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Asymptotic Equilibrium in Prey-Predator Interactions with Nonlinear "Per Capita" Growth Rates

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1. Introduction

We investigate when hereditary terms do not affect the global asymptotic behavior of the nonlinear nonautonomous analog of the prey-predator model. Consider the simple Lotka-Volterra model for prey-predator interactions

$$\dot{x} = x(a_1 - b_1 x - c_1 y), \quad \dot{y} = y(-a_2 + b_2 x - c_2 y). \tag{1}$$

Under mild conditions (e.g. the existence of a positive solution of the system of the algebraic equations $-b_1 x - c_1 y = -a_1$, $b_2 x - c_2 y = a_2$ and the existence of a positive diagonal matrix D such that if A is the community matrix of the system, then $DA + A^T D$ is negatively definite) Goh [5] proved that system (1) has a uniform stable attractor for all paths in the positive quadrant. Similar conditions for such models with linear "per capita" growth rates have been given by many authors, see, e.g., [1, 2, 10, 13, 15] with head Volterra himself [11].

The problem however becomes more difficult if the interspecific interaction terms in (1) are replaced by nonlinear ones, with the simplest case that of Holling response functionals (i.e. $x/(1+x)$, $y/(1+y)$), or if growth rates depend on delay effects, or, generally, if both of these cases occur. To this direction Kolmogoroff [9] considered the system

$$x' = xf(x, y), \quad y' = yg(x, y) \tag{2}$$

and provided conditions for the existence of either a stable critical point or a stable limit cycle. Similar properties are examined by Samuelson [12] for the system (1) while a kind of structural stability for it is examined by Freedmann and Waltman [4]. For the latter case Cushing [3] is able to provide sufficient conditions for the existence of a local or global attractor.

The methods used in most of these cases are analytical. We recall, for instance, Cushing [3] who does use linearization and complex Laplace transform. It is however expected that in such a case a smoothness assumption on the growth rate is required. It is also notable that for the case of linear per capita growth rates it can be used the method of graphical representation of the labeled graph of the system (see, e.g., [13]).

The stable attractor for (1) is simply the solution (ξ, η) of the system $b_1\xi + c_1\eta = -a_1$, $b_2\xi - c_2\eta = a_2$. We shall be interested in conditions guaranteeing that the behavior of (1) described above is maintained when the rates $a_1 - b_1x - c_1y$ and $-a_2 + b_2x - c_2y$ are modified to reflect delay and time varying (i.e. nonautonomous) effects. Thus we will consider a system of the form

$$x' = f(x)F(t, x, x_t, y_t), \quad y' = g(y)G(t, y, y_t, x_t) \tag{3}$$

where x_t, y_t represent the past of x, y at the time t. The functions F, G satisfy some Lipschitz type conditions and no smootheness assumptions are imposed. The factors f, g are general functions non vanishing on $(0, +\infty)$ which guarantee uniqueness of the zero solution of (3).

However the nonautonomous character of (3) does not imply that the attractor (ξ, η) of (3) is itself a solution of (3); it will be if F, G do not depend on time. Thus we will have an attractor which will be, in a certain sense, an asymptotic solution of the system. To achieve this fact at infinity we will impose certain regularity conditions on F, G as the time tends to infinity. Further conditions are also provided in order to insure a correspondence of the function x with the prey species and y with the predators.

The paper is organized as follows: In Section 2 we give the basic assumptions and present the model. Section 3 is devoted to the invariance of the positive quadrant and the boundedness of the solutions. In Sections 4, 5 we discuss the behavior of the species when one of them disappears. Boundedness away from zero is discussed in Section 6 and, in Section 7, we prove our convergence results. This section is closed with some examples presented to illustrate our results.

2. The model and the basic assumptions

We start with some terminology and notations, and then present the system and the basic assumptions.

Let $\boldsymbol{R}$ be the real line; we denote by x or y a function from $\boldsymbol{R}$ into $\boldsymbol{R}$. Given such a function x we denote by x_t the function x_t: $(-\infty, 0] \to \boldsymbol{R}$ defined by $x_t(s) = x(t+s)$. Namely, x_t represents the history of x at t. If x is bounded and continuous, then, for each t, x_t belongs to the space of bounded continuous functions from $(-\infty, 0]$ into $\boldsymbol{R}$. We shall denote this space by C_-. We associate C_- by two metrics. The first metric is generated by the sup-norm $\|\cdot\|$, namely,

$$\|\varphi - \psi\| = \sup_{-\infty < t \leqq 0} |\varphi(t) - \psi(t)|,$$

and the second one will represent the uniform convergence on compact intervals. For definiteness we set

$$\rho(\varphi, \psi) = \sum_{n=0}^{\infty} \frac{1}{2^n} \min \{1, \sup_{-n-1 \leqq t \leqq 0} |\varphi(t) - \psi(t)|\}.$$

The subject of this work is the system of functional differential equations

$$x' = f(x)F(t, x, x_t, y_t) \tag{2.1}$$

$$y' = g(y)G(t, y, y_t, x_t) \tag{2.2}$$

where the functions F, G are defined on $\boldsymbol{R} \times \boldsymbol{R} \times C_- \times C_-$. An initial condition associated with (2.1)–(2.2) is a requirement $x_{t_0} = \varphi$, $y_{t_0} = \psi$ with $\varphi, \psi \in C_-$. The solution of the initial value problem at t_0 is then a pair of continuous functions (x, y) such that $(x_{t_0}, y_{t_0}) \in C_- \times C_-$, and (2.1)–(2.2) holds for all $t > t_0$ in the common domain of x, y. We say that (x, y) is a solution for $t > t_0$ if it is a solution of an initial value problem at t_0. We say that (x, y) is a full solution of (2.1)–(2.2) if it is defined for all $t \in \boldsymbol{R}$ and (2.1)–(2.2) is satisfied for all t.

