GLOBAL STABILITY FOR A STAGE-STRUCTURED PREDATOR-PREY MODEL

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Abstract

The asymptotic behavior of a stage-structured predator-prey system is studied using the theory of finite dimensional competitive systems. Using natural conditions on the persistency constant for prey and on the reproduction rate of the mature predators, it is found that the system under consideration has a unique positive equilibrium, which is globally asymptotically stable. Some considerations on the uniform persistency of the system are also included.

Key words: Stage structure, predator-prey model, global stability, competitive systems, orbital stability, uniform persistence, positive equilibrium.
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1 Introduction

The age factors are important for the dynamics and evolution of many mammals. The rates of survival, growth and reproduction almost always depend heavily on age or developmental stage and it has been noticed that the life history of many species is composed of at least two stages, immature and mature, with significantly different morphological and behavioral characteristics.

The study of stage-structured predator-prey systems has attracted considerable attention in recent years, as a way to overcome the limitations of classical Lotka-Volterra models. Magnusson studied in [15] the destabilizing effect of cannibalism in a predator-prey system in which mature predators prey upon both immature predators and prey individuals. Chen established in [3] the existence of positive periodic solutions for a delayed non-autonomous ratio-dependent predator-prey system with stage structure for predator with the help of coincidence degree theory. Wang [22] and Xiao and Chen [24] studied the global stability of a stage-structured predator-prey system using the theory of competitive systems, while the model in Wang and Chen [23] accounted also for the effect of the delay caused by the crowding of the prey. A comprehensive survey of recent progress in stage structured models, with emphasis on modelling issues, can be found in Liu, Chen and Agarwal [12].

In [22], Wang considered the following predator-prey model with stage structure for predator, in which the immature predators can neither hunt nor reproduce

$$\begin{cases} x'(t) = x(t)\left(r - ax(t)\right) - \dfrac{bx(t)}{1+mx(t)} y_2(t), \\ y_1'(t) = k\dfrac{bx(t)}{1+mx(t)} y_2(t) - (D+d_1)y_1(t), \\ y_2'(t) = Dy_1(t) - d_2 y_2(t). \end{cases} \tag{1.1}$$

Here, $x(t)$ denotes the density of prey at time t, while the densities of immature and mature predators are denoted by $y_1(t)$, respectively by $y_2(t)$. The functional response of the mature predator is characterized by the Holling type II function $x \mapsto bx/(1+mx)$, b being the search rate and m being the search rate multiplied by the handling time. It is assumed that the reproduction rate of the mature predator depends on the quantity of prey consumed, the conversion efficiency of prey into newborn immature predators being denoted by k. It is assumed that the predators become mature after a fixed age. In this respect, D denotes the rate at which immature predators become mature predators, that is, $1/D$ represents the total time spent by a predator in its immature stage. Also, the mortality rates of immature, respectively mature predators are denoted by d_1, respectively by d_2.

It has been proved in [22], among other results, that if

$$d_2(D+d_1) < \frac{kbrD}{a+mr}, \tag{1.2}$$

then there is a unique positive endemic equilibrium $E^* = (x^*, y_1^*, y_2^*)$. By using the first approximation method, Wang also proved that the positive equilibrium E^* is locally asymptotically stable provided that the following inequality holds

$$\begin{aligned} x^*(D+d_1+d_2)(a+2max^*-mr)\left(D+d_1+d_2+\frac{x^*(a+2max^*-mr)}{1+mx^*}\right) \\ > \frac{by_2^* d_2(D+d_1)}{1+mx^*}. \end{aligned} \tag{1.3}$$

It has also been shown in [22] that the positive equilibrium E^* is globally asymptotically stable if the following set of inequalities hold

$$a > b + \frac{bmy_2^*}{1+mx^*}, \quad D+d_1 > \frac{kbr}{a+mr} + \frac{kby_2^*}{1+mx^*}, \quad d_2 > D. \tag{1.4}$$

However, it has been observed by Xiao and Chen in [24] that the last two inequalities in condition (1.4) contradict condition (1.2). Incidentally, let us note here that the same applies to relations (2.2) and (4.1) in Wang and Chen [23], albeit in a slightly different form. Xiao and Chen also proved that E^* is globally asymptotically stable provided that (1.3) and (1.2) hold, together with one of the following two assumptions

$$\text{(H1) } D+d_1 > r \text{ and } \underline{x} > \frac{r}{2a}; \qquad \text{(H2) } D+d_1 < r \text{ and } \underline{x} > \frac{r+D+d_1}{2a},$$

where $\underline{x}$ is such that $\underline{x} \le \liminf_{t\to\infty} x(t)$. Their proof is based on the theory of three-dimensional competitive systems and amounts to showing that (1.1) has the property of stability of periodic orbits. Combined with the uniqueness of the positive equilibrium and its local asymptotic stability, this yields that the positive equilibrium is actually globally asymptotically stable.

It has been proved in Georgescu and Hsieh [7] by using Lyapunov functionals and LaSalle's invariance principle rather than by employing competitive systems theory, as done in [22] and [24], that conditions $\underline{x} > r/(2a)$ and (1.2) are actually sufficient for the global asymptotic stability of (1.1) and that (1.3) follows once $\underline{x} > r/(2a)$ holds.

In the following, we shall employ the theory of competitive systems and Muldowney's necessary and sufficient condition for the orbital stability of a periodic orbit, as done in [24], and obtain the global stability of the positive equilibrium for a system which is slightly more general than the one studied in [22] and [24], under a natural persistency condition and a condition on the reproduction rate of the prey. We shall also provide a different persistency argument, based on the use of Lyapunov-like functionals, as opposed to the study of the flow near the boundary, which was the method employed in [22].

