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Lyapunov functions for a generalized Gause-type model*

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Abstract. Lyapunov functions are given to prove the global asymptotic stability of a large class of predator-prey models, including the ones in which the intrinsic growth rate of the prey follows the Ricker-law or the Odell generalization of the logistic law, and the functional predator response is of Holling type.

Key words: Global stability – Lyapunov function – Predator-prey system

1 Introduction

The main purpose of this paper is to establish conditions for the global asymptotic stability of the stationary solution in $\mathbb{R}_+^2$ of the system:

$$\begin{cases} \dot{x} = xg(x) - p(x)y \ , \\ \dot{y} = q(x)y \ , \\ x(0) = x_0 \ , \quad y(0) = y_0 \ . \end{cases} \tag{1.1}$$

We make the following assumptions H:

H_0) for every $(x_0, y_0) \in \mathbb{R}_+^2$ there exists a unique local solution that depends continuously upon the initial data,

H_1) $p(\cdot) \in C([0, +\infty), \mathbb{R})$, $p(0) = 0$ and $p(x) > 0$ for all $x > 0$,

H_2) $q(\cdot) \in C([0, +\infty), \mathbb{R})$; there exists $x_* > 0$ such that $q(x_*) = 0$ and $q(x)(x - x_*) > 0$ for $x \neq x_*$,

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H_3) $g(\cdot) \in C([0, +\infty), \mathbb{R})$ and there exists $k > x_*$ such that $g(x) > 0$, for every $x \in (0, k)$.

Therefore there exists in $\mathbb{R}_+^2$ a unique stationary solution $U_* = (x_*, y_*)$, where

$$y_* \doteq \frac{x_* g(x_*)}{p(x_*)}. \tag{1.2}$$

A large class of biological and bioeconomic models are special cases of systems (1.1) satisfying hypothesis H. For example, the Gause-type models (see Freedman [4]), that are extensively used to mimic predator-prey interactions. For the discussions of the biological aspects of predator-prey systems we refer the reader to [4, 5, 17, 18, 19, 20].

Our approach to the global asymptotic stability (g.a.s., for short) of U_* for system (1.1) is to construct Lyapunov functions (see Hahn [8], La Salle [14]).

Lyapunov function techniques are well developed; the main difficulty is of course to find the right function. Many authors have used Lyapunov functions for the global stability analysis of predator-prey systems (see Goh [6], Harrison [9], Hsu [11]). A good treatment of this topic can be found in Goh [7].

Some partial results on global asymptotic stability for a special case (i.e. $q(x) = \mu p(x) - c, \mu, c \in \mathbb{R}_+$) have been obtained by Cheng et al. [2] and Liou and Cheng [16] using various techniques, e.g. Poincaré–Bendixson theory and comparison methods. Interesting results for systems more general than (1.1) have been given by Kuang [12] and Lindström [15]; the latter considers models that generalize Leslie's model.

The Lyapunov functions introduced below in (2.4) and (3.3) are general enough to be applied to a wide range of predator-prey models; they simplify the study of local stability and the extent of the domain of attraction. One of the advantages of this approach is that the conclusions do not depend so much on the specific functions chosen by the modeler, but rather on their general properties.

In Sect. 2 we exhibit a Lyapunov function that works for Gause-type models even if the response function $p(x)$ is of Holling type III, a case in which the Lyapunov function introduced by Hsu [11] does not work. This Lyapunov function gives results even if the intrinsic growth rate of the prey $g(x)$ follows the Odell generalization of the logistic law (see Segel [22]), or the Ricker law (see Clark [3]).

In Sect. 3 we assume that the intrinsic growth rate of the prey has a logistic behaviour, and we construct another Lyapunov function that gives the global asymptotic stability of U_* when the system (1.1) satisfies the Kolmogorov conditions (see Albrecht et al. [1]).

In Sect. 4 we provide some applications to ecological problems. In model 4 we will show, using Lyapunov functions, that there are solutions having a bounded maximal interval of existence for a model known as "Paradox of Enrichment" in Rosenzweig [21].