In the sequel we shall use the following assumptions:

(A1) f is a continuous function such that $f(0) = 0$, $f(c) > 0$ if $c > 0$, and the Cauchy problem $\dot{z} = f(z)$, $z(0) = 0$, admits the unique solution $z = 0$. The function g satisfies the same assumptions.

(A2) $F, G: \boldsymbol{R} \times \boldsymbol{R} \times C_- \times C_- \to \boldsymbol{R}$ are uniformly continuous and bounded functions on sets of the form $\boldsymbol{R} \times$(bounded subset of $\boldsymbol{R}$)$\times$($\|\cdot\|$-bounded ρ-compact subset of C_-)$\times$($\|\cdot\|$-bounded ρ-compact subset of C_-) where the continuity is meant with respect to the ρ-metric.

(A3) $F(t, c, \varphi, \psi)$, $G(t, c, \varphi, \psi)$ are monotonically decreasing in c for fixed t, φ, ψ and there exist constants $L_1 > M_1 > 0$, $L_2 > M_2 > 0$ and $N_1 \geqq 0$, $N_2 \geqq 0$ such that

$$|F(t, c_1, \varphi, \psi) - F(t, c_2, \varphi, \psi)| \geqq L_1 |c_1 - c_2|,$$

$$|G(t, c_1, \varphi, \psi) - G(t, c_2, \varphi, \psi)| \geqq L_2 |c_1 - c_2|,$$

$$|F(t, c, \varphi_1, \psi_1) - F(t, c, \varphi_2, \psi_2)| \leqq M_1 \|\varphi_1 - \varphi_2\| + N_1 \|\psi_1 - \psi_2\|,$$

$$|G(t, c, \varphi_1, \psi_1) - G(t, c, \varphi_2, \psi_2)| \leqq M_2 \|\varphi_1 - \varphi_2\| + N_2 \|\psi_1 - \psi_2\|.$$

(A4) The constants L_i, M_i, N_i, $i = 1, 2$, satisfy

$$N_1 \cdot N_2 < (L_1 - M_1)(L_2 - M_2).$$

(A5) If $\psi(s) \geqq 0$, $s \leqq 0$ then $F(t, 0, 0, \psi) \leqq F(t, 0, 0, 0)$, for all t.

In the sequel we shall see that these assumptions are appropriate to characterize system (2.1)–(2.2) as a prey-predator model, when $f(w) = g(w) = w$. But in order to distinguish which of the unknown functions x, y behaves like the preys or predators we need some more assumptions given later.

The presence of the functions f, g are quite typical and they are imposed to insure that any solution (x, y) of (2.1)–(2.2) starting from a point in the first quadrant stays away from the x-axis and y-axis in the future. Thus f, g could be replaced by nonautonomous functions which guarantee such a property, or they could be dropped at all, but then this property must be imposed as an assumption.

Next we shall establish the existence of a pair of real numbers $(\xi(t), \eta(t))$ such that for each $t \in \boldsymbol{R}$ it satisfies

$$F(t, \xi(t), \xi(t), \eta(t)) = 0 \tag{2.3}$$

$$G(t, \eta(t), \eta(t), \xi(t)) = 0 \tag{2.4}$$

where $F(t, c, d, e)$ stands for the value $F(t, c, \varphi, \psi)$ with $\varphi(s)=d$, $\psi(s)=e$, $s \leqq 0$. Similarly for $G(t, c, d, e)$.

Lemma 2.1. *Assume that assumptions* (A2) *and* (A3) *are satisfied. Then for each* $t \in \boldsymbol{R}$ *and* $\varphi, \psi \in C_-$ *there exists a unique pair* $(X(t, \psi), Y(t, \varphi)) \in \boldsymbol{R} \times \boldsymbol{R}$ such that

$$F(t, X(t, \psi), X(t, \psi), \psi) = 0, \tag{2.5}$$

$$G(t, Y(t, \varphi), Y(t, \varphi), \varphi) = 0. \tag{2.6}$$

Proof. We shall show (2.5) only, since (2.6) can be proved in the same way. Fix a $t \in \boldsymbol{R}$ and $\psi \in C_-$. Then, for any $c > 0$, we get

$$\begin{aligned} F(t, c, c, \psi) &= F(t, c, c, \psi) - F(t, 0, c, \psi) \\ &\quad + F(t, 0, c, \psi) - F(t, 0, 0, \psi) + F(t, 0, 0, \psi) \\ &\leqq -(L_1 - M_1)c + F(t, 0, 0, \psi) \end{aligned}$$

namely $F(t, c, c, \psi)$ is negative for c large enough. Similarly we can see that $F(t, c, c, \psi)$ is positive for $-c$ large enough. This and the continuity of F imply the existence. To show the uniqueness assume that c, $\bar{c}$ satisfy $c \neq \bar{c}$ and $F(t, c, c, \psi) = 0 = F(t, \bar{c}, \bar{c}, \psi)$. Then we have

$$|F(t, c, c, \psi) - F(t, \bar{c}, c, \psi)| = |F(t, \bar{c}, \bar{c}, \psi) - F(t, \bar{c}, c, \psi)|$$

and by (A3)

$$L_1 |c - \bar{c}| \leqq M_1 |c - \bar{c}|,$$

which is impossible. Thus $c = \bar{c}$ and the lemma is proved.

