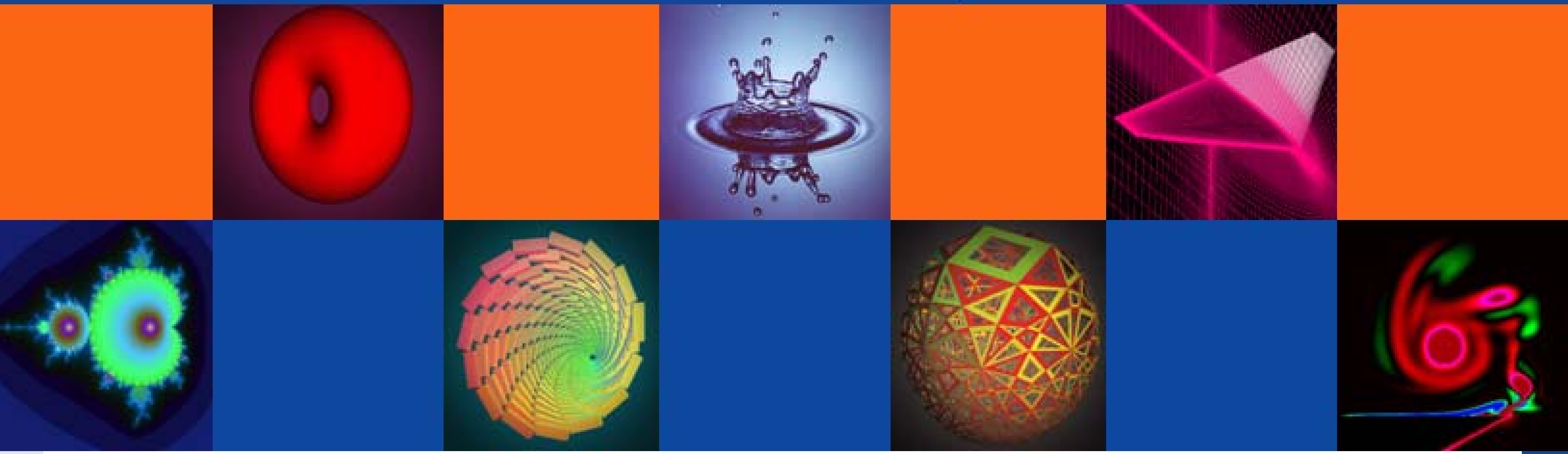

Nonstandard Finite Difference Methods For Predator-Prey Models With General Functional Response

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Technical Report 2007-10

NONSTANDARD FINITE DIFFERENCE METHODS FOR PREDATOR-PREY MODELS WITH GENERAL FUNCTIONAL RESPONSE

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Abstract. Predator-prey systems with linear and logistic intrinsic growth rate of the prey are analyzed. The models incorporate the mutual interference between predators into the functional response which stabilizes predator-prey interactions in the system. Positive and elementary stable nonstandard (PESN) finite-difference methods, having the same qualitative features as the corresponding continuous predator-prey models, are formulated and analyzed. The proposed numerical techniques are based on a nonlocal modeling of the growth-rate function and a nonstandard discretization of the time derivative. This discretization approach leads to significant qualitative improvements in the behavior of the numerical solution. In addition, it allows for the use of an essentially implicit method for the cost of an explicit method. Applications of the PESN methods to specific predator-prey systems are also presented.

1. Introduction

Predator-prey systems are among the most discussed and analyzed topics in mathematical biology. Their relatively simple form as a system of two differential equations allows for detailed understanding of their underlying behavior, even though explicit solutions are not available in a closed form. A general predator-prey model can be written as follows:

$$\begin{aligned} \frac{dx}{dt} &= p(x) - af(x,y)y; \qquad x(0) \geq 0, \\ \frac{dy}{dt} &= f(x,y)y - \mu(y); \qquad y(0) \geq 0, \end{aligned} \tag{1.1}$$

where x and y represent the prey and predator population sizes, and functions $p(x)$ and $\mu(y)$ describe the intrinsic growth rate of the prey and the mortality rate of the predator, respectively. The transformation rate constant a represents the assimilation efficiency of the predator. The function $f(x,y)$ is called "functional response" and represents the per capita predator "feeding rate" per unit time.

The majority of the scientific literature in the field of predator-prey systems assumes that the predator mortality $\mu(y)$ depends linearly on the predator density ($\mu(y) = dy$), while the intrinsic growth rate of the prey $p(x)$ has a linear ($p(x) = bx$) or logistic ($p(x) = bx(1-x/K)$) expression. In this paper we embrace those assumptions and concentrate on the affect of the functional response $f(x,y)$. Functions in the form $f(x,y) = f(x)$ have been used as a predominant "feeding rate" functions

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2000 *Mathematics Subject Classification.* 37M05, 39A11, 65L12, 65L20.