2 The general case

Let be I the set

$$I = \{x \in \mathbb{R}_+ : g(x) > 0\} \tag{2.1}$$

and $G(\cdot)$ the function

$$G : (0, x_*) \cup (x_*, +\infty) \cap I \to \mathbb{R}$$

$$G(x) = \frac{\ln y_* \dfrac{p(x)}{xg(x)}}{\displaystyle\int_{x_*}^{x} \frac{q(t)}{p(t)}\, dt} . \tag{2.2}$$

Let us define

$$\alpha \doteq \sup_{x \in (0, x_*)} G(x) ; \qquad \gamma \doteq \inf_{x \in (x_*, +\infty) \cap I} G(x) . \tag{2.3}$$

Our main result will be the following:

Theorem 2.1. *Let the hypotheses H of* §1 *hold. Assume*

i) $\gamma > 0$ *and* $\alpha \leqq \gamma$,

ii) $\alpha > \overline{\lim}_{x \to x_*^-} G(x)$, *or* $\gamma < \underline{\lim}_{x \to x_*^+} G(x)$,

iii) $\displaystyle\int_{x_*}^{x} \frac{q(t)}{p(t)}\, dt = +\infty$,

iv) $\displaystyle\int_{x_*}^{+\infty} \frac{q(t)}{p(t)}\, dt = +\infty$.

Then the stationary solution U_* of system (1.1) *is globally asymptotically stable in* $\mathbb{R}^2_+$.

Proof. Let $V : \mathbb{R}^2_+ \to \mathbb{R}$

$$V(x, y) = \frac{e^{\gamma y}}{\gamma y_*} \exp\left(\gamma \int_{x_*}^{x} \frac{q(t)}{p(t)}\, dt\right) - \int_{y_*}^{y} \frac{e^{\gamma t}}{t}\, dt - \frac{e^{\gamma y_*}}{\gamma y_*} . \tag{2.4}$$

Then $V \in C^1(\mathbb{R}^2_+, R)$ and $V(x_*, y_*) = 0$.

From assumptions H and hypothesis i), it follows that

$$\frac{e^{\gamma y}}{\gamma y_*} \exp\left(\gamma \int_{x_*}^{x} \frac{q(t)}{p(t)}\, dt\right) > \frac{e^{\gamma y}}{\gamma y_*} \quad \text{for every } x \in (0, x_*) \cup (x_*, +\infty) .$$

Then

$$V(x, y) > 0 \quad \text{for every } (x, y) \in \mathbb{R}^2_+ - \{U_*\}$$

and from (2.3) and i) we get

$$\dot V = \frac{e^{\gamma y}}{y_*} q(x) \left[\frac{xg(x)}{p(x)} \exp\left(\gamma \int_{x_*}^{x} \frac{q(t)}{p(t)}\, dt\right) - y_*\right] \leqq 0 \quad \text{for every } (x, y) \in \mathbb{R}^2_+ \tag{2.5}$$

where $\dot V$ is the derivative of V along the trajectories of system (1.1); therefore V is a Lyapunov function and U_* is stable.

In order to prove that U_* is g.a.s., we observe that from iii) and iv), the function V is "radially unbounded" on $\mathbb{R}_+^2$, given that

$$V(x,y) \to +\infty \quad \text{when } \|(x,y)\| \to +\infty \quad \text{or} \quad \|(x,y)\| \to 0, \quad (x,y) \in \mathbb{R}_2^+ .$$

Thus the set

$$S_l \doteq \{(x,y) \in \mathbb{R}_+^2 : V(x,y) \leqq l\} \tag{2.6}$$

is, for every $l \geqq 0$, a compact set contained in $\mathbb{R}_+^2$. Moreover from (2.5) S_l is positively invariant. Let

$$\mathcal{O} = \{(x,y) \in \mathbb{R}_+^2 : \dot{V}(x,y) = 0\} .$$

From (2.5) and ii) we see that U^* is not an interior point of the set $\mathcal{O}$; the claim follows by application of the Poincaré–Bendixson theorem. Q.E.D.

