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STABILITY OF A DELAYED RATIO-DEPENDENT PREDATOR-PREY SYSTEM

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ABSTRACT. A ratio-dependent predator-prey model is considered in which the predator growth rate depends on past quantities of the prey. Conditions for stability of an equilibrium and its bifurcation are established when special parameters are taken into account.

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1. INTRODUCTION

In [15, 16, 24], a possible generalisation of the traditional Volterra predator-prey system is considered,

$$\begin{aligned} \dot{S}_1 &= S_1 \cdot \alpha(S_1) - S_2 \cdot V(S_1), \\ \dot{S}_2 &= S_2 \cdot K(S_1) \end{aligned} \tag{1.1}$$

where the dot means differentiation with respect to time t, $S_1(t)$ and $S_2(t)$ are the quantities (or densities) of preys and predators, respectively. Here,

- α is smooth with $\alpha'(S_1) < 0$, $S_1 \geq 0$ and $\alpha(0) > 0 > \lim_{+\infty} \alpha$;
- K and V are nonnegative and increasing, and $K(0) = 0 = V(0)$.

If we replace the argument of K and V by the ratio of S_1 and S_2, then we arrive at a ratio-dependent predator-prey system, which is capable of producing richer and more reasonable or acceptable dynamics. The substantial difference from the classical Kolmogorov model [15, 16] is due to the following two facts related to the system:

(i) Equilibrium abundances are positively correlated along a gradient of enrichment [1];
(ii) These models do not produce the so-called paradox of enrichment (see [11, pp. 490, 502] and [17, p. 391]), more exactly, it either completely disappears or enrichment is related to stability in a more complicated way [21].

A simple ratio-dependent type mathematical model of two-species interaction was first presented in [10, 19, 21].

Let us consider a model of ratio-dependent type which has the form

$$\begin{aligned} \dot{S}_1 &= f_1(S_1, S_2), \\ \dot{S}_2 &= f_2(S_1, S_2) \end{aligned} \tag{1.2}$$

with the initial conditions $S_i(0) > 0$ $(i \in \{1, 2\})$, where

$$f_1(S_1, S_2) := \begin{cases} \alpha S_1 \left(1 - \frac{S_1}{K}\right) - \frac{\beta S_1 S_2}{\varepsilon S_2 + S_1} & \text{if } S_1^2 + S_2^2 > 0 \\ 0 & \text{if } S_1 = S_2 = 0 \end{cases}$$

and

$$f_2(S_1, S_2) := \begin{cases} -\gamma S_2 + \frac{\delta S_1 S_2}{\varepsilon S_2 + S_1} & \text{if } S_1^2 + S_2^2 > 0 \\ 0 & \text{if } S_1 = S_2 = 0. \end{cases}$$

Here, $\alpha > 0$ is the intrinsic growth rate of S_1 in the absence of the S_2-population and without environmental limitation. In the absence of the S_2-population, the S_1-population grows logistically to the carrying capacity $K > 0$; the functional response of the S_2-population is of Michaelis–Menten–Holling type with satiation coefficient or conversion rate $\delta > 0$. The specific mortality

$$E(S_2) = -\gamma S_2 \tag{1.3}$$

of the S_2-population in the absence of the S_1-population depends on the quantity of S_2. $\gamma > 0$ is the death rate of the S_2-population.

If we take polar coordinates $x = r\cos\varphi$, $y = r\sin\varphi$, then a routine calculation shows that $f_i \in C^0(\mathbb{R}_+^2, \mathbb{R})$, however, it is easy to see that $f_i \in C^1(\mathbb{R}_+^2, \mathbb{R})$ $(i \in \{1, 2\})$, therefore solution of (1.2) with positive initial condition exists and is unique.