2 The local stability of the positive equilibrium

In the following, we consider the system

$$\begin{cases} x'(t) = n(x(t)) - f(x(t))y_2(t), \\ y_1'(t) = kf(x(t))y_2(t) - (D + d_1)y_1(t), \\ y_2'(t) = Dy_1(t) - d_2y_2(t), \end{cases} \tag{2.1}$$

under the following hypotheses

(H1) $f \in C^1([0,\infty),[0,\infty))$, $f(0) = 0$, f is strictly increasing on $[0,\infty)$.

(H2) (a) $n \in C^1([0,\infty),\mathbb{R})$
  (b) $n(x) = 0$ if and only if $x \in \{0, x_0\}$, with $x_0 > 0$ and $n(x) > 0$ for $x \in (0, x_0)$.
  (c) n is strictly decreasing on $[x_P,\infty)$, $0 < x_P < x_0$.

The significance of the functions x, y_1, y_2 and of the parameters k, D, d_1, d_2 is the same as in (1.1). Note that (H1) is satisfied for some usual examples of predator functional response, namely for $f(x) = bx^p/(1+mx^p)$, $0 < p \leq 1$, that is, the generalized type II Holling functional response (Holling, [10]) and $f(x) = k(1 - e^{-cx})$ (Ivlev, [11]). Also, (H2) is satisfied for some commonly used examples of growth functions n, namely for $n(x) = x(1 - (x/K))$, that is, the classical logistic growth, for $n(x) = x(1 - (x/K)^\theta)$, $\theta \in (0, 1]$, that is, the generalized logistic growth (Richardson [18]) and for $n(x) = x(re^{1-(x/K)} - d)$ (Nisbet and Gurney, [16]). As in Aiello and Freedman [1], it is assumed that the immature predators are either raised by their mature parents or grow on an abondant nutrient for which they do not have to compete with adults and consequently neither crowding terms nor intra-species competition terms are added for predators.

Under these circumstances, it is easy to see that if $x(0)$, $y_1(0)$, $y_2(0) \geq 0$, then $x(t), y_1(t), y_2(t) \geq 0$ on their respective intervals of existence. Namely, it can be noted that the vector (R_1, R_2, R_3) points inside $Q = [0,\infty)^3$ at all points of ∂Q, where R_1, R_2, R_3 are the right-hand sides appearing in (2.1), so Nagumo's tangency conditions are satisfied. See [17] for details.

It can also be proved that $(0,\infty)^3$ is a positively invariant sent for (2.1). To this purpose, suppose that $x(0), y_1(0), y_2(0) > 0$ and note that $\frac{d}{dt}(y_2e^{d_2t}) = Dy_1e^{d_2t} \geq 0$. It follows that $t \mapsto y_2(t)e^{d_2t}$ is increasing and consequently y_2 is strictly positive. Similarly, $t \mapsto y_1(t)e^{(D+d_1)t}$ is increasing and consequently y_1 is strictly positive. The strict positivity of x can now be proved by a uniqueness argument. Namely, suppose that $x(t_0) = 0$ for some $t_0 > 0$. Then the solution which starts from $(0, y_1(t_0), y_2(t_0))$ at $t = t_0$ should coincide with the solution starting from $(x(0), y(0), z(0))$ at $t = 0$, which is obviously a contradiction.

Since $x' \leq n(x)$, it follows that $x(t) \leq \max(x(0), x_0)$ for all t, which insures the boundedness of x. Let us also define $F(x, y_1, y_2) = x + (1/k)y_1 + (1/k)y_2$. Computing the derivative of F along the solutions of (2.1), we obtain that

$$\dot{F} + dF \leq n(x) + dx,$$

where $d = \min(d_1, d_2)$, and so

$$\begin{aligned} F(x(t), y_1(t), y_2(t)) \leq{}& F(x(0), y_1(0), y_2(0))e^{-dt} \\ &+ (n_M + d\max(x(0), x_0))\,\frac{1 - e^{-dt}}{d}, \end{aligned}$$

for all t, where n_M is a boundedness constant for n on $[0, \max(x(0), x_0)]$, that is, on the boundedness interval for x. It follows that x, y_1, y_2 are bounded and consequently, from basic ODE theory, they are defined on all $[0, \infty)$. This means that the system (2.1) is well-defined in a biological (and mathematical) sense. Regarding the behavior of the solutions which start on the boundary of $[0, \infty)^3$, it is easy to see that the solutions which start in the plane y_1Oy_2 tend to the origin while remaining in the plane y_1Oy_2 (obviously, this case is mathematically significant only, as no initial prey population exists), the solutions which start on the semiaxis Ox tend to $(x_0, 0, 0)$, while all other solutions starting on the boundary enter $(0, \infty)^3$.

Moreover, following the lines of Georgescu and Hsieh [7, Theorems 3.1 and 3.2], it is possible to show that $T = d_2(D + d_1)/D$ is a threshold parameter for the stability of (2.1), in the sense that if $d_2(D+d_1)/D \geq kf(x_0)$, then the predator classes tend to extinction and the unique prey-only equilibrium $(x_0, 0, 0)$ is globally asymptotically stable on $(0, \infty)^3$, while if the reverse inequality is satisfied, then the prey-only equilibrium becomes unstable and there is a unique positive equilibrium (x^*, y_1^*, y_2^*). As the dynamics of the system in the case $d_2(D + d_1)/D \geq kf(x_0)$ is now completely determined, we shall assume for the rest of the paper that the reverse inequality is satisfied, that is,

$$d_2(D + d_1)/D < kf(x_0). \tag{2.2}$$

Note that if we define the basic reproduction number of the predator population as

$$R_0 = kf(x_0) \cdot \frac{1}{d_2} \cdot \frac{D}{D + d_1},$$

by analogy with the considerations indicated in [21] for differential systems arising in epidemiology, then (2.2) can simply be rewritten as $R_0 > 1$.

