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HOPF BIFURCATION IN PREDATOR-PREY MODELS WITH AN AGE STRUCTURED PREY

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ABSTRACT. In this paper is analyzed the existence of periodic orbits in a predator-prey interaction, when the predator feeds on each one of the two age classes of prey. Three families of models are considered in correspondence with different prey and predator behaviors. Specifically, a constant predation rate on the non reproductive class of the prey is considered in the first family; a Holling predation of type two on the non reproductive class is incorporated in the second and in the third family; a defense group mechanism of the reproductive class is introduced in the third family. We prove that these three families of models exhibit Hopf bifurcations and that the Hopf periodic orbit is a local attractor.

1. INTRODUCTION

Predator–prey is one of the most important interspecific interaction and it has received extensive attention from many points of view. Recently some models have been built to study the dynamical properties of a system where predation is age–dependent. The study of age structured models is a topic of ecological interest. In nature we find predators that eat only adults, or immature prey, or sometimes they prefer the most conspicuous class. An example is the cicada which is preyed only in adult stage [8], or some species of perch which feed on immature prey [4]. The phenomenon of predation on the more abundant prey known as switching has been considered in many papers, see for example [6], [9], [10], [11]. In [7] a system containing a predator species and a structured prey species with fixed maturity time is analyzed. This model presents a kind of switching from one age class to the other. It is found that the introduction of a time delay is a destabilizing process in the sense that increasing the time delay could cause population's fluctuations. Another important aspect that could be present in a predator-prey relationship is the ability of the prey to better defend themselves when their number is large. Pairs of musk-oxen can be successfully attacked by wolves but groups often are not attacked [12]. Examples of this kind of group defense can be found in [5], [2]. In [3], one of the author has been concerned with the role of the age structure of a prey in the dynamic of a predator-prey model. The scenarios considered in that paper have been modelled by the following three families of differential systems defined

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in $(\mathbb{R}^+)^3$:

$$
\begin{aligned}
\dot{x} &= x\left(a\left(1-\frac{x+y}{k}\right)-\frac{z}{x+y+1}-b\right),\\
\dot{y} &= bx-cy-yz,\\
\dot{z} &= z\left(\frac{dx}{x+y+1}+ey-f\right);
\end{aligned}
\tag{1}
$$

$$
\begin{aligned}
\dot{x} &= x\left(a\left(1-\frac{x+y}{k}\right)-\frac{z}{x+y+1}-b\right),\\
\dot{y} &= bx-cy-\frac{yz}{y+1},\\
\dot{z} &= z\left(\frac{dx}{x+y+1}+\frac{ey}{y+1}-f\right);
\end{aligned}
\tag{2}
$$

$$
\begin{aligned}
\dot{x} &= x\left(a\left(1-\frac{x+y}{k}\right)-\frac{z}{x^2+y+1}-b\right),\\
\dot{y} &= bx-cy-\frac{yz}{y+1},\\
\dot{z} &= z\left(\frac{dx}{x^2+y+1}+\frac{ey}{y+1}-f\right).
\end{aligned}
\tag{3}
$$

All the parameters a, b, c, d, e, f and k are positive. As usual the dot denotes derivative with respect to the time variable t.

In this paper, we prove that these three families of differential systems exhibit Hopf bifurcations and that the Hopf periodic orbit is a local attractor. Some numerical computations provided in [3] show the existence of this kind of orbits for the families (2) and (3), but no proofs are available up to now.

In section 2 we summarize some well known sufficient conditions for showing that a Hopf bifurcation takes place in a differential system in $\mathbb{R}^n$. Finally, in section 3 we shall prove that these sufficient conditions hold in the three differential systems (1), (2) and (3) with a convenient election of their positive parameters.

2. Hopf bifurcation

In this section we summarize for the differential systems in $\mathbb{R}^3$ some basic results on the Hopf bifurcation that will be used for proving the main results. For more details see Marsden and McCracken [14].