Remarks. i) Observe that the function $V(x,y)$ defined in (2.4) is the first integral of the following system:

$$\begin{cases} \dot{x} = p(x)\left[y_* \exp\left(-\gamma \int_{x_*}^{x} \frac{q(t)}{p(t)}\, dt\right) - y\right] , \\ \dot{y} = q(x)y \ , \end{cases}$$

Therefore the same result could have been obtained through comparison methods as in Yan–Qian [23] (see Theorem 3.13).

ii) We want to emphasize that Theorem 2.1 is applicable to system (1.1) in particular when the intrinsic growth rate of the prey-population $g(x)$ follows the Ricker-law (i.e. $g(x) = ae^{-\sigma x}$, a and $\sigma > 0$), and in addition also if $r(0) = 0$, where $r(x)$ is the isocline of the prey-population (see Model 1 §4).

Now, if we assume that the behaviour of $g(\cdot)$ of system (1.1) is only of logistic type, i.e. we add hypothesis H_4) below to hypotheses H, then we have the following theorem:

Theorem 2.2. *Assume hypotheses H,* i), ii) *and* iii) *of Theorem* 2.1, *and*

H_4) *k, as defined in H_3 of* §1, *is unique,* $g(k) = 0$, $g(x)(x-k) < 0$ *for* $x \in (0, +\infty)$, $x \neq k$.

Then U_* is globally asymptotically stable for system (1.1) *in* $\mathbb{R}_+^2$.

Proof. Let us consider the function $V(x,y)$ defined in (2.4); obviously (2.5) holds and U_* is stable.

Let D_l the set:

$$D_l \doteq S_l \cap \{(x,y) \in \mathbb{R}_+^2 : x \leqq k\}$$

where S_l is the set defined in (2.6).

Let $l_k \doteq V\left[k, y_* \exp\left(-\gamma \int_{x_*}^{k} \frac{q(t)}{p(t)}\, dt\right)\right]$ and for $l \geqq l_k$ let $y_1(l)$ and $y_2(l)$ be the solutions of the equation $V(k,y) = l$ with $0 < y_1(l) \leqq y_2(l)$, then:

$$S_l \cap \{(x,y) \in \mathbb{R}_+^2 : x = k\} = \begin{cases} \emptyset & \text{if } l < l_k \\ \{(k,y) : y_1(l) \leqq y \leqq y_2(l)\} & \text{if } l \geqq l_k . \end{cases}$$

From iii) it follows that for every $l \geqq 0$, D_l is a compact set strictly contained in $\mathbb{R}^2_+$ and positively invariant. We are left with showing that there exists $T \geqq 0$, such that $x(T) < k$ for $t > T$ (see the proof of Theorem 2.1).

Let $(x(\cdot), y(\cdot))$, $t \in [0, \tau)$, be the solution of (1.1) and $x_0 < k$; then $x(t) < k$ for $t \in (0, \tau)$. Let us suppose by contradiction that $x(t) = k$ for some t, and t_0 be the first value of t such that $x(t_0) = k$; then $\dot{x}(t_0) \geqq 0$ and from (1.1)

$$\dot{x}(t_0) \leqq -p(x(t_0))y(t_0) < 0 \,,$$

a contradiction.

Let now $x_0 \geqq k$, and suppose by contradiction that $x(t) \geqq k$ for every $t \in [0, \tau)$. From (1.1) we have $\dot{x}(t) < 0$ for every $t \in [0, \tau)$; and

$$k \leqq x(t) \leqq x_0 \quad \text{for } t \in [0, \tau) \,. \tag{2.7}$$

By (1.1) we get

$$\dot{x}(t) + \lambda \dot{y}(t) \leqq g(x(t))(x(t) + \lambda y(t)) \quad \text{for } t \in [0, \tau) \,,$$

where

$$\lambda \doteq \min_{x \in (k, x_0)} \frac{p(x)}{q(x) - g(x)} \,.$$

Then

$$x(t) + \lambda y(t) \leqq e^{\int_0^t g(x(s))\,ds}(x_0 + \lambda y_0) \quad \text{for } t \in [0, \tau) \,,$$

and since

$$y(t) = y_0 e^{\int_0^t q(x(s))\,ds} \quad \text{for } t \in [0, \tau) \tag{2.8}$$

there exists $\bar{y}$ such that

$$0 < y(t) \leqq \bar{y} \quad \text{for every } t \in [0, \tau) \,. \tag{2.9}$$

Then from (2.7) and (2.9) it follows that $\tau = +\infty$, and from (2.8) we have

$$\lim_{t \to +\infty} y(t) = +\infty \,,$$

a contradiction. Q.E.D.