Let $S_1 \cdot M_1(S_1, S_2) := f_1(S_1, S_2)$ and $S_2 \cdot M_2(S_1, S_2) := f_2(S_1, S_2)$, then the system (1.2) is written in the Kolmogorov form of

$$\dot{\mathbf{S}} = \begin{pmatrix} S_1 \cdot M_1(\mathbf{S}) \\ S_2 \cdot M_2(\mathbf{S}) \end{pmatrix} \tag{1.4}$$

(see [19]), which is useful since one can check the following two properties of this system:

- M_1 and M_2 are smooth functions, therefore the positive quadrant of the phase space $[S_1, S_2]$ is an invariant region (see [22], pp. 198–203 and 230–231);
- $\frac{\partial M_1}{\partial S_2}(S_1, S_2) = -\frac{\beta}{\varepsilon + S_1} < 0$ and $\frac{\partial M_2}{\partial S_1}(S_1, S_2) = -\frac{\delta\varepsilon}{(\varepsilon + S_1)^2} > 0$ $(S_1, S_2 > 0)$, i. e., in fact the system is a predator-prey system with prey S_1 and predator S_2.

The ratio-dependent predator-prey model (1.2) has been studied by several authors recently, and very rich dynamics has been observed. In [10] and later in [2], the authors restricted their analysis to parameter values that ensure that the origin as equilibrium behaves as a saddle point and they established conditions for persistence of the model, and showed the existence of eight qualitatively different types of system behaviours realized for various parameter values. In [13] and later in [26] the authors studied the analytical behaviour at the origin and showed that this equilibrium can be either a saddle point or an attractor of certain trajectories, and shown that the origin is indeed a critical point of higher order. In [17] the global behaviour of solutions was investigated and it was showed that if the positive equilibrium is locally asymptotically stable, then the system does not have any nontrivial positive periodic solutions.

Now we are going to show that with respect to certain circumstances this model can have a periodic solution. This happens by incorporating a delay effect into the systems. For the justification and biological relevance of the delay in ratio-dependent systems see [6]. In [14] the most famous delay in the predator-equation was introduced, i. e., $K\left(\frac{S_1(t)}{S_2(t)}\right)$ was replaced by $K\left(\frac{S_1(t-\tau)}{S_2(t-\tau)}\right)$. Starting from the evidence that in such a system the present growth rate of a predator depends not only on the present quantity of food but also on past quantities, we will introduce an infinite distributed delay into the second equation of system (1.2) for prey density, i. e., we replace S_1 in the second equation by

$$R(t) := \int_{-\infty}^{t} S_1(\tau)\rho(t-\tau)d\tau, \quad t \in [0, +\infty), \tag{1.5}$$

where $\rho : \mathbb{R}_0^+ \to \mathbb{R}_0^+$ is the so-called *density function* satisfying the relation

$$\int_0^{+\infty} \rho(s)ds = 1. \tag{1.6}$$

Due to [5, 4, 7, 8, 18, 25], we assume that the influence of the past is fading away exponentially, i. e., $\rho(t) := a \cdot \exp(-at)$ ($a \in (0, +\infty)$) and $a \int_{-\infty}^{t} exp(-a(t-\tau))d\tau = a\int_0^{+\infty} \exp(-as)\, ds = 1$ hold. The smaller a is, the longer the time interval is in the past in which the values of S_1 are taken into account, i. e., $1/a$ is the "measure of the influence of the past".

Clearly, if $\gamma < \delta < \frac{\gamma\beta}{\beta-\varepsilon\alpha}$ for $\gamma > \varepsilon\alpha$ or $\delta > \gamma$ for $\gamma \le \varepsilon\alpha$, then (1.2) has three equilibria, two on the boundary of the positive quadrant: $(0,0)^T$, whose local stability cannot be directly studied (the system cannot be linearised), $(K,0)^T$ that is unstable and a unique equilibrium with positive coordinates: $(\overline{S_1}, \overline{S_2})^2 := \frac{K}{\alpha\varepsilon\delta}(\beta(\gamma-\delta) + \delta\varepsilon\alpha)\left(1, \quad \frac{\delta-\gamma}{\gamma\varepsilon}\right)^T$ which may or may not be stable. To study the local stability of equilibrium $(0,0)^T$ there are several ways, e. g. via introducing the new variable $S := S_1/S_2$ or making a time scale change $dt =: (\varepsilon S_2 + S_1)d\tau$ (cf. [17] and [26]). First we give conditions for the asymptotic stability of the equilibrium of the delayed system and show that under some conditions the increase of the delay $\frac{1}{a}$ destabilises the originally stable equilibrium by a Poincaré–Andronov–Hopf bifurcation (see [9]). While the system without delay has no periodic solutions apart from the trivial one, this one has.

