PERIODIC ORBITS IN PREDATOR-PREY SYSTEMS WITH HOLLING FUNCTIONAL RESPONSES

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Abstract. We study the existence of periodic orbits of the predator–prey systems $\dot{x} = rx - f(x)y$, $\dot{y} = \big(g(x) - \mu\big)y$, for different types of Holling functional responses $f(x)$ of the predator. For the first type we have centers, for the second type there is neither periodic orbits nor limit cycles, and for the third and fourth types there are limit cycles.

1 Introduction Since the seminal work of Kolmogorov [8], extensive work has been done on the study of the dynamic of a predator-prey system modeled by two autonomous differential equations. One very popular version of such a system, the so–called Gause–type model, has the following general form

$$\begin{aligned} \dot{x} &= xh(x) - f(x)y, \\ \dot{y} &= (cf(x) - d(y))y, \end{aligned} \tag{1}$$

As usual the dot denotes derivative with respect to the time variable t.

The global stability of the system is typically determined by the existence of a positive attractor, either an equilibrium or a limit cycle. For this reason, the existence and uniqueness of positive attractors and limit cycles of system (1) has attracted much interest in recent years. For a sample of these studies, see Cheng [3], Xiao and Zhang [15], Hazík [6], Kuang [10], Moghadas [12]. Most of the recent work has employed technical methods, such as transforming the system to an equivalent generalized Lienard system or trying directly to exploit the special structure of the limit cycle and the prey isocline. The models also incorporated non monotonic functional response to simulate defence mechanisms of the prey, see for example González et al [11], Ruan and Xiao [13], Wolkovicz [14], Xiao and Zhang [16], Zhu et al [17].

Roughly speaking all the models which one finds in the literature consider a function $h(x)$ such that $(x - K)h(x) < 0$ for all $x \geq 0$, as in the logistic growth model. The case of exponential growth of the prey has not been considered. Levin in [9] investigated the effect of the density–dependent predator death rate upon the stability of equilibria for the model

$$\begin{aligned} \dot{x} &= ax - f(x)y, \\ \dot{y} &= (cf(x) - d(y))y, \end{aligned} \tag{2}$$

where d is an increasing function and $d(0) > 0$. However the existence of limit cycles was not investigated.

In this work we will study the predator–prey model

$$\begin{aligned} \dot{x} &= rx - f(x)y, \\ \dot{y} &= \big(g(x) - \mu\big)y, \end{aligned} \tag{3}$$

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satisfying

(i) the domain of definition of the system is the closed first quadrant (i.e. $x \geq 0$, $y \geq 0$);

(ii) the parameters r and μ are positive;

(iii) $g : \mathbb{R}^+ \to \mathbb{R}$ is a C^1 increasing function in an interval $[0, L_2]$ and $g(0) = 0$.

(iv) $f : \mathbb{R}^+ \to \mathbb{R}$ is a positive function in $x > 0$ with $f(0) = 0$ and corresponds to the functional response of the predator.

According with Holling we shall analyze system (3) for the following classes of functional responses:

(iv.1) $f(x)$ is linear;

(iv.2) $f'(x)$ is a C^1 positive monotonic function;

(iv.3) $f : \mathbb{R}^+ \to \mathbb{R}$ is a C^m sigmoid function in an interval $[0, L_1)$, $(m \geq 4)$. Namely, f' is an increasing function and there exists $x_0 \in (0, L_1)$ such that $(x_0 - x)f''(x) > 0$ for all $x \neq x_0$ in $(0, L_1)$.

(iv.4) $f_n(x) = x^n/(x^2 + bx + 1)$ where $-2 < b$, $n = 1, 2$, and $g(x) = af_n(x)$ with $a > 0$ for $x \geq 0$.

We also assume that $L_1 \leq L_2$.

The equilibrium points of system (3) in the region $0 \leq x \leq L_1$, are $(0, 0)$ and (x^*, y^*), where $g(x^*) = \mu$ and $y^* = rx^*/f(x^*)$. The Jacobian of system (3) is

$$J(x, y) = \begin{pmatrix} r - f'(x)y & -f(x) \\ g'(x)y & g(x) - \mu \end{pmatrix},$$

where the prime denotes derivative with respect to the variable x. Therefore

$$J(0, 0) = \begin{pmatrix} r & 0 \\ 0 & -\mu \end{pmatrix} \quad \text{and} \quad J(x^*, y^*) = \begin{pmatrix} A & -B \\ D & 0 \end{pmatrix},$$

where

$$A = r - f'(x^*)y^*, \quad B = f(x^*) > 0 \quad \text{and} \quad D = g'(x^*)y^*.$$

So the $(0, 0)$ is a saddle point, and since the eigenvalues of the linear approximation of system (3) at (x^*, y^*) are

$$\lambda_i(\mu, r) = \frac{A \pm \sqrt{A^2 - 4BD}}{2}, \quad i = 1, 2; \tag{4}$$

we have that (x^*, y^*) is

- a stable node if $A < 0 \leq A^2 - 4BD$,
- an unstable node if $A > 0$ and $A^2 - 4BD \geq 0$,
- a stable focus if $A < 0$ and $A^2 - 4BD < 0$,
- an unstable focus if $A > 0$ and $A^2 - 4BD < 0$,
- a center or a weak focus if $A = 0$.

