Hopf bifurcations in predator–prey systems with social predator behaviour

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Abstract

This paper is devoted to the existence of Hopf bifurcations in predator–prey systems under the assumption that the predators show social behaviour. Using the theory of Hopf bifurcation, we prove that the social coefficient appears as an adequate bifurcation parameter. Also, some numerical results are presented in order to discuss the structure of bifurcating solutions. © 1997 Elsevier Science B.V.

Keywords: Predator–prey; Social behaviour; Hopf bifurcation

1. Introduction

General models of the interaction between two populations without spatial structure can be formulated as

\[
\begin{align*}
x' &= xF(x, y) \\
y' &= yG(x, y)
\end{align*}
\]

where the growth rates \( F(x, y) \) and \( G(x, y) \) can assume various forms. As a rule, prey has a limited growth of logistic type and interacts with predators according to some well known formulae. On the other hand, it is customary to adopt—for predators—a malthusian decay balanced by a growth term which accounts for prey consumption. Predators, as a rule, have some kind of social behaviour, either competitive or cooperative, that can be embodied in the definition of \( G(x, y) \) (Murray, 1989). In this paper the following model will be analyzed

\[
\begin{align*}
x' &= rx(1 - \frac{x}{K}) - Axy \\
y' &= -By + yf(y) + Dxy
\end{align*}
\]

where \( r, K, A, B, D \) are positive constants with the usual interpretations: \( r \) and \( K \) are, respectively, the per capita growth rate and the carrying capac-
ity of the prey, $B$ is the death rate of the predator, and $A$ and $D$ represent efficiencies. $A$ is the per capita rate at which the predator captures its prey, while $B$ is the per capita growth rate of the predator resulting from catching prey. They represent observable data on the populations. The ‘social term’ $yf(y)$ can be tuned to describe the various behaviours of the $y$ population by adequate choices of the function $f(y)$.

The simplest choice for the social term is $yf(y) = Sy^2$, where the sign of the constant $S$ shows competition ($S < 0$) or cooperation ($S > 0$). More complex internal relationships in the predator population can be described through an expression $yf(y) = y^\sigma f^*(y)$, where $f^*(y)$ is a close-to-identity function. This last requirement is made in order to enhance the role of the ‘natural’ interaction term $y^2$.

According to the paper of Antonelli and Kazarinoff (1988), an adequate choice is of the type $yf(y) = y Sy^\sigma = Sy^\sigma + 1$, where $S$ is a parameter depending only on factors that determine predator aggregation, and $\sigma \approx 1$. Therefore the model will read:

$$
\begin{align*}
    x' &= rx(1 - \frac{x}{K}) - Axy \\
    y' &= -By + Sy^{\sigma+1} + Dxy.
\end{align*}
$$

These equations can be written in non-dimensional form by taking $x = KX$, $y = (r/A)Y$ and using $1/r$ as a new time unit. The resulting system is

$$
\begin{align*}
    X' &= X(1 - X) - XY \\
    Y' &= -bY + cY^{\sigma+1} + dXY
\end{align*}
$$

where $b = Br^{-1}$, $c = SA^{-\sigma}r^{\sigma-1}$, $d = DKr^{-1}$. The social term has the same form as in the dimensional system. Whenever $\sigma = 1$, the system becomes a Lotka–Volterra one. Following the conjecture of Antonelli and Kazarinoff (1988), the aim of this paper is to provide mathematical proof of the existence of a family of stable periodic solutions to the system.

In the non-dimensional system, $b > 0$ and $d > 0$, whereas $c$ is of variable sign. The problem is to analyze whether social behaviour of the predators can cause oscillatory solutions to appear. It is only natural to look for the possibility of Hopf bifurcations.

In phase space both axes are orbits of the system, so $intR_+^2$ is invariant. Singular points are $(0, 0), (1, 0), (0, (b/c)^{1/\sigma})$ and $(X^*, Y^*) \in intR_+^2$ (whenever it exists) where $X^*$ and $Y^*$ are the solutions of the system

$$
\begin{align*}
    1 - X - Y &= 0 \\
    -b + dX + cY^{\sigma+1} &= 0
\end{align*}
$$

The Jacobian at $(X^*, Y^*)$ is

$$
\begin{bmatrix}
    -X^* & -X^* \\
    dY^* & c\sigma Y^{\sigma+1}
\end{bmatrix}
$$

and the quadratic equation for the eigenvalues, $\lambda^2 - Tr(J^*)\lambda + |J^*| = 0$, yields the conditions for them to be purely imaginary ones: $Tr(J^*) = 0$, i.e. $c = c^\sigma = X^*/\sigma Y^{\sigma+1}$ with

$$|J^*| = X^*Y^*(d - c\sigma Y^{(\sigma - 1)}) > 0.$$ 

2. The density-independent case, $\sigma = 1$

The case $\sigma = 1$ can be easily analyzed. The study is carried on in order to show some heuristic ideas to be applied in the general case. Only the case $P = (X^*, Y^*) \in intR_+^2$ will be studied. The singular points are $(0, 0), (1, 0), (0, b/c)$ if $c > 0$ and $P = (X^*, Y^*) = (c - b/c - d, b - d/c - d)$.