2. The system with delay

We consider the model of predator-prey interaction with time delay which is given by

$$\begin{aligned} \dot{S}_1 &= \alpha S_1\left(1-\frac{S_1}{K}\right)-\frac{\beta S_1 S_2}{\varepsilon S_2+S_1}\\ \dot{S}_1 &= -\gamma S_2+\frac{\delta R S_2}{\varepsilon S_2+R} \end{aligned} \tag{2.1}$$

where R is given by (1.5). Since

$$\dot{R}(t) = a(S_1(t) - R(t)) \quad (t \in [0, +\infty)),$$

we see that (2.1) is equivalent in its qualitative dynamical behaviour to the three dimensional system of ordinary differential equations

$$\begin{aligned} \dot{S}_1 &= \alpha S_1\left(1-\frac{S_1}{K}\right)-\frac{\beta S_1 S_2}{\varepsilon S_2+S_1}\\ \dot{S}_1 &= -\gamma S_2+\frac{\delta R S_2}{\varepsilon S_2+R}\\ \dot{R} &= a(S_1-R) \end{aligned} \tag{2.2}$$

on $[0, \infty)$ in the following sense (see also [7]). If $(S_1, S_2) : [0, +\infty) \to \mathbb{R}^2$ is the solution of (2.1) corresponding to the continuous and bounded initial function $\tilde{S_1} : (-\infty, 0] \to \mathbb{R}$ and the initial value $S_2^0 := S_2(0)$ (i. e., $S_1(t) := \tilde{S_1}(t)$ $(t < 0)$), then $(S_1, S_2, R) : [0, +\infty) \to \mathbb{R}^3$ is the solution of (2.2) satisfying the initial conditions $S_1(0) = \tilde{S_1}(0)$, $S_2(0) = S_2^0$ and $R(0) = R^0 := a\int_{-\infty}^0 \tilde{S_1}(\tau)\exp(a\tau)\,d\tau$ and vice versa. (Clearly, if the initial values $S_1(0)$, S_2^0 and R^0 related to system (2.2) are prescribed then, the function $\tilde{S_1}$ is not uniquely determined.) There are seven parameters in (2.2), thus if we introduce new variables and time with substitutions such as

$$S_1 =: Ku, \quad S_2 =: \frac{K}{\varepsilon}v, \quad R =: Kw, \quad t =: \alpha\tau,$$

then (2.2) takes the following simpler, dimensionless form

$$\begin{aligned} u' &= u(u-1)-\frac{buv}{v+u}\\ v' &= -cdv+\frac{cvw}{v+w}\\ w' &= \mu(u-w) \end{aligned} \tag{2.3}$$

where $b := \frac{\beta}{\alpha\varepsilon}$, $c := \frac{\delta}{\alpha}$, $d := \frac{\gamma}{\delta}$ and $\mu := \frac{a}{\alpha}$, and where the prime, this time, denotes differentiation with respect to the variable τ. With these notations, if $0 < d < 1 < b < \frac{1}{1-d}$ for $b > 1$ or if $0 < d < 1$ for $b \le 1$, then system (2.3) has the following equilibria: firstly, the origin, whose local stability cannot be directly investigated and is of no interest, secondly, the points $(1, 0, 1)^T$ and the unique positive $(\overline{u}, \overline{v}, \overline{w})^T :=$

$\Big(b(d-1)+1, \frac{1-d}{d}(b(d-1)+1), b(d-1)+1\Big)^T$, which represent the extinction state of predator and the coexistence state of predator and prey, respectively.