Key words and phrases. finite-difference; nonstandard; positive; elementary stable; predator-prey; predator interference.

for decades. Among the most popular "prey-dependent" functional responses are the Holling type I, II and III $\left(f = \alpha x,\ f = \dfrac{\alpha x}{x+c},\ f = \dfrac{\alpha x^2}{x^2+c}\right)$ [14]. However, in some situations they predict unrealistic population dynamics of the predator or the prey. The main problem is that the linear expression of the functional response in terms of the predator density does not account for the interference between predators. This fact requires "predator-dependent" forms of $f(x,y)$ as the ratio-dependent type $f = \dfrac{\alpha x}{x+by}$ [3, 15, 19], the Beddington-DeAngelis type $f = \dfrac{\alpha x}{b+wx+y}$ [2, 6], and Nicholson-Bailey form $f = \alpha x e^{-by}$ [13], to name a few. Analysis of the published experimental data shows that "predator-dependence" in the functional response is a nearly ubiquitous property [25]. The following conditions guarantee the biological relevance of the function $f(x,y)$ as a capita "feeding rate" function:

$$f(x,y) > 0, \quad \frac{\partial f}{\partial x} > 0, \quad \frac{\partial f}{\partial y} < 0, \text{ when } (x,y) \in \mathbb{R}^2_+. \tag{1.2}$$

These conditions express that unconditionally positive feeding rate is affected positively by an increase in prey density and negatively by the increase in predator density due to interspecies interference.

Numerical simulations, based on finite difference approximations, such as Euler, Runge-Kutta and Adams methods, are widely used to predict the dynamics of the interacting populations. Unfortunately, their stability and accuracy depend strongly on the time step-size. That raises questions about the truncation errors, the stability regions and, from a dynamical point of view, the accuracy at which the dynamics of the continuous system are represented by the discrete system. Lubuma and Roux [20] and Dimitrov and Kojouharov [9, 10], among others, have used nonstandard techniques, developed by Mickens [22], to design elementary stable nonstandard (ESN) methods that preserve the local stability of equilibria of the approximated differential system for arbitrary time step-sizes. However, the ESN methods, as well as the standard numerical methods, do not guarantee a positive discrete solution for all positive initial values. The positivity condition is natural when predator-prey interactions are modeled and approximated numerically. Failing to satisfy it reflects negatively on the accuracy and efficiency of the numerical methods. Recently, several positive and elementary stable nonstandard (PESN) methods have been designed for some specific predator-prey [11, 12, 23], phytoplankton-nutrient [8] and epidemic [18, 24] systems.

In this paper, we develop PESN numerical methods for predator-prey systems (1.1) with general functional response $f(x,y)$ of the form (1.2) that have only hyperbolic equilibria. The equilibria-assumption is not too restrictive biologically, since most natural predator-prey systems are structurally stable to a variety of plausible biological changes. The new PESN methods preserve both the positivity of the solutions and the stability of the equilibria of the corresponding predator-prey system. In addition, the designed numerical approximations allow us to solve the discrete systems explicitly, which increases the efficiency of the methods.

The paper is organized as follows. In Section 2 we provide some definitions and preliminary results. In Sections 3 and 4 we analyze Systems (1.1) with linear and logistic intrinsic prey growth rate, respectively, and design the corresponding PESN numerical methods. In the last two sections we illustrate our results by numerical examples and outline some future research directions.

2. Definitions and Preliminaries

A general two-dimensional autonomous system has the following form:

$$\frac{dz}{dt} = F(z); \quad z(0) = (x(0), y(0))^T \in \mathbb{R}^2_+, \tag{2.1}$$

where $z(t) = (x(t), y(t))^T$ and the function $F = [F^1, F^2]^T : \mathbb{R}^2 \mapsto \mathbb{R}^2$ is differentiable in $\mathbb{R}^2_+$.

The equilibrium points of System (2.1) are defined as the solutions of $F(z) = 0$. The condition (1.2) implies an existence of only finite number of equilibria of System (1.1).

Definition 2.1. *Let z^* be an equilibrium of System (2.1), $J(z^*)$ be the Jacobian of System (2.1) at z^* and $\sigma(J(z^*))$ denotes the spectrum of $J(z^*)$. An equilibrium z^* of System (2.1) is called linearly stable if $Re(\lambda) < 0$ for all $\lambda \in \sigma(J(z^*))$ and linearly unstable if $Re(\lambda) > 0$ for at least one $\lambda \in \sigma(J(z^*))$.*

Throughout this article, we assume that System (2.1) has only hyperbolic equilibria, i.e., $Re(\lambda) \neq 0$, for $\lambda \in \bigcup_{z^* \in \Gamma} \sigma(J(z^*))$, where Γ represents the set of all equilibria of System (2.1).

A numerical scheme with a step size h, that approximates the solution $z(t_k)$ of System (2.1) can be written in the form:

$$\mathcal{D}_h(z_k) = \mathcal{F}_h(F; z_k), \tag{2.2}$$

where $\mathcal{D}_h(z_k) \approx \left(\frac{dx}{dt}, \frac{dy}{dt}\right)^T$, $\mathcal{F}_h(F; z_k)$ approximates the right-hand side of System (2.1), $z_k \approx z(t_k)$, and $t_k = t_0 + kh$.

The stability of the fixed points of explicit numerical schemes of the form (2.2) can be determined as follows:

Lemma 2.1. *Assume that System (2.2) has the following explicit form:*

$$z_{k+1} = G(z_k), \tag{2.3}$$

where the function $G = [G^1, G^2]^T : \mathbb{R}^2 \mapsto \mathbb{R}^2$ is differentiable. A fixed point z^* of System (2.3) is stable if and only if all eigenvalues of $J(z^*)$ are less than one in absolute values, where $J(z^*)$ denotes the Jacobian of System (2.3).