For competitive behaviour, $c < 0$, $P \in intR_+^2$ if $b < d$, and a Lyapunov type theorem (see (Hofbauer and Sigmund, 1988), p. 49) shows that the $\omega$-limit of every orbit in $intR_+^2$ is contained in the set of critical points of the following Lyapunov function:

$$V(X, Y) = dH(X) + G(Y) \text{ with } H(X) = X^* \log X - X \text{ and } G(Y) = Y^* \log Y - Y$$

where $V'(X(t), Y(t)) \geq 0$. Since the only critical point of $V(X, Y)$ is $P = (X^*, Y^*)$, every solution
in \(\text{int}R^2\) converges to this equilibrium \(P\), a spiral sink.

On the other hand, for cooperative behaviour, \(c > 0\), the condition \(c > b > d\) implies \(|J^*| < 0\). Therefore, \(P\) is a saddle point, an unstable point. If the condition is \(c < b < d\), then \(|J^*| > 0\), and for \(c = c^*\) where

\[
c = c^* = \frac{X^*}{Y^*} = \frac{c - b}{b - d} \quad \text{or} \quad c^* = \frac{-b}{b - d - 1}
\]

then \(\text{Tr}(J^*) = 0\), and \(P\) could be a centre point. In fact, denoting the right hand side of the system for the case \(\sigma = 1\) by the vector field \(F_i = (f(X, Y), g(X, Y))\) and by applying general results on Lotka–Volterra systems (see (Hofbauer and Sigmund, 1988), p. 150), it is possible to choose \(r\) and \(s\) such that the function \(B(X, Y) = X^{-1}Y^{-1}\) satisfies

\[
div(BF_i) = \frac{\partial}{\partial X} (Bf) + \frac{\partial}{\partial Y} (Bg) = \text{Tr}(J^*)B
\]

Then the condition for the eigenvalues to be purely imaginary is just the integrability condition for the two dimensional vector field \(G = (Bg, -Bf)\). Hence there exists a function \(V(X, Y)\) on \(\text{int}R^2\) such that \(G = \text{grad}V(X, Y)\). Taking the derivative of \(t \to V(X(t), Y(t))\) we have

\[
V'(X(t), Y(t)) = \frac{\partial V}{\partial X} X + \frac{\partial V}{\partial Y} Y = fg(B - B) = 0
\]

and hence \(V\) is a constant of motion, in general of the form \(V(X, Y) = X^pY^q(M + NX + RY)\), and it attains its single maximum at \(P = (X^*, Y^*)\) which will be, undoubtedly, a centre.

Nevertheless, when \(c \neq c^*\) the Bendixson–Dulac criterion shows that no closed orbits around \(P\) can exist, and \(P\) becomes a spiral source. The above discussion can be summed up in the following:

**Proposition 1.** Under the hypothesis \(c < b < d\), a centre exists at \(P\) if \(c = c^*\) and no other periodic orbits can exist. In other words, the system has a neutral Hopf bifurcation at \(P\) (see Fig. 1a–c).

3. The density-dependent case, \(\sigma \neq 1\)

It has been shown that a neutral Hopf bifurcation can exist when \(\sigma = 1\). Next it will be proved

![Fig. 1. (a) (\(\sigma = 1\)) \(c = 0.3 < b = 0.8 < d = 2\); (b) (\(\sigma = 1\)), \(c = 0.36 < b = 0.8 < d = 2\); (c) (\(\sigma = 1\)), \(c = 0.4 < b = 0.8 < d = 2\).](image-url)
that a somewhat different situation arises when \( \sigma \neq 1 \). In this case, the system reads
\[
\begin{align*}
X' &= X(1 - X) - X Y \\
Y' &= -b Y + c Y^{\sigma+1} + d X Y
\end{align*}
\]
and can be considered as a perturbation of the case \( \sigma = 1 \), so it will be written as \( X' = F_\sigma(X) \), where \( X = (X, Y) \) and the components of the vector field \( F_\sigma \) are given by the right hand side terms in the system. Closeness between \( F_\sigma \) and \( F_1 \) is measured in the \( L^1 \) norm:
\[
\|F_\sigma - F_1\| = \sup_{X \in U} \| (F_\sigma - F_1)(X) \|_1
\]
\[
+ \sup_{X \in U} \| (J_\sigma - J_1)(X) \|_L
\]
\[
= \sup_Y |c (Y^{\sigma+1} - Y^2)|
\]
\[
+ \sup_Y (\max_{\eta} |c (\sigma - 1) \eta Y^\sigma|).
\]
Here \( U \) is some open subset of \( \mathbb{R}^2 \), \( \| \cdot \|_1 \) is the euclidean norm, \( \| \cdot \|_L \) is the usual norm for linear maps and \((\xi, \eta)\) is any vector in the unit ball of \( \mathbb{R}^2 \).

