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Predator-prey system model of singular equations ; back to D'Ancona's question

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Abstract. We shall propose a new predator-prey system model which not only answers D'Ancona's question but also explains Gause's experiment.

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1 Introduction

In this paper we shall study a new type of predator-prey system model. As is known, for example see [1, Chapter15], the biologist Umberto D'Ancona studied why the predator fish dramatically rose in the percentages-of-total-catch of fish in Mediterranean Sea during the years that spanned World War I, and the mathematician Vito Volterra answered this question by innovating the equation for the number of individuals of prey fish $x(t)$ for time t and the number of individuals of predator fish $y(t)$ for t :

$$(1.1) \quad \frac{\dot{x}(t)}{x(t)} = a - by(t), \quad \frac{\dot{y}(t)}{y(t)} = -c + dx(t),$$

where a, b, c and d are positive constants ; the equilibrium point (x^*, y^*) , where $x^* = \frac{c}{d}$ and $y^* = \frac{a}{b}$, represents the average of the numbers of individuals of prey fish and predator fish respectively, the reduced level of fishing caused by the war may be represented as the increment of a and decrement of c , which implies the increment of y^* , and this result is known as Volterra's

principle [1, p.255]. However does this explanation really answer D'Ancona's question ? First of all he also thought both numbers of individuals of prey fish and predator fish would have increased, which is not the case for (1.1). This lack has made the author reconsider (1.1). Moreover as another lack, (1.1) never explains the extinction of species ; in fact the mathematical biologist G.F.Gause [2, Chapter IV] experimented the predator-prey system of two species of protozoa and found that the prey first of all extincts while the predator exists, which yielded the equation

$$(1.2) \quad \frac{\dot{x}(t)}{x(t)} = a - b \frac{y(t)}{\sqrt{x(t)}}, \quad \frac{\dot{y}(t)}{y(t)} = d\sqrt{x(t)} \quad \text{for } x(t) \neq 0.$$

The purpose of this paper is to show a new type of predator-prey system model, which not only completely answers D'Ancona's question but also explains Gause's experiments. Let $x(t)$ and $y(t)$ be the numbers of individuals of prey and predator for t respectively, and whenever prey and 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 number of individuals of prey, may depend on the number of individuals of predator per unit of the number of individuals of prey, that is $\frac{y(t)}{x(t)}$, but not on $y(t)$ itself, and hence we get the equation for $x(t)$

$$(1.3) \quad \frac{1}{x(t)} \frac{dx(t)}{dt} = a - b \left(\frac{y(t)}{x(t)} \right)^\alpha,$$

where a, b and α are positive constants. 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 number of individuals of predator, that is $\frac{x(t)}{y(t)}$, but not on $x(t)$ itself, and hence

$$(1.4) \quad \frac{1}{y(t)} \frac{dy(t)}{dt} = -c + d \left(\frac{x(t)}{y(t)} \right)^\beta,$$

where c, d and β are positive constants. Since solutions of (1.3) and (1.4) may be unbounded as $t \rightarrow \infty$, we shall add the saturation term $g(t)$ to (1.3), and hence

$$(1.5) \quad \frac{1}{x(t)} \frac{dx(t)}{dt} = a - b \left(\frac{y(t)}{x(t)} \right)^\alpha - g(x(t)),$$

where $g(x)$ is continuous for $x \geq 0$ and $g(x) \rightarrow \infty$ as $x \rightarrow \infty$, which guarantees the boundedness of positive solutions for (1.4) and (1.5).

2 Equilibrium points and solution behaviors

Our predator-prey system is the following

$$(2.1) \quad \frac{\dot{x}}{x} = a - b \left(\frac{y}{x} \right)^\alpha - g(x), \quad \frac{\dot{y}}{y} = -c + d \left(\frac{x}{y} \right)^\beta.$$

First of all we shall assume the existence of equilibrium point of (2.1), (x^*, y^*) , where x^* is the solution of the equation

$$(2.2) \quad g(x) = a - b \left(\frac{d}{c} \right)^{\frac{\alpha}{\beta}}$$

and

$$(2.3) \quad y^* = \left(\frac{d}{c} \right)^{\frac{1}{\beta}} x^*.$$

Therefore $\frac{y^*}{x^*}$ increases as c decreases, which may answer one of D'Ancona's questions why a reduced level of fishing is more beneficial to the predator than to their prey. Furthermore we must answer another question of D'Ancona such that the number of individuals of not only predator but also of prey would increase under the reduced level of fishing, which means that

$$(2.4) \quad \frac{\partial x^*}{\partial a} > 0, \quad \frac{\partial y^*}{\partial c} < 0.$$

Theorem 1

(2.4) holds if and only if

$$(2.5) \quad g'(x) > 0, \quad g'(x)x > b\alpha \left(\frac{d}{c} \right)^{\frac{\alpha}{\beta}} \quad \text{for } x = x^*.$$

