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NUMERICAL INVESTIGATION OF DIFFUSIVE PREDATOR-PREY MODEL WITH APPLICATION TO ANNULAR HABITAT

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Abstract

A predator-prey model of the Lotka-Volterra type is considered in annular habitat with the domain which demonstrates 2π-periodicity properties for all species at fixed time. The model is described by two nonlinear partial differential equations of parabolic type. Initial conditions are formulated so that predator and prey do not interact with each other at initial time interval. Dynamics of migration and further interaction between the species is investigated by solution of the formulated mixed problem by the numerical method of lines. The inverse problem of the parameter identification of the problem is also solved by the method of lines. In this case, it is assumed that the information about the predator and prey is incomplete, i.e., the populations are assumed to be known in small domain of the habitat. It is shown that the formulated solution method guarantees accurate identification of all unknown parameters of the model and hence, the

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complete reconstruction of the predator-prey interaction on the habitat. The obtained parameters can be used for prediction of further dynamics of the species interaction and values of their steady-states.

1. Introduction

The term "annular habitat" appeared in the seventies of 20th century in Russian School of Mathematical Ecology governed by Markman and Bazykin [1]. Their fundamental book [2], which was first published in Russian, was further translated in English and contained a chapter devoted to the annular habitats where spatially homogeneous oscillations of populations and stable dissipative structures were investigated. The annular habitats demonstrate a 2π-periodicity of species distributions at fixed time and also well known as the periodic habitats. The last name is the most popular between mathematicians, which demonstrates interest to this type of problems [3-6]. In this paper, we use the original term "annular habitat". There are numerous examples of species living in habitats, which can be theoretically treated as the annular habitats. For example, bacteria population surrounding circular edges of puddles, plants and animals living at constant height levels of mountains, species co-existing on banks surrounding big lakes, etc. Mathematical models of population dynamics have to take into consideration different aspects of species competition and co-existence in the annular habitats, such as growing and saturation of prey, predator-prey interaction, formalized in different types of trophic functions, prey and predator migrations in the habitat, etc.

2. Problem Statement

The paper is devoted to numerical analysis of the diffusive predator-prey system of the Lotka-Volterra type in the annular habitat. The following assumptions are as follows:

- in the absence of predator, the prey population is growing in accordance with the logistic law, which is formalized in the model by combination of linear and quadratic terms,

- in the absence of prey, the predator population demonstrates decay proportional to combination of linear and quadratic terms, i.e., it takes into consideration internal competition of prey for the food,

- the trophic function has type one in accordance with the classification proposed in [1] and [2], as it was accepted in the classical Lotka-Volterra model, and

- the species migration in the annular habitat is described by the dissipative terms proportional to second partial derivatives of predator and prey populations with respect to polar angle, characterizing the spatial distribution in the habitat.

3. Governing Equations, Periodic and Initial Conditions

Following the assumptions in Section 2, the governing system of equations is as follows:

$$\frac{\partial x}{\partial t} = a_{11}x - a_{12}x^2 - a_{13}xy + D_x \frac{\partial^2 x}{\partial \varphi^2},$$

$$\frac{\partial y}{\partial t} = -a_{21}y - a_{22}y^2 - a_{23}xy + D_y \frac{\partial^2 y}{\partial \varphi^2}, \tag{1}$$

where $x = x(t, \varphi)$ is population of prey depending on time t and polar angle, φ, characterizing the spatial coordinate of the annular habitat, $y = y(t, \varphi)$ is population of predator, coefficients for a_{ij} for $(i, j = 1, 2, 3)$ and D_x, D_y and are assumed to be positive constants. This is the system of two nonlinear partial differential equations of parabolic type. The system is considered in the finite time interval $t \in [0, T]$, for $T > 0$, and $\varphi \in [0, 2\pi]$. Due to 2π-periodicity of the annular habitat, the corresponding periodicity conditions of the prey and predator populations are:

$$x(t,\ \varphi = 0) = x(t,\ \varphi = 2\pi); \quad \frac{\partial x}{\partial \varphi}(t,\ \varphi = 0) = \frac{\partial x}{\partial \varphi}(t,\ \varphi = 2\pi),$$

$$y(t,\ \varphi = 0) = y(t,\ \varphi = 2\pi); \quad \frac{\partial y}{\partial \varphi}(t,\ \varphi = 0) = \frac{\partial y}{\partial \varphi}(t,\ \varphi = 2\pi). \tag{2}$$

