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Mathematical approach to biological outbreak and crash

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1 Introduction

The outbreak and crash of population has been observed in many species; plankton in sea water, which is known as a red water, insect and fish [6], and small animals [4]. Moreover several known reseaches in biology may be penetrated from this view-point; for example the famous data of fishing studied by U.D'Anconna and V.Volterra [10], Gause's experiment [3] and Luckenbill's experiment [7].

The purpose of this note is to propose a mathematical model representing the outbreak and crash of population. Any species, which causes the outbreak and crash, may be considered as not only the predator from one hand but also the prey from another hand, and hence we shall appeal the predator-prey system model which has homoclinic orbits to null state ; this orbit starts from null state for some time, goes to the maximal state as the time increases, which implies the outbreak, and then backs to the null state as the time furthermore increases, which implies the crash. Our system is the following :

$$\dot{x} = ax - b\sqrt{xy}\,, \quad \dot{y} = -cy + d\sqrt{xy}\,, \quad \left(\cdot = \frac{d}{dt}\right) \tag{1}$$

where a, b, c and d are positive constants and $x = x(t)$ and $y = y(t)$ denote the populations of prey and predator, respectively. We may see that (1) is reduced to Malthusian law in the case where either $x(t) \equiv 0$ or $y(t) \equiv 0$, and to the ratio dependent model in the case where $x(t) > 0$ and $y(t) > 0$:

$$\frac{\dot{x}}{x} = a - b\sqrt{\frac{y}{x}}, \quad \frac{\dot{y}}{y} = -c + d\sqrt{\frac{x}{y}}, \tag{2}$$

although this model is different from the known ratio dependent model [1]. The solution $(x(t), y(t))$ is said to be homoclinic to origin if $x(t) \to 0$

and $y(t) \to 0$ as $t \to \pm\infty$, where either $x(t) \not\equiv 0$ or $y(t) \not\equiv 0$. The meaning of (2) is the following [8]. Whenever the prey and the predator encounter each other, $x(t)$ decreases and $y(t)$ increases. The relative ratio of $x(t)$, $\frac{1}{x(t)}\frac{dx(t)}{dt}$, which is an increment of the number of individuals of prey per unit of the population of prey, may depend on the number of individuals of predator per unit of the population of prey, $\frac{y(t)}{x(t)}$, but not on $y(t)$. Similarly the relative ratio of $y(t)$, $\frac{1}{y(t)}\frac{dy(t)}{dt}$, may depend on the number of individuals of prey per unit of the population of predator, $\frac{x(t)}{y(t)}$, but not on $x(t)$.
Our first result is the following.

Theorem 1
Assume either that $(a+c)^2 < 4bd$ or that $(a+c)^2 \geq 4bd$ and $bd > ac$. Then solution $(x(t), y(t))$, where either $x(t) \not\equiv 0$ or $y(t) \not\equiv 0$, is homoclinic to origin.

Next we shall treat the exceptional case of Theorem 1 :

$$bd < ac\,. \tag{3}$$

In this case we shall require the existence of saturation term $g(x)$ for the prey equation of (1), that is ,

$$\dot{x} = (a - g(x))x - b\sqrt{xy}\,, \qquad \dot{y} = -cy + d\sqrt{xy}\,, \tag{4}$$

where $g(x)$ is differentiable with respect to $x > 0$, $g'(x) > 0$, $g(0) = 0$ and $g(x)$ is bounded for $x \geq 0$, and hence clearly $g(\infty)$ exists.
Our second result is the following.

Theorem 2
We assume that (3) holds and furthermore that $c^2 \geq bd$ and $g(\infty) > a+c$. Then there exist the unique equilibrium point E, which is asymptotically stable, and a solution $(x(t), y(t))$ such that $x(t) \to 0$, $y(t) \to 0$ as $t \to \infty$, where $x(0) > x^*$ and $y(0) = y^*$ for $E = (x^*, y^*)$.

Remark 1 The conclusion of Theorem 2 may explain the paradox of enrichment (cf.see [5], [9]).