Here, $1/d_2$ represents the time spent by a predator into the mature stage (the only one in which the predators can hunt and consume prey) and $D/(D + d_1)$ represents the fraction of immature predators which survive to the mature stage. As $f(x_0)$ represents the functional response of the mature predators introduced into a prey-only population at carrying capacity of the environment and k measures the efficience of the conversion of prey into new immature predators, the significance of R_0 is quite clear: R_0 represents the average number of offsprings produced by a predator during its lifetime. Of course, if $R_0 > 1$, that is, if few mature predators introduced in a prey population at carrying capacity have the capability to reproduce fast enough, then the survival of the predator population is guaranteed, so the prey-only equilibrium is unstable.

We first attempt to characterize the local stability of (2.1) at (x^*, y_1^*, y_2^*). It is easy to see that the Jacobian matrix of (2.1) at a generic point (x, y_1, y_2) is given by

$$J_{(2.1)}(x, y_1, y_2) = \begin{pmatrix} n'(x) - f'(x)y_2 & 0 & -f(x) \\ kf'(x)y_2 & -(D + d_1) & kf(x) \\ 0 & D & -d_2 \end{pmatrix}. \tag{2.3}$$

Moreover, the coordinates x^*, y_1^*, y_2^* of the equilibrium point E^* verify the following equilibrium relations

$$\begin{cases} n(x^*) = f(x^*)y_2^*, \\ kf(x^*)y_2^* = (D + d_1)y_1^*, \\ Dy_1^* = d_2y_2^*. \end{cases}$$

From the above equilibrium relations, it follows that the characteristic equation at (x^*, y_1^*, y_2^*) is given by

$$\begin{aligned} &\lambda^3 + [(D + d_1 + d_2) + f'(x^*)y_2^* - n'(x^*)]\,\lambda^2 \\ &\quad + \lambda\,[(D + d_1 + d_2)(f'(x^*)y_2^* - n'(x^*))] + (D + d_1)d_2f'(x^*)y_2^* = 0. \end{aligned} \tag{2.4}$$

By the Routh-Hurwitz theorem, all roots of (2.4) have negative real parts if

$$\begin{aligned}&[(D+d_1+d_2)+f'(x^*)y_2^*-n'(x^*)]\,[(D+d_1+d_2)(f'(x^*)y_2^*-n'(x^*))]\\&\qquad > (D+d_1)d_2f'(x^*)y_2^*,\end{aligned} \tag{2.5}$$

while if the reverse of (2.5) is satisfied, then two characteristic roots have positive real parts. Note that if $x^* > x_P$, then $n'(x^*) < 0$ and consequently

$$\begin{aligned}&[(D+d_1+d_2)+f'(x^*)y_2^*-n'(x^*)]\,[(D+d_1+d_2)(f'(x^*)y_2^*-n'(x^*))]\\&\qquad > (D+d_1+d_2)^2f'(x^*)y_2^*\\&\qquad \geq 4(D+d_1)d_2f'(x^*)y_2^*,\end{aligned}$$

so (2.5) is satisfied if the inequality $x^* > x_P$ holds and consequently any positive equilibrium $E^* = (x^*, y_1^*, y_2^*)$ for which $x^* > x_P$ is locally asymptotically stable.

3 The uniform persistence of the system

Let $\underline{x}$ such that $\liminf_{t\to\infty} x(t) \geq \underline{x}$. We now prove that if $\underline{x} > x_P$, then (2.1) is uniformly persistent, that is, there are $m, M \in (0,\infty)$ such that

$$m \leq \liminf_{t\to\infty} \varphi(t) \leq M \qquad \text{for } \varphi \in \{x, y_1, y_2\}\,.$$

From a biological viewpoint, it is clear that the uniform persistence of the system insures the survival of all populations, which reach in the long term at least a certain numerical level not depending on the initial population sizes. Let us denote

$$h = n/f|_{[x_P,\infty)}\,.$$

It is easy to see that $h(x_0) = 0$ and h is strictly decreasing on $[x_P, +\infty)$. We start by proving a quantitative property of the solutions of (2.1).

Lemma 3.1. *For all $\rho > 0$ small enough, if*

$$\limsup_{t\to\infty} y_2(t) \leq \rho$$

then

$$\liminf_{t\to\infty} x(t) \geq h^{-1}(\rho).$$

Proof. It is seen that

$$\begin{aligned}x'(t) &= f(x(t))\left[\frac{n(x(t))}{f(x(t))} - y_2\right]\\&\geq f(x(t))\,[h(x(t)) - (\rho+\varepsilon)]\end{aligned}$$

for t large enough and $\varepsilon > 0$ arbitrary. The conclusion follows easily, if ρ is chosen small enough, so that h is well-defined. □

We now introduce a few notions regarding the persistence of a semidynamical system. Let π_1 be a semidynamical system defined on a closed subset F of a locally compact metric space (X, d).

Definition 3.1. *It is said that a subset S of F is a uniform repeller if there is $\eta > 0$ such that for each $x \in F\backslash S$, $\liminf_{t\to\infty} d(\pi_1(x,t), S) > \eta$.*

Of course, the semidynamical system is then uniformly persistent if the boundary of F is a uniform repeller. We now state an elegant result of Fonda ([6, Corollary 1]) about uniform repellers for semidynamical systems on abstract metric spaces.