Our main result is the following.

Theorem 1. *We consider system* (3) *satisfying the assumptions* (i), (ii), (iii) *and* (iv.k) *for some* $k \in \{1, 2, 3\}$*. Then the following statements hold.*

(a) The singular point (x^*, y^*) *of system* (3) *under the assumption* (iv.1) *is a center.*

(b) There are no periodic orbits for system (3) *if the assumption* (iv.2) *hold and* $L_2 = \infty$.

(c) For convenient values of r *and* μ *there exist periodic orbits surrounding the singular point* (x^*, y^*) *of system* (3) *under the assumption* (iv.3)*, due to a Hopf bifurcation.*

(d) If $f(x) = x^2/(x^2 + 1)$ *and* $g(x) = x$*, then the global phase portraits of system* (3) *in the Poincaré disc and in a sufficiently small neighborhood of* $\mu = 1$ *are given in Figure 1 assuming that the unique limit cycle of these systems is the one coming from the Hopf bifurcation of statement* (c).

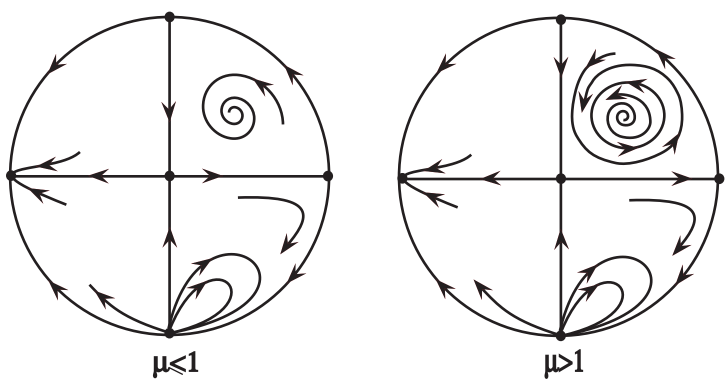

Figure 1: The global phase portrait of the system of statement (d) of Theorem 1 for values of μ near 1.

Statement (a) in the particular case that $g(x) = f(x)$ was proved by Volterra in [19]. The proof of statement (a) is given in Section 2.

Statement (b) can be obtained from the results of Harrison [5] who proved that under the assumptions of statement (b) the singular point (x^*, y^*) of system (3) is a global attractor or repellor in the first quadrant. For proving this he used a Liapunov function. Here we provide a new and shorter proof of statement (b) using the Bendixson–Dulac criterion, see Section 3.

Statement (c) is proved showing the existence of a Hopf bifurcation, see Section 4.

Statement (d) is proved in Section 5. There we also recall the basic results of the Poincaré compactification for planar polynomial differential systems that we shall need for doing the global phase portrait of system (3) in the whole compactified plane.

Finally in Section 6 we study system (3) when the function f satisfies (iv.4).

2 Proof of statement (a) **of Theorem 1** We assume that we are under the assumptions of statement (a) of Theorem 1. Then we have that $f(x) = ax$ with $a > 0$. Then the function

$$H(x, y) = y^r \exp\left(-ay + \int_0^x \frac{\mu - g(s)}{s}\, ds\right)$$

is a first integral of system (3), because

$$\frac{\partial H}{\partial x}\,\dot{x} + \frac{\partial H}{\partial y}\,\dot{y} = \frac{\partial H}{\partial x}\,x(r-ay) + \frac{\partial H}{\partial y}\,\big(g(x)-\mu\big)y = 0.$$

The eigenvalues (4) at the singular point (x^*, y^*) are $\pm\sqrt{rx^*g'(x^*)}\,i$. So from [1] or [4] it follows that this singular point is either a weak focus or a center. But since the first integral $H(x,y)$ is well defined at (x^*, y^*), this singular point is a center. Hence statement (a) of Theorem 1 is proved.

3 Proof of statement (*b*) of Theorem 1

First we recall the Bendixson–Dulac criterion, for a proof see [4].

Proposition 2. *We consider the differential system $\dot{x} = F(x,y)$ and $\dot{y} = G(x,y)$, where $F, G : U \to \mathbb{R}$ are C^1 functions defined in the simple connected open subset $U \subset \mathbb{R}^2$. If there exists a nonzero C^1 function $B : U \to \mathbb{R}^2$ such that $\partial(BF)/\partial x + \partial(BG)/\partial y$ does not change sign in U, then this differential system has no periodic orbits in U.*

We shall apply Proposition 2 to system (3) under the assumptions of statement (b). Let $F(x,y) = rx - f(x)y$ and $G(x,y) = \big(g(x)-\mu\big)y$. Take $B(x,y) = 1/(yf(x))$, then

$$\frac{\partial(BF)}{\partial x} + \frac{\partial(BG)}{\partial y} = \frac{r(f(x) - xf'(x))}{yf^2(x)} \begin{cases} > 0 & \text{if } f \text{ is concave down,} \\ < 0 & \text{if } f \text{ is concave up,} \end{cases} \tag{5}$$

for all $x > 0$ and $y > 0$. Otherwise there exists an $x_0 > 0$ such that $f(x_0) - x_0 f'(x_0) = 0$. This implies that the tangent line to the graphic $\Gamma = \{(x, f(x)) : x > 0\}$ at the point $(x_0, f(x_0))$ pass through the origin of coordinates. This contradicts the fact that this tangent line cannot intersect Γ, because the curve Γ is concave down, or concave up, and $f(x) > 0$ for all $x > 0$.