Remark. Let us observe that Theorem 2.2 holds for system (1.1). In particular it applies when $g(x)$ follows the Odell-law (i.e. $g(x) = x^a(k - x), a > 0$), and if $r(0) = 0$, where $r(x)$ is the isocline of the prey-population (see Model 2 §4).

Given the role played by the hypothesis $\alpha \leqq \gamma$, where α and γ are defined in (2.3), we now state some sufficient conditions for it to occur.

Lemma 2.3. *If hypothesis H of* §1 *holds and if*

$$\left(\frac{xg(x)}{p(x)} - y_*\right)(x - x_*) \leqq 0, \quad \text{for } x \in (0, +\infty) \tag{2.10}$$

then $\alpha \leqq \gamma$.

Proof. Taking into account (2.2) we have

$$G(x)(x - x_*) \geqq 0 \quad \text{for every } x \in (0, x_*) \cup (x_*, +\infty) \cap I \,,$$

from which the assertion follows. Q.E.D.

If the behaviour of $g(x)$ is of logistic type, we have the following.

Lemma 2.4. *Suppose that H and H_4 of Theorem 2.2 hold and that*

i) $r:(0,k)\to \mathbb{R}$, *where* $r(x) = xg(x)/p(x)$ *is such that* $r \in C^1((0,k),\mathbb{R})$ *and* $r'(x_*) \leqq 0$,

ii) $S:(0,k)\to\mathbb{R}$, $S(x) = (r'(x_*)p'(x_*) - r'(x)p(x))/r(x)q(x)$ *is a continuous, monotone nondecreasing function,*

iii) $\overline{\lim}_{x\to 0^+} G(x) < S(x_*)$ *where $G(x)$ is defined in* (2.2).

Then $\alpha \leqq \gamma$.

Proof. Let $\varphi:(0,x_*)\cup(x_*,k)\to\mathbb{R}$, where

$$\varphi(x) = \frac{-r'(x)p(x)}{r(x)q(x)},$$

it is easy to verify that if $\bar{x}\in(0,x_*)\cup(x_*,k)$, then:

$$G'(\bar{x}) = 0 \quad \text{iff } G(\bar{x}) = \varphi(\bar{x})$$

moreover

$$(\varphi(x) - S(x))(x - x_*) \leqq 0 \quad \text{for } x\in(0,k),\ x \neq x_*,$$

which proves the lemma. Q.E.D.

3 Other results for the logistic case

Hypothesis H_4 of Theorem 2.2 allows us to obtain another result. Let

$$F:(0,x_*)\cup(x_*,k)\to\mathbb{R}$$

$$F(x) = \frac{y_* - \dfrac{xg(x)}{p(x)}}{\displaystyle\int_{x_*}^{x}\frac{q(t)}{p(t)}\,dt} \tag{3.1}$$

and

$$\beta \doteq \sup_{x\in(0,x_*)} F(x), \qquad \theta \doteq \inf_{x\in(x_*,k)} F(x). \tag{3.2}$$

Theorem 3.1. *Assume hypotheses H and H_4 of Theorem 2.2 and*

i) $\theta > 0$ *and* $\beta \leqq \theta$,

ii) $\beta > \overline{\lim}_{x\to x_*^-} F(x)$ *or* $\theta < \underline{\lim}_{x\to x_*^+} F(x)$,

where F, θ and β are defined in (3.1) *and* (3.2),

Then U_* is locally asymptotically stable for (1.1) *and there are no periodic orbits in* $\mathbb{R}^2_+$.