Consider an autonomous system of ordinary differential equations

$$\frac{du}{dt} = F(u,\mu), \tag{4}$$

where $F : \mathbb{R}^3 \times \mathbb{R} \to \mathbb{R}^3$ is C^∞ and μ is the bifurcation parameter. Suppose that $a(\mu)$ is a singular point of (4) for every μ in a neighborhood U of $\mu = 0$, i.e. $F(a(\mu),\mu) = 0$ if $\mu \in U$. Assume that $DF|_{(a(\mu),\mu)}$ has eigenvalues of the form $\alpha(\mu) \pm i\beta(\mu)$.

Poincaré [15], Andronov and Witt [1] and Hopf [13] (a translation to the English of the Hopf's original paper can be found in section 5 of [14]) showed that an one–parameter family of periodic orbits of (4) arises from $(u,\mu)=(0,0)$ if

(i) $DF|_{(0,0)}$ has eigenvalues $\pm i\beta(0)\neq 0$,
(ii) $DF|_{(0,0)}$ the third eigenvalue $\rho\neq 0$, and
(iii) $(d\alpha/d\mu)|_{\mu=0}\neq 0$.

We say that $\mu=0$ is the value of the *Hopf bifurcation.*

In order to describe how to compute the kind of stability of the periodic orbit (*Hopf periodic orbit*) which appears at a Hopf bifurcation, we write the differential system (4) in a neighborhood of the origin of $\mathbb{R}^3$ and of $\mu=0$ as

$$
\begin{aligned}
\dot x &= P(x,y,z,\mu)=\alpha(\mu)x+\beta(\mu)y+\sum_{i+j+k=2}^{\infty} a_{ijk}x^iy^jz^k,\\
\dot y &= Q(x,y,z,\mu)=-\beta(\mu)x+\alpha(\mu)y+\sum_{i+j+k=2}^{\infty} b_{ijk}x^iy^jz^k,\\
\dot z &= R(x,y,z,\mu)=\rho z+\sum_{i+j+k=2}^{\infty} c_{ijk}x^iy^jz^k.
\end{aligned}
\tag{5}
$$

Let $z=f(x,y,\mu)$ be the *local central surface* associated to the singular point $(a(\mu),\mu)$ for $\mu\in U$. Then from the equality

$$R(x,y,f(x,y,\mu),\mu)=\frac{\partial f}{\partial x}(x,y,\mu)P(x,y,f(x,y,\mu),\mu)+\frac{\partial f}{\partial y}(x,y,\mu)Q(x,y,f(x,y,\mu),\mu),$$

we can compute the first terms of the Taylor series of $f(x,y,\mu)$.

Let $\tilde P(x,y,\mu)=P(x,y,f(x,y,\mu),\mu)$ and $\tilde Q(x,y,\mu)=Q(x,y,f(x,y,\mu),\mu)$ be. We define the number

$$
\begin{aligned}
V = &\ \frac{3\pi}{4|\beta(0)|}\left(\frac{\partial^3\tilde P}{\partial x^3}+\frac{\partial^3\tilde P}{\partial x\partial y^2}+\frac{\partial^3\tilde Q}{\partial x^2\partial y}+\frac{\partial^3\tilde Q}{\partial y^3}\right)\Bigg|_{(x,y,\mu)=(0,0,0)}+\\
&\frac{3\pi}{4\beta(0)^2}\left(-\frac{\partial^2P}{\partial x^2}\frac{\partial^2P}{\partial x\partial y}+\frac{\partial^2Q}{\partial y^2}\frac{\partial^2Q}{\partial x\partial y}+\frac{\partial^2Q}{\partial x^2}\frac{\partial^2Q}{\partial x\partial y}\right.\\
&\left.-\frac{\partial^2P}{\partial y^2}\frac{\partial^2P}{\partial x\partial y}+\frac{\partial^2P}{\partial x^2}\frac{\partial^2Q}{\partial y^2}-\frac{\partial^2P}{\partial y^2}\frac{\partial^2Q}{\partial y^2}\right)\Bigg|_{(x,y,z,\mu)=(0,0,0,0)}.
\end{aligned}
$$

Without loss of generality we can assume that $\rho<0$, otherwise we can reverse the sign of time t in the differential system. If $V<0$ then an attracting Hopf periodic orbit exists for $\mu>0$ sufficiently small. If $V>0$ then an unstable Hopf periodic orbit exists for $\mu<0$ sufficiently small.