From (5) and Proposition 2 it follows that system (3) has no periodic orbits in $x > 0$ and $y > 0$. Hence statement (b) of Theorem 1 is proved.

4 Proof of statement (*c*) of Theorem 1

We assume that system (3) satisfies the assumption of statement (c) of Theorem 1.

From the definition of sigmoid curve there exists a unique value $x_1 \in (0, L_1)$ such that $f'(x_1) = f(x_1)/x_1$. Since $g(x)$ is increasing in $(0, L_2)$, there is a unique value μ_1 of μ such that $g(x_1) = \mu_1$.

First we claim that there is an interval I for which if $\mu \in I$ then $\Delta = A^2 - 4BD < 0$. Now we shall prove the claim.

Note that $\Delta < 0$ if and only if

$$r^2\left(1 - \frac{x^* f'(x^*)}{f(x^*)}\right)^2 - 4rx^*g'(x^*) < 0.$$

We know that $g'(x) > 0$ for all $x \in (0, L_2)$, therefore there is an interval I' containing μ_1 and a number $K > 0$ such that $x^*g'(x^*) > K$ for all $x^* \in J'$, where J' is the inverse image of I' by g. Then we have $-4rx^*g(x^*) < -4rK$, which implies

$$\Delta < r^2\left(1 - \frac{x^* f'(x^*)}{f(x^*)}\right) - 4rK.$$

When $\mu = \mu_1$ we have $x^* = x_1$ and $\Delta < -4rK$, by continuity we have that $\Delta < 0$ in one interval $J \subset J'$ containing x_1. This implies that there exists an interval $I \subset I'$ containing μ_1 on which, if $\mu \in I$ then $\Delta < 0$. Hence the claim is proved.

For $\mu \in I$ the matrix $J(x^*, y^*)$ has two distinct conjugate complex eigenvalues with negative real part if $\mu < \mu_1$, zero real part if $\mu = \mu_1$ and positive real part if $\mu > \mu_1$, see (4) for more details.

We now check that the derivative of the real part with respect to μ at μ_1 is different from zero. Let

$$\begin{aligned}\frac{d}{d\mu}\mathrm{Re}(\lambda_i(\mu)) &= \frac{d}{d\mu}\left[\frac{r}{2}\left(1 - \frac{x^* f'(x^*)}{f(x^*)}\right)\right] \\ &= -\frac{r}{2}\frac{d}{d\mu}\left[\frac{x^* f'(x^*)}{f(x^*)}\right] \\ &= -\frac{r}{2}\left[\frac{\big(f(x^*) - x^* f'(x^*)\big) f'(x^*) + x^* f(x^*) f''(x^*)}{f^2(x^*)}\right]\frac{dx^*}{d\mu}.\end{aligned}$$

Since $g(x^*) = \mu$ and g^{-1} exists, then $x^* = g^{-1}(\mu)$. So, from $x^* = (g^{-1} \circ g)(x^*)$ we have that

$$1 = \frac{d}{dx^*}\big(g^{-1} \circ g\big)(x^*) = \big(g^{-1}\big)'(\mu) \cdot g'(x^*).$$

Then

$$\frac{dx^*}{d\mu} = \big(g^{-1}\big)'(\mu) = \frac{1}{g'(x^*)},$$

so

$$\frac{d}{d\mu}\mathrm{Re}(\lambda_i(\mu)) = -\frac{r}{2}\left[\frac{\big(f(x^*) - x^* f'(x^*)\big) f'(x^*) + x^* f(x^*) f''(x^*)}{g'(x^*) f^2(x^*)}\right].$$

We remember that if $\mu = \mu_1$ then $x^* = x_1$ and that $f'(x_1) = f(x_1)/x_1$. Therefore

$$\begin{aligned}\frac{d}{d\mu}\mathrm{Re}(\lambda_i(\mu))\bigg|_{\mu=\mu_1} &= -\frac{r}{2}\left[\frac{\big(f(x_1) - x_1 f'(x_1)\big) f'(x_1) + x_1 f(x_1) f''(x_1)}{g'(x_1) f^2(x_1)}\right] \\ &= -\frac{r x_1 f''(x_1)}{2 f(x_1) g'(x_1)} \neq 0.\end{aligned}$$

So by the Hopf's bifurcation theorem (see [18]) system (3) contains a periodic orbit for some values of $\mu \in I$. Indeed, there exists an $\bar{\varepsilon} > 0$ and a C^{m-1} function $\mu(\varepsilon)$,

$$\mu(\varepsilon) = \sum_{i=1}^{[\frac{m-2}{2}]} \alpha_{2i}\varepsilon^{2i} + O(\varepsilon^{m-1}), \quad (0 < \varepsilon < \bar{\varepsilon}), \tag{6}$$

such that for each $\varepsilon \in (0, \bar{\varepsilon})$ there exist a periodic solution of system (3) for $\mu = \mu(\varepsilon)$, see [7] pages 16-17.

