

A ratio-dependent predator-prey system model

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1 Introduction

The classical Lotka-Volterra model:

$$\dot{x} = ax - bxy \quad \dot{y} = -cy + dxy \quad (1)$$

where a, b, c and d are positive constants, has an extreme character such that all solutions are periodic and the average of each solution is equal to the equilibrium value, $x = \frac{c}{d}$ and $y = \frac{a}{b}$ [1]. However, once the saturation term is added as in the case of (2), there exists no non-constant periodic solution

$$\dot{x} = ax - bxy - x^2 \quad \dot{y} = -cy + dxy \quad (2)$$

(see [2]). This gap make the author doubt the validity of Lotka-Volterra type models.

On the other hand the author proposed a kind of ratio-dependent model for predator-prey system [3]. In this paper, first of all we shall show that our model possesses a non-constant periodic solution in spite of the appearance of saturation term and that the average of non-constant periodic solutions is less than the equilibrium value. Secondly we shall show that FitzHugh-Nagumo equation is a special case of our model, and hence FitzHugh-Nagumo equation is a kind of predator-prey system model. Thirdly we shall propose the model with time lag, which is reasonable from the aspect of biological theory and guarantees the positiveness of solutions.

2 Ratio-dependent model

The author proposed a kind of ratio-dependent model for prey and predator system such that

$$\frac{\dot{x}}{x} = a - \frac{by}{x} - g(x) \quad \frac{\dot{y}}{y} = -c + \frac{dx}{y} \quad (3)$$

where a, b, c and d are positive constants, x and y represent the populations of prey and predator, $x > 0$ and $y > 0$, and $g(x)$ represents the saturation effect, that is, $g(x) > a$ for large x (see [3]). Obviously (3) is equivalent to that

$$\dot{x} = ax - by - g(x)x \quad \dot{y} = -cy + dx \quad (4)$$

We shall consider the existence of non-constant periodic solution of (4), which is positive valued. First of all we assume that the equation (5) has the positive root x^*

$$g(x) = a - \frac{bd}{c}, \quad (5)$$

and hence $E = (x^*, y^*)$, where $y^* = \frac{d}{c}x^*$, is an equilibrium point.

Theorem 1

Let $g(x)$ be once continuously differentiable with respect to $x > 0$, and assume that $g'(x^*) > 0$, $g'(x^*)x^* = \frac{bd}{c} - c > 0$ and that $\frac{\partial}{\partial a}g'(x^*)x^* \neq 0$. Then there exists two continuously differentiable functions $a(\varepsilon)$ and $\omega(\varepsilon)$, $a(0) = a$ and $\omega(0) = \frac{\pi}{\sqrt{cg'(x^*)x^*}}$, such that (4), where $a = a(\varepsilon)$, has a non-constant $\omega(\varepsilon)$ -periodic solution $(x(t, \varepsilon), y(t, \varepsilon))$ for $\varepsilon \neq 0$ and $(x(t, \varepsilon), y(t, \varepsilon)) \rightarrow E$ as $\varepsilon \rightarrow 0$. Consequently $x(t, \varepsilon)$ and $y(t, \varepsilon)$ are positive for small ε .

Proof The linear variational system of (4) around E is the following :

$$\begin{pmatrix} \dot{\xi} \\ \dot{\eta} \end{pmatrix} = \begin{pmatrix} \frac{bd}{c} - g'(x^*)x^* & -b \\ d & -c \end{pmatrix} \begin{pmatrix} \xi \\ \eta \end{pmatrix},$$

and hence the characteristic equation is

$$\lambda^2 + \left(g'(x^*)x^* - \frac{bd}{c} + c \right) \lambda + cg'(x^*)x^* = 0,$$

which, by our assumption, has the pure imaginary root $\lambda = \pm 2i\sqrt{g'(x^*)x^*}$. Since $\frac{\partial}{\partial a}\{g'(x^*)x^* - \frac{bd}{c} + c\} \neq 0$, our conclusion follows from Hopf bifurcation theorem [4, Theorem 4.1].

Example 1 We shall treat the case where $g(x) = x$, and hence (4) is the following

$$\dot{x} = ax - by - x^2 \quad \dot{y} = -cy + dx \quad (6)$$

where $bd > c^2$ and $a = \frac{2bd}{c} - c$. Then we may see that $x^* = a - \frac{bd}{c} > 0$ and that $g'(x^*)x^* - \frac{bd}{c} + c = a - \frac{2bd}{c} + c$. Therefore we can verify

that all assumptions of Theorem 1 are satisfied, and consequently the conclusion of Theorem 1 holds for (6). Next let $(x(t), y(t))$ be an existing non-constant periodic solution of (6) with period $\omega > 0$, and set $x_0 = \frac{1}{\omega} \int_0^\omega x(t)dt$ and $y_0 = \frac{1}{\omega} \int_0^\omega y(t)dt$. From (6), we get that $x_0 = \frac{c}{d}y_0$ and $ax_0 = by_0 + \frac{1}{\omega} \int_0^\omega x^2(t)dt$. Since $\frac{1}{\omega} \int_0^\omega x^2(t)dt > x_0^2$, it follows that $(a - \frac{bd}{c})x_0 > x_0^2$, which implies that $x^* > x_0$, and hence $y^* > y_0$. Namely the average of periodic solutions are smaller than the equilibrium values.

