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Analysis of the stochastic model “prey–migration area–predator–superpredator”

Irina I. Vasilyeva¹, Olga V. Druzhinina², Olga N. Masina¹, Anastasia V. Demidova³

¹ Bunin Yelets State University, 28 Kommunarov St, Yelets, 399770, Russian Federation

² Federal Research Center “Computer Science and Control” of Russian Academy of Sciences, 44 building 2 Vavilov St, Moscow, 119333, Russian Federation

³ RUDN University, 6 Miklukho-Maklaya St, Moscow, 117198, Russian Federation

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Abstract. Current research areas of dynamic migration and population models include the analysis of trajectory dynamics and solving parametric optimization problems using computer methods. In this paper we consider the population model “prey–migration area–predator–superpredator”, which is given by a system of four differential equations. The model takes into account trophic interactions, intraspecific and interspecific competition, as well as migration of the prey to the refuge. Using differential evolution parameters are found that ensure the coexistence of populations of prey, predator and superpredator, respectively, in the main habitat and the existence of a population of prey in a refuge. The transition to stochastic variants of the model based on additive noise, multiplicative noise and the method of constructing self-consistent models is performed. To describe the structure of the stochastic model the Fokker–Planck equations are used and a transition to a system of equations in the Langevin form is performed. Numerical solution of stochastic systems of differential equations is implemented by the Euler–Maruyama method. Computer experiments are conducted using a Python software package, and trajectories for deterministic and stochastic cases are constructed. A comparative analysis of deterministic model and corresponding stochastic models is carried out. The results can be used in solving problems of mathematical modeling of biological, ecological, physical, chemical and demographic processes.

Key words and phrases: system of differential equations; migration flows; stochastization; method of constructing self-consistent models; differential evolution

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1. Introduction

Among the key directions in the study of dynamic population models with migration flows one can highlight the investigation of trajectory dynamics and the development of computational methods for analyzing these models. The construction and study of deterministic and stochastic models of population dynamics taking into account trophic interactions between species and competition or considering species competition and migration flows are addressed, in particular, in [1–10]. In [1] a modification of the “predator–prey” model is proposed accounting for competition among predators for additional food. In [2] a “predator–prey” model is studied where the prey is characterized by an additive Allee effect and controlled migration flows are considered for the predator. In [6] a four-dimensional dynamic model with two migration habitats is proposed corresponding to the predator and prey respectively.

In [3] several types of three-dimensional models are considered, including species competition and trophic interactions of the “prey–predator–superpredator” type taking into account the possibility of prey infection by viral diseases. Complex trophic interactions with predator and superpredator saturation effects according to Holling are studied in [4]. For each considered model equilibrium states are obtained, trajectory dynamics are investigated and phase portraits are constructed. In most of the proposed models with trophic interactions, migration flows of populations are not taken into account, therefore, studying the impact of prey migration to refuges presents scientific interest. In [5] a distributed three-dimensional system of partial differential equations of the “prey–predator–superpredator” type is considered based on the reaction-diffusion equation which accounts for various factors of population growth and mortality as well as migration flows between habitats. However there arises a need to construct similar models based on systems of ordinary differential equations.

Stochastic population models represent significant theoretical and applied interest. Models with trophic interactions in the stochastic case is insufficiently studied. In [7] the impact of environmental fluctuations on a “prey–predator” model with a stage-structured prey population is investigated, a stochastic analysis of the model is carried out and conditions for stochastic stability are derived. In [8] the dynamical behavior of a “prey–predator” system is studied where both the prey and predator exhibit herd behavior. The stochastization of the model is performed by adding Gaussian white noise to the prey reproduction rates and the predator extinction rates.

One of the effective methods of stochastization is the method of constructing self-consistent stochastic models proposed in [11–15]. In [16] a stochastic model is obtained using an original software package that includes calculations of the interaction scheme, drift vector and diffusion matrix. In [9, 10] a “two competitors–two migration areas” model is considered which takes into account intraspecific and interspecific competition in two populations as well as bidirectional migration of both populations. The transition to the stochastic case for this model is carried out based on the method of constructing self-consistent one-step models.