Lemma 2.2. *Assume that in addition to the conditions of Lemma* 2.1, (A4) *is satisfied. Then for each* $t \in \boldsymbol{R}$ *there exists a unique pair* $(\xi(t), \eta(t)) \in \boldsymbol{R} \times \boldsymbol{R}$ *such that* (2.3), (2.4) *are satisfied.*

Proof. Set $\eta_1 = 0$ and for each $n = 1, 2, \cdots$ let $\xi_n = X(t, \eta_n)$ and $\eta_{n+1} = Y(t, \xi_n)$, where $X(t,\cdot)$, $Y(t,\cdot)$ satisfy (2.5), (2.6) respectively. Then we can easily see that for each $n=2, 3,\cdots$ it holds on one hand

$$|F(t, \xi_n, \xi_n, \eta_n)-F(t, \xi_{n-1}, \xi_n, \eta_n)| = |F(t, \xi_{n-1}, \xi_{n-1}, \eta_{n-1})-F(t, \xi_{n-1}, \xi_n, \eta_n)|$$

and so, by (A3),

$$(2.7)\qquad (L_1-M_1)|\xi_n-\xi_{n-1}| \leqq N_1|\eta_n-\eta_{n-1}|$$

and on the other hand

$$|G(t, \eta_{n+1}, \eta_{n+1}, \xi_n)-G(t, \eta_n, \eta_{n+1}, \xi_n)| = |G(t, \eta_n, \eta_n, \xi_{n-1})-G(t, \eta_n, \eta_{n+1}, \xi_n)|$$

and so, by (A3),

$$(2.8)\qquad (L_2-M_2)|\eta_{n+1}-\eta_n| \leqq N_2|\xi_n-\xi_{n-1}|\,.$$

Combining (2.7) and (2.8) we get

$$(2.9)\qquad |\eta_{n+1}-\eta_n| \leqq \theta|\eta_n-\eta_{n-1}|,\quad |\xi_{n+1}-\xi_n| \leqq \theta|\xi_n-\xi_{n-1}|$$

where

$$\theta = \frac{N_1\cdot N_2}{(L_1-M_1)(L_2-M_2)}\,,$$

which is less than 1, because of (A4). Now, (2.9) implies that (ξ_n), (η_n) are Cauchy sequences and thus they converge, say, to $\bar{\xi}$, $\bar{\eta}$ respectively. This proves the existence.

To prove the uniqueness assume that $\hat{\xi}$, $\hat{\eta}$ is another pair satisfying $F(t, \hat{\xi}, \hat{\xi}, \hat{\eta}) =0=G(t, \hat{\eta}, \hat{\eta}, \hat{\xi})$. Then we can easily verify that $|\hat{\xi}-\bar{\xi}|\leqq\theta|\hat{\xi}-\bar{\xi}|$ and $|\hat{\eta}-\bar{\eta}|\leqq \theta|\hat{\eta}-\bar{\eta}|$, which imply $(\hat{\xi}, \hat{\eta})=(\bar{\xi}, \bar{\eta})$. Put $\xi(t)=\bar{\xi}$ and $\eta(t)=\bar{\eta}$ and the lemma is proved.

Once the functions X, Y, ξ, η are found we make the following assumptions:

(A6) $(X(t, 0), Y(t, 0))$ converges, as $t\to+\infty$, to (X_0, Y_0), where $X_0>0$ and $Y_0<0$.

(A7) $(\xi(t), \eta(t))$ converges, as $t\to+\infty$, to (ξ_0, η_0), where $\xi_0>0$ and $\eta_0>0$.

(A8) $\liminf_{t\to+\infty} Y(t, X_0) > 0$.

Remark 2.1. The assumptions (A6)–(A8) are essential in characterizing (2.1)–(2.2) as a prey-predator model. To be more specific, $x(t)$ corresponds to the preys and $y(t)$ to the predators at each time t. We will see that the solution $(\xi(t), \eta(t))$ of (2.5), (2.6) is that quantity which attracts any positive path in the phase space of (2.1)–(2.2), as $t\to+\infty$, i.e. (ξ_0, η_0) will be the limit, as $t\to+\infty$, of any such a path.

3. Invariance of the positive quadrant and boundedness

For each $K>0$ we denote by $C_-(K)$ the set of all $\varphi\in C_-$ such that $0\leqq\varphi(s)\leqq K$, $s\leqq 0$ and $\varphi(0)>0$.

We shall show the following result:

Proposition 3.1. *Assume that* (A1), (A2) *hold and that* (2.1)–(2.2) *admits a solution* (x, y) *on* $t\geqq t_0$, *where* $(x_{t_0}, y_{t_0})\in C_-(K_1)\times C_-(K_2)$ *for some* $K_1>0$, $K_2>0$. *Then* $(x(t), y(t))\in(0, +\infty)\times(0, +\infty)$ *for each* $t>t_0$.