When analyzing the eigenvalues of $J(z^*)$ we will make use of the following lemma [5, p. 82]:

Lemma 2.2. *Roots of the quadratic equation $\lambda^2+\alpha\lambda+\beta = 0$ satisfy $|\lambda_i| < 1, i = 1, 2$ if and only if the following three conditions hold:*

- (a) $1 + \alpha + \beta > 0$;
- (b) $1 - \alpha + \beta > 0$; *and*
- (c) $\beta < 1$.

The next definition deals with the dynamical correspondence between a differential system and a numerical method regarding the stability of their equilibrium points [1].

Definition 2.2. *The finite difference method (2.2) is called elementary stable, if, for any value of the step size h, its only fixed points z^* are the equilibria of the differential system (2.1), the linear stability properties of each z^* being the same for both the differential system and the discrete method.*

The form of the predator-prey system (1.1) guarantees that any solution with positive initial conditions remains positive in time. The corresponding requirement for numerical methods is formulated in the following definition:

Definition 2.3. *The finite difference method (2.2) is called unconditionally positive, if, for any value of the step size h, and $z(0) \in \mathbb{R}^2_+$ its solution remains positive, i.e., $z_k \in \mathbb{R}^2_+$ for $k = 1, 2, 3, \ldots$.*

The numerical methods developed in this paper are dynamically consistent with the differential system (1.1), by means of the above two definitions, and belong to the class of nonstandard finite-difference methods according to the following definition [1]:

Definition 2.4. *The one-step method (2.2) for solving System (2.1) is called a nonstandard finite-difference method if at least one of the following conditions is satisfied:*

- $\mathcal{D}_h(z_k) = \dfrac{z_{k+1} - z_k}{\varphi(h)}$, *where* $\varphi(h) = h + \mathcal{O}(h^2)$ *is a nonnegative function;*
- $\mathcal{F}_h(F; z_k) = f(z_k, z_{k+1}, h)$, *where* $f(z_k, z_{k+1}, h)$ *is a nonlocal approximation of the right-hand side of System (2.1).*

3. PESN METHODS FOR PREDATOR-PREY SYSTEMS WITH LINEAR INTRINSIC GROWTH RATE OF THE PREY

In this section we analyze System (1.1) with linear intrinsic growth rate of the prey, i.e., $p(x) = bx$, which has the following non-dimensional form:

$$\begin{aligned} \frac{dx}{dt} &= x - af(x,y)y; \qquad x(0) \geq 0, \\ \frac{dy}{dt} &= f(x,y)y - dy; \qquad y(0) \geq 0. \end{aligned} \tag{3.1}$$

Depending on the values of the parameters, System (3.1) has the following equilibria:

(1) The trivial equilibrium $(x_0, y_0) = (0, 0)$;
(2) An interior equilibrium (x^*, y^*) satisfying $f(x^*, y^*) = d$ and $x^* = ady^*$.

Analyzing the global qualitative behavior of all solutions of System (3.1), the following statements about the stability of the equilibria are true:

(1) The trivial equilibrium (x_0, y_0) is always linearly unstable;
(2) The interior equilibrium (x^*, y^*) is linearly stable if

$$D(x^*, y^*) = \frac{\partial f}{\partial y}(x^*, y^*) + ad\frac{\partial f}{\partial x}(x^*, y^*) > 0$$

and

$$T(x^*, y^*) = 1 + \frac{\partial f}{\partial y}(x^*, y^*)y^* - a\frac{\partial f}{\partial x}(x^*, y^*)y^* < 0$$

are satisfied simultaneously.

The numerical schemes described in the following theorem represent PESN methods, provided that System (3.1) with linear intrinsic growth rate of the prey population has only hyperbolic equilibria:

Theorem 3.1. *Let ϕ be a real-valued function on $\mathbb{R}$ that satisfies the property:*

$$\phi(h) = h + O(h^2) \quad \text{and} \quad 0 < \phi(h) < 1 \quad \text{for all} \quad h > 0. \tag{3.2}$$

There exists a constant $Q > 0$ such that the following scheme for solving System (3.1) represents a PESN method:

$$\begin{aligned} \frac{x_{k+1} - x_k}{\varphi(h)} &= x_k - a g(x_k, y_k) x_{k+1} y_k, \\ \frac{y_{k+1} - y_k}{\varphi(h)} &= f(x_k, y_k) y_k - d y_{k+1}, \end{aligned} \tag{3.3}$$

where $g(x,y) = \frac{f(x,y)}{x}$ is differentiable in $\bar{\mathbb{R}}^2_+$ and $\varphi(h)$ has the form $\varphi(h) = \phi(hq)/q$ for some $q > Q$.

Proof. Let us denote $h_1 = \varphi(h) = \dfrac{\phi(hq)}{q}$. Note that if $q > Q$ then $0 < h_1 < \dfrac{1}{Q}$. The explicit expression of the nonstandard scheme (3.3) has the form:

$$\begin{aligned} x_{k+1} &= \frac{(1 + h_1) x_k}{1 + a h_1 g(x_k, y_k) y_k}, \\ y_{k+1} &= \frac{(1 + h_1 f(x_k, y_k)) y_k}{1 + h_1 d}. \end{aligned} \tag{3.4}$$

Since the constants a, e and d are positive then the scheme (3.4) is unconditionally positive and its fixed points are exactly the equilibria of System (3.1).