Proof. Let $W:\mathbb{R}^2_+\to\mathbb{R}$

$$W(x,y) = \frac{1}{\theta+1}(y^{\theta+1} - y_*^{\theta+1}) - \frac{y_*}{\theta}(y^\theta - y_*^\theta) + y^\theta\int_{x_*}^{x}\frac{q(t)}{p(t)}\,dt. \tag{3.3}$$

It is obvious that $W\in C^1(\mathbb{R}^2_+,\mathbb{R})$, $W(x_*,y_*) = 0$.

From i), H_1 and H_2 we have

$$W(x,y) > 0 \quad \text{for } (x,y) \in \mathbb{R}^2_+ - \{U_*\} ,$$

and from (3.1) and i) for every $(x,y) \in \mathbb{R}^2_+$,

$$\dot{W} = y^\theta q(x)\left[\frac{xg(x)}{p(x)} - y_* + \theta \int_{x_*}^{x} \frac{q(t)}{p(t)}\,dt\right] \leqq 0 , \tag{3.4}$$

where $\dot{W}$ is the derivative of W along the solutions of (1.1).

Let

$$\lambda_1 \doteq \sup_{y \in (0, y_*)} W(x_*, y) ,$$

$$\lambda_2 \doteq \sup_{x \in (x_*, k)} W(x, y_*) ,$$

$$\lambda_3 \doteq \sup_{x(0, x_*)} W(x, y_*) .$$

If $\lambda_1 \leqq \min(\lambda_2, \lambda_3)$ then, for every $0 \leqq l < \lambda_1$ we have that the set

$$D_l = \{(x,y) \in \mathbb{R}^2 : W(x,y) \leqq l\}$$

is a compact set strictly contained in the region defined by

$$0 < x < k \qquad \text{and} \qquad 0 < y < h^{-1}(l) ,$$

where $h:[y_*, +\infty) \to \mathbb{R}_+$, and $h(y) = W(x_*, y)$ is a continuous monotone increasing function where $\lim_{y \to +\infty} h(y) = +\infty$.

Then from ii) we have, as in Theorem 2.1, that U_* is asymptotically stable and its domain of attraction contains the set

$$\{(x,y) \in \mathbb{R}^2_+ : W(x,y) < \lambda_1\}$$

and hence the segment $x = x_*$, $0 < y < y_*$. The claim follows.

For the other cases we can argue in a similar way. Q.E.D.

Remarks. i) Let us observe that the function $W(x,y)$ defined in (3.3) is the first integral of the following system:

$$\begin{cases} \dot{x} = p(x)\left[y_* - \theta \displaystyle\int_{x_*}^{x} \frac{q(t)}{p(t)}\,dt - y\right] \\ \dot{y} = q(x)y \end{cases} .$$

Thus the same result follows as in Yan-Qian [23] (Theorem 3.13).

ii) If system (1.1) satisfies Kolmogorov's conditions, so that $\mathbb{R}^2_+$ is positively invariant and the solutions are bounded in the future (see Albrecht et al. [1]), then Theorem 3.1 implies that U_* is globally asymptotically stable in $\mathbb{R}^2_+$. Let us observe that under the assumption that the Kolmogorov conditions hold, Liou and Cheng [16] have introduced a nice method to obtain the global asymptotical stability of U_* in a special case of system (1.1). Under the same hypotheses, Kuang [12] generalized this result. It is very easy to verify that condition i) of our Theorem 3.1 is a sufficient condition for the one they require (see [16], assumption (d), p. 67).

The following lemma is proved as Lemma 2.3 and Lemma 2.4.

Lemma 3.2. *If hypotheses H and H_4 of Theorem* 3.1 *hold, and if*

$$\left(\frac{xg(x)}{p(x)} - y_*\right)(x - x_*) \leqq 0 \quad \text{for } x \in (0, k) \tag{3.5}$$

then $\beta \leqq \theta$.

Lemma 3.3. *Suppose that H and H_4 of Theorem* 3.1 *hold and moreover*
i) $r:(0,k) \to \mathbb{R}$, $r(x) = \frac{xg(x)}{p(x)}$ *is such that*

$$r \in C^1((0,k), \mathbb{R}) \quad \text{and} \quad r'(x_*) \leqq 0\,,$$

ii) $T:(0,k) \to \mathbb{R}$, $T(x) = (r'(x_*)p(x_*) - r'(x)p(x))/q(x)$ *is a continuous monotone non decreasing function,*
iii) $\overline{\lim}_{x \to 0^+} F(x) < T(x_*)$ *where $F(\cdot)$ is defined in* (3.1).
Then $\beta < \theta$.