Initial conditions are:

$$x(t = 0,\ \varphi) = X(\varphi) \text{ and } y(t = 0,\ \varphi) = Y(\varphi). \tag{3}$$

The system of equations (1), periodicity conditions (2) and initial conditions (3) form a mixed problem, which will be solved numerically using the method of lines (Section 4).

4. Method of Lines: Solution of the Annular Habitat Predator(prey) Problem (1)-(3)

In the method of lines [7], the following three-points finite difference scheme for approximation of the second derivatives [8]:

$$\frac{\partial^2 x_m}{\partial \varphi^2} \cong \frac{x_{m-1} - 2x_m + x_{m+1}}{\partial \varphi^2},$$

$$\frac{\partial^2 y_m}{\partial \varphi^2} \cong \frac{y_{m-1} - 2y_m + y_{m+1}}{\partial \varphi^2}, \tag{4}$$

where $\Delta\varphi = \frac{2\pi}{M}$ - interval between two neighbor lines, $x_m = x_m(t)$ and $y_m = y_m(t)$ are functions of time only. That is why the method of lines can be interpreted as the method of conversion of the original system of two partial differential equations (1) of order four into the truncated system of $2M$ ordinary differential equations. This system is as follows:

$$\dot{x}_m = \dot{z}_m = a_{11}x_m - a_{12}x_m^2 - a_{13}x_m y_m + D_x x_m'',$$

$$\dot{y}_m = \dot{z}_m + M = -a_{21}y_m - a_{22}y_m^2 + a_{23}x_m y_m + D_y y_m'', \tag{5}$$

where $m = 1, 2, \ldots, M$, $x_m = z_m$, $y_m = z_{m+M}$ and

$$x_m'' = \frac{1}{\Delta\varphi^2}\begin{cases} z_m - 2z_1 + z_2 & \text{if } m = 1, \\ z_{m-1} - 2z_m + z_{m+1} & \text{if } 1 < m < M, \\ z_{M-1} - 2z_M + z_1 & \text{if } m = M, \end{cases}$$

$$y_m'' = \frac{1}{\Delta\varphi^2}\begin{cases} z_{2M} - 2z_{M+1} + z_{M+2} & \text{if } m = 1, \\ z_{m+M-1} - 2z_{m+M} + z_{m+M+1} & \text{if } 1 < m < M, \\ z_{2M-1} - 2z_{2M} + z_{M+1} & \text{if } m = M \end{cases} \tag{6}$$

due to 2π -periodicity (2).

Initial conditions (3) for system (5)-(6) are formulated so that the initial distribution of prey at $(t = 0)$ is given in points $m = 1, 2, ..., M$, and initial distribution of predators is given in points $m + M = M + 1, M + 2, ..., 2M$. Solution of the formulated initial value problem is performed by one of the standard numerical ODEs.

5. Solution of Direct Initial Value Problems

For the solution of the direct problem, it is assumed that coefficients $a_{11}, a_{12}, ..., a_{23}, D_x, D_y$ are known. Let us assume that these coefficients are: $a_{11} = 0.75$, $a_{12} = 5.0 \cdot 10^{-4}$, $a_{13} = 6.25 \cdot 10^{-3}$, $a_{21} = 1.0$, $a_{22} = 7.5 \cdot 10^{-3}$, $a_{23} = 6.25 \cdot 10^{-3} = a_{13}$, $D_x = 4.0 \cdot 10^{-3}$ and $D_y = 8.0 \cdot 10^{-3}$. Duration of time interval is assumed to be $T = 40$ and $t \in [0, T]$. Let us select number of intervals in the annular habitat to be $M = 360$. It means that lines of solution will be separated by angular increment $\Delta\varphi = \frac{2\pi}{M} = 1^\circ$ (one arc degree). Number of temporal intervals in $[0, T = 40]$ is selected as $N = 400$. Hence, $2M = 720$ nonlinear ordinary differential equations will be solved and solution of the problem in $2M \cdot N = 720 \cdot 400 = 288 \cdot 10^3$ points will be obtained.