Proof. Let $t_1>t_0$ be fixed. By (A2) the function

$$\delta(t) = F(t, x(t), x_t, y_t), \quad t\in[t_0, t_1]$$

is continuous and thus there is a $\delta\in\boldsymbol{R}$ such that $\delta(t)\geqq\delta$, $t\in[t_0, t_1]$. Since x satisfies

$$\dot{x} = f(x)\delta(t) \quad \text{on} \quad (t_0, t_1]$$

it satisfies $x(t)\geqq z(t)$, $t\in[t_0, t_1]$, where z is a minimal solution of

$$\dot{z} = f(z)\delta, \quad z(t_0) = x(t_0) > 0.$$

Defining $w(t)=z(t_0+(t-t_0)/\delta)$, $t\in[t_0, t_0+\delta(t_1-t_0)]$ observe that w solves the initial value problem

$$\dot{w}(t) = f(w), \quad w(t_0) = x(t_0) > 0$$

on $(t_0, t_0+\delta(t_1-t_0)]$ and, by (A1), $w(t)>0$, $t\in[t_0, t_0+\delta(t_1-t_0)]$. This implies that $x(t)>0$ on $[t_0, t_1]$ and since t_1 is arbitrary it follows that $x(t)>0$ for all $t\geqq t_0$. The proof for y is similar.

We are now ready to show that any positive path for (2.1)–(2.2) in the phase space remains bounded for all $t\geqq t_0$.

Proposition 3.2. *Let f, F satisfy* (A1), (A2), (A3), (A5), *let g, G satisfy* (A1), (A2) *and let* (x, y) *be a solution of* (2.1)–(2.2) *on* $t\geqq t_0$, *with* $(x_{t_0}, y_{t_0})\in C_-(K)\times C_-(K)$, *for some* $K>0$. *Then there exists* $B_1>0$ *such that* $0<x(t)\leqq B_1$, *for all* $t\geqq t_0$.

Proof. The fact that $0<x(t)$, $t\geqq t_0$, has been proved above.

Assume that x is unbounded. This implies the existence of a sequence (t_n) such that $t_n\to+\infty$, $x(t_n)\to+\infty$, $x(s)<x(t_n)$ for $s<t_n$ and $\dot{x}(t_n)>0$. The last inequality implies that

$$F(t_n, x(t_n), x_{t_n}, y_{t_n}) > 0. \tag{3.1}$$

On the other hand we can see that

$$F(t_n, x(t_n), x_{t_n}, y_{t_n}) \leqq -(L_1-M_1)x(t_n) + \varepsilon_n \tag{3.2}$$

where

$$\varepsilon_n = F(t_n, 0, 0, y_{t_n}).$$

By (A5) and (A2) the sequence (ε_n) is bounded (above). Combining (3.1) and (3.2) we conclude that $(x(t_n))$ is bounded and thus x is bounded.

Proposition 3.3. *Let g, G satisfy* (A1), (A2), (A3) *and let* (x, y) *be a solution of* (2.1)–(2.2) *on* $t \geqq t_0$, *with* $(x_{t_0}, y_{t_0}) \in C_-(K) \times C_-(K)$, *for some* $K>0$. *If x is bounded on* $[t_0, +\infty)$ *then there is a* B_2 *such that* $0<y(t) \leqq B_2$ *for all* $t \geqq t_0$.

Proof. This goes as the proof of Proposition 3.2 where now boundedness of $G(t_n, 0, 0, x_{t_n})$ is coming from boundedness of x and (A2).

4. Preys without predators

We shall discuss what is the behavior of the prey species in the absence of predators. First we will show the following:

Proposition 4.1. *Assume that g, G satisfy* (A1) *and* (A2). *If* y $(\geqq 0)$ *solves* (2.2) *on* $t>t_0$ *for a certain continuous function* $x\colon \boldsymbol{R} \to \boldsymbol{R}$, *where* $y_{t_0} \in C_-(K)$ $(K>0)$ *and if* $y(t_1)=0$ *for a certain* $t_1>t_0$, *then* $y(t)=0$ *for all* $t \geqq t_1$.

Proof. Let (t_1, t_2) be a maximal interval (if such exists) such that $y(t_1)=0$ and $y(t)>0$ for $t \in (t_1, t_2)$. Fix a $\tau \in (t_1, t_2)$ and let δ_1, δ_2 be such that

$$\delta_1 \leqq G(t, y(t), y_t, x_t) \leqq \delta_2$$

for all $t \in [t_1, \tau]$. Then clearly y satisfies

$$z_1(t) \leqq y(t) \leqq z_2(t), \quad t \in [t_1, \tau] \tag{4.1}$$

where z_1 is a minimal solution of the problem $\dot{z}=g(z)\delta_1$, $z(t_1)=0$ and z_2 is a maximal solution of $\dot{z}=g(z)\,\delta_2$, $z(t_1)=0$. By (A1) we can easily see that $z_1(t)=z_2(t)=0$, $t \in [t_1, \tau]$, which, by (4.1), implies $y(t)=0$, $t \in [t_1, \tau]$. This shows that $y(t)=0$ for all $t \geqq t_1$ and the proof is complete.

Remark 4.1. The result of the preceding paragraph biologically means that if for a certain moment the species dies, then there does not exist any sourse of reproduction and thus death will be for all future over that.

Here is the place to refer to [7], where the behavior of one-species populations is discussed under the effect of seasonal variations. It is however expected that, whenever predatory do not exist, the (deterministic) environment of preys follows its biological evolution without exterior effects. In this case the preys approach the asymptotic carrying capacity of the environment. Under the assumption (A6) the asymptotic carrying capacity of the environment (in the absence of predators) is identified with the value X_0. Indeed, we have the following result:

Proposition 4.2. *Let assumptions* (A1), (A2), (A3), (A6) *be satisfied. If* (x, y) *is a solution of the system* (2.1)–(2.2) *on* $t \geqq t_0$ *such that* $x_{t_0}, y_{t_0} \in C_-(K)$, *for a certain* $K>0$, *and if* $y(t_1)=0$ *for a certain* $t_1>t_0$, *then, as* $t \to +\infty$, *the solution* x *of* (2.1) *converges to* X_0.