Remark. Hsu in Theorem 3.2 of [11] (see also [10, 12]) states the global asymptotic stability of U_* using condition (3.5). Cheng et al. in Theorem 2 of [2] claim that U_* is globally asymptotically stable under conditions equivalent to those of our Lemma 3.3. In both cases the authors make use of the positivity of the solutions of (1.1) without requiring the proper conditions for this to be the case. However the result of Hsu is true, because from (3.5) it easily follows that $\overline{\lim}_{x \to 0^+} \frac{p(x)}{x} < +\infty$ and this implies the positivity of the solutions. On the other hand, Cheng et al. [2] under their own hypotheses only prove that there are no periodic orbits in $\mathbb{R}^2_+$ (see Model 4 in §4 below).

4 Applications

We present some models from the ecological literature.

Model 1. This is a typical model from fisheries in which the intrinsic growth rate of the prey it is assumed to follow the Ricker-law (see Clark [3])

$$\begin{cases} \dot{x} = mx^a e^{-bx} - pxy \\ \dot{y} = (qx - c)y \end{cases}$$

where $m, p, q, c, b \in \mathbb{R}_+$, $a \geqq 1$ and $\frac{c}{q} > \frac{a-1}{b}$.

Let $x_* \doteq \frac{c}{q}$ and $y_* \doteq \frac{m}{p} x_*^{a-1} e_*^{-bx}$, then from Theorem 2.1, $U_* = (x_*, y_*)$ is g.a.s. in $\mathbb{R}^2_+$.

The assertion is easy to verify by observing that if $G(\cdot)$ is the function defined in (2.2), it follows that:

$$G(x)=\frac{p}{q}b\left[1+\left(x_*-\frac{a-1}{b}\right)\frac{\ln\dfrac{x}{x_*}}{x-x_*-x_*\ln\dfrac{x}{x_*}}\right]$$

$$\text{for } x\in(0,x_*)\cup(x_*,+\infty)$$

then

$$\alpha=\frac{p}{c}(a-1)<\gamma=\frac{bp}{q}\,.$$

Observe that if $a=1$, this model can also be studied by making use of the Lyapunov function of Hsu [11], but this function does not work for $a>1$.

Model 2. Let us consider a model in which the intrinsic growth rate of the prey follows the Odell-law (see Segel [22])

$$\begin{cases}\dot{x}=mx^2(1-x)-pxy\\ \dot{y}=(qx-c)y\end{cases}$$

where $m,p,q,c\in\mathbb{R}_+$ $\frac{1}{2}<\frac{c}{q}<1$. Let $x_*\doteq\frac{c}{q}$ and $y_*\doteq\frac{m}{p}x_*(1-x_*)$, then from Theorem 2.2 U_* *is g.a.s.* in $\mathbb{R}^2_+$. The assertion follows by observing that:

$$G(x)=\frac{\dfrac{p}{q}\ln\dfrac{x_*(1-x_*)}{x(1-x)}}{x-x_*-x_*\ln\dfrac{x}{x_*}}\quad\text{for } x\in(0,x_*)\cup(x_*,1)$$

where $G(x)$ is the function defined in (2.2) and $G'(\bar{x})=0$ iff $G(\bar{x})=h(\bar{x})$ where

$$h(x)=\frac{p}{q}\frac{(2x-1)}{(1-x)(x-x_*)}\quad\text{for } x\in(0,x_*)\cup(x_*,1)\,.$$

Then

$$\sup_{(0,x_*)}G(x)=\sup_{(0,x_*)}h(x)\quad\text{and}\quad\inf_{(x_*,1)}G(x)=\inf_{(x_*,1)}h(x)$$

and so after some calculations it is easy to see that $\gamma>0$ and $\alpha\leqq\gamma$ where α and γ are defined in (2.3).