Theorem 3.2. *Let π be a semidynamical system defined on a locally compact metric space X and let S be a compact subset of X such that $X\backslash S$ is positively invariant. A necessary and sufficient condition for S to be a uniform repeller is that there exists a neighborhood U of S and a continuous function $P : X \to \mathbb{R}_0^+$ satisfying*

1. *$P(x) = 0$ if and only if $x \in S$.*
2. *For all $x \in U\backslash S$ there is a $T_x > 0$ such that $P(\pi(x, T_x)) > P(x)$.*

Using the above result, it is possible to prove that the set $B = \big\{(x, y_1, y_2) \in [0, M]^3; y_2 = 0\big\}$ is a uniform repeller, where M is a suitable boundedness constant.

Theorem 3.3. *Suppose that (2.2) is satisfied. Then B is a uniform repeller.*

Proof. It is seen that B is compact and that $[0, M]^3\backslash B$ is positively invariant. Let $P : [0, M]^3 \to \mathbb{R}_0^+$ defined by $P(x, y_1, y_2) = y_2$. Define also

$$U = \big\{(x, y_1, y_2) \in [0, M]^3, P(x, y_1, y_2) < \rho\big\}$$

where ρ is small enough, so that $kf(h^{-1}(\rho))D/(D + d_1) > d_2$ and $h^{-1}(\rho)$ is well defined.

Suppose by contradiction that there is $z \in U$ such that for all $t > 0$ one has

$$P(\pi(z, t)) \le P(z) < \rho,$$

where $z = (x^z, y_1^z, y_2^z)$ and $\pi(z, \cdot)$ is the solution of (2.1) with initial data $x(0) = x^z$, $y_1(0) = y_1^z$, $y_2(0) = y_2^z$.

Let us consider

$$\xi(t) = y_2(t) + \frac{D}{D + d_1}(1 - \rho^*)y_1(t)$$

with ρ^* small enough, so that

$$\frac{D}{D + d_1}(1 - \rho^*)kf(h^{-1}(\rho)) - d_2 > 0$$

One then has

$$\begin{aligned}
\xi'(t) &= (Dy_1(t) - d_2y_2(t)) + \frac{D}{D + d_1}(1 - \rho^*)\left[kf(x)y_2 - (D + d_1)y_1\right] \\
&= Dy_1 - d_2y_2 - D(1 - \rho^*)y_1 + \frac{D}{D + d_1}(1 - \rho^*)kf(x)y_2 \\
&= \rho^* y_1 + \left[\frac{D}{D + d_1}(1 - \rho^*)kf(x) - d_2\right] y_2 \\
&\ge \rho^* y_1 + \left[\frac{D}{D + d_1}(1 - \rho^*)kf(h^{-1}(\rho)) - d_2\right] y_2.
\end{aligned}$$

As a result, $\xi'(t) \ge C\xi(t)$ for some sufficiently small C and consequently $\xi(t) \to \infty$ as $t \to \infty$, which contradicts the boundedness of x, y_1, y_2. It then follows by Theorem 3.2 that B is an uniform repeller, which finishes the proof. □

It is then easy to see that under the hypotheses of Theorem 3.3, the system (2.1) is uniformly persistent provided that condition $\underline{x} > x_P$ holds. Consequently, we obtain the following result.

Theorem 3.4. *If (2.2) is satisfied and $\underline{x} > x_P$ holds, then (2.1) is uniformly persistent.*

Proof. By Theorem 3.3, the boundedness of x, y_1, y_2 and inequality $\underline{x} > x_P$, there are $m, M > 0$ such that

$$m \leq \liminf_{t\to\infty} \varphi(t) \leq \limsup_{t\to\infty} \varphi(t) \leq M \tag{3.1}$$

for $\varphi \in \{x, y_2\}$. From the second equation in (2.1) one infers that

$$y_1(t_2) = e^{-(D+d_1)(t_2-t_1)} y_1(t_1) + \int_{t_1}^{t_2} kf(x(s)) y_2(s) e^{-(D+d_1)(t_2-s)} ds,$$

so

$$y_1(t_2) \geq e^{-(D+d_1)(t_2-t_1)} y_1(t_1) + kf(m)\rho \frac{1 - e^{-(D+d_1)(t_2-t_1)}}{D + d_1}$$

for $t_2 \geq t_1 \geq t^*$, t^* great enough, which implies that

$$\liminf_{t\to\infty} y_1(t) \geq \frac{kf(m)\rho}{D + d_1}.$$

Since y_1 is bounded, it follows that (3.1) holds for $\varphi = y_1$ as well, with suitable m, M and consequently (2.1) is persistent and in the long term both the predator and prey populations reach at least a certain level not depending on the initial population sizes. ☐

The biological interpretation of the above result is very simple. Once few mature predators introduced in a prey-only equilibrium can reproduce fast enough ($kf(x_0) > d_2(D+d_1)/D$) and there is an abondance of prey on the long term ($\underline{x} > x_P$), then the survival of all populations is assured for all future time. For other related arguments pertaining to the persistence of certain epidemiologic systems, see Margheri and Rebelo [14].

To prove the global stability of the positive endemic equilibrium E^*, we need now introduce a few notions and results about competitive systems and the orbital stability of their periodic orbits. See Smith [19] for a comprehensive treatment of asymptotic behavior of finite and infinite dimensional competitive systems.

Definition 3.2. *The autonomous differential system*

$$x' = f(x), \quad f : \mathcal{D} \subset \mathrm{I\!R}^n \to \mathrm{I\!R}^n, \tag{3.2}$$

is said to be competitive in $\mathcal{D}$ *if there is a diagonal matrix* $H = \mathrm{diag}(\varepsilon_1, \varepsilon_2, \ldots, \varepsilon_n)$, $\varepsilon_i \in \{-1, 1\}$, $i = 1, .., n$ *such that* $HJ_{(3.2)}H$ *has nonpositive off-diagonal elements for all* $x \in \mathcal{D}$.