Proof. By Proposition 4.1 we have $y(t)=0$, $t \geqq t_1$; thus $y(t+s) \to 0$, as $t \to +\infty$, uniformly for all s in compact intervals. We shall show that

$$\lim_{t \to +\infty} X(t, y_t) = X_0 . \tag{4.2}$$

Indeed, letting $\varepsilon(t)=|F(t, X(t, 0), X(t, 0), y_t)-F(t, X(t, 0), X(t, 0), 0)|$, we observe that $\varepsilon(t) \to 0$, as $t \to +\infty$. On the other hand we get

$$|F(t, X(t, y_t), X(t, y_t), y_t)-F(t, X(t, 0), X(t, y_t), y_t)|$$
$$\leqq |F(t, X(t, 0), X(t, y_t), y_t)-F(t, X(t, 0), X(t, 0), y_t)| + \varepsilon(t).$$

By (A3) then we have

$$|X(t, y_t)-X(t, 0)| \leqq \frac{\varepsilon(t)}{L_1-M_1},$$

which in view of (A6) proves (4.2).

Define now a function H by the type

$$H(t, c, \varphi) = F(t, c, \varphi, y_t)$$

where y is the solution above. Thus, x satisfies

$$\dot{x} = f(x)H(t, x, x_t) \tag{4.3}$$

and $\sigma(t) \overset{\text{def}}{=\!=} X(t, y_t)$ satisfies $H(t, \sigma(t), \sigma(t))=0$, where, by the previous arguments, $\sigma(t) \to X_0>0$. Apply now the results of [7, Th. 3.2] and obtain that $x(t) \to X_0$ as $t \to +\infty$.

5. Predators without preys

The situation of the model is such that whenever preys do not exist the number of predators approaches zero as the time increases. Indeed, we have the following result:

Proposition 5.1. *Let the assumptions* (A1), (A2), (A3), (A6) *be satisfied. If* (x, y) *is a solution of the system* (2.1)–(2.2) *on* $t \geqq t_0$ *such that* $x_{t_0}, y_{t_0} \in C_-(K)$ *for a certain* $K>0$, *and if* $x(t_1)=0$ *for a certain* $t_1>t_0$, *then* $x(t)=0$, $t \geqq t_1$, *and the solution* $y(t)$ *of* (2.2) *approaches zero, as* $t \to +\infty$.

Proof. The fact that $x(t)=0$, $t \geqq t_1$, can be proved if we will follow the steps of Proposition 4.1. Thus $x(t+s) \to 0$, as $t \to +\infty$, uniformly for all s in compact intervals of $\boldsymbol{R}$. In particular x is bounded and so, by Proposition 3.3, y is bounded and positive.

Assume that $\limsup_{t \to +\infty} y(t) \equiv r$. We have to show that $r=0$, which will imply that $\lim_{t \to \infty} y(t)=0$.

Indeed, let $r>0$. By (2.2) $\dot{y}$ is bounded and thus y is uniformly continuous and bounded on $[t_0, +\infty)$. By Arzelà-Ascoli Theorem there exists a function $\bar{y}\colon \boldsymbol{R} \to \boldsymbol{R}$ such that $\bar{y}(0)=r$, and for some sequence $t_n \to +\infty$, $y(t_n+s) \to \bar{y}(s)$, uniformly for all s in compact intervals of $\boldsymbol{R}$. By (A2), the sequence (t_n) produces a limiting equation of (2.2), which is of the form

$$\dot{z} = g(z)\bar{G}(t, z, z_t, 0)$$

and it is satisfied by $\bar{y}(t)$, for all $t \in \boldsymbol{R}$. Since $r=\bar{y}(0)$ is maximal we have $\dot{\bar{y}}(0)=0$ and since $\bar{y}(0)>0$ it follows that

$$\bar{G}(0, \bar{y}(0), \bar{y}_0, 0) = 0. \tag{5.1}$$

Notice that $\bar{G}$ is a function satisfying (A2) and (A3) with the same constant coefficients L_2, M_2, N_2 (More facts about the limiting equations theory for general causal operator equations can be found e.g. in Karakostas [8], Markus and Mizel [11]).

On the other hand we can see that

$$\bar{G}(0, Y_0, Y_0, 0) = 0 \tag{5.2}$$

where Y_0 is the constant appearing in assumption (A6). Recall that $Y_0<0$ and so

$$|Y_0 - \bar{y}(0)| = \|Y_0 - \bar{y}_0\|. \tag{5.3}$$

Now, from (5.1) and (5.2) we observe that

$$|\bar{G}(0, \bar{y}(0), \bar{y}_0, 0) - \bar{G}(0, Y_0, \bar{y}_0, 0)| = |\bar{G}(0, Y_0, Y_0, 0) - \bar{G}(0, Y_0, \bar{y}_0, 0)|$$

which, by (A3), gives

$$L_2|Y_0 - \bar{y}(0)| \leqq M_2\|Y_0 - \bar{y}_0\|. \tag{5.4}$$

Since $L_2>M_2$, (5.4) leads to a contradiction because of (5.3). The proof is finished.