Remark 3. *From the proof of item (c) it follows that the bifurcation value μ_1 is given by $\mu_1 = g(x_1)$, where x_1 is the positive root of the equation $f'(x) = f(x)/x$. It is no hard to see that condition* (iv.3) *implies that* $\frac{d}{d\mu}\mathrm{Re}(\lambda_i(\mu))\Big|_{\mu=\mu_1} > 0$. *This derivative will be denoted in what follows by d.*

5 Proof of statement (d) **of Theorem 1** We suppose that we are in the hypotheses of statement (d) of Theorem 1. Then doing the change of time $dt = (x^2+1)ds$ and denoting again the derivative with respect to the new time s by a dot, system (3) becomes

$$\begin{aligned} \dot{x} &= x(r + rx^2 - xy), \\ \dot{y} &= (x-\mu)(x^2+1)y. \end{aligned} \tag{7}$$

The singular point $(x^*(\mu), y^*(\mu))$ is $(\mu, (1+\mu^2)r/\mu)$ and its eigenvalues are $\pm 2\sqrt{r}\,i$ for $\mu = 1$, and

$$\frac{1}{2}\left((\mu^2-1)r \pm \sqrt{(-4\mu^5 + r\mu^4 - 8\mu^3 - 2r\mu^2 - 4\mu + r)r}\right),$$

for any $\mu > 0$. Then by statement (c) of Theorem 1 it follows that system (7) exhibits a Hopf bifurcation at $\mu = 1$. Moreover the point $(x^*(\mu), y^*(\mu))$ is a stable focus if $\mu < 1$ and $1-\mu$ is sufficiently small, and an unstable focus if $\mu > 1$ and $\mu - 1$ is sufficiently small. Since system (7) is a polynomial differential system we can compute the first nonzero Liapunov constant at the singular point $(x^*(1), y^*(1))$. This Liapunov constant is negative, so the singular point $(x^*(1), y^*(1))$ is a stable weak focus. For more details about the Liapunov constants and their computations see Chapter 6 of [4].

Of course system (7) has a saddle at the origin of coordinates, its two unstable separatrices are the x half–axes and its two stable separatrices are the y half–axes.

System (7) has no other finite singular points. Now we shall study his infinite singular points using the Poincaré compactification, see the appendix.

In the local chart U_1 system (7) goes over to

$$\begin{aligned} \dot{z}_1 &= z_1\big(1 - (r+\mu)z_2 + z_1 z_2 + z_2^2 - (r+\mu)z_2^3\big), \\ \dot{z}_2 &= -z_2^2(r - z_1 + rz_2^2). \end{aligned}$$

So the unique infinite singular point in the local chart U_1 is its origin, and consequently in the local chart U_2 the unique possible infinite singular point would be also its origin, which is a singular point because is the endpoint of the positive y half–axis, one of the stable separatrices of the saddle located at the origin of $\mathbb{R}^2$.

The $(0,0)$ of the local chart U_1 is a semi–hyperbolic singular point because it has eigenvalues 1 and 0, applying the characterization of the local phase portraits for these kind of singular points (see [1] or [4]), we get that it is a saddle–node located as it is described in Figure 1.

Now in order to characterize all the local behaviors at the finite and infinite singular points only remains to study the origin of the local chart U_2. System (7) in this local chart becomes

$$\begin{aligned} \dot{z}_1 &= -z_1\big(z_1 z_2 + z_1^3 - (r+\mu)z_1^2 z_2 + z_1 z_2^2 - (r+\mu)z_2^3\big), \\ \dot{z}_2 &= -z_2(z_1 - \mu z_2)(z_1^2 + z_2^2). \end{aligned} \tag{8}$$

The linear part at the origin of this system is identically zero, so in order to study its local phase portrait we must do blow ups, see [2] or [4].

We start doing the blow up given by the change of variables $(z_1, z_2) \mapsto (z_1, w = z_2/z_1)$. In these new variables system (8) can be written as

$$\begin{aligned} \dot{z}_1 &= z_1^3\big(-z_1 - w + (r+\mu)z_1 w^2 + (r+\mu)z_1 w^3\big), \\ \dot{w} &= z_1^2 w^2(1 - rz_1 - rz_1 w^2). \end{aligned} \tag{9}$$

Now we rescale the time variable and eliminate the common factor z_1^2 between the two equations of system (9). Thus we get

$$\begin{aligned} \dot{z}_1 &= z_1\big(-z_1 - w + (r+\mu)z_1w^2 + (r+\mu)z_1w^3\big), \\ \dot{w} &= w^2(1 - rz_1 - rz_1w^2). \end{aligned} \tag{10}$$

Note that we continue denoting by w the rescaled variable. But the origin of system (10) has again the linear part identically zero, so we do a second blow up.