It is known (see, for instance, Smith [19, Theorem 4.1]) that three-dimensional competitive systems defined on convex sets have the Poincare-Bendixson property, in the sense that any nonempty compact w-limit set of (3.2) which contains no equilibria is a closed orbit of (3.2).

Definition 3.3. *An orbit* $\mathcal{O}$ *of (3.2) is called orbitally stable if and only if for all* $\varepsilon > 0$ *there is* $\delta > 0$ *with the property that any solution* $x(t)$ *starting in a point* $x(0)$ *with the property that the distance from* $x(0)$ *to* $\mathcal{O}$ *is less than* δ *remains at distance less than* ε *from* $\mathcal{O}$ *for any* $t \geq 0$. *The orbit* $\mathcal{O}$ *is then called orbitally asymptotically stable if it is orbitally stable and the distance from* $x(t)$ *to* $\mathcal{O}$ *tends to* 0 *as* $t \to \infty$.

Definition 3.4. *The system (3.2) is then said to have the property of stability of periodic orbits if all its periodic orbits are orbitally asymptotically stable in the sense mentioned above.*

Of great interest in the study of orbital stability of periodic solutions is the following result of Muldowney [15, Theorem 4.2], which converts a somewhat nonstandard problem associated to an autonomous dynamical system (the orbital stability of a periodic solution) into a more standard one, but associated to a nonautonomous system.

Proposition 3.5. *A sufficient condition for a periodic trajectory* $\gamma = \{p(t); 0 \le t \le T\}$ *of (3.2) to be orbitally asymptotically stable is that the nonautonomous linear system*

$$Z' = J^{[2]}_{(3.2)}(p(t))Z$$

be asymptotically stable.

Here, $J^{[2]}_{(2.1)}$ is the second additive compound of the Jacobian matrix of (3.2). For the definition of k-th additive and multiplicative compound matrices of dimension n, see Muldowney [15]. We here only indicate that if $n = 3$, $k = 2$ and $A = (a_{ij})_{1 \le i,j \le 3}$, then the second additive compound of A is given by the formula

$$A^{[2]} = \begin{pmatrix} a_{11} + a_{22} & a_{23} & -a_{13} \\ a_{32} & a_{11} + a_{33} & a_{12} \\ -a_{31} & a_{21} & a_{22} + a_{33} \end{pmatrix}$$

We now show that our system (2.1) is competitive and that, under certain conditions, it has the property of stability of periodic orbits.

Theorem 3.6. *Suppose that (2.2) is satisfied and that* $\underline{x} > x_P$ *holds. Then the system (2.1) is competitive and has the property of stability of periodic orbits.*

Proof. Consider

$$\mathcal{D} = [0, M]^3, \quad H = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

By (2.3), one has

$$HJ_{(2.1)}H = \begin{pmatrix} n'(x) - f'(x)y_2 & 0 & -f(x) \\ -kf'(x)y_2 & -(D + d_1) & -kf(x) \\ 0 & -D & -d_2 \end{pmatrix},$$

and so $HJ_{(2.1)}H$ has nonpositive off-diagonal entries on $\mathcal{D}$, that is, it is competitive on $\mathcal{D}$.

We attempt to show that the system (2.1) has the property of stability of periodic orbits by applying Proposition 3.5. Let $p = (x(t), y_1(t), y_2(t))$ be a positive periodic orbit of (2.1).

Let us consider the system

$$Z' = J^{[2]}_{(2.1)}(p(t))Z, \quad Z = (z_1, z_2, z_3)^T \tag{3.3}$$

and prove that this system is asymptotically stable. Let us define

$$V(z_1(t), z_2(t), z_3(t)) = \left\| \left(z_1(t), \frac{y_1(t)}{y_2(t)} z_2(t), \frac{y_1(t)}{ky_2(t)} z_3(t) \right) \right\|,$$

where $\|\cdot\|$ is a norm on $\mathbb{R}^3$, defined by

$$\|(z_1, z_2, z_3)\| = \max(|z_1|, |z_2| + |z_3|).$$

Note that V is well defined, since (2.1) is persistent under the given hypotheses. Then system (3.3) can be expanded as

$$\begin{cases} z_1' = -(-n'(x) + f'(x)y_2 + (D + d_1))z_1 + kf(x)z_2 + f(x)z_3, \\ z_2' = Dz_1 + (n'(x) - f'(x)y_2 - d_2)z_2, \\ z_3' = kf'(x)y_2z_2 - (D + d_1 + d_2)z_3. \end{cases} \tag{3.4}$$

By using (3.4), it is possible to derive the estimations

$$\begin{cases} D_+ \left|z_1\right| \leq -(-n'(x) + f'(x)y_2 + (D + d_1)) \left|z_1\right| + kf(x) \left|z_2\right| + f'(x) \left|z_3\right|, \\ D_+ \left|z_2\right| \leq D \left|z_1\right| - (-n'(x) + f'(x)y_2 + d_2) \left|z_2\right|, \\ D_+ \left|z_3\right| \leq kf'(x)y_2 \left|z_2\right| - (D + d_1 + d_2) \left|z_3\right|. \end{cases} \tag{3.5}$$

Then

$$D_+ \left|z_1\right| \leq -(-n'(x) + f'(x)y_2 + (D + d_1)) \left|z_1\right| + \frac{kf(x)y_2}{y_1} \left(\frac{y_1}{y_2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \right) \tag{3.6}$$

and

$$D_+ \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \leq D \left|z_1\right| - (d_2 + \min(-n'(x), D + d_1)) \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right). \tag{3.7}$$