Proof. Since (2.2) yields that $g'(x)\frac{\partial x}{\partial a} = 1$, it follows that $\frac{\partial x^*}{\partial a} > 0$ if and only if $g'(x^*) > 0$. Moreover since $y^* = \left(\frac{d}{c} \right)^{\frac{1}{\beta}} x^*$, we get

$$\frac{\partial y^*}{\partial c} = -\frac{1}{\beta} \left(\frac{d}{c} \right)^{\frac{1}{\beta}} \frac{1}{c} x^* + \left(\frac{d}{c} \right)^{\frac{1}{\beta}} \frac{\partial x^*}{\partial c}$$

and

$$g'(x^*) \frac{\partial x^*}{\partial c} = \frac{b}{c} \left(\frac{d}{c} \right)^{\frac{\alpha}{\beta}} \alpha.$$

Therefore

$$\frac{\partial y^*}{\partial c} = \frac{1}{\beta c} \left(\frac{d}{c} \right)^{\frac{1}{\beta}} \left\{ -x^* + \frac{b\alpha \left(\frac{d}{c} \right)^{\frac{\alpha}{\beta}}}{g'(x^*)} \right\},$$

which completes the proof.

Example 1 We shall treat the case of (2.1) where $g(x) = ex$ for positive constant e . Then $x^* = \frac{1}{e} \left(a - b \left(\frac{d}{c} \right)^{\frac{\alpha}{\beta}} \right)$ and $y^* = \left(\frac{d}{c} \right)^{\frac{1}{\beta}} x^*$. By

Theorem 1, if $a > b(\alpha + 1)\left(\frac{d}{c}\right)^{\frac{\alpha}{\beta}}$, then $\frac{\partial x^*}{\partial a} > 0$ and $\frac{\partial y^*}{\partial c} < 0$. Although we can see that $\frac{\partial x^*}{\partial c} > 0$, above all x^* increases if the amount of increment of a is much larger than the amount of the decrement of c by the reduced level of fishing ; namely if this reduced level of fishing is more effective to prey fish than to predator fish, then the population of prey fish would increase.

Volterra's equation (1.1) is also known to be succeeded in the explanation for insecticide treatments to the cottony cushion scale insect as prey and a ladybird beetle as predator, where the application of DDT to this system above all terminated in the increment of the population of scale insects [1, p.225]. This phenomenon may be explained by (2.1) too. In fact, since $\frac{\partial x^*}{\partial a} > 0$ and $\frac{\partial x^*}{\partial c} > 0$, above all x^* increases if the amount of increment of c is much larger than the amount of decrement of a by the application of the insecticide ; namely if DDT is more effective to kill the lady bird beetle than to kill the scale insects, then the population of the scale insects would increase by this application of DDT.

Theorem 2

If $g'(x) > 0$ and $g'(x)x - \alpha b\left(\frac{d}{c}\right)^{\frac{\alpha}{\beta}} + \beta c > 0$ for $x = x^*$, then (x^*, y^*) is asymptotically stable.

Proof. (2.1) is reduced to

$$(2.6) \quad \dot{x} = ax - by^\alpha x^{1-\alpha} - g(x)x, \quad \dot{y} = -cy + dx^\beta y^{1-\beta}.$$

The linear variational system with respect to (x^*, y^*) is

$$\begin{pmatrix} \dot{\xi} \\ \dot{\eta} \end{pmatrix} = \begin{pmatrix} \alpha b\left(\frac{d}{c}\right)^{\frac{\alpha}{\beta}} - g'(x)x & -b\alpha\left(\frac{d}{c}\right)^{\frac{\alpha-1}{\beta}} \\ \beta c\left(\frac{d}{c}\right)^{\frac{1}{\beta}} & -\beta c \end{pmatrix} \begin{pmatrix} \xi \\ \eta \end{pmatrix},$$

and the characteristic equation is

$$\lambda^2 + \left(g'(x)x - \alpha b\left(\frac{d}{c}\right)^{\frac{\alpha}{\beta}} + \beta c \right) \lambda + \beta c g'(x)x = 0$$

where $x = x^*$, whose roots has negative roots. Thus the proof is completed.

Remark 1 (2.5) implies the conditions of Theorem 2, and in the case of Example 1, (x^*, y^*) is asymptotically stable if $a + \beta c > (\alpha + 1)b\left(\frac{d}{c}\right)^{\frac{\alpha}{\beta}}$.

Our system(2.1) may explain Gause's experiments.

Theorem 3

Assume that $g(x) \geq 0$ for $x \geq 0$ and that $\alpha \geq 1$. Then there exists a large positive number A such that if $y(0) \geq Ax(0)$ and $x(0) > 0$, then exists a finite positive number T such that $x(t) > 0$ and $y(t) > 0$ for $0 \leq t < T$ and $x(t) \rightarrow 0$ as $t \rightarrow T$, where $y(T) > 0$.