Initial distribution of the prey population at time $(t = 0)$ is assumed to be:

$$x(t = 0, \varphi) = \text{Prey}(\varphi) = 10^3 \cdot \exp\left[-17 \cdot \left(\varphi - \frac{\pi}{4}\right)^4\right]. \tag{7}$$

Initial distribution of the predator population at initial time is:

$$y(t = 0, \varphi) = \text{Predator}(\varphi) = 5 \cdot 10^3 \cdot \exp\left[-17 \cdot \left(\varphi - \frac{3\pi}{4}\right)^4\right]. \tag{8}$$

The initial distribution of the prey and predator is shown in Figure 1. So, at the initial time instant, the species are practically isolated from each other.

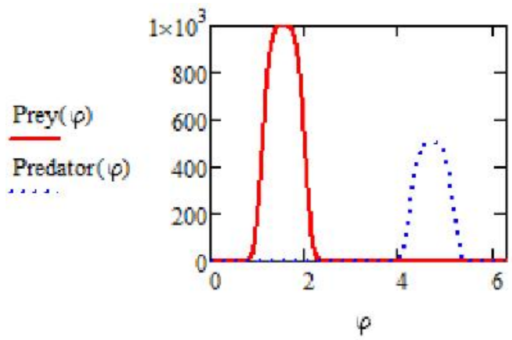

Figure 1. Initial distribution of the prey and predator in annular habitat $\varphi \in [0, 2\pi]$.

Reformulation of the initial value conditions for the method of lines is shown in Figure 2, where $kk = 1, 2, ..., 2M = 720$ and for $m = 1, 2, ..., M = 360$:

$$z_m = \text{Prey}(\varphi_m = \Delta\varphi \cdot m), \quad z_{m+M} = \text{Predator}(\varphi_{m+M} = \Delta\varphi \cdot (m + M)). \tag{9}$$

It follows from Figure 2 that what follows the distribution of prey will be displayed as a surface of contour plots for lines with number $m = 1, 2, ..., 360$ and population of predator will be displayed as the corresponding plots for lines with numbers $m + M = M + 1, \; M + 2, ..., 2M = 361, 362, ..., 720.$

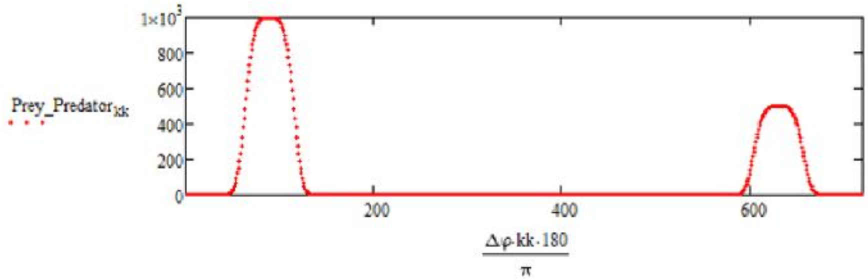

Figure 2. Initial distribution of prey and predator in annular habitat for the method of lines.

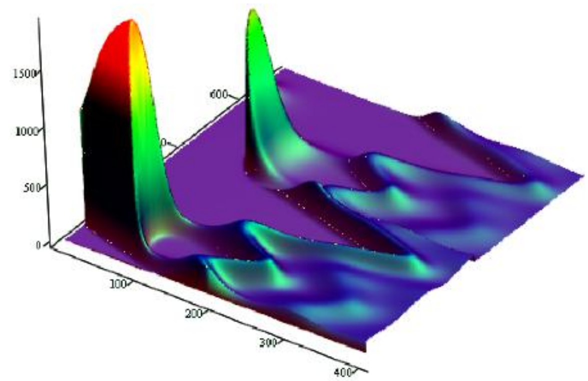

Figure 3. Surface plot of prey-predator interactions.