We do the change of variables $(z_1, w) \mapsto (z_1, v = w/z_1)$. In these new variables system (10) can be written as

$$\begin{aligned} \dot{z}_1 &= z_1^2\big(-1 - v + (r+\mu)z_1v - z_1^2v^2 + (r+\mu)z_1^3v^3\big), \\ \dot{v} &= z_1v\big(1 + 2v - (2r+\mu)z_1v + z_1^2v^2 - (2r+\mu)z_1^3v^3\big). \end{aligned} \tag{11}$$

Again we rescale the time variable and eliminate the common factor z_1 between the two equations of system (11). Thus we get

$$\begin{aligned} \dot{z}_1 &= z_1\big(-1 - v + (r+\mu)z_1v - z_1^2v^2 + (r+\mu)z_1^3v^3\big), \\ \dot{v} &= v\big(1 + 2v - (2r+\mu)z_1v + z_1^2v^2 - (2r+\mu)z_1^3v^3\big). \end{aligned} \tag{12}$$

Note that we continue denoting by v the rescaled variable. System (12) has only one singular point on the v–axis, the origin which is a saddle, see Figure 2(a).

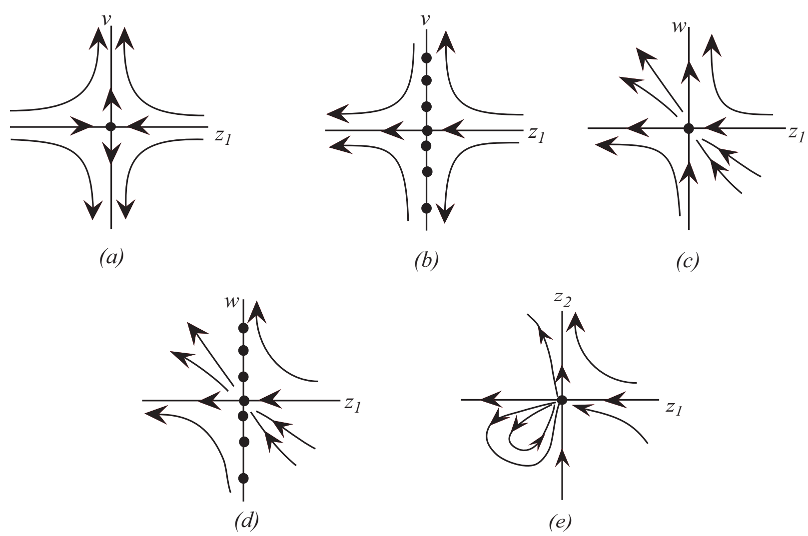

Figure 2: The sequence of the blow ups for studying the origin of the local chart U_2.

Going back through the changes of variables the phase portrait in the neighborhood of the v–axis for system (11) is given in Figure 2(b). The phase portrait in the neighborhood of the w–axis for system (10) is described in Figure 2(c). The phase portrait in the neighborhood of the w–axis for system (9) is given in Figure 2(d). Finally the phase portrait in the neighborhood of the origin of the local chart U_2 is shown in Figure 2(e).

Putting together all the information about the finite and infinite singular points and taking into account the Hopf bifurcation we obtain the global phase portraits of Figure 1 near $\mu = 1$, assuming that the unique limit cycle that system (3) has under the assumptions of statement (d) of Theorem 1 is the one coming from the Hopf bifurcation. Hence statement (d) of Theorem 1 is proved.

6 Examples As an application of Theorem 1 we analyze the system

$$\begin{aligned} \dot{x} &= rx - f(x)y, \\ r\dot{y} &= (g(x) - \mu)y, \end{aligned} \tag{13}$$

with

$$f(x) = \frac{x^n}{x^2 + bx + 1},$$

for $n = 1, 2$, $g(x) = af(x)$ and $b \neq 0$ is a real number greater than -2. The parameters r and μ are positive. The case $n = 2$ and $b = 0$ was analyzed in Theorem 1(d).

From now on we say that an equilibrium point (x, y) is a *coexistence equilibrium point* (*ce* point) if $xy \neq 0$.

Theorem 4. *We consider the predator–prey model defined by* (13)*.*

(a) Let $n = 1$ and $-2 < b < 0$. If $0 < \mu < a/(b + 2)$ there exist two ce equilibrium points $P_i(\mu) = (x_i(\mu), y_i(\mu))$ for $i = 1, 2$, with $x_1(\mu) < x_2(\mu)$ and for $\mu \leq \mu_1$ but close enough to $\mu_1 = 2ab/(b^2 - 4)$ an unstable limit cycle appears around to $P_1(\mu)$ due to a Hopf bifurcation. The point $P_2(\mu)$ is a saddle.

(b) Let $\mu_1 = a/(b + 2)$. For $n = 2$ we have

(b.1) If $b > 0$ and $0 < \mu < a$ then there exists a unique ce equilibrium point and for $\mu > \mu_1$ a stable periodic orbit appears due to a Hopf bifurcation.