In order to check the stability of the last two equilibria we linearise system (2.3) at these points. The coefficient matrix is

$$A(u,v,w) := \begin{bmatrix} 1-2u-\frac{bv^2}{(v+u)^2} & -\frac{bu^2}{(v+u)^2} & 0 \\ 0 & \frac{cw^2}{(v+w)^2}-cd & \frac{cv^2}{(v+w)^2} \\ \mu & 0 & -\mu \end{bmatrix}.$$

In particular,

$$A(1,0,1) = \begin{bmatrix} -1 & -b & 0 \\ 0 & c(1-d) & 0 \\ \mu & 0 & -\mu \end{bmatrix}, \qquad A(\overline{u},\overline{v},\overline{w}) = \begin{bmatrix} ek-1 & -bd^2 & 0 \\ 0 & cdk & ck^2 \\ \mu & 0 & -\mu \end{bmatrix},$$

where $e := b(1+d)$, $k := 1-d$, and the characteristic polynomials take the form

$$p_{101}(\lambda) := \lambda^3 + (1+\mu-c(1-d))\lambda^2 + (\mu-\mu c(1-d)-c(1-d))\lambda + \mu c(1-d)$$

and

$$p_{\overline{uvw}}(\lambda) := \lambda^3+(\mu+cdk-ek+1)\lambda^2+(cdk(\mu+1)-ek(\mu-cdk)+\mu)\lambda+\mu cdk(ek+1+bdk).$$

Applying the Routh–Hurwitz criterion, we conclude that they are stable polynomials if and only if the following inequalities hold:

$$1+\mu > c(1-d), \tag{2.4a}$$

$$\mu(1-c(1-d)) > c(1-d), \tag{2.4b}$$

$$\mu c(1-d) > 0, \tag{2.4c}$$

$$P_{101}(\mu) := (1-c(1-d))\mu^2 + (1-4c(1-d)+c^2(1-d))\mu + c(1-d)(c-1) > 0$$

and

$$\mu + cdk + 1 > ek \tag{2.5a}$$

$$\mu(cdk-ek+1) > -cdk(1-ek) \tag{2.5b}$$

$$\mu cdk(ek+1+bdk) > 0, \tag{2.5c}$$

and

$$\begin{aligned} P_{\overline{uvw}}(\mu) := (cdk-ek+1)\mu^2 + (cdk(cdk+2-2ek-bdk) \\ + ek(ek-2)+1))\mu + cdk(1+cdk(1+ek)-ek) > 0. \end{aligned} \tag{2.5d}$$

If we assume that

$$1-ek > 0 \tag{2.6a}$$

i. e.,

$$\frac{1}{1-d} > b(1+d), \tag{2.6b}$$

then (2.5a) and (2.5b) hold. Clearly, (2.5c) holds automatically, thus (2.5d) and (2.6a) (resp. (2.6b)) atogether form a sufficient condition of asymptotic stability of the equilibrium $(\overline{u}, \overline{v}, \overline{w})^T$.

In view of (2.6a), the following three cases can be distinguished.

2.1. Case $ek < 1$.

In this case the inequalities (2.5a-c) hold true. If

$$cdk(cdk + 2 - 2ek - bdk) + ek(ek - 2) + 1 \geq 0, \tag{2.7}$$

then (2.5d) holds for all μ and $(\overline{u}, \overline{v}, \overline{w})^T$ is asymptotically stable. If (2.7) does not hold, then since the constant term of the quadratic polynomial $P_{\overline{uvw}}$ is positive, this polynomial has either no real roots or has two roots of the same sign. If $P_{\overline{uvw}}$ has no real roots or has two negative roots, then (2.7) holds again for all μ and the equilibrium $(\overline{u}, \overline{v}, \overline{w})^T$ is asymptotically stable. If $P_{\overline{uvw}}$ has two positive roots, $0 < \mu_1 < \mu_0$, say, then the equilibrium $(\overline{u}, \overline{v}, \overline{w})^T$ is asymptotically stable for large values of μ, i. e., for small delays. At μ_0, the characteristic polynomial $p_{\overline{uvw}}$ has the form

$$p_{\overline{uvw}}(\lambda) \equiv (\lambda^2 + cdk(\mu_0 + 1) - ek(\mu_0 - cdk) + \mu_0)(\lambda + \mu_0 + cdk - ek + 1),$$

and its roots are

$$\lambda_0(\mu_0) = -\mu_0 - cdk + ek - 1 < 0 \quad \text{and} \quad \lambda_{1,2}(\mu_0) = \pm i\omega,$$

where

$$\omega := \sqrt{cdk(\mu_0 + 1) - ek(\mu_0 - cdk) + \mu_0}.$$

A routine calculation shows that

$$\frac{d\Re(\lambda_1(\mu_0))}{d\mu} = -\frac{\left(cdk(\mu_0 + 1) - ek(\mu_0 - cdk) + \mu_0 - 3\omega^2\right)\left(cdk(ek + 1) + bdk - \omega^2\right)}{(cdk(\mu_0 + 1) - ek(\mu_0 - cdk) + \mu_0 - 3\omega^2)^2 + 4\omega^2(\mu_0 + cdk - ek + 1)^2}.$$