3 FitzHugh-Nagumo equation

We shall consider the case of (4) with external force (I, J) , that is,

$$\dot{x} = ax - by - g(x)x + I \quad \dot{y} = -cy + dx + J \quad (7)$$

Now we shall refer to the Bohnhoeffer-Van del Pol equation [5, p.447]

$$\dot{x} = c \left(y + x - \frac{x^3}{3} + z \right) \quad \dot{y} = -(x - a - by)/c$$

where a, b, c and z are constants. Replacing x by $-x$, we shall get

$$\dot{x} = cx - cy - \frac{c}{3}x^3 - cz \quad \dot{y} = \frac{1}{c}x - \frac{b}{c}y + \frac{a}{c},$$

which is the case of (7), where $I = -cz$ and $J = \frac{a}{c}$. Next we shall refer to Nagumo's partial differential equation [6, p.2064]

$$h \frac{\partial^2 u}{\partial s^2} = \frac{1}{c} \frac{\partial u}{\partial t} - w - \left(u - \frac{u^3}{3} \right)$$

$$c \frac{\partial w}{\partial t} + bw = a - u,$$

where a, b, c and h are constants. Replacing u by $-x$ and w by y respectively, we shall get that

$$\frac{\partial x}{\partial t} = ch \frac{\partial^2 x}{\partial s^2} + cx - cy - \frac{cx^3}{3}$$

$$\frac{\partial y}{\partial t} = -\frac{b}{c}y + \frac{1}{c}x + \frac{a}{c},$$

which is the case of (7), where $I = ch \frac{\partial^2 x}{\partial s^2}$ and $J = \frac{a}{c}$.

4 Delay system

The domain $\{x \geq 0, y \geq 0\}$ may not be invariant for (4) as t increases. In order to cover this defect, we shall consider the case where (3) has partially a delay term such that

$$\frac{\dot{x}(t)}{x(t)} = a - b \frac{y(t-1)}{x(t-1)} - g(x(t)), \quad \frac{\dot{y}(t)}{y(t)} = -c + d \frac{x(t)}{y(t)} \quad (8)$$

where the initial condition is that $x(\theta) > 0, y(\theta) > 0$ for $-1 \leq \theta \leq 0$. Let $(x(t), y(t))$ denote the solution of (8).

Theorem 2

$(x(t), y(t))$ is defined for $t \geq 0$, $x(t) > 0$ and $y(t) > 0$ for $t \geq 0$, and $(x(t), y(t))$ is bounded for $t \geq 0$.

Proof Setting that $f(t) = a - b \frac{y(t-1)}{x(t-1)}$ for $0 \leq t \leq 1$, we shall obtain the ordinary differential equation such that

$$\dot{x}(t) = f(t)x(t) - g(x(t))x(t) \quad \dot{y} = -cy(t) + dx(t), \quad (9)$$

where $0 \leq t \leq 1$, and therefore by the usual existence theorem, (9) has the solution $(x(t), y(t))$ for $0 \leq t \leq 1$. Repeating this argument infinitely, we may claim that the solution of (9) is defined for $t \geq 0$. Now the first equation of (9) yields that

$$x(t) = x(0) \exp \left(\int_0^t f(s) - g(x(s)) ds \right) > 0$$

and the second one that

$$y(t) = e^{-ct}y(0) + \int_0^t de^{-c(t-s)}x(s) ds > 0. \quad (10)$$

Since $\dot{x}(t) < (a - g(x(t))x(t))$ and since there is a positive number A such that $g(x) > a$ for $x \geq A$, it follows that $x(t) < A$ for large t , and therefore (10) implies that $y(t)$ is bounded for $t \geq 0$. The proof completed.

References

1. Braum, M., Coleman, C.S., and Drew, D.A., edited (1983). Differential Equation Models, Springer-Verlag, New York.
2. Morita, Y.(1996). The Chaos of Biological Model (in Japanese), Asakura-shoten L.T.D., Japan.
3. Nakajima, F.(2004). Predator-prey system model of singular equations ; back to D'Ancona's question, Hokkaido Univ. Preprint in Mathematics, No.635, Japan
4. Chow, S.N. and Hale, J.K.(1982). Methods of Bifurcation Theory, Chapt.1, Springer-Verlag, New York.
5. FitzHugh, R.(1961). Impulses and physiological states in theoretical models of nerve membrane, Biophysical J. Vol.1, 445-466.
6. Nagumo, J., Arimoto, s., and Yoshizawa, S.(1962). An active pulse transmission line simulating nerve axon, proceeding of the IRE, 2061-2070.

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