(b.2) If $-2 < b < 0$, the system has a Hopf bifurcation with an unstable periodic orbit around $P_1(\mu)$ for $\mu < \mu_1$. If $-2 < b < -1$ and $a < \mu < \mu_1$, then the system has also a saddle equilibrium point $P_2(\mu)$.

Proof. We give a sketch of the proof. It is easy to verify that $f(x)$ is a sigmoid function in $[0, L_1]$ where L_1 is given by

(i) $L_1 = \infty$ if $n = 2$ and $b \geq 0$,

(ii) $L_1 = -2/b$ if $n = 2$ and $-2 < b < 0$,

(iii) $L_1 = 1$ if $n = 1$ and $-2 < b < 0$.

We also have that bifurcation parameter values are given by (see Remark (3))

(iv) $\mu_1 = 2ab/(b^2 - 4)$ for $n = 1$ and $x_1 = -b/2$,

(v) $\mu_1 = a/(b + 2)$ for $n = 2$ and $x_1 = 1$.

In case (i) the function f increases monotonically to 1, when x tends to infinity, then system (13) posses a unique coexistence equilibrium point $P_1(\mu) = (x_1(\mu), y_1(\mu)$ if $\mu < a$.

In cases (ii) and (iii) where $-2 < b < 0$, f is a decreasing function in $[L_1, \infty)$. Therefore there exists two *ce* points $P_i(\mu) = (x_i(\mu), y_i(\mu))$, $i = 1, 2$ with $x_1(\mu) < x_2(\mu)$, for $l_0 < \mu < g(L_1)$ where $l_0 = \lim_{x \to \infty} g(x)$. Indeed

$$l_0 = \begin{cases} 0 & \text{if } n = 1, \\ a & \text{if } n = 2, \end{cases}$$

and

$$g(L_1) = \begin{cases} \dfrac{a}{2 + b} & \text{if } n = 1, \\[2ex] \dfrac{4a}{4 - b^2} & \text{if } n = 2. \end{cases}$$

We stand y_1 for $y_1(\mu_1)$. At the bifurcation value $\mu = \mu_1$ through some linear change of variables system (13) becomes

$$\begin{aligned} \dot{x} &= -a\delta f(x_1)\, y - F(x,y) + O(4), \\ \dot{y} &= a\delta f(x_1)\, x + G(x,y) + O(4), \end{aligned}$$

where

$$F(x,y) = \frac{f''(x_1)y_1}{2a\delta}\, x^2 + f'(x_1)\, xy + \frac{f''(x_1)}{2a\delta}\, x^2 y + \frac{f'''(x_1)y_1}{6a^2\delta^2}\, x^3,$$

and

$$G(x,y) = \frac{1}{\delta} F(x,y),$$

with $\delta = \sqrt{r/\mu_1}$. Moreover the equilibrium point (x_1, y_1) becomes $(0,0)$.

According to Wiggins (see [20], pp. 270–278), the kind of bifurcation is determined by the sign of d (d is defined in Remark 3) and α is defined by

$$\begin{aligned} \alpha &= \frac{1}{16}(F_{xxx} + F_{xyy} + G_{xxy} + G_{yyy}) + \frac{1}{16\omega}(F_{xy}(F_{xx} + F_{yy}) \\ &\quad -G_{xy}(G_{xx} + G_{yy}) - F_{xx}G_{xx} + F_{yy}G_{yy}), \end{aligned}$$

where the derivatives are evaluated at $(0,0)$ and $\omega = \sqrt{\mu_1 r} = a\delta f(x_1)$.

In the proof of Theorem 1 we have shown that d is positive. The computations to obtain α are straightforward and we omit details. If $n = 2$ we get

$$\alpha = -\frac{b}{8a(b+2)^3},$$

for all $a, r > 0$ and $-2 < b < \infty$. Hence if $b < 0$ the system has a subcritical bifurcation with an unstable periodic orbit surrounding the stable equilibrium point $P_1(\mu)$ for $\mu < \mu_1$. For $\mu \geq \mu_1$ only remains the equilibrium point $P_1(\mu)$ which becomes unstable. If $b > 0$ a supercritical bifurcation arises with a stable equilibrium point for $\mu \leq \mu_1$ and a stable periodic orbit for $\mu > \mu_1$. If $n = 2$ in order to have simultaneously a Hopf bifurcation and a saddle point it is necessary that $\mu_1 = a/(2+b)$ be greater than a, then the condition $-1 > b$ must be satisfied.

In the case $n = 1$ we have that α is given by

$$\alpha = \frac{8b}{a\,(b^2-4)^3}.$$

In this case $\alpha > 0$ for all $-2 < b < 0$. Hence a subcritical bifurcation occurs at μ_1, with a unstable periodic orbit for $\mu < \mu_1$ and a unstable equilibrium point for $\mu \geq \mu_1$.

The matrix of the linear approximation of system (13) around the point $P_2(\mu)$ is

$$J = \begin{pmatrix} r - f'(x_2(\mu))y_2(\mu) & -f(x_2(\mu)) \\ af(x_2(\mu))y_2(\mu) & 0 \end{pmatrix}.$$

Since $Tr(J) > 0$ and $\det J < 0$, $P_2(\mu)$ is a saddle point. So the theorem is proved. □

Although we do not pretend here to give a complete description of the phase portrait of system (13), we notice that the coexistence of a limit cycle and a saddle point implies that the positive quadrant is separated in two invariant regions. In one of them (the coexistence region) the trajectories are bounded and in the other one, all the trajectories tend to infinity. Indeed there are three types of coexistence.