We analyze the stability of those fixed points using Lemma 2.1. The Jacobian J of Scheme (3.4) has the form $J(x,y) = (j_{ij}(x,y))_{2\times 2}$, where

$$j_{11}(x,y) = \frac{(1+h_1)(1 + a h_1 g(x,y) y) - a h_1 (1 + h_1) \frac{\partial g}{\partial x}(x,y) x y}{(1 + a h_1 g(x,y) y)^2},$$

$$j_{12}(x,y) = -\frac{a h_1 (1 + h_1) x}{(1 + a h_1 g(x,y) y)^2} \left(g(x,y) + \frac{\partial g}{\partial y}(x,y) y \right),$$

$$j_{21}(x,y) = \frac{h_1 \frac{\partial f}{\partial x}(x,y) y}{1 + h_1 d}, \quad \text{and} \quad j_{22}(x,y) = \frac{1 + h_1 f(x,y) + h_1 \frac{\partial f}{\partial y}(x,y) y}{1 + h_1 d}.$$

Eigenvalues of J at the trivial equilibrium $(0,0)$ are $1 + h_1$ and $\frac{1}{1+h_1 d}$, i.e., $(0,0)$ is always unstable. Therefore the behavior of System (3.3) around the trivial equilibrium is dynamically consistent with the behavior of System (3.1)

Since $f(x,y) = g(x,y)x$ then $\frac{\partial f}{\partial x}(x,y) = \frac{\partial g}{\partial x}(x,y)x + g(x,y)$ and $\frac{\partial f}{\partial y}(x,y) = \frac{\partial g}{\partial y}(x,y)x$. In addition, $ag(x^*,y^*)y^* = 1$ at any interior equilibrium (x^*,y^*). Therefore the Jacobian $J^* := J(x^*,y^*)$ can be simplified as follows:

$$J^* = \begin{pmatrix} \frac{1+2h_1}{1+h_1} - \frac{ah_1}{1+h_1}\frac{\partial f}{\partial x}(x^*,y^*)y^* & -\frac{adh_1}{1+h_1} - \frac{ah_1}{1+h_1}\frac{\partial f}{\partial y}(x^*,y^*)y^* \\ \frac{h_1}{1+dh_1}\frac{\partial f}{\partial x}(x^*,y^*)y^* & 1 + \frac{h_1}{1+dh_1}\frac{\partial f}{\partial y}(x^*,y^*)y^* \end{pmatrix}$$

Eigenvalues λ_1 and λ_2 of $J(x^*,y^*)$ are roots of the quadratic equation:

$$\lambda^2 - \alpha\lambda + \beta = 0,$$

where

$$\alpha = \frac{2+3h_1}{1+h_1} - \frac{ah_1}{1+h_1}\frac{\partial f}{\partial x}(x^*,y^*)y^* + \frac{h_1}{1+dh_1}\frac{\partial f}{\partial y}(x^*,y^*)y^*$$

and

$$\beta = \frac{1+2h_1}{1+h_1} - \frac{ah_1}{(1+h_1)(1+dh_1)}\frac{\partial f}{\partial x}(x^*,y^*)y^* + \frac{h_1(1+2h_1)}{(1+h_1)(1+dh_1)}\frac{\partial f}{\partial y}(x^*,y^*)y^*.$$

The fixed point (x^*,y^*) is stable if and only if all three conditions of Lemma 2.2 hold and (x^*,y^*) is unstable if at least one of the conditions fails. Note that $\alpha = \alpha(h_1)$ and $\beta = \beta(h_1)$ are continuous functions of h_1 for $h_1 > 0$. In addition, $\alpha(0) = 2$ and $\beta(0) = 1$, which implies that there exist constants $\tilde{A}_{(x^*,y^*)} > 0$ such that $1 + \alpha(h_1) + \beta(h_1) > 0$ for all $0 < h_1 < \tilde{A}_{(x^*,y^*)}$.

Assume that (x^*,y^*) is a stable equilibrium of System (3.1). Therefore $D(x^*,y^*) > 0$ and $T(x^*,y^*) < 0$. Since $D(x^*,y^*) > 0$ then

$$1 - \alpha + \beta = \frac{h_1^2}{(1+h_1)(1+dh_1)} y^* D(x^*,y^*) > 0$$

and Condition (b) of Lemma 2.2 holds. The last condition of Lemma 2.2 is equivalent to

$$T(x^*,y^*) + h_1\left(d + 2\frac{\partial f}{\partial y}(x^*,y^*)y^*\right) < 0. \tag{3.5}$$

Clearly, if $d + 2\frac{\partial f}{\partial y}(x^*,y^*)y^* \leq 0$ then the above inequality is always satisfied. If $d + 2\frac{\partial f}{\partial y}(x^*,y^*)y^* > 0$ the inequality (3.5) is true when $h_1 < A_{(x^*,y^*)}$, where $A_{(x^*,y^*)} = \dfrac{|T(x^*,y^*)|}{|d + 2\frac{\partial f}{\partial y}(x^*,y^*)y^*|}$. Therefore, if $h_1 < \min(A_{(x^*,y^*)}, \tilde{A}_{(x^*,y^*)})$ all three conditions of Lemma 2.2 are satisfied and (x^*,y^*) is a stable fixed point of System (3.3).

