

Proposition 2:

Let E^* be a positive equilibrium of (4).

- If $E^* \notin \mathcal{A}$ and in addition $h'(x^*) < \varphi'(x^*)$, then E^* is a stable focus or node.
- If E^* is in the interior of \mathcal{A} and in addition $h'(x^*) < \varphi'(x^*)$, then E^* is an unstable focus or node.
- If $h'(x^*) > \varphi'(x^*)$, then E^* is a saddle point.

Proof. Let \mathcal{J} be the Jacobian matrix at E^* . From the proof of Theorem 2 it is seen that the condition $h'(x^*) < \varphi'(x^*)$ is equivalent to $\det(\mathcal{J}) > 0$, while the condition $H(x^*) < G(x^*)$ is equivalent to $\text{tr}(\mathcal{J}) < 0$. \square

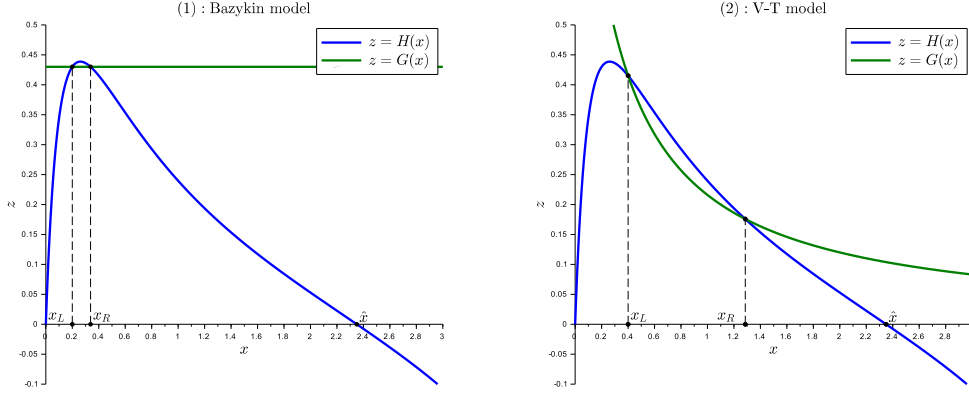


Figure 1: The graphs of the functions H and G for (a) Bazykin model : $K = 5$, $r = 0.19$, $a = 0.6$, $\alpha = 0.43$ and $c = 0.3$; (b) V-T model : $K = 5$, $r = 0.19$, $a = 0.6$, $\alpha = 0.27$, $c = 0.3$ and $\delta = 0.25$.

III SOME APPLICATIONS

We will restrict our attention to two cases which were considered in the literature (see Table 1). The first one is Bazykin's model [1, 3, 9] in which the regulation was introduced by intraspecific mechanisms, that is a competition among predators for resources other than prey. To do this, Bazykin subtracted a quantity αy , called a self-limitation term, from the predator equation. The term $1/\alpha$ can be considered as a constant carrying capacity of the predators, d is depending only on the predator density and it is given by $d(x, y) = \alpha y$, with $\alpha \geq 0$. The second one is variable-territory model in which α in Bazykin's model is made inversely proportional to resource availability, that is $\alpha = b/x$. The dynamics are described by the so-called variable-territory model (V-T) [5–7] because it can be derived by assuming that the territory size changes in response to food availability : the carrying capacity of the predator is now inversely proportional to the density of the prey. Note that the V-T model in Table 1, where by/x is replaced by $by/(\delta + x)$ (actually, we used the letter α instead of b) is a biologically justified modification of the model of Turchin-Batzli [5] proposed by Jiang and Wang [7], to make limited the self-limitation term of the predator $by/(\delta + x)$ when $x \rightarrow 0$. In the Variable-Territory model (V-T), d depends on both densities x and y , and it is given by $d(x, y) = \frac{\alpha y}{\delta + x}$, with $\alpha \geq 0$ and $\delta > 0$. In Table 1, we also give the expression of the function φ for Bazykin's and V-T models. For Bazykin's and V-T models, the equation $H(x) = G(x)$ where H and G are defined by (11), can have two positive real roots x_L and x_R in $[0, \hat{x}]$ (see Figure 1). Therefore, \mathcal{A} is the closed arc

$$\mathcal{A} = \{(x, h(x)), x_L \leq x \leq x_R\}.$$

Remark 1:

In Bazykin's and V-T models, when $\alpha \rightarrow 0$, then $x_L \rightarrow 0$ and $x_R \rightarrow \hat{x}$. Therefore, the stability condition $x \notin [x_L, x_R]$ reduces to $x > \hat{x}$, which is the condition of stability for the RMA model.