3. Statement of the main results

In this section we present three theorems proving the existence of Hopf bifurcations in systems (1), (2) and (3), when all their parameters are positive.

Recall that a *polynomial differential system* in $\mathbb{R}^3$ is a differential system of the form

$$\dot x=P(x,y,z),\quad \dot y=Q(x,y,z),\quad \dot z=R(x,y,z),$$

where P, Q and R are real polynomials in the variables x, y and z. The *degree* of this polynomial differential system is the maximum of the degrees of the polynomials P, Q and R.

Notice that the three differential systems (1), (2) and (3) can be written as polynomial differential systems of degrees 3, 4 and 5 respectively. This is achieved rescaling the time variable from t to s doing $dt = (x+y+1)ds$, $dt = (x+y+1)(y+1)ds$ and $dt = (x^2+y+1)(y+1)ds$ respectively.

Due to the big number of parameters that these differential systems have and that they are equivalent to a polynomial differential system of degree greater than 2, it was not possible to determine their equilibrium points neither to analyze the local stability around them. This forced us to impose certain constraints on the equilibrium points in order to reduce the number of parameters. Details of our method are given in the following.

We force that the point $(1,1,r)$ be a singular point of systems in any of the considered cases(1), (2) and (3). We get this equilibrium point by choosing conveniently the parameters b, c and f. In fact, a linear system of three equations is solved for computing b, c and f. After, we make that the characteristic polynomial of the Jacobian matrix at the singular point $(1,1,r)$, have two eigenvalues $\mu \pm i$ and one real eigenvalue ρ. We obtain these eigenvalues by taking conveniently the parameters d, e and ρ. then, the values of d, e and ρ are the solutions of a linear system of three equations. Finally, since these linear systems have a unique solution, the differential systems (1), (2) and (3) corresponding to the above determined parameters satisfy the sufficient conditions stated in section 2 for exhibiting a Hopf bifurcation at the singular point $(1,1,r)$ when $\mu = 0$. It is checked that the solutions of the considered linear systems are positive.

In the following three theorems we present the differential systems (1), (2) and (3) with the coefficients b, c, d, e and f computed as we have explained in the previous paragraph. Then we prove, by taking conveniently the coefficient a and the third component r of the singular point, that every one of these three differential systems exhibits a Hopf bifurcation at the singular point $(1,1,r)$ when $\mu = 0$.

Theorem 1. *Consider the differential system* (1) *defined in* $(\mathbb{R}^+)^3$ *with the parameter values* $a > 0$, $r > 0$, $k > 10$,

$$b = \frac{3a(k-2) - kr}{3k}, \qquad c = \frac{3a(k-2) - 4kr}{3k},$$

$$d = \frac{d_1}{2k^2r(3a(k-8)+kr)}, \qquad e = \frac{e_1}{18k^2r(3a(k-8)+kr)},$$