Assume that (x^*,y^*) is an unstable equilibrium of System (3.1). Therefore $D(x^*,y^*) < 0$ or $T(x^*,y^*) > 0$. As we describe above $D(x^*,y^*) < 0$ implies that Condition (b) of Lemma 2.2 fails. On the other hand, if $T(x^*,y^*) > 0$ then Inequality (3.5) is never satisfied, provided that $d + 2\frac{\partial f}{\partial y}(x^*,y^*)y^* \geq 0$. Condition (c) of Lemma 2.2 also fails if $d + 2\frac{\partial f}{\partial y}(x^*,y^*)y^* < 0$ and $h_1 < A_{(x^*,y^*)}$. Therefore the unstable behavior of the system (3.1) around (x^*,y^*) is preserved when $h_1 < A_{(x^*,y^*)}$.

Finally, if we select

$$Q = \max_{(x^*,y^*)\in\tilde{\Gamma}} \left(\frac{1}{A_{(x^*,y^*)}}, \frac{1}{\tilde{A}_{(x^*,y^*)}} \right),$$

where $\tilde{\Gamma}$ represents the set of all equilibria of System (3.1), then

$$h_1 < \min(A_{(x^*,y^*)}, \tilde{A}_{(x^*,y^*)})$$

for every equilibrium point (x^*, y^*), which guarantee dynamical consistence between the differential system (3.1) and the numerical scheme (3.3) around all equilibria. □

Remark 3.1. *If we want to determine a specific value for* Q *we need to evaluate the constants* $\tilde{A}_{(x^*,y^*)}$. *After some lengthy calculations one derives the following:*

$$1 + \alpha(h_1) + \beta(h_1) > 0 \iff Bh_1^2 + Ch_1 + 4 > 0,$$

where $B = 6d + \left(4\frac{\partial f}{\partial y}(x^*, y^*) - D(x^*, y^*)\right) y^*$ *and* $C = 4 + 4d + 2T(x^*, y^*)$. *Therefore, the constant* $\tilde{A}_{(x^*,y^*)}$ *can be selected as follows:*

$$\tilde{A}_{(x^*,y^*)} = \begin{cases} \frac{2}{\sqrt{|B|}}, & C = 0 \\ \frac{4}{|C|}, & B = 0 \\ \min\left(\frac{|C|}{|B|}, \frac{2}{|C|}\right), & \textit{otherwise} \end{cases}$$

4. PESN METHODS FOR PREDATOR-PREY SYSTEMS WITH LOGISTIC INTRINSIC GROWTH RATE OF THE PREY

In this section we analyze System (1.1) with logistic intrinsic growth rate of the prey, i.e., $P(x) = bx(1 - x/K)$, which has the following non-dimensional form:

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - af(x,y)y; \qquad x(0) \ge 0, \\ \frac{dy}{dt} &= f(x,y)y - dy; \qquad y(0) \ge 0. \end{aligned} \tag{4.1}$$

Depending on the values of the parameters, System (4.1) has the following equilibria:

1. The trivial equilibrium $(x_0, y_0) = (0, 0)$;
2. A boundary equilibrium $(x_1, y_1) = (1, 0)$; and
3. An interior equilibrium (x^*, y^*) satisfying $f(x^*, y^*) = d$ and $x^*(1 - x^*) = ady^*$.

According the stability analysis of System (3.1), the following statements about the stability of the equilibria are true:

1. The trivial equilibrium (x_0, y_0) is always linearly unstable;
2. The boundary equilibrium (x_1, y_1) is stable if $f(1, 0) < d$ and unstable otherwise;
3. The interior equilibrium (x^*, y^*) exist only if $f(1, 0) > d$, i.e., when the boundary equilibrium (x_1, y_1) is unstable. The interior equilibrium is linearly stable if

$$D(x^*, y^*) = (1 - 2x^*)\frac{\partial f}{\partial y}(x^*, y^*) + ad\frac{\partial f}{\partial x}(x^*, y^*) > 0$$

and

$$T(x^*, y^*) = 1 - 2x^* + \frac{\partial f}{\partial y}(x^*, y^*)y^* - a\frac{\partial f}{\partial x}(x^*, y^*)y^* < 0$$

are satisfied simultaneously.

The numerical schemes described in the following theorem represent PESN methods, provided that System (4.1) with logistic intrinsic growth rate of the prey population has only hyperbolic equilibria:

Theorem 4.1. *Let ϕ be a real-valued function on $\mathbb{R}$ that satisfies the property (3.2). There exists a constant $Q > 0$ such that the following scheme for solving System (4.1) represents a PESN method:*

$$\begin{aligned} \frac{x_{k+1} - x_k}{\varphi(h)} &= x_k - x_{k+1}x_k - ag(x_k, y_k)x_{k+1}y_k, \\ \frac{y_{k+1} - y_k}{\varphi(h)} &= f(x_k, y_k)y_k - dy_{k+1}, \end{aligned} \tag{4.2}$$

where $g(x,y) = \frac{f(x,y)}{x}$ is differentiable in $\bar{\mathbb{R}}^2_+$ and $\varphi(h)$ has the form $\varphi(h) = \phi(hq)/q$ for $q > Q$.

Proof. Since this proof repeats all of the major steps in the proof of Theorem 3.1, most of the same extensive calculations are omitted here. We again denote $h_1 = \varphi(h) = \dfrac{\phi(hq)}{q}$. The explicit expression of the nonstandard scheme (4.2) has the form:

$$\begin{aligned} x_{k+1} &= \frac{(1 + h_1)x_k}{1 + ah_1 g(x_k, y_k)y_k + h_1 x_k}, \\ y_{k+1} &= \frac{(1 + h_1 f(x_k, y_k))y_k}{1 + h_1 d}. \end{aligned} \tag{4.3}$$

Positivity of constants a, e and d implies unconditionally positivity of the scheme (4.3). Note that the fixed points of the method (4.3) are exactly the equilibria of System (4.1).