3.1 Applications to Bazykin's model

Bazykin's model is given by

$$\begin{cases} \dot{x} = rx \left(1 - \frac{x}{K}\right) - \frac{axy}{c+x}, \\ \dot{y} = \left(e \frac{ax}{c+x} - \alpha y - m\right) y, \end{cases} \quad (12)$$

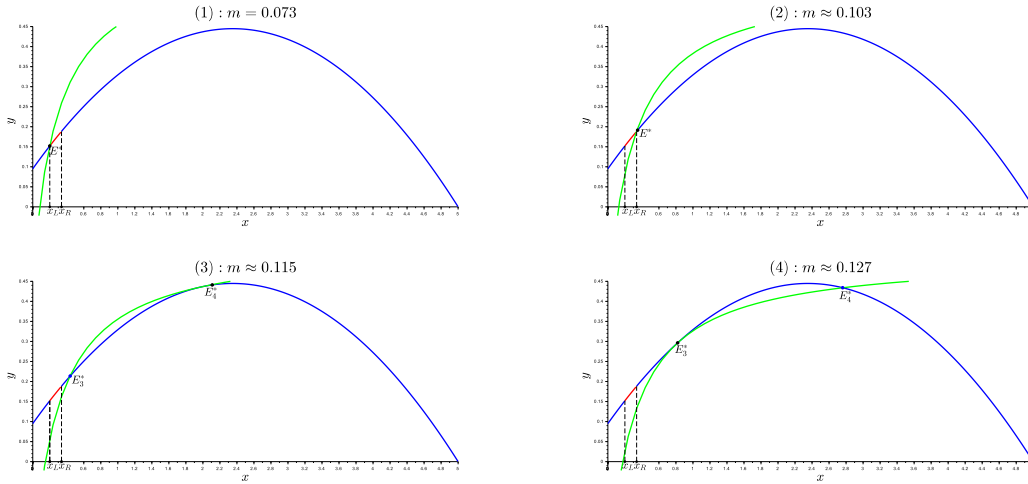


Figure 2: Hopf and Saddle-Node bifurcations in Bazykin model (12) with the parameter values of Figure 1, and $e = 0.58$. The curve $y = h(x)$, in blue, and the curves $y = \varphi(x)$, in green. Stable equilibria are plotted in blue dots. Non-hyperbolic equilibria are plotted in black. The values of m correspond to Hopf bifurcations for the cases (1),(2) and Saddle-Node bifurcations for cases (3),(4).

In Figure 2 we plot the prey and predator isoclines of system (12). Note that the prey isocline $y = h(x)$ does not depend on m , while the predator isocline $y = \varphi(x)$ does. When the parameter m increases, different values of bifurcations are to be considered. If the predator isocline passes through the point $(x_L, h(x_L))$ [resp. $(x_R, h(x_R))$], with m increasing, the positive equilibrium can move from stable to unstable (resp. unstable to stable) equilibrium. This leads to the appearance of a Poincaré-Andronov-Hopf bifurcation. Furthermore, Saddle-Node bifurcations can be observed when the isoclines become tangent to each other. More precisely, we consider m as a bifurcation parameter and we consider the bifurcation values of m depicted on the figure. These bifurcations values are obtained as follows:

1. The values x_L and x_R are obtained by solving the equation $H(x) = \alpha$, with respect to x . It is an algebraic equation of degree 3. We keep only its positive roots. We obtain $x_L = 0.2$ and $x_R \approx 0.338$.
2. The corresponding bifurcation values m_L and m_R are obtained by solving equation $\varphi(x_i) = h(x_i)$, $i = L, R$, with respect to m . We obtain $m_L \approx 0.074$ and $m_R \approx 0.103$. Actually, these bifurcation values correspond to Poincaré-Andronov-Hopf bifurcations.
3. The values x_1^{SN} and x_2^{SN} are obtained by solving the equation $h'(x) = \varphi'(x)$, with respect to x . Which leads to solving an algebraic equation of degree 3 given by

$$-27.00008721 + 20.90000000x + 27.70833334x^2 - 15.83333334x^3 = 0.$$

We keep only its positive roots. We obtain $x_1^{SN} \approx 2.11$ and $x_2^{SN} \approx 0.819$.

