The paradox of enrichment

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1 Introduction.

It is natural to expect that an increasing the supply of food for human beings may support an increasing its populations. However, to the contray in 1963, Huffaker, Shea and Herman reported in their experiments the destabilization of a stable exploitation ecosystem which resulted in the extinction of both the exploiter (an acarophagous mite) and its victim (an herbivorous mite). This fact was confirmed by Luckenbill in 1973 who conducted more sophisticated experiment using the protozoan of a paramecium aurelia and its predator didinium nasutum and showed that the enrichment of the system by supplying excess bacteria resulted in the extinction of the paramecium aurelia. In 1971, Rosenzweig appealed that the increasing the supply of limiting nutrients or energy tends to destroy the steady state, and thus that human beings must be very careful in attempting to enrich an ecosystem in order to increase its food yield ; this concept is now known as the paradox of enrichment. On the other hand, as the theoretical studies of this paradox Rosenzweig and Harrison stated several mathematical models, which are the type of Lotka-Volterra equations, and showed numerically the situation of the extinction. The purpose of this paper is to state a new type of model for predator-prey system, by which we shall prove the paradox of enrichment rigorously but not numerically.

2 Main result

Our model is the following. Let $x(t)$ and $y(t)$ be the populations of prey and predator for time t, respectively :

$$\frac{\dot{x}(t)}{x(t)} = a - g(x(t)) - b\frac{y(t)}{x(t)}, \quad \frac{\dot{y}(t)}{y(t)} = -c + d\frac{x(t)}{y(t)} \quad \left(\cdot = \frac{d}{dt}\right) \tag{1}$$

where $x(t) > 0$, $y(t) > 0$, a, b, c and d are positive constants and $g(x)$ is a continuous, non-negative valued function. In (1), a represents the birth rate per capita of prey, c the death rate per capita of predator and $g(x)$ the effect of circumstances caused by x. We assume simply that $g(x) = x$ for $0 < x < e$ and for some number $e > a + c$, and $g(x) = e$ for $x \geq e$. Moreover assume that $ac > bd$, and hence we may see that the point $E := (x^*, y^*)$, where $x^* = a - \frac{bd}{c}$ and $y^* = \frac{d}{c}x^*$, is an equilibrium point. Our result is the following :

Theorem 1
Assume that $ac > 2bd - c^2$. Then E is asymptotically stable, and there exists a special solution $(x_0(t), y_0(t))$ such that $x_0(0) > x^*$ and $y_0(0) = y^*$ and that $x_0(t) \to 0$ and $y_0(t) \to 0$ as $t \to \infty$. Moreover for any solution $(x(t), y(t))$ with $x(0) > x_0(0)$ and $y(0) = y^*$ there exists a positive number T such that $y(T) > 0$ and $x(t)$ approaches zero as t approaches T.

Remark 1 The proof of Theorem 1 is a kind of phase plane method, and we may see that $y_0(t) > y^*$ for some $t > 0$. Moreover the existence of T may be observed in the data of [1] and [2]. The author thinks that the conclusion of Theorem 1 may describe the paradox of enrichiment.

We shall comment on the existence of non-constant periodic solution of (1). The following fact is known as [Example 1,5].

Theorem 2
Assume that $a = \frac{2bd}{c} - c$ and $bd > c^2$. Then there exists two continuously differentiable function $a(\varepsilon)$ and $w(\varepsilon), a(0) = a$, and $w(0) = \frac{\pi}{\sqrt{bd - c^2}}$, such that (1), where $a = a(\varepsilon)$, has a non-constant $w(\varepsilon)$-periodic solution $(x(t, \varepsilon), y(t, \varepsilon))$, which is close to E as ε is sufficiently small.

Theorem 2 was proved by the method of Hopf bifurcation.

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