Eigenvalues of J at the trivial equilibrium (x_0, y_0) are $1 + h_1$ and $\frac{1}{1+dh_1}$, i.e., (x_0, y_0) is always unstable, which is consistent with the dynamical behavior of System (4.1). The Jacobian at the boundary equilibrium (x_1, y_1) has eigenvalues $\frac{1}{1+h_1}$ and $\frac{1+h_1 f(1,0)}{1+dh_1}$. Therefore, the fixed point (x_1, y_1) is stable if $f(1, 0) < d$, which is precisely when (x_1, y_1) is a stable equilibrium of System (4.1). Using that $f(x, y) = g(x, y)x$ and the fact that $ag(x^*, y^*)y^* + x^* = 1$, the Jacobian $J(x^*, y^*) = (j_{ij}(x^*, y^*))_{2\times 2}$, at an interior equilibrium (x^*, y^*), can be simplified as follows:

$$\begin{aligned} j_{11}(x^*, y^*) &= \frac{1 + 2h_1}{1 + h_1} - \frac{h_1}{1 + h_1}\left(2x^* + a\frac{\partial f}{\partial x}(x^*, y^*)y^*\right), \\ j_{12}(x^*, y^*) &= -\frac{ah_1}{1 + h_1}\left(d + \frac{\partial f}{\partial y}(x^*, y^*)y^*\right), \\ j_{21}(x^*, y^*) &= \frac{h_1}{1 + dh_1}\frac{\partial f}{\partial x}(x^*, y^*)y^*, \quad \text{and} \\ j_{22}(x^*, y^*) &= 1 + \frac{h_1}{1 + dh_1}\frac{\partial f}{\partial y}(x^*, y^*)y^*. \end{aligned}$$

Eigenvalues λ_1 and λ_2 of $J(x^*,y^*)$ are roots of the quadratic equation:

$$\lambda^2 - \alpha\lambda + \beta = 0,$$

where

$$\alpha = \frac{2+3h_1-2h_1x^*}{1+h_1} - \frac{ah_1}{1+h_1}\frac{\partial f}{\partial x}(x^*,y^*)y^* + \frac{h_1}{1+dh_1}\frac{\partial f}{\partial y}(x^*,y^*)y^*$$

and

$$\begin{aligned}\beta = \frac{1+2h_1(1-x^*)}{1+h_1} &- \frac{ah_1}{(1+h_1)(1+dh_1)}\frac{\partial f}{\partial x}(x^*,y^*)y^* \\ &+ \frac{h_1(1+2h_1(1-x^*))}{(1+h_1)(1+dh_1)}\frac{\partial f}{\partial y}(x^*,y^*)y^*.\end{aligned}$$

Functions $\alpha = \alpha(h_1)$ and $\beta = \beta(h_1)$ are continuous in h_1 for $h_1 > 0$ and they take values $\alpha(0) = 2$ and $\beta(0) = 1$ at zero. Therefore, there exist constants $\tilde{A}_{(x^*,y^*)} > 0$ such that $1 + \alpha(h_1) + \beta(h_1) > 0$ for all $0 < h_1 < \tilde{A}_{(x^*,y^*)}$.

Condition (b) of Lemma 2.2, i.e., $1 - \alpha + \beta > 0$, is equivalent to $D(x^*,y^*) > 0$ while Condition (c) of Lemma 2.2 leads to

$$T(x^*,y^*) + h_1\left(d(1-2x^*) + 2\frac{\partial f}{\partial y}(x^*,y^*)y^*(1-x^*)\right) < 0. \tag{4.4}$$

The former inequality is satisfied when $h_1 < A_{(x^*,y^*)}$, where

$$A_{(x^*,y^*)} = \frac{|T(x^*,y^*)|}{|d(1-2x^*) + 2\frac{\partial f}{\partial y}(x^*,y^*)y^*(1-x^*)|}.$$

Similarly to the proof of Theorem 3.1 we conclude that if $h_1 < \min(A_{(x^*,y^*)}, \tilde{A}_{(x^*,y^*)})$ then the dynamical behavior of the numerical scheme (4.2) around an equilibrium (x^*,y^*) is consistent with the behavior of System (4.1). When (x^*,y^*) is a stable equilibrium of System (4.1) then it is also a stable fixed point of System (4.2) and vice versa.

Selection of

$$Q = \max_{(x^*,y^*)\in\tilde{\Gamma}}\left(\frac{1}{A_{(x^*,y^*)}}, \frac{1}{\tilde{A}_{(x^*,y^*)}}\right),$$

where $\tilde{\Gamma}$ represents the set of all interior equilibria of System (4.1), guarantees that $h_1 < \min(A_{(x^*,y^*)}, \tilde{A}_{(x^*,y^*)})$ for every equilibrium point (x^*,y^*). □

Remark 4.1. *Similarly to the case in the previous section, the calculation of a specific value for Q requires evaluations of the constants $\tilde{A}_{(x^*,y^*)}$. Condition (a) of Lemma 2.2 is equivalent to*