Heuristic methods of parametric optimization inspired by nature are applied to study dynamic models [17]. In particular, [18] describes the differential evolution algorithm for numerical optimization. Differential evolution is based on the genetic annealing algorithm and is applied to real-valued input data. In [19] the results of development a software package for optimizing the parameters of population dynamic models are presented. The model “two competitors–one migration area” is considered which takes into account interspecific competition and bidirectional uneven migration of the first population to a refuge. Using differential evolution, a set of parameters satisfying the specified conditions for the coexistence of two species in the main habitat and the survival of the migrating specie in the refuge is found.

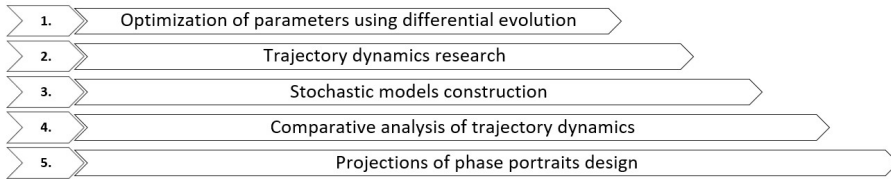


Figure 1. Stages of the algorithm for model (1) research

This paper is devoted to the study of a four-dimensional population model of the “prey–migration area–predator–superpredator” type which takes into account complex trophic interactions as well as prey migration to a refuge. In Section 2 the construction of the “prey–migration area–predator–superpredator” model with bidirectional species migration is considered. A search for model parameters is conducted using an evolutionary algorithm. The deterministic four-dimensional model is studied and projections of phase portraits are constructed. In Section 3 stochastic models of the “prey–migration area–predator–superpredator” type are developed taking into account the addition of additive and multiplicative noises as well as random migration coefficients. In this section stochastization is also performed using the method of constructing self-consistent stochastic models. The results of computational experiments are presented and an interpretation of these results is provided including a comparison of the stochastic models with the deterministic model. As a software tool for investigating the models a program complex developed in Python using the numpy, sympy, and scipy libraries is utilized. Section 4 presents a discussion of the results.

2. Description of the deterministic model and search for optimal parameters

We propose a description of a four-dimensional dynamic model that takes into account trophic interactions and prey migration based on a system of differential equations of the form

$$\begin{aligned}
 \dot{x}_1 &= a_1 x_1 - p_{11} x_1^2 - q_{13} x_1 x_3 - q_{14} x_1 x_4 + \beta x_2 - \gamma x_1, \\
 \dot{x}_2 &= a_2 x_2 - p_{22} x_2^2 - \beta x_2 + \gamma x_1, \\
 \dot{x}_3 &= -c_3 x_3 - p_{33} x_3^2 - q_{34} x_3 x_4 + d_{13} x_1 x_3, \\
 \dot{x}_4 &= -c_4 x_4 - p_{44} x_4^2 + d_{34} x_3 x_4 + d_{14} x_1 x_4,
 \end{aligned} \tag{1}$$

where x_1 is the population density of prey in the main habitat, x_2 is the population density of prey in the refuge, x_3 is the population density of predator, x_4 is the population density of superpredator; a_i ($i = 1, 2$) are the natural growth rate coefficients of prey in the main habitat (a_1) and in the refuge (a_2); q_{13} is the interaction coefficient between prey in the main habitat and predator, q_{14} is the interaction coefficient between prey in the main habitat and superpredator; p_{ii} ($i = 1, 2, 3, 4$) are the intraspecific competition coefficients; q_{34} is the interaction coefficient between predator and superpredator; c_i ($i = 3, 4$) are the natural loss rate coefficients of predator (c_3) and superpredator (c_4); d_{13} is the growth coefficient of predator due to consumption of prey in the main habitat; d_{14} is the growth coefficient of superpredator due to consumption of prey in the main habitat; d_{34} is the growth coefficient of superpredator due to consumption of predator; β is the migration coefficient of prey from the main habitat to the refuge, γ is the migration coefficient of prey from the refuge to the main habitat.