From the above, we may infer that

$$\begin{aligned} D_+ \left(\frac{y_1}{y_2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \right) &= \frac{\dot{y_1}\ y_2 - y_1\ \dot{y_2}}{y_2^2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) + \frac{y_1}{y_2} \left(D_+ \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \right) \\ &\leq \left(\frac{\dot{y_1}}{y_1} - \frac{\dot{y_2}}{y_2} \right) \frac{y_1}{y_2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \frac{y_1}{y_2} D \left|z_1\right| - k \frac{y_1}{y_2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \end{aligned}$$

and therefore

$$\begin{aligned} & D_+ \left(\frac{y_1}{y_2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \right) \\ & \leq \frac{y_1}{y_2} D \left|z_1\right| + \left(\frac{\dot{y_1}}{y_1} - D \frac{y_1}{y_2} - \min\left(-n'(x), D + d_1\right) \right) \frac{y_1}{y_2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \end{aligned}$$

It is now possible to evaluate the time derivative of V. Let $t_0 > 0$. If $V(t) = \left|z_1(t)\right|$ in a vicinity of t_0, then

$$\begin{aligned} D_+ V(t_0) &\leq -(-n'(x) + f'(x)y_2 + (D + d_1)) \left|z_1\right| + \frac{kf(x)y_2}{y_1} \left(\frac{y_1}{y_2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \right) \\ &\leq \left[\frac{kf(x)y_2}{y_1} + n'(x) - f'(x)y_2 - (D + d_1) \right] \left|z_1\right| \\ &\leq \left[\frac{\dot{y_1}}{y_1} + n'(x) - f'(x)y_2 \right] V(t_0). \end{aligned}$$

If $V(t) = \frac{y_1(t)}{y_2(t)} \left[\left|z_2(t)\right| + \frac{z_3(t)}{k} \right]$ in a vicinity of t_0, then

$$\begin{aligned} D_+ V(t_0) &\leq \frac{y_1}{y_2} D \left|z_1\right| + \left(\frac{\dot{y_1}}{y_1} - D \frac{y_1}{y_2} - \min\left(-n'(x), D + d_1\right) \right) \frac{y_1}{y_2} \left(\left|z_2\right| + \frac{\left|z_3\right|}{k} \right) \\ &\leq \left[\frac{\dot{y_1}}{y_1} - \min\left(-n'(x), D + d_1\right) \right] V(t_0). \end{aligned}$$

If neither of these situations happens, then

$$\begin{aligned} \left|z_1(t_0)\right| &= \frac{y_1(t_0)}{y_2(t_0)} \left[\left|z_2(t_0)\right| + \frac{\left|z_3(t_0)\right|}{k} \right] \\ D_+ \left|z_1(t)\right| \Big|_{t=t_0} &= D_+ \left[\frac{y_1(t)}{y_2(t)} \left(\left|z_2(t)\right| + \frac{\left|z_3(t)\right|}{k} \right) \right] \Big|_{t=t_0} \end{aligned}$$

and consequently, by the same argument,

$$D_+V(t_0) \le \min\left(\left[\frac{\dot{y}_1}{y_1} + n'(x) - f'(x)y_2\right], \left[\frac{\dot{y}_1}{y_1} - \min\left(-n'(x), D + d_1\right)\right]\right) V(t_0)$$

Then, for all $t > 0$, one has

$$\begin{aligned} D_+V(t) &\le \max\left(\left[\frac{\dot{y}_1}{y_1} + n'(x) - f'(x)y_2\right], \left[\frac{\dot{y}_1}{y_1} - \min\left(-n'(x), D + d_1\right)\right]\right) V(t) \\ &\le \max\left(\left[\frac{\dot{y}_1}{y_1} + n'(x) - f'(x)y_2\right], \left[\frac{\dot{y}_1}{y_1} + \max\left(n'(x), -(D + d_1)\right)\right]\right) V(t) \\ &\le \frac{\dot{y}_1}{y_1} + \max\left(n'(x), -(D + d_1)\right) V(t). \end{aligned}$$

Note that if $\underline{x} > x_P$, then $n'(x(t))$ is strictly negative on some $[t_*, \infty)$. It follows that

$$V(t) \le V(t^*)\frac{y_1(t)}{y_1(t^*)}e^{-\delta(t-t^*)},$$

so $\lim_{t\to\infty} V(t) = 0$. It then follows from the persistence of (2.1) that

$$\lim_{t\to\infty} z_1(t) = \lim_{t\to\infty} z_2(t) = \lim_{t\to\infty} z_3(t) = 0,$$

so the null solution of (3.3) is asymptotically stable. By Proposition 3.5, the system (2.1) has the property of stability of periodic solutions. □

It is then possible to prove that for three-dimensional competitive systems which are permanent, the local asymptotic stability of a unique positive equilibrium and the property of stability of periodic orbits insure that the endemic equilibrium is actually globally asymptotically stable. More precisely, the following result ([24, Theorem 2.2]) holds.

Proposition 3.7. *Assume that $n = 3$ and that D is convex and bounded. If (3.2) is competitive and permanent in D, it has a unique equilibrium in D and it also has the property of stability of periodic orbits, then the interior equilibrium is globally asymptotically stable in* Int D.

By Theorem 3.6 and Proposition 3.7, it then follows that the positive equilibrium is globally asymptotically stable in $(0, \infty)^3$ since condition $\underline{x} > x_P$ implies that $x^* > x_P$ and consequently, as previously noted, the positive equilibrium is locally asymptotically stable. From all our previous considerations, it is then possible to conclude with the following global stability result, which characterizes the global asymptotic stability of the positive equilibrium.