(i) A stable limit cycle. This occurs for $n = 2$, $\mu > \mu_1$ and $b > 0$.

(ii) A stable *ce* equilibrium point. The conditions are $n = 2$, $\mu \leq \mu_1$ and $b > 0$.

(iii) An unstable limit cycle. This happens for $n = 1, 2$ when $\mu < \mu_1$.

If $n = 2$ then b must be negative. The corresponding phase portraits are showed in Figure 3. Notice that in the presence of the prey defense mechanism (case (3) above), only a some sort of weak coexistence is possible, because the limit cycle is unstable and small perturbations can lead to the predator extinction. In fact the coexistence is only feasible inside the region bounded by the limit cycle. So it can be conjectured that global coexistence is no possible for a predator–prey model as (3) when the prey grows exponentially and presents a defense mechanism.

Appendix: The Poincaré compactification Let $X = (P, Q)$ be a quadratic vector field. The Poincaré compactified vector field $p(X)$ corresponding to X is a vector field induced in $\mathbb{S}^2$ as follows (see for instance [4] and [1]).

Let $\mathbb{S}^2 = \{y = (y_1, y_2, y_3) \in \mathbb{R}^3 : y_1^2 + y_2^2 + y_3^2 = 1\}$ (called the *Poincaré sphere*) and $T_y\mathbb{S}^2$ be the tangent space to $\mathbb{S}^2$ at point y. Consider the central projections $f_+ : T_{(0,0,1)}\mathbb{S}^2 \longrightarrow \mathbb{S}^2_+ = \{y \in \mathbb{S}^2 : y_3 > 0\}$ and $f_- : T_{(0,0,1)}\mathbb{S}^2 \longrightarrow \mathbb{S}^2_- = \{y \in \mathbb{S}^2 : y_3 < 0\}$. These maps define two copies of X, one in the northern hemisphere and the other in the southern hemisphere. Denote by X' the vector fields $Df_+ \circ X$ and $Df_- \circ X$ in $\mathbb{S}^2$ except on its equator $\mathbb{S}^1 = \{y \in \mathbb{S}^2 : y_3 = 0\}$. Obviously $\mathbb{S}^1$ is identified to the infinity of $\mathbb{R}^2$. In order to extend X' to an analytic vector field in $\mathbb{S}^2$ (including $\mathbb{S}^1$) it is necessary that X satisfies suitable hypotheses. For the quadratic vector fields the *Poincaré compactification* $p(X)$ is the only analytic extension of y_3X' to $\mathbb{S}^2$.

For the flow of the compactified vector field $p(X)$, the equator $\mathbb{S}^1$ is invariant. On $\mathbb{S}^2\backslash\mathbb{S}^1$ there are two symmetric copies of X, and knowing the behaviour of $p(X)$ around $\mathbb{S}^1$, we know the behaviour of X near infinity. The projection of the closed northern hemisphere of $\mathbb{S}^2$ in $y_3 = 0$ under $(y_1, y_2, y_3) \longmapsto (y_1, y_2)$ is called the *Poincaré disc*. Due to these two symmetric copies of X on $\mathbb{S}^2$, it follows that the *infinite singular points* (i.e. the singular points on $\mathbb{S}^1$) appear in pairs of diametrally opposite points.

As $\mathbb{S}^2$ is a differentiable manifold, for computing the expression of $p(X)$, we can consider the six local charts $U_i = \{y \in \mathbb{S}^2 : y_i > 0\}$, and $V_i = \{y \in \mathbb{S}^2 : y_i < 0\}$ where $i = 1, 2, 3$, and the diffeomorphisms $F_i : U_i \longrightarrow \mathbb{R}^2$ and $G_i : V_i \longrightarrow \mathbb{R}^2$ defined as the inverses of the central projections from the tangent planes at the points $(1, 0, 0)$, $(-1, 0, 0)$, $(0, 1, 0)$, $(0, -1, 0)$, $(0, 0, 1)$ and $(0, 0, -1)$, respectively. If we denote by $z = (z_1, z_2)$ the value of $F_i(y)$ or $G_i(y)$ for any $i = 1, 2, 3$, then z represents different things according to the local charts under consideration. Some straightforward calculations give for $p(X)$ the following expressions:

$$z_2^2\Delta(z)\left[Q\left(\frac{1}{z_2}, \frac{z_1}{z_2}\right) - z_1P\left(\frac{1}{z_2}, \frac{z_1}{z_2}\right), -z_2P\left(\frac{1}{z_2}, \frac{z_1}{z_2}\right)\right] \quad \text{in} \quad U_1,$$

$$z_2^2\Delta(z)\left[P\left(\frac{z_1}{z_2}, \frac{1}{z_2}\right) - z_1Q\left(\frac{z_1}{z_2}, \frac{1}{z_2}\right), -z_2Q\left(\frac{z_1}{z_2}, \frac{1}{z_2}\right)\right] \quad \text{in} \quad U_2,$$

$$\Delta(z)[P(z_1, z_2),\, Q(z_1, z_2)] \qquad \text{in} \quad U_3,$$

where $\Delta(z) = (z_1^2 + z_2^2 + 1)^{-\frac{1}{2}}$. The expression for V_i is the same as that for U_i except for the multiplicative factor -1. In these coordinates for $i = 1, 2$, $z_2 = 0$ always denotes the