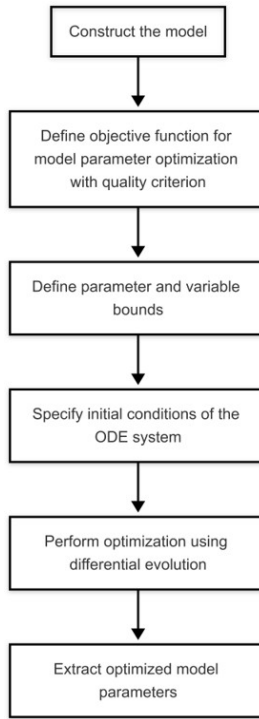


Figure 2. Stages of applying the differential evolution algorithm for parameters search

Figure 1 presents the stages of the algorithm for model (1) research in the form of a diagram.

For the four-dimensional system (1) an optimization search method is applied to find a parameter set that ensures the coexistence of prey, predator and superpredator in the main habitat as well as the survival of the species in the migration area. A computational experiment is conducted to adjust the parameters of model (1) considering the given initial conditions $(x_1(0), x_2(0), x_3(0), x_4(0)) = (3.0, 2.0, 1.0, 0.5)$. The optimization search for the parameter set is based on differential evolution taking into account a special choice of quality criterion consistent with ecological sense [19].

The algorithm of the modified differential evolution implements the minimization of a numerical criterion characterizing the deviation from the specified equilibrium state of differential equations system (1). The minimization criterion has the form

$$\frac{1}{n(s_1 - s_0)} \sum_{i=s_0}^{s_1} \|x_i - S^*\| \rightarrow \min, \quad (2)$$

where n is the number of trajectories considering different initial conditions, s_1 is the index of the last step of the ODE trajectory calculation algorithm, s_0 is the index of the initial step of the ODE trajectory calculation algorithm, x_i is the phase vector of the system at the i -th step.

The parameter search algorithm developed with consideration of criterion (2) allows for the identification of parameter sets under which model (1) exhibits a transition to stationary regimes. In particular the following set of parameters is obtained: $a_1 = 20.00$, $a_2 = 20.00$, $p_{11} = 4.00$, $p_{22} = 2.00$, $q_{13} = 0.30$, $q_{14} = 0.30$, $q_{34} = 0.38$, $\beta = 0.50$, $\gamma = 0.10$, $c_3 = 7.74$, $p_{33} = 0.12$, $c_4 = 0.10$, $p_{44} = 4.80$, $d_{13} = 4.36$, $d_{14} = 3.06$, $d_{34} = 3.76$. Using the identified parameter set a positive equilibrium state is obtained: $x_1 = 3.31$, $x_2 = 9.77$, $x_3 = 14.08$, $x_4 = 13.09$. The performed verification of the model based on the numerical solution of the differential equations system demonstrated that the solutions are close to the identified positive equilibrium state.

3. Stochastization of the model and comparative analysis of the deterministic model with stochastic variants

We proceed to the stochastic models corresponding to system (1), taking into account the introduction of additive and multiplicative noises. The stochastic differential equation (SDE) in the form of the Langevin equation has the following form:

$$dx = a(x, t)dt + b(x, t)dW, \quad (3)$$

where $x \in R^4$ is the system state function, $W \in R^4$ is the standard Brownian motion described by a random Wiener process, and $a(x, t)$ is the right-hand side of the differential equations system (1) presented in vector form. The matrix $b(x, t)$ in (3) is defined depending on the type of random noise. For SDE with additive noise, $b(x, t)$ is the identity matrix of size 4×4 . For SDE with multiplicative noise in the trivial case we have

$$b(x, t) = \begin{pmatrix} \sigma x_1 & 0 & 0 & 0 \\ 0 & \sigma x_2 & 0 & 0 \\ 0 & 0 & \sigma x_3 & 0 \\ 0 & 0 & 0 & \sigma x_4 \end{pmatrix},$$

where σ is the noise intensity parameter.