2 Proof of Theorem 1

We shall consider the solution $(x(t), y(t))$ of (1) with initial condition $x(0) = x_0$ and $y(0) = 0$, where x_0 is an arbitrary positive number and $y(t) > 0$ for $0 < t < \varepsilon$ and for a positive number ε. We shall set $X(t) = \sqrt{x(t)}$ and $Y(t) = \sqrt{y(t)}$ as long as $x(t) > 0$ and $y(t) > 0$, and hence reduce (1) to the linear system :

$$2\begin{pmatrix} \dot{X}(t) \\ \dot{Y}(t) \end{pmatrix} = \begin{pmatrix} a & -b \\ d & -c \end{pmatrix}\begin{pmatrix} X(t) \\ Y(t) \end{pmatrix}, \tag{5}$$

where $X(0) = \sqrt{x_0}$ and $\lim_{t\to+0} Y(t) = 0$.

First of all we shall consider the case where $(a+c)^2 < 4bd$, which implies that the eigenvalues of coefficient matrix is not real. Therefore solution curve $(X(t), Y(t))$ rotates around origin counter-clockwisely as t increases, and hence there exists a positive number T such that $X(t) > 0$ for $0 < t < T$, $Y(t) > 0$ for $0 < t \le T$ and $X(T) = 0$. Now we shall construct a special solution $(x(t), y(t))$ of (1) with $x(0) = x_0$ and $y(0) = 0$:

$$\begin{array}{rr} x(t) = x_0 e^{at}, \quad y(t) \equiv 0 & \text{for } t \le 0, \\ x(t) = X^2(t), \quad y(t) = Y^2(t) & \text{for } 0 < t < T, \\ x(t) \equiv 0, \quad y(t) = Y^2(T)e^{-c(t-T)} & \text{for } t \ge T. \end{array}$$

Then we can verify that both $x(t)$ and $y(t)$ are continuously differentiable for t and satisfies (1). Clearly $(x(t), y(t))$ satisfies the property of homoclinic orbit to origin.

Next we shall consider the remaining case where $(a+c)^2 \ge 4bd$ and $bd > ac$, which implies that both eigenvalues of the coefficient matrix of (5) are real and of the same sign. We may assume that the eigenvalues are negative, if necessary, by changing the direction of t ; the definition of homoclinic orbit is invariant to this change. Considering the solution $(X(t), Y(t))$ of (5) with $X(0) > 0$ and $Y(0) = 0$, we may see either that $X(t) > 0$, $Y(t) > 0$ for $t > 0$ and $X(t) \to 0$, $Y(t) \to 0$ as $t \to \infty$ or that there exists a positive number T such that $X(t) > 0$ for $0 < t < T$, $X(T) = 0$ and $Y(t) > 0$ for $0 < t \le T$. To the both cases we may construct the homoclinic orbit to origin, $(x(t), y(t))$ with $x(0) = X^2(0)$ and $y(0) = 0$, by the same way as the first part of this proof. The proof of Theorem 1 is completed.

3 Proof of Theorem 2

The system (4) has the unique equilibrium point $E = (x^*, y^*)$ such that x^* is the unique solution of the equation $g(x) = a - \frac{bd}{c}$ and $y* = \left(\frac{d}{c}\right)^2 x^*$, where we used that $g(0) = 0$ and $g(\infty) > a$.
The variational system of (4) with respect to E is the following :

$$\begin{pmatrix} \dot{\xi} \\ \dot{\eta} \end{pmatrix} = \begin{pmatrix} \frac{bd}{2c} - g'(x^*)x^* & -\frac{bc}{2d} \\ \frac{d^2}{2c} & -\frac{c}{2} \end{pmatrix} \begin{pmatrix} \xi \\ \eta \end{pmatrix},$$

and hence the equation of λ, the eigenvalues of the coefficient matrix, is the following :

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

Since $g'(x^*) > 0$, it follows from our assumption that the real part of λ is negative, which implies the asymptotic stability of E. Setting $X = \sqrt{x}$ and $Y = \sqrt{y}$ for $x > 0$ and $y > 0$, we reduce (4) to the equation :

$$\begin{aligned} 2\dot{X} &= (a - g(X^2))X - bY, \\ 2\dot{Y} &= dX - cY. \end{aligned} \tag{6}$$

Clearly the point P, $P = (\sqrt{x^*}, \sqrt{y^*})$, is an equilibrium point of this system, which is asymptotically stable. The linear part of (6) is the following :

$$2\begin{pmatrix} \dot{X} \\ \dot{Y} \end{pmatrix} = \begin{pmatrix} a & -b \\ d & -c \end{pmatrix} \begin{pmatrix} X \\ Y \end{pmatrix},$$