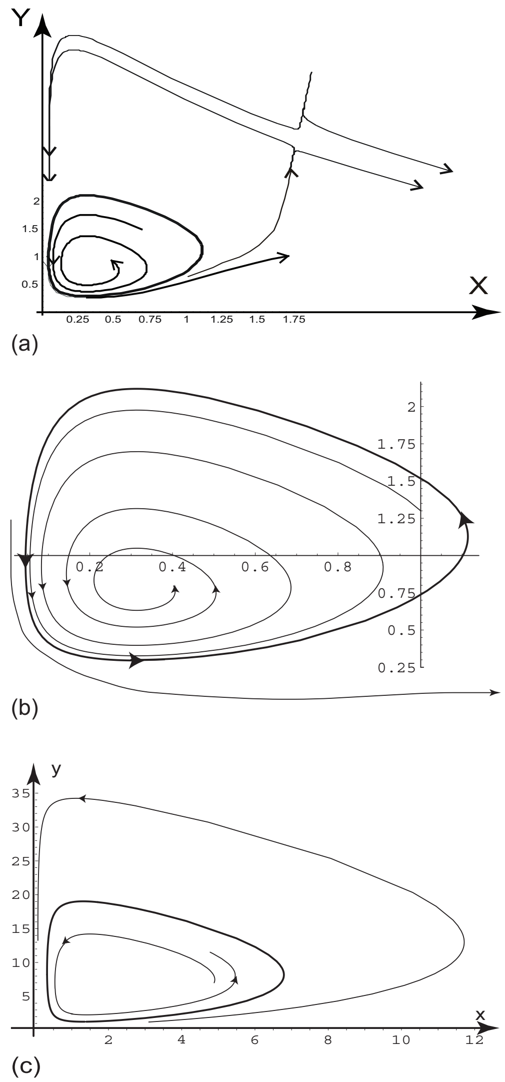

Figure 3: The phase portrait of system (13), for (a) $n = 1$, $\mu < \mu_1$, or $n = 2$, $-2 < b < -1, \mu < \mu_1$; (b) $n = 2$, $\mu < \mu_1$, $-1 \leq b < 0$; (c) $n = 2$, $\mu > \mu_1$, $b > 0$.

points of $\mathbb{S}^1$. In what follows we omit the factor $\Delta(z)$ by rescaling the vector field $p(X)$. Thus we obtain a polynomial vector field of degree at most 3 in each local chart.

Since the unique singular point at infinity which cannot be contained into the charts $U_1 \cup V_1$ are the origins $(0,0)$ of U_2 and V_2, when we study the infinity singular points on the charts $U_2 \cup V_2$, we only consider if the $(0,0)$ of these charts are or not singular points.

A singular point q of $p(X)$ is called an *infinite* (respectively *finite*) singular point if $q \in \mathbb{S}^1$ (respectively $q \in \mathbb{S}^2 \setminus \mathbb{S}^1$).

We want to study the local phase portrait at infinite singular points. For this we choose an infinite singular point $(z_1, 0)$ and start by looking at the expression of the linear part of the field $p(X)$. For $i = 0, 1, 2$ we denote by P_i and Q_i the homogeneous polynomials of degree i of P and Q, respectively. Then, $(z_1, 0) \in \mathbb{S}^1 \cap (U_1 \cup V_1)$ is an infinite singular point of $p(X)$ if and only if

$$F(1, z_1) = Q_2(1, z_1) - z_1 P_2(1, z_1) = 0.$$

Similarly $(z_1, 0) \in \mathbb{S}^1 \cap (U_2 \cup V_2)$ is an infinite singular point of $p(X)$ if and only if

$$G(z_1, 1) = P_2(z_1, 1) - z_1 Q_2(z_1, 1) = 0.$$

Note that these two polynomials $F(1, z_1)$ and $G(z_1, 1)$ in one variable can be unified to a unique homogeneous polynomial in two variables, namely $F(x, y) = xQ_2(x, y) - yP_2(x, y) = -G(x, y)$.

The Jacobian matrix of the vector field $p(X)$ at an infinite singular point $(z_1, 0)$ is

$$\begin{pmatrix} F'(1, z_1) & Q_1(1, z_1) - z_1 P_1(1, z_1) \\ 0 & -P_2(1, z_1) \end{pmatrix},$$

or

$$\begin{pmatrix} G'(z_1, 1) & P_1(z_1, 1) - z_1 Q_1(z_1, 1) \\ 0 & -Q_2(z_1, 1) \end{pmatrix},$$

if $(z_1, 0)$ belongs to U_1 or U_2, respectively.

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