4. The corresponding bifurcation values m_1^{SN} and m_2^{SN} are obtained by solving equation $\varphi(x_i^{SN}) = h(x_i^{SN})$, $i = 1, 2$, with respect to m . We obtain $m_1^{SN} \approx 0.114$ and $m_2^{SN} \approx 0.127$. Actually, these bifurcation values correspond to Saddle-Node bifurcations.

Using Proposition 2 we can make the following conclusions :

- If $0 \leq m < m_L$ or $m_R < m < m_1^{SN}$ or $m > m_2^{SN}$, then the system has a unique positive equilibrium satisfying $E^* \notin \mathcal{A}$ and in addition $\varphi'(x^*) > h'(x^*)$. Therefore, E^* is LES. Actually, it is a stable focus or node.

- If $m_L < m < m_R$, then the system has a unique positive equilibrium E^* which is in the interior of \mathcal{A} and in addition $\varphi'(x^*) > h'(x^*)$. Therefore, E^* is unstable. Actually, it is an unstable focus or node which is surrounded by a stable limit.
- If $m_1^{SN} < m < m_2^{SN}$, then the system has three positive equilibria, one being unstable and the two others being LES. Actually, the unstable equilibrium is a saddle whose stable manifolds separate the positive cone in the basins of attraction of the stable equilibria.

We give in Appendix A some plots illustrating the above mentioned behaviors.

3.2 Application to V-T model

V-T model is given by

$$\begin{cases} \dot{x} = rx \left(1 - \frac{x}{K}\right) - \frac{axy}{c+x}, \\ \dot{y} = \left(e \frac{ax}{c+x} - \frac{\alpha}{\delta + x} y - m\right) y, \end{cases} \quad (13)$$

In Figure 3 we plot the prey and predator isoclines of system (13). We consider m as a bifurcation parameter and we consider the bifurcation values of m depicted on the figure. These bifurcations values are obtained as follows:

1. The values x_L and x_R are obtained by solving the equation $H(x) = G(x)$, with respect to x . It is an algebraic equation of degree 3. We keep only its positive roots. We obtain $x_L \approx 0.4$ and $x_R \approx 1.285$.
2. The corresponding bifurcation values m_L and m_R are obtained by solving equation $\varphi(x_i) = h(x_i)$, $i = L, R$, with respect to m . We obtain $m_L \approx 0.114$ and $m_R \approx 0.216$. Actually, these bifurcation values correspond to Poincaré-Andronov-Hopf bifurcations.

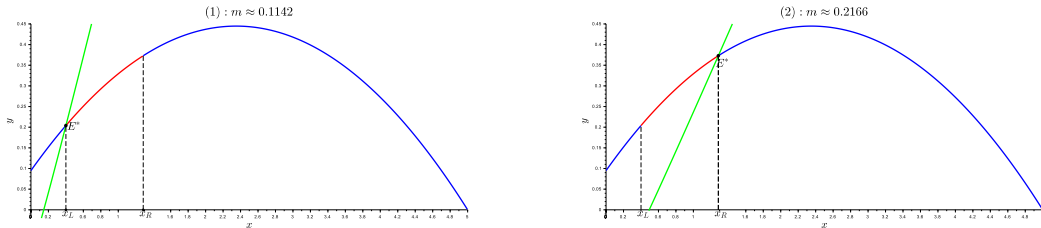


Figure 3: Hopf bifurcation in VT model (13) with the parameter values of Figure 1, and $e = 0.58$. The curve $y = h(x)$, in blue, and the curves $y = \varphi(x)$, in green. Non-hyperbolic equilibria are plotted in black. The values of m correspond to Hopf bifurcations.

Using Proposition 2 we can make the following conclusions :

- If $0 \leq m < m_L$ or $m > m_R$, then the system has a unique positive equilibrium satisfying $E^* \notin \mathcal{A}$ and in addition $\varphi'(x^*) > h'(x^*)$. Therefore, E^* is LES. Actually, it is a stable focus or node.
- If $m_L < m < m_R$, then the system has a unique positive equilibrium E^* which is in the interior of \mathcal{A} and in addition $\varphi'(x^*) > h'(x^*)$. Therefore, E^* is unstable. Actually, it is an unstable focus or node which is surrounded by a stable limit cycle.

We give in Appendix B some plots illustrating the above mentioned behaviors.