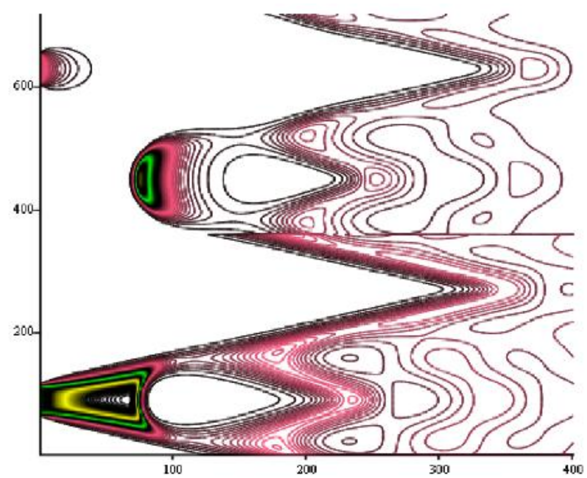

Figure 4. Contour plot of prey-predator interactions.

Solution of the initial value problem (5)-(9) is performed by the Adams-Backward Differential Formula (AdamsBDF) built-in algorithm in the MathCad15 software. Laptop with 8GB RAM INTEL CORE I7, 2.8GHz processor needs less than 250 seconds for solution of this problem. The solution is shown in Figure 3 as a surface plot and in Figure 4 as a contour plot.

Graphs of both prey and predator at polar angle $\varphi = \frac{\pi}{2}$, which correspond to lines 90 and 450, are shown in Figure 5, where prey $(t) = x\left(t, \varphi = \frac{\pi}{2}\right)$ and predator $(t) = y\left(t, \varphi = \frac{\pi}{2}\right)$.

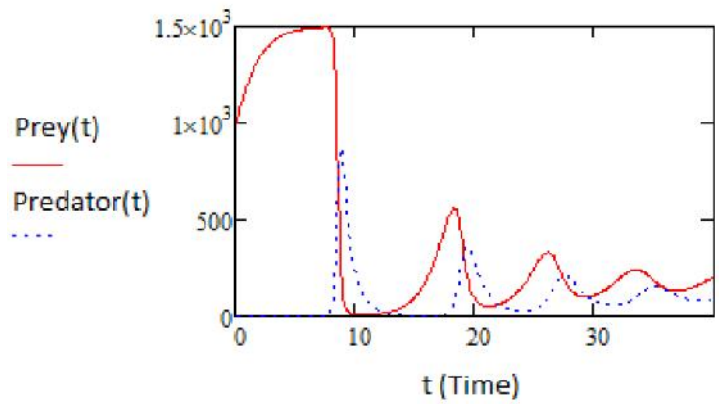

Figure 5. Graphs of prey (solid line) and predator (dashed line) at $\varphi = \frac{\pi}{2}$.