6. Boundedness away from zero

What is going on to be shown here is that the (positive) solutions for (2.1)–(2.2) stay away from zero as the time increases. First we need the following lemma:

Lemma 6.1. *Assume that F, G are continuous and satisfy the conditions* (A3), (A4), (A6), (A8). *Then there exists an $\varepsilon>0$ such that for all large t*

$$F(t, 0, 0, 0) \geqq \varepsilon \quad \textit{and} \quad G(t, 0, 0, X_0) \geqq \varepsilon.$$

Proof. For all large t we have $X(t, 0) \geqq (1/2)X_0 \equiv a_1$ and $Y(t, X_0) \geqq (1/2) \liminf_{t\to+\infty} Y(t, X_0) \equiv a_2$. Taking any $\varepsilon>0$ with $\varepsilon \leqq \min\{(L_i - M_i)a_i$: $i=1, 2\}$, we get on one hand that

$$\begin{aligned} F(t, 0, 0, 0) &= F(t, 0, 0, 0) - F(t, X(t, 0), 0, 0) \\ &\quad + F(t, X(t, 0), 0, 0) - F(t, X(t, 0), X(t, 0), 0) \\ &\geqq L_1 X(t, 0) - M_1 X(t, 0) \geqq (L_1 - M_1)a_1 \geqq \varepsilon \end{aligned}$$

and on the other hand that

$$\begin{aligned} G(t, 0, 0, X_0) &= G(t, 0, 0, X_0) - G(t, Y(t, X_0), 0, X_0) \\ &\quad + G(t, Y(t, X_0), 0, X_0) - G(t, Y(t, X_0), Y(t, X_0), X_0) \\ &\geqq L_2 Y(t, X_0) - M_2 Y(t, X_0) \geqq (L_2 - M_2)a_2 \geqq \varepsilon, \end{aligned}$$

for all large t.

Proposition 6.2. *Assume the conditions* (A1)–(A6) *and* (A8) *hold and let $(x(t), y(t))$, $t \geqq t_0$, be a solution of* (2.1)–(2.2) *with $(x_{t_0}, y_{t_0}) \in C_-(K) \times C_-(K)$ for some $K>0$. Then there is a real number $\eta>0$ such that $x(t) \geqq \eta$ and $y(t) \geqq \eta$ for all $t \geqq t_0$.*

Proof. We shall show first that $\liminf_{t\to+\infty} x(t) > 0$. Indeed, let us assume that $\liminf_{t\to+\infty} x(t) = 0$. (Notice that $x(t)>0$, $t \geqq t_0$, because of Proposition 3.1.). This means that $x(t_k) \to 0$, for some sequence $t_k \to +\infty$. We can assume that $\dot{x}(t_k) \leqq 0$.

Since x and y are uniformly continuous and bounded functions, there exist x^*, y^*: $\boldsymbol{R} \to \boldsymbol{R}$ and a subsequence $(t_{n(k)})$ of (t_k) such that $x(t_{n(k)}+t) \to x^*(t)$ and $y(t_{n(k)}+t) \to y^*(t)$ uniformly for all t in compact intervals of $\boldsymbol{R}$. The sequence $(t_{n(k)})$ produces limiting equations

$$\dot{u} = f(u)F^*(t, u, u_t, v_t), \quad \dot{v} = g(v)G^*(t, v, v_t, u_t) \tag{6.1}$$

satisfied for $u=x^*$ and $v=y^*$ on all of $\boldsymbol{R}$. But $x^*(0)=0$, so that $x^*(t)=0$, $t\in\boldsymbol{R}$ because of (A1). Thus y^* satisfies

$$\dot{y}^* = g(y^*)G^*(t, y^*, y_t^*, 0), \quad t\in\boldsymbol{R}.$$

Since G^* satisfies (A2) and (A3) with the same constants L_2, M_2, N_2, from Proposition 5.1 we get that $y^*(t)\to 0$, as $t\to+\infty$.

By Lemma 6.1 and the continuity condition on F there exist $\delta>0$ and $r\geqq t_0$ such that if z, w satisfy $\rho(z_t, 0)\leqq\delta$ and $\rho(w_t, 0)\leqq\delta$, $t\geqq r$, then $F(t, z, z_t, w_t)\geqq\varepsilon/2$, where $\varepsilon>0$ is sufficiently small. By the definition of the ρ metric there exist $T>0$ and $\eta_1>0$ such that $\varphi\in C_-$ and $|\varphi(s)|\leqq\eta_1$, $s\in[-T, 0]$, implies $\rho(\varphi, 0)\leqq\delta$.

Since $y^*(t)\to 0$, as $t\to+\infty$, there is a t_1 such that $0<y^*(t)\leqq\eta_1/2$, $t\geqq t_1$. Thus there is an index k_1 such that $0<y(t_{n(k)}+t)\leqq\eta_1$, $k\geqq k_1$, $t\in[-T, 0]$. For the same reason we can assume that $0<x(t_{n(k)}+t)\leqq\eta_1$, $k\geqq k_1$ and $t\in[-T, 0]$. Therefore we have $\rho(x_{t_{n(k)}}, 0)\leqq\delta$ and $\rho(y_{t_{n(k)}}, 0)\leqq\delta$, $k\geqq k_1$. This implies that

$$F(t_{n(k)}, x(t_{n(k)}), x_{t_{n(k)}}, y_{t_{n(k)}}) \geqq \frac{\varepsilon}{2}, \quad k\geqq k_1$$

and so

$$\dot{x}(t_{n(k)}) \geqq \frac{\varepsilon}{2} f(x(t_{n(k)})) > 0, \quad k \geqq k_1 .$$

This contradicts the fact that $\dot{x}(t_{n(k)})\leqq 0$ and so $\liminf_{t\to+\infty} x(t)>0$. By Proposition 3.1 we have $x(t)>0$, $t\geqq t_0$, so that an $\eta>0$ exists with $x(t)\geqq\eta$, $t\geqq t_0$.