IV CONCLUSION AND REFERENCES

We considered the modified RMA prey-predator model (4) obtained by adding to the natural mortality m of the predator a non-constant disappearance rate $d(x, y)$. We first showed the positiveness and the boundedness of the solutions with non-negative initial conditions. In addition to the boundary equilibria $E_1(0, 0)$ and $E_2(K, 0)$ that always exist and for which the stability conditions are as for the RMA model where $d(x, y) = 0$, we showed that the modified model can have positive equilibria. The condition of existence of a positive equilibrium is the same as for the RMA, that is $x_1 < K$ where x_1 is given by (2). The main stability properties are, when $E^*(x^*, y^*)$ exists, that the boundary equilibria E_1 and E_2 are saddle points, and E^* is LES if and only if inequalities (10) are verified (Theorem 2). Then, We defined a closed subset \mathcal{A} of the ascending branch of the prey isocline such that, if $E^* \in \mathcal{A}$, then E^* is unstable. We gave a geometrical description of the stability of a positive equilibrium which mainly says that E^* is LES if and only if $E^* \notin \mathcal{A}$ and the slope at E^* of the x -isocline $y = h(x)$ is smaller than the slope of the y -isocline $y = \varphi(x)$. If the slope at E^* of the x -isocline is larger than the slope of the y -isocline E^* is a saddle point. We applied then our study to two cases which were considered in the literature : the Bazykin's model for which the disappearance rate $d(x, y) := \alpha y$ depends only on the predator density, and the variable territory model (V-T) for which the disappearance rate $d(x, y) := \frac{\alpha y}{\delta + x}$ depends on both densities. We noticed that the set \mathcal{A} for Bazykin's and V-T models is a closed arc with ends the points $(x_L, h(x_L))$ and $(x_R, h(x_R))$ where $0 < x_L < x_R < \hat{x} := (K - c)/2$. Since the prey isocline $y = h(x)$ does not depend on m , while the predator isocline $y = \varphi(x)$ does, we could obtain in Figures 2 and 3 for Bazykin's and V-T models respectively, and for increasing values of m , different values of bifurcations, namely Poincaré-Andronov-Hopf bifurcations and Saddle-Node bifurcations. Notice that one can have multiple positive equilibria and bistability. Using Theorem 2, we could give a description of the local properties of both models near the equilibria. We confirmed our results by numerical simulations.

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A NUMERICAL SIMULATIONS FOR BAZYKIN’S MODEL

We give in this section some plots illustrating our results. We consider the numerical values of the parameters used in Section 3.1 and we plot the isoclines for typical values of m , see Figure 4. For $m = 0.04$ or $m = 0.22$, see Figure 4(1,4), the system has a unique positive equilibrium E^* satisfying the following properties: $E^* \notin \mathcal{A}$ (the red arc of the prey isocline) and, in addition, at E^* the slope of the predator isocline is larger than the slope of the prey isocline. Therefore, according to Proposition 2, the equilibrium E^* is LES. Actually it is a stable focus for $m = 0.04$, see Figure 5(1) and a stable node for $m = 0.221$, see Figure 5(4). For $m = 0.089$, see Figure

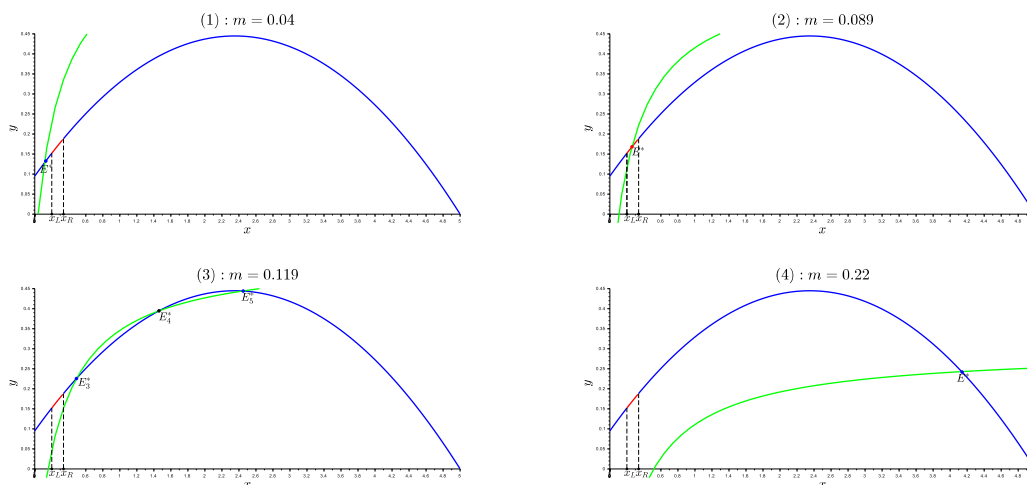


Figure 4: Bazykin’s model with the parameter values of Figure 1, and $e = 0.58$. The curve $y = h(x)$, in blue, and the curves $y = \varphi(x)$, in green. Stable [resp. unstable] equilibria are plotted in blue [resp. red] dots. Saddle point is plotted in black dot.