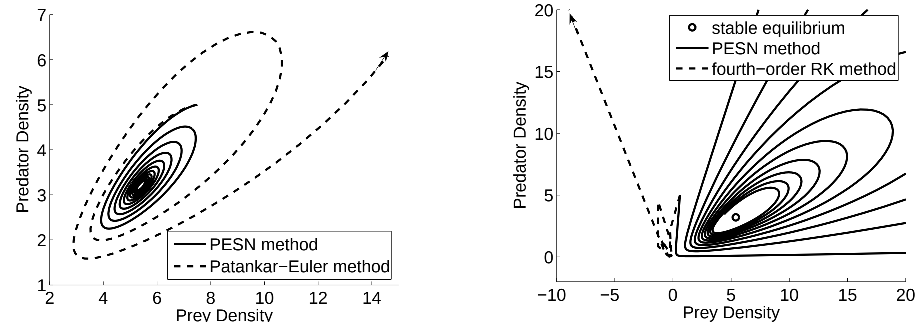
$$Bh_1^2 + Ch_1 + 4 > 0,$$

where

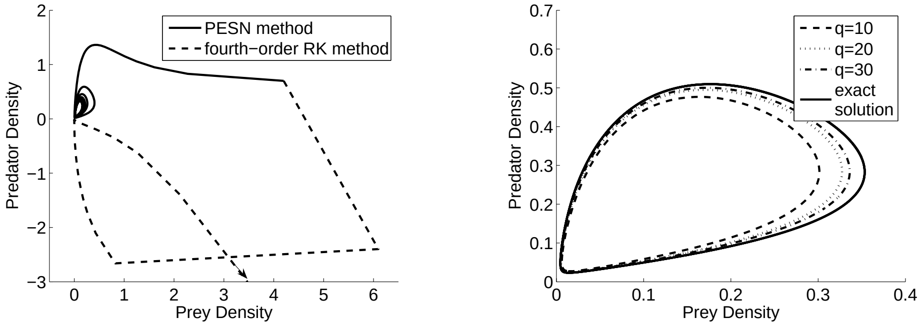
$$B = 2d(3-2x^*) + \left(4(1-x^*)\frac{\partial f}{\partial y}(x^*,y^*) - D(x^*,y^*)\right)y^*$$

and

$$C = 4 + 4d + 2T(x^*,y^*).$$



(a) $h = 0.4$, $x(0) = 7.5$, $y(0) = 5.0$ (b) $h = 0.8$, $x(0) = 0.6$, $y(0) = 5.0$



(c) $h = 0.4$, $x(0) = 4.2$, $y(0) = 0.7$ (d) $h = 0.4$, $x(0) = 4.2$, $y(0) = 0.7$

FIGURE 1. Numerical approximations of the solutions of Beddington-DeAngelis predator-prey systems with linear (top) and logistic (bottom) intrinsic growth rate of the prey.

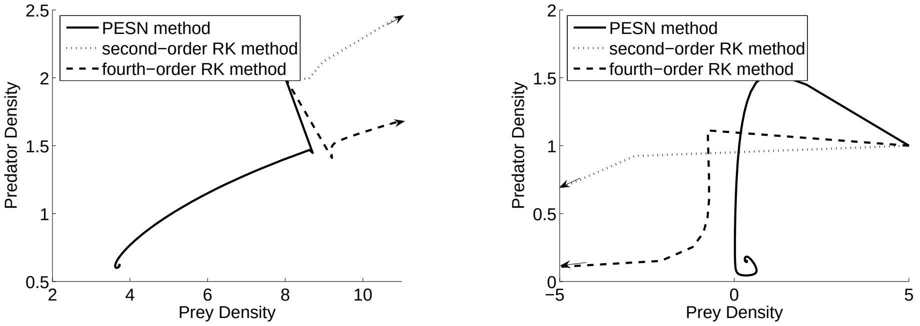
Therefore, the constant $\tilde{A}_{(x^*,y^*)}$ *can be selected as follows:*

$$\tilde{A}_{(x^*,y^*)} = \begin{cases} \frac{2}{\sqrt{|B|}}, & C = 0 \\ \frac{4}{|C|}, & B = 0 \\ \min\left(\frac{|C|}{|B|}, \frac{2}{|C|}\right), & otherwise \end{cases}$$

5. NUMERICAL SIMULATIONS

To illustrate the advantages of the designed PESN finite-difference methods, we first consider predator-prey systems with Beddington-DeAngelis functional response $f(x, y) = \dfrac{ex}{b + x + y}$.

The first set of simulations (Fig.1-a,b) compares different numerical approximations of the system with a linear intrinsic growth (3.1). Mathematical analysis of System (3.1) with Beddington-DeAngelis functional response and constants $a = 0.75$, $d = 2.25$, $b = 1.0$ and $e = 4.0$ shows that the equilibrium $(x_0, y_0) = (0, 0)$ is unstable, while the equilibrium $(x^*, y^*) = (\frac{27}{5}, \frac{16}{5})$ is globally asymptotically stable in the interior of the first quadrant [7]. The scheme (3.3) represents a PESN method for $q > Q = 4$, so we select $q = 4.5$ in our experiment. The first simulation (Fig.1-a) compares approximations obtained by the PESN method (3.3) and



(a) $h = 0.76$, $x(0) = 8.0$, $y(0) = 2.0$

(b) $h = 0.33$, $x(0) = 5.0$, $y(0) = 1.0$

FIGURE 2. Numerical approximations of the solutions of Nicholson-Bailey predator-prey systems with linear (left) and logistic (right) intrinsic growth rate of the prey.

the Patankar-Euler method [4]. The Patankar Euler method is positive, but not elementary stable, which leads to divergence of its solution for a step-size $h = 0.4$. The second simulation (Fig.1-b) compares the PESN method (3.3) and the fourth-order Runge-Kutta method. In this example, the Runge-Kutta method, which is not elementary stable, fails to express the correct asymptotic behavior of the corresponding predator-prey system and the numerical solution diverges.