We shall show that $\liminf_{t\to+\infty} y(t)>0$. Indeed, assume that $\liminf_{t\to+\infty} y(t)=0$. Thus again as in the case above we have $y(t_k)\to 0$, for some sequence $t_k\to+\infty$, for which we can assume that $\dot{y}(t_k)\leqq 0$. Again, as above, there are functions x^*, y^*: $\boldsymbol{R}\to\boldsymbol{R}$ and a subsequence $(t_{n(k)})$ of (t_k) such that $x(t_{n(k)}+t)\to x^*(t)$ and $y(t_{n(k)}+t)\to y^*(t)$, uniformly for all t in compact intervals of $\boldsymbol{R}$. The sequence $(t_{n(k)})$ produces limiting equations (6.1) satisfied for $u=x^*$ and $v=y^*$ on all of $\boldsymbol{R}$. But $y^*(0)=0$, so that $y^*(t)=0$, $t\in\boldsymbol{R}$, because of (A1). Thus x^* satisfies

$$\dot{x}^* = f(x^*)F^*(t, x^*, x_t^*, 0).$$

Since F^* satisfies (A2) and (A3) with the same constants L_1, M_1, N_1, from Proposition 4.2 and the fact that $\lim X(t_{n(k)}+t, 0)=X_0$, we conclude that $x^*(t)\to X_0$ as $t\to+\infty$.

By Lemma 6.1 and the continuity condition on G we get a $\delta>0$ and $r\geqq t_0$ such that if z, w satisfy $\rho(z_t, 0)<\delta$ and $\rho(w_t, X_0)<\delta$, $t\geqq r$, then $G(t, z, z_t, w_t)\geqq\varepsilon/2$. Now, the proof goes as above in the case of x. Finally we obtain

$$\dot{y}(t_{n(k)}) \geqq \frac{\varepsilon}{2} g(y(t_{n(k)})) > 0,$$

for all large k, which contradicts the hypothesis that $\dot{y}(t_{n(k)}) \leqq 0$. This completes the proof of the proposition.

7. Global convergence

We shall provide in this section the main result of this work, given in the following theorem.

7.1. Theorem. *Let the conditions* (A1)–(A8) *hold. If* (ξ_0, η_0) *is the pair of real numbers appearing in* (A7), *then any solution* $(x(t), y(t))$, $t \geqq t_0$, *of* (2.1)–(2.2), *with* $(x_{t_0}, y_{t_0}) \in C_-(K) \times C_-(K)$ *for some* $K > 0$, *has the property that*

$$\lim_{t \to +\infty} (x(t), y(t)) = (\xi_0, \eta_0).$$

Proof. Let (x, y) be a solution of (2.1)–(2.2) on $(t_0, +\infty)$, with $(x_{t_0}, y_{t_0}) \in C_-(K) \times C_-(K)$, for some $K > 0$. Then by Propositions 3.1 and 6.2 the functions x, y are both positive bounded and stay away from zero.

Let $\bar{\xi} = \limsup_{t \to +\infty} x(t)$. Then there are functions $\bar{x}$: $\boldsymbol{R} \to \boldsymbol{R}$, y': $\boldsymbol{R} \to \boldsymbol{R}$ and a sequence (t_k) with $t_k \to +\infty$ such that $\bar{x}(0) = \bar{\xi}$ and $x(t_k + t) \to \bar{x}(t)$, $y(t_k + t) \to y'(t)$, uniformly for all t in compact intervals. The sequence (t_k) produces a limiting equation

$$\dot{u} = f(u) F^*(t, u, u_t, y'_t)$$

satisfied by $\bar{x}$. But $\dot{\bar{x}}(0)$ must be zero because of maximality of $\bar{x}(0)$, so that

$$F^*(0, \bar{x}, \bar{x}_0, y'_0) = 0. \tag{7.1}$$

On the other hand we see that

$$F^*(0, \xi_0, \xi_0, \eta_0) = 0.$$

This and (7.1) give

$$\begin{aligned} &F^*(0, \bar{\xi}, \bar{x}_0, y'_0) - F^*(0, \xi_0, \bar{x}_0, y'_0) \\ &\quad = F^*(0, \xi_0, \xi_0, \eta_0) - F^*(0, \xi_0, \bar{x}_0, y'_0) \end{aligned}$$

which, in view of (A3), implies that

$$L_1 |\bar{\xi} - \xi_0| \leqq M_1 \|\xi_0 - \bar{x}_0\| + N_1 \|\eta_0 - y'_0\|. \tag{7.2}$$

Similarly we obtain that

$$L_1 |\underline{\xi} - \xi_0| \leqq M_1 \|\xi_0 - \underline{x}_0\| + N_1 \|\eta_0 - y''_0\| \tag{7.3}$$

where $\underline{x}$: $\boldsymbol{R} \to \boldsymbol{R}$, $\underline{x}(0) = \underline{\xi} = \liminf_{t \to +\infty} x(t)$ and $x(t_\ell + t) \to \underline{x}(t)$, $y(t_\ell + t) \to y''_0(t)$, uniformly for t in compact intervals, for some sequence $t_\ell \to +\infty$.

For y we obtain similar relations, i.e.