Since $ac > bd$, one of the eigenvalues of coefficient matrix is negative, say λ_1, and furthermore, since $g(X^2)X = o(X)$ as $X \to 0$, it follows from [2] that (6) has a solution $(X(t), Y(t))$ such that $X(t) \to 0$, $Y(t) \to 0$ as $t \to \infty$ and that $\frac{Y(t)}{X(t)} \to \frac{a-\lambda_1}{b}$ as $t \to \infty$. Since the tangent line of C_1 for origin has the slope $\frac{a}{b}$, curve $(X(t), y(t))$ is located above C_1 for large t, say $t \geq 0$. Now we shall show that there is a t_0 such that $X(t_0) > \sqrt{x^*}$ and $Y(t_0) = \sqrt{y^*}$, which implies the conclusion of Theorem 2 by translation of t. Let A and B be positive constants such that $g(A^2) > a + c$ and $B > \frac{d}{c}A$, and hence it is seen that $\dot{X} < 0$ for $X > A$ and $\dot{Y} < 0$ for $0 < X < A$ and $Y > B$, and that P is contained in the domain : $0 < X < A$ and $0 < Y < B$. The isoclines of $\dot{X} = 0$ and $\dot{Y} = 0$ are represented by $bY = aX - g(X^2)X$ and $cY = dX$, respectively, which meet at P each other. Let e be the number such that $g(e^2) = a$

and set $k = \sqrt{x^*}$ and $q = \frac{d}{c}A$. The C_1, C_2 and l_i, $0 \le i \le 4$, are defined by the equations, respectively,

$$\begin{array}{rcll} C_1 & : & bY = aX - g(X^2)X, & 0 < X < k, \\ C_2 & : & bY = aX - g(X^2)X, & k < X < e, \\ l_0 & : & X = 0, & 0 < Y < B, \\ l_1 & : & Y = B, & 0 < X < A, \\ l_2 & : & X = A, & q < Y < B, \\ l_3 & : & cY = dX, & k < X < A, \\ l_4 & : & X = A, & 0 < Y < q. \end{array}$$

We shall illustrate these lines in Figure 1. In the following argument, it is assumed that t is decreasing. First of all it is seen that curve $(X(t), Y(t))$ never crosses l_0, because $\dot{X} < 0$ on l_0, and furthermore that this curve never approaches P, because of the stability of P. We can verify that $(X(t), Y(t))$ cannot cross C_1 without crossing previously one of l_1, l_2 and l_3, because $\dot{Y} < 0$ on C_1. Assume that $(X(t), Y(t))$ crosses l_2 for some $t_1 < 0$, which implies that $X(t) > A$ for $t < t_1$, because $\dot{X} < 0$ for $X > A$. Setting $X = r\cos\theta$, $Y = r\sin\theta$, we get

$$\begin{aligned} \dot{\theta} &= b\sin^2\theta + (g(X^2) - a - c)\sin\theta\cos\theta + d\cos^2\theta, \\ \dot{r} &= -f(\theta, r)r, \end{aligned}$$

where $f(r,\theta) = (g(X^2) - a)\cos^2\theta + (b - d)\sin\theta\cos\theta + c\sin^2\theta$, which is bounded. The second equation of the above implies that $r(t) < \infty$ for $t < \infty$, that is, $(X(t), Y(t))$ never blows up for finite time. Moreover, since $g(X^2) > a + c$ for $X > A$, it follows from the first equation that

$$\dot{\theta} > b\sin^2\theta + d\cos^2\theta,$$

which implies that $(X(t), Y(t))$ rotates around origin negatively as t decreases, and that this curve intersects the line $Y = 0$ for some t_3, $t_2 > t_3$. Thus there exists a number t_4, $t_2 > t_4 > t_3$, such that $X(t_4) > k$ and $Y(t_4) = \sqrt{y^*}$. Next assume that $(X(t), Y(t))$ crosses l_1 for some $t_1 < 0$. Since $2\dot{Y} < 0$ and $2\dot{X} < aA - bB < 0$ for $0 < X < A$ and $Y > B$, it follows that $(X(t), Y(t))$ crosses the line $X = A$ for some $t_2 < t_1$, which is contained in the argument of l_2. The remaining case is that $(X(t), Y(t))$ crosses l_3 for some $t_1 < 0$. Since $\dot{X} < 0$ on l_3, $(X(t), Y(t))$ never crosses l_3 from the right hand side to the left hand side as t decreases, and above all $(X(t), Y(t))$ must cross one of l_4, the line $Y = 0$, and C_2 for some t_2, $t_1 > t_2$. The case of l_4 is the same as in the case of l_2, and these two cases guarantee the existence of that number t_4. This completes the proof.