$$f = \frac{e_1 + 3d_1}{18k^2r(3a(k-8)+kr)},$$

where

$$\begin{aligned} d_1 = \ & (3a(k-2) - kr)\big(27(ka^2 + a^2 + k^2) + kr(2kr - 3ka - 21a)\big) + \\ & 3\mu\big(27k^2a^2 - 27a^2 - 30k^2ra + 6kra + 81k^2 + 8k^2r^2\big)k + \\ & 27\mu^2(9a - 5r)k^3 + 243\mu^3k^3, \\ e_1 = \ & -81k^2a^3 + 1053ka^3 - 1782a^3 + 9k^3ra^2 - 144k^2ra^2 + 9kra^2 + \\ & 81k^3a - 486k^2a + 3k^3r^2a + 39k^2r^2a - 2k^3r^3 + 9k^3r - \\ & 3\mu k\big(27k^2a^2 - 324ka^2 + 297a^2 + 6k^2ra + 114kra - 27k^2 - 8k^2r^2\big) - \\ & 9\mu^2k^2(9ka - 144a + 11kr) + 81\mu^3k^3, \end{aligned}$$

satisfying $1 \gg a \gg r$. *Then in a neighborhood* U *sufficiently small of* $\mu = 0$ *such that* $|\mu| \ll r$ *the following statements hold.*

(a) *All the parameters of system* (1) *are positive.*
(b) *The point* $(1, 1, r) \in (\mathbb{R}^+)^3$ *is a singular point of system* (1) *for all* $\mu \in U$, *and this system has a Hopf bifurcation at this singular point for* $\mu = 0$.
(c) *An attracting Hopf periodic orbit exists for* $\mu > 0$ *sufficiently small.*

Proof. First, we prove that the parameters b, c, d, e and f of system (1) are positive. Parameters a and k are positive by hypohesis.

Since $1 \gg a \gg r \gg \mu > 0$ and $k > 10$ we have that

$$b = \frac{3a(k-2) - kr}{3k} \approx \frac{a(k-2)}{k} > 0.$$

The same arguments shows that $c > 0$.

Since μ is the smallest parameter and it is as small as we want we have that

$$d \approx \frac{(3a(k-2) - kr)\big(27(ka^2 + a^2 + k^2) + kr(2kr - 3ka - 21a)\big)}{2k^2 r(3a(k-8) + kr)}.$$

Since $1 \gg r$ we get that

$$d \approx \frac{27(k-2)(ka^2 + a^2 + k^2)}{2k^2 r(k-8)}.$$

Again since $1 \gg a$ it follows that

$$d \approx \frac{27(k-2)}{2r(k-8)} > 0.$$

In a similar way to the case $d > 0$, we obtain that

$$e \approx \frac{\overline{e}}{18k^2 r(3a(k-8) + kr)},$$

where $\overline{e} = -81k^2a^3 + 1053ka^3 - 1782a^3 + 9k^3ra^2 - 144k^2ra^2 + 9kra^2 + 81k^3a - 486k^2a + 3k^3r^2a + 39k^2r^2a - 2k^3r^3 + 9k^3r$. Therefore we get that

$$e \approx \frac{3(-k^2a^2 + 13ka^2 - 22a^2 + k^3 - 6k^2)}{2k^2 r(k-8)} \approx \frac{3(k-6)}{2r(k-8)} > 0.$$

Finally we shall see that $f > 0$. Indeed taking into account the expression of f and the computations done for d and e if follows easily that

$$f \approx \frac{6(k-3)}{r(k-8)} > 0.$$

Hence statement (a) is proved.

An easy but tedious computation shows that the point $(1, 1, r)$ is a singular point of system (1). The Jacobian matrix at this singular point is

$$\begin{pmatrix} \dfrac{kr - 9a}{9k} & \dfrac{kr - 9a}{9k} & -\dfrac{1}{3} \\ \dfrac{3a(k-2) - kr}{3k} & \dfrac{3a(2-k) + kr}{3k} & -1 \\ \dfrac{2dr}{9} & \dfrac{1}{9}(9e - d)r & 0 \end{pmatrix}.$$

After another tedious computation their eigenvalues are $\mu \pm i$ and

$$\rho = \frac{9a(1-k)+4kr}{9k} - 2\mu.$$

Now the proof of statement (b) follows directly from section 2.

