WORKING PAPER

MULTIPLE LIMIT CYCLES FOR PREDATOR-PREY MODELS

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Foreword

One of the classical objects of study in mathematical ecology is the predator-prey interaction. In particular, the well-known model by Gause exhibits a rich dynamical structure. In this paper, a Gause type predator-prey model with concave prey isocline and (at least) two limit cycles is constructed. This serves as a counterexample to a global stability criterion of Hsu [3].

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Multiple Limit Cycles for Predator-Prey Models[1]

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1. Introduction.

We consider the classical Gause predator prey model

$$\begin{aligned} \dot{x} &= xg(x) - yp(x), \\ \dot{y} &= y(-s + cp(x)), \end{aligned} \tag{1.1}$$

where x represents the density of the prey and y that of the predator. The death rate s of the predator and the conversion factor c are positive numbers. The growth rate $g(x)$ of the prey and the predator response function $p(x)$ are assumed to satisfy

$$(x - K)g(x) < 0 \qquad \text{for} \quad x \geq 0, x \neq K, \tag{1.2}$$

for some $K > 0$ and

$$p(0) = 0, \quad p(K) > \frac{s}{c}, \quad p'(x) > 0 \qquad \text{for } x \geq 0. \tag{1.3}$$

The prey isocline is given by $y = h(x) := \frac{xg(x)}{p(x)}$ and is assumed to be concave down, i.e.

$$h''(x) < 0 \qquad \text{for } x \geq 0. \tag{1.4}$$

Under these assumptions, the interior equilibrium $E^* = (x^*, y^*)$ exists and is unique. Let $\hat{x}$ be the unique point where $h(x)$ attains its maximum. Then $0 \leq \hat{x} < K$. E^* is locally stable if $h'(x^*) < 0$ or equivalently $x^* > \hat{x}$ and it is

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unstable if $h'(x^*) > 0$, that is $x^* < \hat{x}$. It is known that if $\hat{x} = 0$, i.e. the prey isocline is always decreasing, then E^* is globally stable, see Hsu [3, Theorem 3.2].

In [3, Theorem 3.3], it was claimed that (1.4) together with local stability implies the global stability of the interior equilibrium. Later it was pointed out in [1] that the proof was 'not rigorously correct'. In spite of this, this condition seems to be still believed by some as a criterion for global stability. The purpose of this note is to construct counterexamples which satisfy the above conditions, but with the (locally stable) interior equilibrium being surrounded by (at least) two limit cycles.

2. Multiple Limit Cycles.

The idea for constructing an example with multiple limit cycles is as follows. We will use s as a bifurcation parameter. For $s < \hat{s} := p(\hat{x})$, the interior equilibrium $E_s^* = (x_s^*, y_s^*)$ is unstable and hence, by boundedness of solutions, there is an attracting limit cycle or an attracting invariant annulus surrounding E_s^*. When s increases beyond $\hat{s}$, x_s^* passes $\hat{x}$, so that E_s^* becomes stable and there is a Hopf bifurcation at $s = \hat{s}$. If we can make this Hopf bifurcation subcritical, there will be an unstable limit cycle bifurcating from E_s^* for s slightly larger than $\hat{s}$. Hence there will be at least two limit cycles.

Multiplying the vector field (1.1) by the positive function $p(x)^{-1}y^{\beta-1}$ (where the real number β will be fixed later) we get

$$\begin{aligned} \dot{x} &= y^{\beta-1}h(x) - y^{\beta}, \\ \dot{y} &= y^{\beta}\left(\frac{-s}{p(x)} + c\right), \end{aligned} \tag{2.1}$$

Clearly (1.1) and (2.1) have identical phase portraits. The divergence of the vector field (2.1) is given by

$$\text{div} = y^{\beta-1}h'(x) + \beta y^{\beta-1}\left(\frac{-s}{p(x)} + c\right) =: y^{\beta-1}D_s(x).$$

Evaluating $D_s(x)$ at $x = x_s^*$ we have $D_s(x_s^*) = h'(x_s^*)$, in particular $D_{\hat{s}}(\hat{x}) = 0$. Hence $h'(x_s^*)$ equals the real part of the eigenvalues at E_s^*, up to a positive constant. Since $\frac{\partial}{\partial s}h'(x_s^*) = h''(x_s^*)\frac{\partial}{\partial s}x_s^* < 0$, the transversality condition for a Hopf bifurcation is satisfied.

Differentiating with respect to x we obtain $D_s'(x) = h''(x) + \beta\frac{sp'(x)}{p^2(x)}$. Now we choose β such that $D_{\hat{s}}'(\hat{x}) = 0$ i.e. $\beta = -\frac{p(\hat{x})^2h''(\hat{x})}{\hat{s}p'(\hat{x})}$. Then

$$D_s''(x) = h'''(x) + \beta s\frac{p(x)p''(x) - 2p'(x)^2}{p(x)^3}$$

and

$$D_s''(\hat{x}) = h'''(\hat{x}) - h''(\hat{x}) \left(\frac{p''(\hat{x})}{p'(\hat{x})} - \frac{2p'(\hat{x})}{p(\hat{x})} \right). \tag{2.2}$$

We will show in section 3 that it is possible to find functions h and p obeying the assumptions (1.2) – (1.4) and satisfying

$$D_s''(\hat{x}) > 0. \tag{2.3}$$

Then $D_s(x) > 0$ for x close to (but different from) $\hat{x}$. Hence, by a theorem of Bendixson, E_s^* is repelling. Consequently the Hopf bifurcation is subcritical and there are small limit cycles for s slightly larger than $\hat{s}$.

Alternatively, one could also follow the procedure as described in [2]. In their notation (see p. 90 of [2]) Re $c_1(0)$ leads to the same expression as given in (2.2) for our $D_s(\hat{x})$, up to a positive factor, and hence is positive by assumption (2.3). Consequently, their μ_2 and β_2 are both positive. Therefore there is a unique unstable limit cycle bifurcating from E_s^* for s slightly larger than $\hat{s}$.

3. An Example.

We conclude by giving a concrete example satisfying all the assumptions in sections 1 and 2. Let

$$c = 1, \quad g(x) = (1+x)(1-\frac{x}{3})(3-4x+2x^2) \quad \text{and} \quad p(x) = x(3-4x+2x^2).$$

Then g and p satisfy (1.2) and (1.3) with $K = 3$. Also

$$h(x) = (1+x)(1-\frac{x}{3})$$

satisfies (1.4). Moreover, $\hat{x} = 1$ and $\hat{s} = 1$. Using (2.2), $D_s''(\hat{x}) = \frac{4}{3}$ and (2.3) is also satisfied.

References.

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3. S.-B. Hsu, On global stability of a predator-prey system, *Math. Biosci.* **39**, 1-10 (1978).