4(2), the system has a unique positive equilibrium E^* satisfying the following properties: E^* is in the interior of \mathcal{A} and, in addition, at E^* the slope of the predator isocline is larger than the slope of the prey isocline. Therefore, according to Proposition 2, the equilibrium E^* is unstable. Actually it is an unstable focus, surrounded by a stable limit cycle as shown in Figure 5(2). For $m = 0.119$, see Figure 4(3), the system has three positive equilibria E_3^* , E_4^* and E_5^* , satisfying the following properties: $E_j^* \notin \mathcal{A}$, for $j = 3, 4, 5$ and, in addition, at E_3^* and E_5^* , the slope of the predator isocline is larger than the slope of the prey isocline, while at E_4^* , the slope of the predator isocline is smaller than the slope of the prey isocline. Therefore, according to Proposition 2, the equilibrium E_4^* is a saddle point, while E_3^* and E_5^* are LES. Actually E_3^* is a stable focus and E_5^* is a stable node, as shown in Figure 5(3). The figure shows that the stable manifold W_s of E_4^* separate the positive cone into the basins of attraction of E_3^* and E_5^* .

B NUMERICAL SIMULATIONS FOR V-T MODEL

We give in this section some plots illustrating our results. We consider the numerical values of the parameters used in Section 3.2 and we plot the isoclines for typical values of m , see Figure 6. For $m = 0.04$ or $m = 0.24$, see Figure 6(1,3), the system has a unique positive equilibrium E^* satisfying the following properties: $E^* \notin \mathcal{A}$ (the red arc of the prey isocline) and, in addition, at E^* the slope of the predator isocline is larger than the slope of the prey isocline. Therefore, according to Proposition 2, the equilibrium E^* is LES. Actually it is a stable focus as shown in Figures 7(1,3). For $m = 0.089$, see Figure 6(2), the system has a unique positive equilibrium E^* satisfying the following properties: E^* is in the interior of \mathcal{A} and, in addition, at E^* the slope of the predator isocline is larger than the slope of the prey isocline. Therefore, according to Proposition 2, the equilibrium E^* is unstable. Actually it is an unstable focus, surrounded by a stable limit cycle as shown in Figure 7(2).

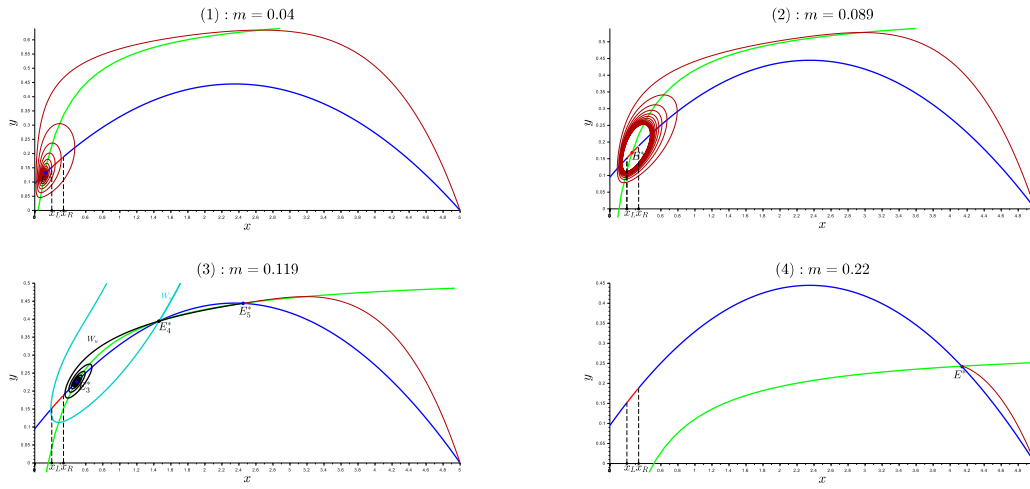


Figure 5: Some phase portraits of Bazykin model with the parameter values of Figure 1 with $e = 0.58$. (1) and (4) : E^* of abscissa $x^* = 0.13$ and $x^* = 4.14$ respectively is LES. (2) : E^* of abscissa $x^* = 0.26$ is unstable, surrounded by a limit cycle. (3) : E_4^* of abscissa $x_4^* = 1.46$ is a saddle point, while E_3^* and E_5^* of abscissa $x_3^* = 0.49$ and $x_5^* = 2.45$ respectively are LES.