For this model, the Lyapunov function, given by Hsu [11] and the methods used by Cheng et al. [2] and by Liou and Cheng [16] do not work. This is because they need $r(0)\geqq 0$ in the prey isocline $r(x)=\frac{xg(x)}{p(x)}$, and this is not true in this model.

Model 3. Let us consider the following model, where the functional response is of Holling type III:

$$\begin{cases} \dot{x} = \gamma x\left(1 - \dfrac{x}{k}\right) - \dfrac{mx^n y}{a + x^n} \\ \dot{y} = \left[c\dfrac{mx^n}{a + x^n} - D\right] y \end{cases}$$

where $\gamma, k, m, a, c, D \in \mathbb{R}_+$ and n for the sake of simplicity is a positive integer.

Let

$$x_* \doteq \left(\frac{aD}{cm - D}\right)^{1/n}, \quad \text{with } 0 < x_* < k$$

and

$$r(x) = \frac{\gamma}{m} x^{1-n}(a + x^n)\left(1 - \frac{x}{k}\right).$$

Suppose that

$$r'(x_*) < 0$$

then $U_* = (x_*, y_*)$ where $y_* = r(x_*)$, is g.a.s. in $\mathbb{R}^2_+$. Recalling the remark after Lemma 3.3, and observing that the model satisfies Kolmogorov's conditions, from Example 2 in Cheng et al. [2], the assertion easily follows.

Model 4. Let us consider the following model that in the case $\mu < 1$ is known as the "Paradox of Enrichment" (see Rosenzweig [21]).

$$\begin{cases} \dot{x} = ax(1 - x) - bx^\mu y \\ \dot{y} = c(x^\mu - d)y \end{cases}$$

where $a, b, c, \mu \in \mathbb{R}_+$, $0 < d < 1$.

If $\mu \geqq 1$ then from Theorem 2.2 we have that $U_* = (x_*, y_*)$, where

$$x_* \doteq d^{1/\mu} \quad \text{and} \quad y_* \doteq \frac{a}{b} d \frac{1 - \mu}{\mu}(1 - d^{1/\mu})$$

is g.a.s. in $\mathbb{R}^2_+$.

If $\mu < 1$ we have that if $x_* < \frac{1-\mu}{2-\mu}$, from the linear analysis, U_* is unstable, while if $x_* > \frac{1-\mu}{2-\mu}$ from Theorem 3.1, U_* is asymptotically stable and there exist no periodic orbits in $\mathbb{R}^2_+$.

Actually if $T(\cdot)$ is the function defined in ii) of Lemma 3.3, we have

$$T(x) = \begin{cases} \dfrac{a}{c}(2 - \mu)\dfrac{x - x_*}{x^\mu - x_*^\mu} & \text{for } x \in [0, 1], \quad x \neq x_* \\ \dfrac{a}{c}\dfrac{2 - \mu}{\mu} x_*^{1-\mu} & \text{for } x = x_* \end{cases}$$

$$T'(x) = \frac{a}{c}(2 - \mu)\frac{x^\mu - x_*^\mu - \mu x^{\mu-1}(x - x_*)}{(x^\mu - x_*^\mu)^2}$$

so that (see Cheng et al. [2], Example 1) $T'(x) \geqq 0, x \in (0,1)$ and $F(0) < T(x_*)$, where $F:(0,x_*)\cup(x_*,1) \to \mathbb{R}$,

$$F(x) = \frac{a}{c}\,\frac{x_*^{1-\mu}(1-x_*) - x^{1-\mu}(1-x)}{(x-x_*) - \dfrac{x_*^{\mu}}{1-\mu}(x^{1-\mu} - x_*^{1-\mu})}$$

is the function defined in (3.1).

Therefore $\beta \leqq \theta$, where β and θ are defined in (3.2).

Now $F(1) > 0$, and:

$$\lim_{x \to x_*^{\pm}} F(x) = \begin{cases} \pm\infty & \text{for } x_* \neq \dfrac{1-\mu}{2-\mu} \\ \dfrac{a}{c}\dfrac{2-\mu}{\mu} x_*^{1-\mu} & \text{for } x_* = \dfrac{1-\mu}{2-\mu} \end{cases}$$

so that $\theta > 0$ and $\beta > \lim_{x \to x_*^-} F(x)$.