For proving statement (c) we need to compute the number V defined in section 2. For simplifying the computations, first we write the differential system (1) as a polynomial differential system doing the rescaling of the independent variable given by $dt = (x+y+1)ds$, i.e. taking s as the new independent variable. Second we translate the singular point $(1,1,r)$ at the origin of $\mathbb{R}^3$. Third we do a linear change of variables which writes the linear part of the differential system in its real Jordan form, i.e. as in (5) but now $\alpha(\mu) = 3\mu$, $\beta(\mu) = 3$ and

$$\rho = \frac{9a(1-k)+4kr}{3k} - 6\mu.$$

Due to the rescaling of the independent variable the new eigenvalues are the previous ones multiplied by 3. But now our system (5) is a polynomial differential system of degree 3. We do not write this system because its complete statement should need several pages as the coefficients expressions are too long.

From section 2, to get the number V we need to compute for our system (5) the central surface $z = f(x,y,0)$ around the singular point $(0,0,0)$ for $\mu = 0$. We only need this central surface up to terms of degree 3 in the variables x and y. We have computed it, and only has terms of degree 2 and 3, the linear terms are zero. Then, following the steps indicated in section 2 we obtain the number V. We do not provide the complete expression of V because it needs more than three pages. Here we only provide his approximate expression, first taking into account that $1 \gg r > 0$, then V is approximately

$$-\frac{27a^3(k-2)(k-1)\left(2ka^2-4a^2+k^2\right)\left(4(k-2)^2a^4+(k-3)^2k^2a^2+k^4\right)\pi}{k^3\left(a^2(k-5)^2+k^2\right)\left(a^2(k-1)^2+k^2\right)\left(a^2(k-1)^2+4k^2\right)r^2},$$

and second taking into account that $1 \gg a \gg r > 0$, a simpler approximation of V is

$$-\frac{27a^3(k-2)(k-1)\pi}{4k^3r^2} < 0.$$

Since for $\mu = 0$ we have that

$$\rho = \frac{9a(1-k)+4kr}{3k} \approx \frac{3a(1-k)}{k} < 0,$$

from the summary of section 2 we know that the Hopf periodic orbit exists for $\mu > 0$ sufficiently small and is attracting. Hence statement (c) is proved. □

Theorem 2. *Consider the differential system* (2) *defined in* $(\mathbb{R}^+)^3$ *with the parameter values* $a > 0$, $r > 0$, $k > 13$,

$$b = \frac{3a(k-2)-kr}{3k}, \qquad c = \frac{6a(k-2)-5kr}{6k},$$

$$d = \frac{d_1}{2k^2r(2a(19-2k)+kr)}, \quad e = \frac{e_1}{27k^2r(2a(19-2k)+kr)},$$

$$f = \frac{2d+3e}{6},$$

where

$$\begin{aligned} d_1 = \;& -432k^2a^3 + 1080ka^3 - 432a^3 + 48k^3ra^2 + 294k^2ra^2 - 483kra^2 - \\ & 108k^3a + 216k^2a - 46k^3r^2a - 40k^2r^2a + 11k^3r^3 + 117k^3r - \\ & 6\mu k\big(72k^2a^2 - 108ka^2 + 36a^2 - 86k^2ra + 61kra + 108k^2 + 25k^2r^2\big) - \\ & 9\mu^2k^2(108ka - 72a - 61kr) - 648\mu^3k^3, \end{aligned}$$

$$\begin{aligned} e_1 = \;& 2\Big(1296k^2a^3 - 11016ka^3 + 16848a^3 - 144k^3ra^2 + 198k^2ra^2 + 2853kra^2 - \\ & 324k^3a + 3888k^2a + 114k^3r^2a - 327k^2r^2a - 22k^3r^3 - 9k^3r + \\ & 6\mu k\big(216k^2a^2 - 1620ka^2 + 1404a^2 - 222k^2ra + 1047kra + 108k^2 + 50k^2r^2\big) + \\ & 9\mu^2k^2(252ka - 1440a - 97kr) + 648\mu^3k^3\Big), \end{aligned}$$

satisfying $1 \gg a \gg r$. Then in a neighborhood U sufficiently small of $\mu = 0$ such that $|\mu| \ll r$ the following statements hold.