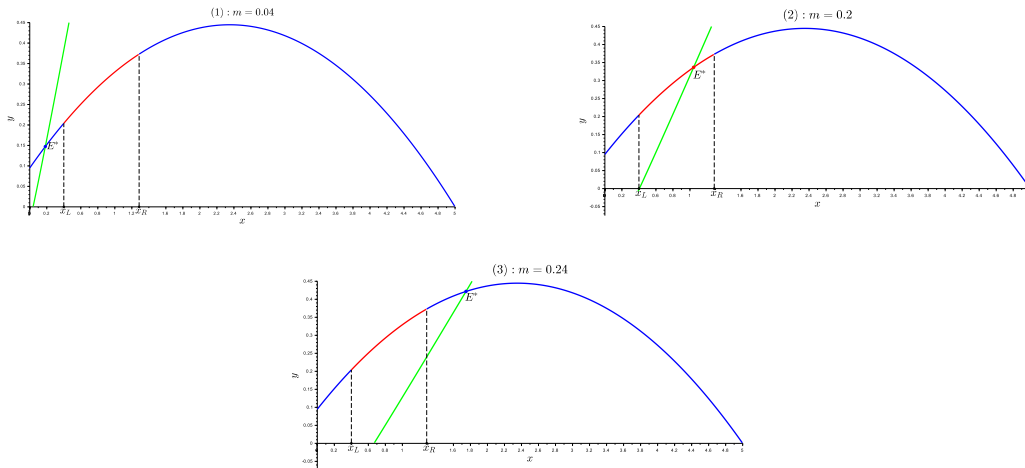


Figure 6: V-T model with the parameter values of Figure 1, and $e = 0.58$. The curve $y = h(x)$, in blue, and the curves $y = \varphi(x)$, in green. Stable [resp. unstable] equilibrium is plotted in blue [resp. red] dot.

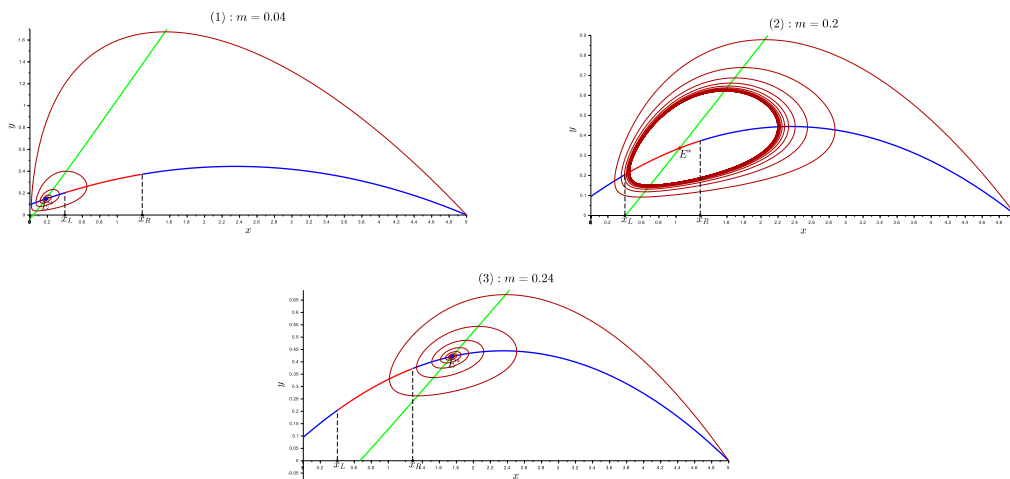


Figure 7: Some phase portraits of V-T model with the parameter values of Figure 1 with $e = 0.58$. (1) and (3) : E^* of abscissa $x^* = 0.18$ and $x^* = 1.74$ respectively is LES. (2) : E^* of abscissa $x^* = 1.04$ is unstable, surrounded by a limit cycle.