The next set of simulations (Fig.1-c,d) compares approximations of the system with a logistic intrinsic growth (4.1) and Beddington-DeAngelis functional response. Mathematical analysis of System (4.1) with constants $a = 1.5$, $d = 0.25$, $b = 0.02$ and $e = 1.0$ shows that equilibria $(x_0, y_0) = (0, 0)$, $(x_1, y_1) = (1, 0)$ and $(x^*, y^*) = (0.0443, 0.1127)$ are unstable and all solutions approach an unique limit cycle, which is globally asymptotically stable in the interior of the first quadrant [16, 17]. The scheme (4.2) represents a PESN method for $q > Q = 0.549$, so we select $q = 1$ in this example. The first simulation (Fig.1-c) compares the approximations of the solution, starting at $(4.2, 0.7)$, obtained by the PESN method (3.3) and the fourth-order Runge-Kutta method with step-size $h = 0.4$. The Runge-Kutta approximation diverges, while the PESN method expresses the correct asymptotic behavior of the predator-prey system and converges to a limit cycle. However, this limit cycle does not exactly coincide with the real attractor. The last simulation (Fig.1-d) shows that we can a obtain better approximation of the limit cycle by increasing the value of q in the PESN method.

Our second example of a "predator-dependent" functional response, $f(x, y)$, is the Nicholson-Bailey form $f(x, y) = xe^{-by}$. Mathematical analysis of System (3.1) with Nicholson-Bailey functional response and constants $a = 3.0$, $d = 2.0$ and $b = 1.0$ shows that the equilibrium $(x_0, y_0) = (0, 0)$ is unstable, while the equilibrium $(x^*, y^*) = (3.7144, 0.6191)$ is asymptotically stable, but not globally stable in the interior of the first quadrant. Solutions that start outside of its basin of attraction are unbounded. The scheme (3.3) represents a PESN method without restrictions for q. Therefore we can use the scheme (3.3) with $\varphi(h) = h$. The simulation (Fig.1-a) compares approximations of the solution, starting at point $(8, 2)$, which is inside of the basin of attraction of the equilibrium (x^*, y^*), obtained by the PESN method (3.3) and second- and fourth-order Runge-Kutta methods. For a step-size $h = 0.76$ the Runge-Kutta approximations diverge, while the PESN approximation converges to the equilibrium (x^*, y^*).

Finally, we consider the predator-prey system with a logistic intrinsic growth (4.1) and Nicholson-Bailey functional response. Mathematical analysis of System (4.1) with constants $a = 5.0$, $d = 0.3$ and $b = 1.0$ shows that the equilibria $(x_0, y_0) = (0, 0)$, $(x_1, y_1) = (1, 0)$ are unstable, while $(x^*, y^*) = (0.3216, 0.165)$ is globally asymptotically stable in the interior of the first quadrant. The scheme (4.2) represents a PESN method for $q > Q = 0.107$, so we select $q = 0.2$ in this example. The simulation (Fig.1-b) compares the approximations of the solution, starting at $(5.0, 1.0)$, obtained by the PESN method (3.3) and second- and the fourth-order Runge-Kutta methods with step-size $h = 0.33$. The Runge-Kutta approximations diverge, while the PESN method expresses the correct asymptotic behavior of System (4.1) and converges toward the equilibrium (x^*, y^*).

In all of the above simulations the PESN method follows accurately the dynamics of System (2.1), while the standard numerical methods are dynamically inconsistent and fail to preserve the stability of equilibria, the positivity of the trajectories, and/or the regions of attraction for a variety of time-step sizes. Problems in the use of the standard numerical methods arise not only because they are not elementary stable but also because the methods are not unconditionally positive, which is a natural requirement to have when approximating biological systems. However, the positivity-preserving property is not a sufficient condition that guarantees the asymptotic consistence of numerical solutions. An example of that is the Patankar-Euler method, which is unconditionally positive but not elementary stable and expresses serious numerical problems for large time-steps.

6. Conclusions

Positive and elementary stable nonstandard (PESN) numerical methods were developed for predator-prey systems with general functional response that have only hyperbolic equilibria. The designed new PESN methods preserve two of the most important dynamical characteristics of the corresponding systems, namely the stability of all equilibria and the positivity of all solutions with positive initial conditions. The value of the constant Q in the PESN methods depends on the particular system (1.1) and the specific functional response function $f(x, y)$. Usually, it requires some information about the existing equilibria and can be defined as a simple expression in terms of the parameters of the systems.

The numerical solutions of the developed PESN methods are dynamically consistent and express the correct asymptotic behavior of the corresponding predator-prey systems for arbitrary large time-steps. In addition, the PESN approach allows for the use of an essentially implicit method for the cost of an explicit one, which makes the methods a computationally effective tool in simulations of the dynamics of predator-prey systems.

Future research directions include the design and analysis of PESN methods for biological systems with non-hyperbolic equilibria.

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