As in the case \( \sigma = 1 \), a unique singular point \( P = (X^*, Y^*) \) exists in \( \mathbb{R}^2 \). It is the intersection of the line \( y = 1 - x \) and the curve \( y = ((b - dx)/c)^{1/\sigma} \), whose graph resembles that of the line \( y = (b - dx)/c \) for \( \sigma \approx 1 \). It is obvious that \( X^* < 1 \) and \( Y^* < 1 \), so for \( U = (0, 1) \times (0, 1) \), the following holds: \( \|F_\sigma - F_1\| \leq 2c \).

Eigenvalues of the jacobian \( J^* \) at \( P \) will be purely imaginary if \( c = c_\sigma^* = X^*/\sigma Y^{\sigma} \) and \( |J^*| = X^* Y^*(d - c \sigma Y^{(\sigma - 1)}) > 0 \).

If \( c = c_\sigma^* \), \( P \) is not hyperbolic, so it is obvious that periodic solutions can appear as \( c \) crosses the bifurcation value, so a possible Hopf bifurcation is at hand. In order to show that it is an actualHopf bifurcation the transversality condition
\[
\frac{d}{dc} (Re \lambda)_{c = c_\sigma^*} > 0
\]
must be fulfilled at the value \( c = c_\sigma^* = X^*/\sigma Y^{\sigma} \), but this is true because
\[
\frac{d}{dc} (Re \lambda)_{c = c_\sigma^*} = \frac{1}{2} \frac{d}{dc} (c \sigma Y^{\sigma} - X^*)
\]
\[
= \frac{1}{2} \sigma Y^{\sigma-1}
\]
\[
+ \frac{1}{2} (1 + c \sigma^2 Y^{\sigma-1}) \left( \frac{dY^*}{dc} \right)_{c = c_\sigma^*}
\]
\[
\left( \frac{dY^*}{dc} \right)_{c = c_\sigma^*} > 0
\]
so \( (dY^*/dc)_{c = c_\sigma^*} > 0 \) implies \( d/dc (Re \lambda)_{c = c_\sigma^*} > 0 \), and taking the derivative of \( -b + d X^* + c Y^* = 0 \) with respect to \( c \) at \( c_\sigma^* \) it follows that
\[
\left( \frac{dY^*}{dc} \right)_{c = c_\sigma^*} (d - c \sigma Y^{(\sigma - 1)}) = Y^{\sigma} > 0
\]
since \( d - c \sigma Y^{(\sigma - 1)} > 0 \).

As in the previous case, by using the Hopf bifurcation theorem (see Arrowsmith and Place, 1990, p. 205), the discussion can be summed up in the following:
Theorem 2. If $|J^*| > 0$, the system representing the case $\sigma \neq 1$ has a Hopf bifurcation at the value $c = c^*_\sigma = X^*/\sigma Y^*/\sigma$.

4. Numerical simulations and comments.

This section contains some numerical simulations showing the qualitative analysis of the model.

Fig. 1a–c, show very clearly that the Lotka–Volterra model ($\sigma = 1$) has three possible phase portraits corresponding to a neutral Hopf bifurcation.

For the case of a Hopf bifurcation when $\sigma \neq 1$, we present two numerical simulations. The first one corresponds to the parameters values $b = 1$, $\sigma = 0.5$ and $d = 1$. It shows a spiral sink at the singular point $P = (X^*, Y^*)$ for $c = 0.8119$ while it displays a spiral source for the value $c = 0.8165$ (see Fig. 2a, b). In the same way, for the parameters values $b = 0.5$, $\sigma = 0.5$ and $d = 2$ we can observe that when the bifurcation parameter $c$ crosses from the value $c = 0.25$ to 0.3 the stable equilibrium point turns into an unstable equilibrium surrounded by a periodic attractor (see Fig. 3a, b).

The Hopf bifurcation obtained is a supercritical one, i.e. when the bifurcation parameter $c$ crosses the bifurcation value $c^*_\sigma$, a family of small amplitude periodic solutions occurs, and all of them are stable ones, as our numerical experiments suggest.

From the ecological viewpoint, a Hopf bifurcation describes the appearance of cyclic stable population patterns for certain parameter combinations. These parameters can be adequately interpreted in terms of the original populational features.

Numerical experiments were carried on for several other parameter combinations, with similar qualitative behaviour. All computations were performed with the MacMath system.

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References