When stochastization is based on additive and multiplicative noise the random processes do not follow from the internal structure of the model. Next we consider a stochastic model that incorporates multipliers containing a random Wiener process applied to migration rates

$$\begin{aligned} \dot{x}_1 &= a_1 x_1 - p_{11} x_1^2 - q_{13} x_1 x_3 - q_{14} x_1 x_4 + \sigma_1 W x_2 - \sigma_2 W x_1, \\ \dot{x}_2 &= a_2 x_2 - p_{22} x_2^2 - \sigma_1 W x_2 + \sigma_2 W x_1, \\ \dot{x}_3 &= -c_3 x_3 - p_{33} x_3^2 - q_{34} x_3 x_4 + d_{13} x_1 x_3, \\ \dot{x}_4 &= -c_4 x_4 - p_{44} x_4^2 + d_{34} x_3 x_4 + d_{14} x_1 x_4, \end{aligned} \quad (4)$$

where σ_1, σ_2 are the noise intensities, and W is the Wiener process. Thus, system (4) accounts for the random nature of the migration parameters.

In the computer program developed in Python within the Jupyter Notebook environment the solution of the SDE is implemented using the Euler–Maruyama method [14]. The essence of this method is in the discretization of time and the step-by-step approximate computation of the SDE solution taking into account both the deterministic and stochastic components.

Figure 3 shows the trajectories of model (1) and the trajectories of the corresponding stochastic models. The trajectories are obtained using the identified set of parameters and the specified initial conditions. Each of the four plots depicts the dynamics of the corresponding phase variable.

The results of the analysis of the system (1) trajectories and its stochastic variants presented in Fig. 3 show the coexistence of prey, predator and superpredator species as well as the survival of the species in the refuge. The introduction of additive noise has a minor effect on the behavior of the model. Adding a random process to the migration parameters significantly affects not only the population density of prey that can migrate to the refuge but also the population densities of predator and superpredator in the main habitat. The solution trajectories of the stochastic differential equations system reach a stationary regime. Fig. 4 shows the projections of phase portraits onto the planes (x_1, x_2) and (x_1, x_4) respectively.