When $x_* > \frac{1-\mu}{2-\mu}$, our result is the same as that of Cheng et al. [2]. However, they draw the conclusion that U_* is g.a.s. in $\mathbb{R}_+^2$, and this is not true because there are solutions having a bounded maximal interval of existence as we shall now show.

Let us consider the function $V(x,y)$ defined in (2.4) with $\lambda \doteq \theta$ where θ is defined in (3.2).

It is obvious that there exists x_1, $0 < x_1 < x_*$ such that:

$$\dot{V} > 0 \quad \text{for every } (x,y) \in \mathbb{R}_+^2, \quad 0 \leqq x \leqq x_1 \,. \tag{4.1}$$

Let

$$\mathscr{C}_1 : W(x,y) = W(0,2y_*); \quad x > 0 \quad y > y_*$$

where W is defined in (3.3), and

$$\mathscr{C}_2 : V(x,y) = V(0,y_*), \quad x > 0, \quad y > \frac{2a}{b} x_1^{1-\mu}(1-x_1)\,.$$

Then there exists $x_2 < \frac{x_*}{2}$ such that $\mathscr{C}_1 \cap \mathscr{C}_2 = \emptyset$ for every $(x,y) \in \mathbb{R}_+^2$, $0 \leqq x \leqq x_2$.

Define the set D by:

$$D = \{(x,y) \in \mathbb{R}_+^2 : W(x,y) \leqq W(0,2y_*)\,,$$
$$V(x,y) \geqq V(0,y_*)\,, \quad 0 < x \leqslant \min(x_1,x_2)\}\,;$$

then every trajectory starting in D cannot cross $\mathscr{F}D$ either through $\mathscr{C}_1$ because of (4.1), or through $\mathscr{C}_2$ because of (3.4), or through $\mathscr{C}_3$, where $\mathscr{C}_3$ is the segment intersection between $\mathscr{C}_1, \mathscr{C}_2$ and the line $x = \min(x_1,x_2)$, because $\dot{x} < 0$ on $\mathscr{C}_3$. Therefore the trajectory must reach the y-axis in finite time.

Model 5. Let us now consider a model in which the mortality rate of the predator population is a function of the density of the prey population (see [13]).

$$\begin{cases} \dot{x} = ax(1-x) - \dfrac{px}{b+x}y \\ \dot{y} = \left[\dfrac{cx}{b+x} - \dfrac{ex+f}{dx+s}\right]y \end{cases}$$

where a, b, c, d, e, f, p, s are positive constants and

$$\begin{cases} fd - es > 0 \\ cd - e > 0 \\ cd - e + cs - be - f - bf > 0 \ . \end{cases}$$

Then there exist $\bar{x} < \min(-b, -s/d)$ and $0 < x_* < 1$, such that we can rewrite the problem as

$$\begin{cases} \dot{x} = ax(1-x) - \dfrac{px}{b+x}y \\ \dot{y} = \dfrac{cd-e}{(b+x)(dx+s)}(x-\bar{x})(x-x_*)y \ . \end{cases}$$

If $x_* > \max(0, \frac{1-b}{2})$, and $y_* = \frac{a}{p}(b+x_*)(1-x_*)$, then $U_* = (x_*, y_*)$, the unique stationary solution of the problem in $\mathbb{R}^2_+$, is g.a.s. in $\mathbb{R}^2_+$. The assertion follows from Lemma 3.3, taking into account the remark of Theorem 3.1. In fact the function $T(x)$, defined in Lemma 3.3, becomes, after some calculations,

$$T(x) = \frac{a}{(cd-e)(b+x_*)}[2(b+x_*)x + b(2x_* - 1 + b)]h(x)$$

where $h(x) = (dx+s)/(x-\bar{x})$. Since $h(x)$ is a monotone increasing function in $\mathbb{R}_+$, then $T(x)$ is also a monotone increasing function in $\mathbb{R}_+$.

We note that if $(1-b)/2$ is positive, the Lyapunov function introduced by Hsu [11] does not work.

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