It follows from Figures 3, 4 and 5 that at small initial time interval of living in the habitat, the prey and predator do not interact and hence, the population of prey is increasing in accordance with the logistic law and demonstrates tendency to saturation while the predator population is decreasing substantially in the absence of food. Simultaneously both the populations start migrating in the habitat and meet each other, thus, stipulating intensive interaction between themselves. There are two different mechanisms of this interaction: on one hand, the intensive nonlinear oscillatory behavior of interaction between two populations is occurred when maximum of prey stipulates maximum growth of the predator and vice versa. At maximum of the predator, the prey population demonstrates maximum rate of its drop. On the other hand, the species interaction gives rise to two pairs of quasi-travelling waves of approximately constant amplitudes, which propagate in opposite directions with equal speed. The first pair of the quasi-travelling waves belongs to the prey population, which propagates in the habitat with maximum possible speed. The second pair of the quasi-travelling waves, which has slight delay with respect to the first pair of waves, belongs to the predator. In principle, the predator can migrate in the habitat faster than the prey because the diffusion coefficient of the predator is larger than the diffusion coefficient of prey $(D_x > D_y)$, but as we see from Figures 3 and 4, both the populations migrate in the habitat with the same rate. By means of this propagation, the amplitudes of both the populations of predator and prey are maintained at constant levels. Eventually, the two pairs of travelling waves collide, forming characteristic spikes, and this means that the whole annular habitat becomes populated. Starting from that moment, the two domains of decaying oscillatory behavior exist in the habitat. In the first zone, the decaying oscillations exist in the domain surrounding the area, where the maximum of prey population occurred. In the first domain, the decaying oscillations exist in the area surrounding the place where the colliding of two pairs of quasi-travelling waves has occurred. Amplitude of oscillations in the first domain is larger than in the second one. Eventually, the decaying oscillations tend to steady state values and distribution of the predator and prey populations equalizes over the whole annular habitat. The steady state values, corresponding conditions $\frac{\partial x}{\partial t} = \frac{\partial y}{\partial t} = 0$ and $\frac{\partial^2 x}{\partial \varphi^2} = \frac{\partial^2 y}{\partial \varphi^2} = 0$ are calculated from (1). They are as follows:

$$x^{(st-ts)} = \det\begin{bmatrix} a_{11} & a_{13} \\ a_{21} & a_{23} \end{bmatrix} \cdot \det^{-1}\begin{bmatrix} a_{12} & a_{13} \\ a_{23} & -a_{22} \end{bmatrix} \approx 172.74,$$

$$y^{(st-ts)} = \det\begin{bmatrix} a_{21} & a_{11} \\ a_{23} & a_{21} \end{bmatrix} \cdot \det^{-1}\begin{bmatrix} a_{12} & a_{13} \\ a_{23} & -a_{22} \end{bmatrix} \approx 106.18. \tag{10}$$

6. Solution of Inverse Problem of Parameter Identification with Incomplete Information

Let us assume that the values of parameters $a_{11}, a_{12}, ..., a_{23}, D_x, D_y$ for the problem, considered in Section 3, are unknown, but information about prey and predator populations is available on three neighbor lines, say $z_{89,n} = x_{89,n}$, $z_{90,n} = x_{90,n}$, $z_{91,n} = x_{91,n}$ and $z_{449,n} = y_{89,n}$, $z_{450,n} = y_{90,n}$, $z_{451,n} = y_{91,n}$ for $n = 2, 3, ..., N-1 = 2, 3, ..., 399$. Hence, the information about the species interaction in the habitat is incomplete because we do not know what is going on $2M - 6 = 714$ lines. Moreover, it will also mean that the knowledge of, say, initial (or terminal, or intermediate) conditions on the habitat gives us the possibility to make predictions on predator-prey populations for every finite time interval. It is necessary to mention that the line selection is not arbitrary in general case and it must be done so that the lines are located in the domain where interactions between species are the most intensive. To solve the problem, let us formulate the following overdetermined system of equations from (5), which is linear with respect to the unknown parameters of the system $a_{11}, a_{12}, ..., a_{23}, D_x, D_y$:

$$\begin{aligned} & a_{11}(z_{90,n}) + a_{12}(-z_{90,n}^2) + a_{13}(-z_{90,n} \cdot z_{450,n}) \\ & + D_x(d2z_{90,n}) = (dzt_{90,n}), \\ & a_{21}(z_{450,n}) + a_{22}(-z_{450,n}^2) + a_{23}(-z_{90,n} \cdot z_{450,n}) \\ & + D_y(d2z_{450,n}) = (dzt_{450,n}), \end{aligned} \tag{11}$$

where $n = 2, 3, ..., 399$ and

$$d2z_{90,n} \cong \frac{z_{89,n} - 2z_{90,n} + z_{91,n}}{\Delta\varphi^2}, \quad d2zt_{90,n} \cong \frac{z_{90,n+1} - z_{90,n-1}}{2\Delta t},$$

$$d2z_{450,n} \cong \frac{z_{449,n} - 2z_{450,n} + z_{451,n}}{\Delta\varphi^2}, \quad d2zt_{450,n} \cong \frac{z_{450,n+1} - z_{450,n-1}}{2\Delta t},$$

$$\Delta\varphi = \frac{2\pi}{M} = \frac{\pi}{180}, \quad \Delta t = \frac{T}{N} = \frac{40}{400} = 0.1. \tag{12}$$