Theorem 3.8. *Suppose that (2.2) is satisfied and that $\underline{x} > x_P$ holds. Then (2.1) is uniformly persistent and there is a unique positive equilibrium $E^* = (x^*, y_1^*, y_2^*)$, which is globally asymptotically stable on $(0, \infty)^3$.*

For $f(x) = bx/(1 + mx)$ and $n(x) = x(r - ax)$, our Theorem 3.8 improves [24, Theorem 2.1], since (H1) and (H2) in [24] are unified in a single weaker assumption, while being observed that there is no need to assume *a priori* the local asymptotic stability of the positive endemic equilibrium.

4 Numerical examples and concluding remarks

It has been seen in Theorem 3.8, our main result, that the positive equilibrium E^* is globally asymptotically stable provided that $\underline{x} > x_P$ and $R_0 > 1$. However, while condition $R_0 > 1$ is both necessary and sufficient for the stability of the positive equilibrium (if $R_0 \leq 1$, then the positive equilibrium E^* does not even exist), condition $\underline{x} > x_P$ is only sufficient and not necessary.

Conceptually, the a-priori estimate $\underline{x} > x_P$ has a distinct advantage over lengthy computational conditions arising from coefficient estimations in Lyapunov functionals, the use of Routh-Hurwitz theorem or other similar theoretical devices, which can be found in many papers. These conditions often heavily depends on the particulars of the problem under consideration (on the particular form of n and f, for instance) and do not generally possess any sort of biological interpretation. In contrast, our a-priori estimation has a clear meaning and no futher assumptions on the shape of the functional response f of the mature predator are needed.

However, x_P does not appear to be a threshold parameter for the stability of the positive equilibrium as far as $\underline{x}$ is concerned and it also appears to be difficult to determine one. Also, while natural and transparent, this sort of estimations cannot generally be used to determine domains of attraction since the persistency constant which can be computed with the help of the general results such as Theorem 3.3 is often not large enough to verify the estimate needed in Theorem 3.8.

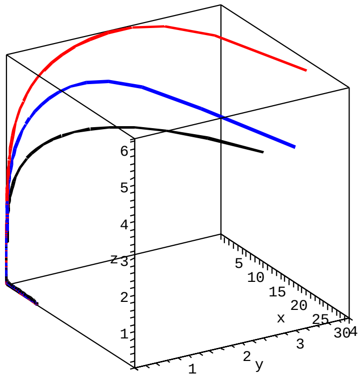
To illustrate our theoretical discussion, we have also provided a set of MATLAB simulations. Our data has been scaled and the examples are illustrative only; the numerical figures do not correspond to a particular predator-prey interaction. The prey population x, respectively the predator populations y_1, y_2 are represented in a system of three-dimensional Cartesian coordinates by x, respectively by y and z.

We denote by LT and RT the left, respectively right-hand side of (2.5), that is

$$LT = \left[D + d_1 + d_2 + x^*\left(2a - \frac{rm+a}{1+mx^*}\right)\right] x^*\left(2a - \frac{rm+a}{1+mx^*}\right)(D + d_1 + d_2),$$
$$RT = \frac{r - ax^*}{1+mx^*} d_2(D + d_1)$$

The first situation is the one in which $R_0 < 1$ and consequently the predator classes tend to extinction. To illustrate this case, we choose $a = 0.5$, $d_1 = 0.8$, $d_2 = 0.45$, $r = 3.5$, $D = 1.2$, $k = 0.01$, $m = 0.1$, $b = 3$. Then $R_0 = 0.164 < 1$ and it seen in Figure 1 that the trajectories of our system tend to the prey-only equilibrium indeed (by coming very close to the origin first).

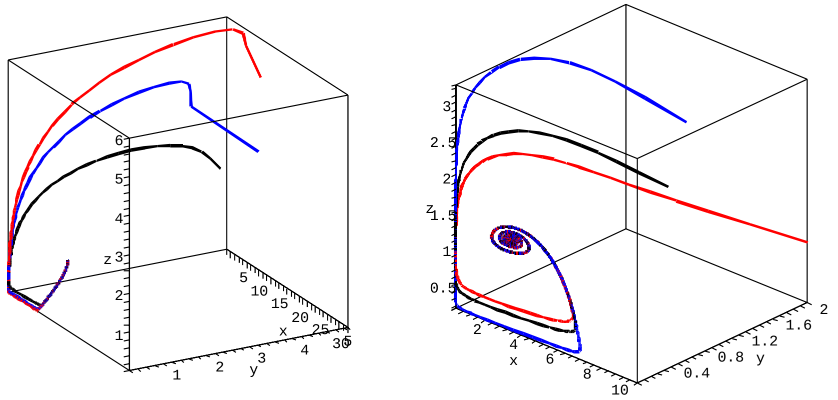
Figure 1: Simulation for case 1. E^* does not exist. All trajectories approach the prey-only equilibrium.



The second situation is the one in which $R_0 > 1$ and E^* is locally asymptotically stable. In this case, the behavior of the trajectories is more complicated, as E^* may or may not globally asymptotically stable. Also, the persistency constant $\underline{x}$ may or may not verify the estimation sought after in Theorem 3.8.

We first picture the situation in which $\underline{x}$ is large enough. For this case, labeled as case 2a, we choose $a = 0.5$, $d_1 = 0.8$, $d_2 = 0.45$, $r = 3.5$, $D = 0.4$, $k = 0.2$, $m = 0.2$, $b = 3$. Then $R_0 = 1.296 > 1$, $\underline{x} = 4.09 > r/(2a) = 3.5$, so the positive equilibrium E^* is globally asymptotically stable, by Theorem 3.8. See Figure 2 for details.

Figure 2: Simulations for cases 2a and 2b. 2a)E^* is GAS, due to the inequality $\underline{x} > r/(2a)$, 2b)E^* is GAS, even though $\underline{x} < r/(2a)$.