Proof Setting $x = r \cos \theta$ and $y = r \sin \theta$ for (2.1) we get

$$\dot{\theta}(t) = -(a+c) \sin \theta \cos \theta + b \sin \theta \cos \theta (\tan \theta)^\alpha + d \sin \theta \cos \theta (\cot \theta)^\beta + g(x) \cos \theta \sin \theta,$$

where $x = r \cos \theta$, and hence

$$\dot{\theta}(t) \geq -(a+c) \sin \theta \cos \theta + b(\sin \theta)^{\alpha+1}(\cos \theta)^{1-\alpha} + d(\sin \theta)^{1-\beta}(\cos \theta)^{1+\beta}$$

for $0 < \theta < \frac{\pi}{2}$. We can take a constant θ_0 , $0 < \theta_0 < \frac{\pi}{2}$, which is sufficiently close to $\frac{\pi}{2}$, and furthermore a positive constant ε such that $\dot{\theta}(t) \geq \varepsilon$ for $\theta_0 < \theta < \frac{\pi}{2}$. Therefore $\theta(t)$ increases as t increases until $\theta(t) = \frac{\pi}{2}$, and $\theta(t)$ approaches $\frac{\pi}{2}$ in finite time, while $x(t)$ and $y(t)$ never blow up for t . This completes the proof.

Example 2 We shall consider more special case of Example 1, where $\alpha = \beta = 1$, and hence

$$(2.7) \quad \dot{x} = ax - by - ex^2, \quad \dot{y} = -cy + dx,$$

where $ac > 2bd$. Then it follows from Remark 1 that the equilibrium point (x^*, y^*) is asymptotical stable, where $x^* = \frac{1}{e} \left(a - \frac{bd}{c} \right)$ and $y^* = \frac{d}{c} x^*$. We can verify that the eigenvalues of the matrix of linear part of (2.7) is a positive number and a negative number, and moreover can take two independent eigenvectors in the first quadrant. Therefore it follows from the argument of [3, p.103] that there exists solution $(x(t), y(t))$ for $t > 0$ such that $x(t) > 0$, $y(t) > 0$ for $t > 0$ and $x(t) \rightarrow 0$, $y(t) \rightarrow 0$ as $t \rightarrow \infty$. Namely there is a possibility of simultaneous extinction for prey and predator.

3 Periodic solutions

We shall show a sufficient condition that (2.1) has no nonconstant periodic solution.

Theorem 4

There exists no nonconstant periodic solution if $(g(x)x)' \geq 0$ for $x > 0$, $0 < \alpha \leq 1$, $\beta \geq 1$ and $a < c + m$, where

$$m = b^{\frac{\beta}{\alpha+\beta}} d^{\frac{\alpha}{\alpha+\beta}} (1-\alpha)^{\frac{\beta}{\alpha+\beta}} (\beta-1)^{\frac{\alpha}{\alpha+\beta}} \left\{ \left(\frac{\beta}{\alpha} \right)^{\frac{\alpha}{\alpha+\beta}} + \left(\frac{\alpha}{\beta} \right)^{\frac{\beta}{\alpha+\beta}} \right\}.$$

Proof The variational equations for (2.6) is

$$\begin{pmatrix} \dot{\xi} \\ \dot{\eta} \end{pmatrix} = \begin{pmatrix} a - b(1 - \alpha) \left(\frac{y}{x}\right)^\alpha - (g(x)x)' & -b\alpha \left(\frac{y}{x}\right)^{\alpha-1} \\ d\beta \left(\frac{x}{y}\right)^{\beta-1} & -c + d(1 - \beta) \left(\frac{x}{y}\right)^\beta \end{pmatrix} \begin{pmatrix} \xi \\ \eta \end{pmatrix},$$

and hence we can see that (2.1) has no nonconstant periodic solution if the coefficient matrix of the above system is negative for $x > 0$ and $y > 0$, that is

$$a < c + (g(x)x)' + \left\{ b(1 - \alpha) \left(\frac{y}{x}\right)^\alpha + d(\beta - 1) \left(\frac{x}{y}\right)^\beta \right\}$$

for $x > 0$ and $y > 0$. Since m is the minimum of the bracket $\{ \}$ for $x > 0$ and $y > 0$, this completes the proof.

Remark 2 We can verify that $\lim_{\alpha \rightarrow 0} m = b$ for each $\beta > 1$ and moreover that conditions of Theorem 4 is compatible with the conditions of Example 1. Theorem 4 suggests that if the death rate of predator c is larger than the birth rate of prey a , then there exists no periodic fluctuations to predator-prey system.

In spite of the significant result such that all solutions of (1.1) are periodic, we have not seemed to be able to observe any evidence of periodic fluctuation in ecology [4, Table 5.2]. Which state is more optimal in ecology, periodic fluctuations or equilibrium points? The author thinks that the state of equilibrium points is more optimal than the state of periodic fluctuations. For, suppose that some species has been in a periodic fluctuation. Then this species would have avoided to get the minimum of this fluctuation in order for its safety survival, and thus it would evolutionally settle some medium value between minimum and maximum, which is an equilibrium.

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