The overdetermined system (11) is solved by the least squares method [7]. To realize this, we compose four matrices:

$$M_1 = \begin{bmatrix} z_{90,2} & -z_{90,2}^2 & -z_{90,2} \cdot z_{450,2} & d2z_{90,2} \\ z_{90,3} & -z_{90,3}^2 & -z_{90,3} \cdot z_{450,3} & d2z_{90,3} \\ \vdots & \vdots & \vdots & \vdots \\ z_{90,N-1} & -z_{90,N-1}^2 & -z_{90,N-1} \cdot z_{450,N-1} & d2z_{90,N-1} \end{bmatrix},$$

$$M_2 = \begin{bmatrix} dzt_{90,2} \\ dzt_{90,3} \\ \vdots \\ dzt_{90,N-1} \end{bmatrix},$$

$$M_3 = \begin{bmatrix} -z_{450,2} & -z_{450,2}^2 & z_{90,2} \cdot z_{450,2} & d2z_{450,2} \\ -z_{450,3} & -z_{450,3}^2 & z_{90,3} \cdot z_{450,3} & d2z_{450,3} \\ \vdots & \vdots & \vdots & \vdots \\ -z_{450,N-1} & -z_{450,N-1}^2 & -z_{90,N-1} \cdot z_{450,N-1} & d2z_{450,N-1} \end{bmatrix},$$

$$M_4 = \begin{bmatrix} dzt_{450,2} \\ dzt_{450,3} \\ \vdots \\ dzt_{450,N-1} \end{bmatrix}, \tag{13}$$

and obtain the result as following estimations of the unknown parameters:

$$[\bar{a}_{11} \quad \bar{a}_{12} \quad \bar{a}_{13} \quad \overline{D}_x]^T = (M_1^T \cdot M_1)^{-1}(M_1^T \cdot M_2),$$

$$[\bar{a}_{21} \quad \bar{a}_{22} \quad \bar{a}_{23} \quad \overline{D}_y]^T = (M_3^T \cdot M_3)^{-1}(M_3^T \cdot M_4). \tag{14}$$

Application of this method to the data, generated in the previous section, gives the following parameters estimation (in the brackets, we reproduce original values of the corresponding parameters):

Table 1. Comparison of exact and estimated values of parameters

Parameter	Exact	Estimated	Relative error %
a_{11}	0.750000	0.752000	0.23
a_{12}	0.000500	0.000501	0.24
a_{13}	0.006250	0.006264	0.23
D_x	0.004000	0.003942	1.45
a_{21}	1.000000	1.002000	0.23
a_{22}	0.000745	0.000749	0.07
a_{23}	0.006250	0.006260	0.15
D_y	0.008000	0.008180	2.25

As we see accuracy of determination of a_{ij} $(i,\ j = 1, 2, 3)$, parameters are higher than accuracy of estimation of D_x, D_y parameters. This can be explained by more accurate numerical calculation of the first derivatives than the second ones.

7. Conclusions

The mixed problem including the system of two nonlinear partial differential equations of parabolic type, 2π -periodicity conditions and initial conditions was formulated on the annular habitat. In the direct approach, it is assumed that the values of all parameters are known and the problem was solved by the method of lines. The solution is given in terms of the surface and contour plots of the interacting prey and predator populations versus time and polar angle of the habitat. It was shown that the species migrations in the habitat are described by the quasi-travelling waves with constant rates of propagation. After populating the habitat, the predator-prey interaction is characterized by the decaying oscillatory behavior, which eventually tends to the theoretically predicted steady-state values. The method of inverse problem solution by the method of lines was proposed.

It was shown that complete identification of the unknown constants can be achieved at incomplete information about species in the domain, where their interaction is the most effective. The relative errors of the estimated unknown parameters have been calculated.

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