We then describe the case in which $\underline{x} < r/(2a)$, but E^* retains its global asymptotic stability. For this case, labeled as case 2b, we choose $a = 0.5$, $d_1 = 0.8$, $d_2 = 0.45$, $r = 3.5$, $D = 1.2$, $k = 0.1$, $m = 0.2$, $b = 3$. Then $R_0 = 2.1 > 1$, $LT = 1.446 > RT = 0.916$ (so E^* is locally asymptotically stable), $\underline{x} = 1.92 < r/(2a) = 3.5$, but the positive equilibrium E^* is still globally asymptotically stable. See Figure 2 for details.

Finally, it may happen that $\underline{x} < r/(2a)$ and E^* loses its global asymptotic stability. For this case, labeled as case 2c, we choose $a = 0.5$, $d_1 = 0.8$, $d_2 = 0.20$, $r = 3.5$, $D = 1.2$, $k = 0.2172$, $m = 0.01$, $b = 3$. Then $R_0 = 12.788 > 1$, $LT = 1.2913 > RT = 1.2905$ (so E^* is locally asymptotically stable), $\underline{x} = 0.514 < (r/2a) = 3.5$ and the positive equilibrium E^* is not globally asymptotically stable. See Figure 3 for details.

The third situation is the one in which $R_0 > 1$ and E^* is unstable. To illustrate this case, labeled as case 3, we choose $a = 0.5$, $d_1 = 0.8$, $d_2 = 0.20$, $r = 3.5$, $D = 1.2$, $k = 0.3$, $m = 0.005$, $b = 3$. Then $R_0 = 18.260 > 1$ and $LT = 0.939 < RT = 1.323$ (so E^* is unstable) and it is seen from Figure 4 that the trajectories of the system approach a periodic orbit.

By essentially the same argument as in Georgescu and Hsieh [7, Theorem 4.1], it is seen that that in case 3 there is at least a periodic solution, but no more than finitely many and at least one of these is orbitally asymptotically stable. Also, in this case any solution which does not start on the one-dimensional stable manifold of E^* tends to a periodic solution. Similarly, in case 2c, there is at least a periodic solution which is necessarily orbitally unstable.

This model, or similar ones accounting for the effects of further biological interactions, may be used to provide details abouth the survival of endangered mammal and reptilian species. See Zhang, Chen and Neumann [25], where the problem of optimal harvesting is also addressed, for a somewhat more complicated model, but under the assumption that all the functions which are used to model the biological

Figure 3: Simulation for case 2c. E^* is LAS but not GAS.

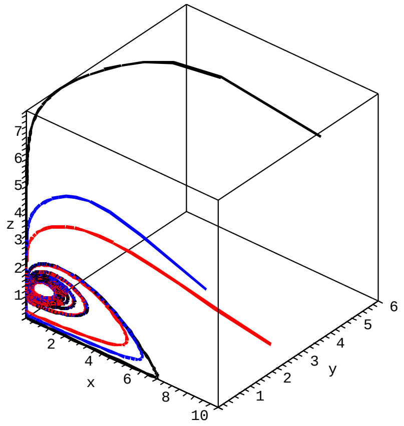
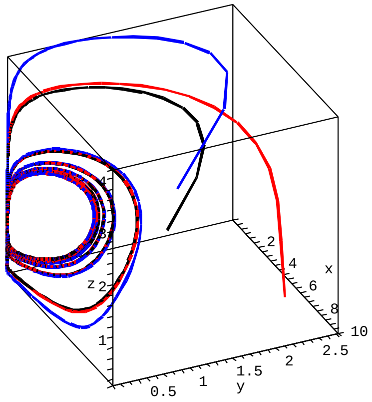


Figure 4: Simulation for case 3. E^* is unstable.



interactions are linear, except for the logistic term. In [25], the case of the Chinese Alligator is considered, as a stage-structured species preying on aquatic animals, and some recommendations for the species preservation are provided. Similarly, the conclusion which arises from our Theorem 3.8 is very simple: to guarantee the survival of the endangered predators at a stable and sure level, its reproduction rate should be improved, so that $R_0 > 1$ (perhaps by artificial insemination) and the prey should be kept numerically above a certain level, so that $\underline{x} > x_P$ (perhaps by raising prey offsprings in dedicated facilities and subsequently releasing them into the natural habitat). Both measures are necessary and an improvement in a single area is not enough.

Our abstract functional response of the mature predator f, which has been modeled after the widely used Holling type II functional response, does not depend on the sizes of the predator populations y_1 and y_2, but only on the prey abundance x, so predators are not assumed to interact with each other during their daily feeding activities. However, other types of functional responses which account for interference between predators have been proposed (Beddington-DeAngelis, [2],[5], Crowley and Martin [4], Hassell and Varley [9]). See the comprehensive paper of Skalski and Gilliam [20] for a comparison of the accuracy provided by these alternative functional responses based on statistical data for a wide range of predator-prey systems.

The population ecology models involving ordinary differential equations are often not as descriptive or as realistic as those using delay differential equations. In this regard, it has been observed by Harrison in [8] by validating a variety of predator-prey models against a known data set regarding the interaction between *Paramecium aurelia* and its predator *Didinium nasutum* presented by Luckinbill in [13] that the best numerical fit has been given by a delayed numerical response of the predator coupled with a sigmoid functional response. However, unlike for the latter, the stability analysis for the former is much easier to be carried out, as time delays generally have a destabilizing effect and may introduce bifurcations and other rich dynamics under certain conditions. This simplification has been done for our model, where the delaying effect of the gestation period for predators is not taken under consideration. Also, the logistic part of the equation which models the growth of the prey class may need to contain a delay term, for similar reasons. We plan to address these issue in a subsequent work.

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