Example. Let $b = 2.0000$, $d = 0.1000$, $c = 0.1000$, then the expression on the left hand side in (2.7) is negative, $\mu_0 = 0.4319$ and $\omega = 0.5970$, furthermore,

$$\frac{d\Re(\lambda_1(\mu_0))}{d\mu} = -\frac{0.2187}{2.5511} < 0,$$

therefore using μ as bifurcation parameter, the equilibrium $(\overline{u}, \overline{v}, \overline{w})^T$ looses its stability by a Poincaré-Andronov-Hopf bifurcation when μ is decreased below μ_0, i. e., the delay is increased, while the other equilibrium becomes asymptotically stable.

2.2. Case $ek = 1$. In this case the inequalities (2.5a-c) hold true, (2.5d) is equivalent to

$$P_{\overline{uvw}}(\mu) := \mu^2 + dk(c - b)\mu + 2cdk > 0. \tag{2.8}$$

If $c - d \geq 0$, then (2.8) holds for all μ and $(\overline{u}, \overline{v}, \overline{w})^T$ is asymptotically stable. If $c < d$, then since the constant term of the quadratic polynomial $P_{\overline{uvw}}$ is positive, this polynomial has either no real roots or has two roots of the same sign. If $P_{\overline{uvw}}$ has no real roots or has two negative roots, then (2.8) holds again for all μ and the equilibrium $(\overline{u}, \overline{v}, \overline{w})^T$ is asymptotically stable. If $P_{\overline{uvw}}$ has two positive roots, $0 < \mu_1 < \mu_0$, say, then the equilibrium $(\overline{u}, \overline{v}, \overline{w})^T$ is asymptotically stable for large values of μ, i. e., for small delays. At μ_0 the characteristic polynomial $p_{\overline{uvw}}$ has the form

$$p_{\overline{uvw}}(\lambda) \equiv (\lambda^2 + cdk(\mu_0 + 1) - (\mu_0 - cdk) + \mu_0) \times (\lambda + \mu_0 + cdk),$$

whose roots are

$$\lambda_0(\mu_0) = -\mu_0 - cdk < 0, \quad \text{and} \quad \lambda_{1,2}(\mu_0) = \pm i\omega,$$

where $\omega := \sqrt{2cdk(\mu_0 + 1)}$. A routine calculation shows that

$$\frac{d\Re(\lambda_1(\mu_0))}{d\mu} = -\frac{\omega^2 \left(3\omega^2 + cdk\left(4\mu_0 - 2cdk(1 + \mu_0) - 2 - 3cd^2k^2\right)\right) + 2c^2d^2k^2(2 + bdk)}{\left(2cdk(\mu_0 + 1) - 3\omega^2\right)^2 + 4\omega^2(\mu_0 + cdk)^2}.$$

Example. Let $b = 0.999900000$, $c = 0.000000001$, then $d = 0.000050003$ and (2.8) is negative, $\mu_0 = 0.00054791$ and $\omega = 0.999999998$, furthermore,

$$\frac{d\Re(\lambda_1(\mu_0))}{d\mu} = -0.031314697 < 0,$$

therefore in this case the equilibrium $(\overline{u}, \overline{v}, \overline{w})^T$ looses its stability if μ is decreased below μ_0. This loss of stability occurs again by a Poincaré-Andronov-Hopf bifurcation, while the other equilibrium becomes asymptotically stable.

2.3. Case $ek > 1$. In this case (2.5a-b) are not satisfied automatically. If we assumed that $cd > e$, then (2.5a) would hold but we have no guarantee that (2.5b) will hold, so it is not sure even for the value μ ($\mu < \mu_0$) that the polynomial $p_{\overline{uvw}}(\lambda)$ is stable.

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