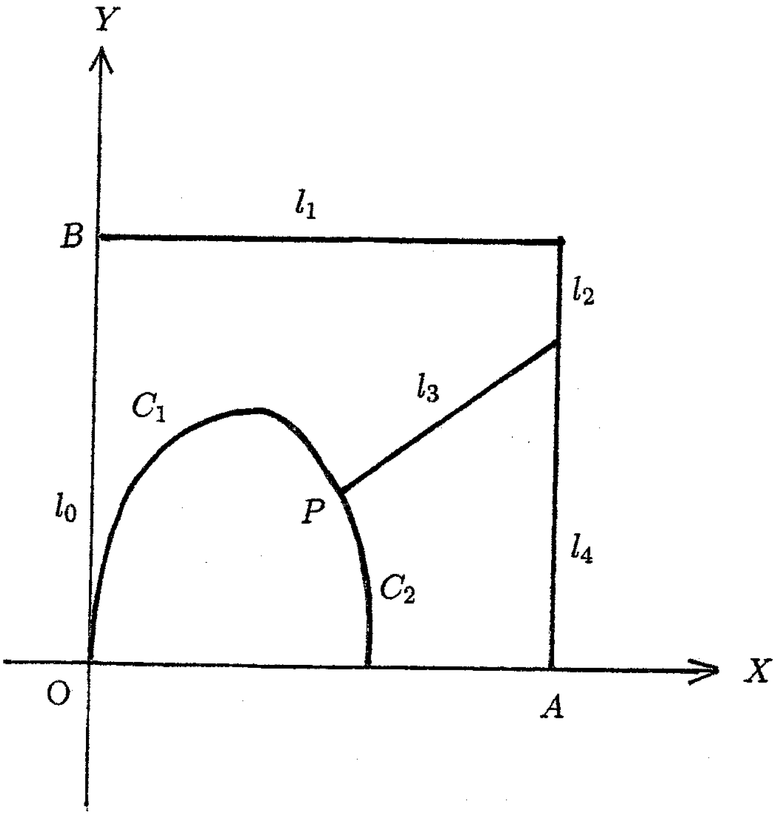

Figure 1

References

1. Arditi, R., Ginzburg, L.R. (1989). Coupling in predator-prey dynamics: ratio-dependence, J.Theo.Biol. 139, 311-326.

2. Coppel, W.A.(1965). Stability and Asymptotic Behavior of Differential Equations, Boston: D.C.Heath and Company, 100-103.

3. Gause, G.F.(1934). The Struggle for Existence, Baltimore : Williams and Wilkins. (Reprint, 1971, New York: Dover)

4. Hansson, L., Henttonen, H.(1988). Rodent dynamics as community processes,TREE 3(8), 195-200.

5. Harrison, G.W.(1995). Comparing predator-prey models to Luckinbill's experiment with Didinium and Paramecium, Ecology, 76(2), 357-374.

6. Iwasa, S., Hanaoka, T.(1972). Seibutu no ijou-hassei(biological outbreaks in Japanese). Tokyo: Kyoritu-Shuppan.

7. Luckinbill, L.S.(1973). Coexistence in laboratory populations of Paramecium Aurelia and its predator Didinium Nasutum, Ecology 54: 1320-1327.

8. Nakajima, F.(2004). Predator-prey system model of singular equations, Kyoto University, Suuriken Koukyuroku 1372, 139-143.

9. Rosenzweig, M.L.(1971). Paradox of enrichment: destabilization of exploitation ecosystems in ecological time, Science, New York, 171, 385-387.

10. Volterra, V.(1931). Lecons Sur la Theorie Mathematique de la Lutte pour la Vie. Paris: Gauthier-Villors.