(7.4) $$L_2|\bar{\eta}-\eta_0| \leqq M_2\|\eta_0-\bar{y}_0\| + N_2\|\xi_0-x_0'\|$$

and

(7.5) $$L_2|\underline{\eta}-\eta_0| \leqq M_2\|\eta_0-\underline{y}_0\| + N_2\|\xi_0-x_0''\|,$$

where $\underline{y}$, $\bar{y}: \boldsymbol{R}\to\boldsymbol{R}$, $\underline{y}(0)=\underline{\eta}=\liminf_{t\to+\infty} y(t)$, $\bar{y}(0)=\bar{\eta}=\limsup_{t\to+\infty} y(t)$, $y(t_m+t)\to\underline{y}(t)$, $\underline{y}(t_n+t)\to\bar{y}(t)$, $x(t_m+t)\to x'(t)$, $x(t_n+t)\to x''(t)$, uniformly in compact intervals of the real line, for some sequences $t_m\to+\infty$ and $t_n\to+\infty$.

Now we distinguish the following four cases:

Case 1. $\xi_0 \geqq \frac{1}{2}(\bar{\xi}+\xi)$, $\eta_0 \geqq \frac{1}{2}(\bar{\eta}+\eta)$:

Then we have $|\underline{\xi}-\xi_0|=\|\underline{x}_0-\xi_0\|\geqq\|x_0''-\xi_0\|$ and $|\underline{\eta}-\eta_0|=\|\underline{y}_0-\eta_0\|\geqq \|y_0''-\eta_0\|$ and so by (7.3), (7.5) obtain

$$(L_1-M_1)|\underline{\xi}-\xi_0| \leqq N_1|\underline{\eta}-\eta_0|, \quad (L_2-M_2)|\underline{\eta}-\eta_0| \leqq N_2|\underline{\xi}-\xi_0|,$$

which give $\underline{\xi}=\xi_0$ and $\underline{\eta}=\eta_0$ because of (A4). Thus $\liminf_{t\to+\infty} x(t)=\xi_0= \limsup_{t\to+\infty} x(t)$ and $\liminf_{t\to+\infty} y(t)=\eta_0=\limsup_{t\to+\infty} y(t)$, that is $x(t)\to\xi_0$ and $y(t)\to\eta_0$, as $t\to+\infty$.

Case 2. $\xi_0 \geqq \frac{1}{2}(\bar{\xi}+\xi)$, $\eta_0 < \frac{1}{2}(\bar{\eta}+\eta)$:

Then $|\underline{\xi}-\xi_0|=\|\underline{x}_0-\xi_0\|\geqq\|x_0'-\xi_0\|$ and $|\bar{\eta}-\eta_0|=\|\bar{y}_0-\eta_0\|\geqq\|y_0''-\eta_0\|$. So, by (7.3), (7.4) obtain

$$(L_1-M_1)|\underline{\xi}-\xi_0| \leqq N_1|\bar{\eta}-\eta_0|, \quad (L_2-M_2)|\bar{\eta}-\eta_0| \leqq N_2|\underline{\xi}-\xi_0|,$$

which, in view of (A4), imply $\lim_{t\to+\infty} x(t)=\xi_0$ and $\lim_{t\to+\infty} y(t)=\eta_0$.

Case 3. $\xi_0 < \frac{1}{2}(\bar{\xi}+\underline{\xi})$ and $\eta_0 < \frac{1}{2}(\bar{\eta}+\underline{\eta})$:

Then $|\bar{\xi}-\xi_0|=\|\bar{x}_0-\xi_0\|\geqq\|x_0'-\xi_0\|$ and $|\bar{\eta}-\eta_0|=\|\bar{y}-\eta_0\|\geqq\|y_0'-\eta_0\|$. We use (7.2), (7.4) as above to get $\lim_{t\to+\infty}(x(t), y(t))=(\xi_0, \eta_0)$.

Case 4. $\xi_0 < \frac{1}{2}(\bar{\xi}+\underline{\xi})$ and $\eta_0 \geqq \frac{1}{2}(\bar{\eta}+\underline{\eta})$:

Similarly, by (7.2), (7.5) we conclude that $\lim_{t\to+\infty}(x(t), y(t))=(\xi_0, \eta_0)$ and the proof is complete.

Example A. Consider the system

$$\dot{x} = x^a(3-x(t)-y(t-1))$$
$$\dot{y} = y^b\Big(-2+\frac{4}{5}x(t)-y(t)-\int_{t-1}^{t} e^{-(t-s)}y(s)ds\Big)$$

where $a \geqq 1$, $b \geqq 1$. Applying the results of our theorem above we conclude that the point $((35e-15)/(14e-5),\ 2e/(14e-5))$ is the carrying capacity of the system, i.e., this is the point to which all positive paths converge.

Example B. Consider the nonlinear nonautonomous system

$$\dot{x} = x^a\Big(3-x(t)-\frac{y(t-1)}{1+y^2(t-1)}\Big)$$
$$\dot{y} = y^b\Big(-1+\frac{3+e^{-t}}{5}x(t)-y(t)-\int_{-\infty}^{t} e^{-(t-s)}y(s)ds\Big)$$

where $a \geqq 1$, $b \geqq 1$. If p is the unique real root of the cubic equation $r^3+(1663/1225)r-(15584/42875)=0$, then we can easily see that, the point $(19/9+35p/18,\ 8/35+p)$ is the limit as $t \to +\infty$ of any positive solution $(x(t),\ y(t))$.

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