(a) *All the parameters of system (2) are positive.*
(b) *The point $(1, 1, r) \in (\mathbb{R}^+)^3$ is a singular point of system (2) for all $\mu \in U$, and this system has a Hopf bifurcation at this singular point for $\mu = 0$.*
(c) *The Hopf periodic orbit exists for $\mu > 0$ sufficiently small and is attracting.*

Proof. The proof follows the same steps than in the proof of Theorem 1. □

Theorem 3. *Consider the differential system (3) defined in $(\mathbb{R}^+)^3$ with the parameter values $a > 0$, $r > 0$, $k > 10$,*

$$b = \frac{3a(k-2) - kr}{3k}, \qquad c = \frac{6a(k-2) - 5kr}{6k},$$
$$d = \frac{d_1}{k^2r(6a(2k-19) + kr)}, \quad e = \frac{e_1}{k^2r(6a(2k-19) + kr)},$$
$$f = \frac{2d + 3e}{6},$$

where

$$\begin{aligned} d_1 = \;& 3\Big(3\big(144a^3 - 360a^3k - 72ak^2 + 144a^3k^2 + 36ak^3 + 201a^2kr - 102a^2k^2r - \\ & 39k^3r - 24a^2k^3r + 6ak^2r^2 + 28ak^3r^2 - 8k^3r^3\big) + \\ & 2\mu k\big(108a^2 - 324a^2k + 324k^2 + 216a^2k^2 + 231akr - 318ak^2r + 116k^2r^2\big) + \\ & 9\mu^2k^2(-72a + 108ak - 77kr) + 648\mu^3k^3\Big), \end{aligned}$$

$$\begin{aligned} e_1 = \;& 2\Big(-1728a^3 + 864a^3k - 504ak^2 + 72ak^3 + 36a^2kr - 216a^2k^2r - 22k^3r + \\ & 81ak^2r^2 + 12ak^3r^2 - 6k^3r^3 + 2\mu k(-432a^2 + 432a^2k + 72k^2 - 312akr - \\ & 36ak^2r + 29k^2r^2) + 2\mu^2k^2(612a + 36ak - 83kr) + 144\mu^3k^3\Big), \end{aligned}$$

satisfying $1 \gg a \gg r$. Then in a neighborhood U sufficiently small of $\mu = 0$ such that $|\mu| \ll r$ the following statements hold.

(a) *All the parameters of system (3) are positive.*
(b) *The point $(1, 1, r) \in (\mathbb{R}^+)^3$ is a singular point of system (3) for all $\mu \in U$, and this system has a Hopf bifurcation at this singular point for $\mu = 0$.*
(c) *The Hopf periodic orbit exists for $\mu > 0$ sufficiently small and is attracting.*

Proof. Again the proof can be done following the same steps than in the proof of Theorem 1. □

4. Concluding remark

Even though the existence of Hopf periodic orbits has been proved for values small enough of a and r, the formulas in Theorems 1-3 can be used to search for this kind of orbits in other regions of the parameter space. A careful exploration of these regions could provide some insights in order to understand which is the effect of the selective predation on the different age classes of the prey in the dynamics of the predator-prey interaction. For instance, in the case of the first model, when k varies on the interval [14,60] (fixing $r = 1$ and $a = 2$), the corresponding values of d for which there are Hopf periodic orbits are always greater than the values of f. However, in the case of the third model, when k increases d changes from values greater than f up to values lesser than f, for k big enough. In this last case, as k increases the predation rate on the x class diminishes due to the defense mechanism. Consequently, a small dependence on this class (d small) is necessary to have stable oscillations when k is big.

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