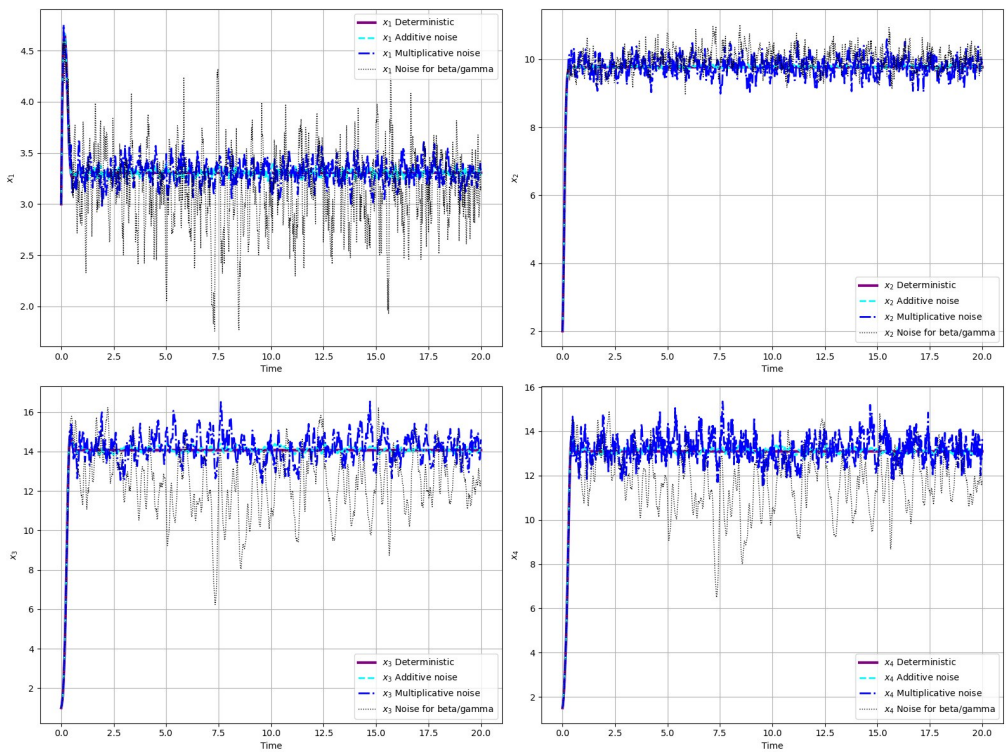


Figure 3. Trajectories of model (1) and the corresponding stochastic models

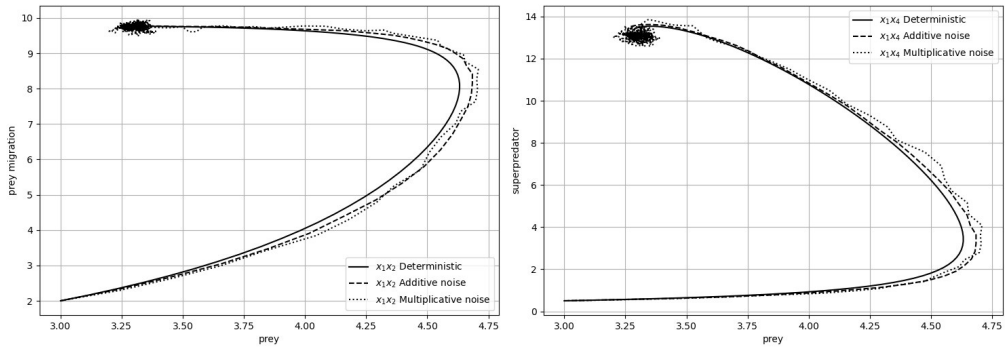


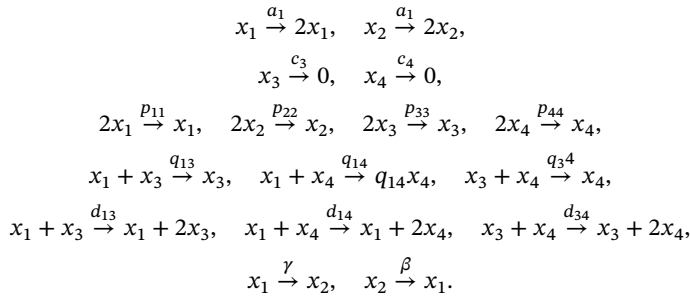
Figure 4. Projections of phase portraits onto the planes (x_1, x_2) and (x_1, x_4)

Projections of phase portraits are constructed which provide a geometric representation of the trajectories of the dynamical system for the specified set of parameters. The equilibrium state has the character of a stable node. The trajectories in the deterministic case and in the stochastic cases exhibit similar behavior.

We also consider the stochastization of model (1) based on the method of constructing self-consistent models [11–15]. This method involves deriving a stochastic differential equation with

consistent stochastic and deterministic parts. The specified stochastic differential equation is obtained through mathematical transformations from an interaction scheme which is a symbolic representation of all possible interactions within the system. In this paper the stochastic model is obtained using a software package developed in Python, the description of which is provided in [16].

As input data the software package uses a description of the interactions occurring in the system. One of the outputs of the software package is the interaction scheme which is represented using the Jupyter interactive interface. The following interaction scheme corresponds to system (1)



The coefficients of the Fokker–Planck equation are as follows:

$$\begin{aligned}
 A &= \begin{bmatrix} a_1x_1 - p_{11}x_1^2 - q_{13}x_1x_3 - q_{14}x_1x_4 + \beta x_2 - \gamma x_1, \\ a_2x_2 - p_{22}x_2^2 - \beta x_2 + \gamma x_1, \\ -c_3x_3 - p_{33}x_3^2 - q_{34}x_3x_4 + d_{13}x_1x_3, \\ -c_4x_4 - p_{44}x_4^2 + d_{34}x_3x_4 + d_{14}x_1x_4, \end{bmatrix}, \\
 B &= \begin{bmatrix} B_{11} & -\beta x_2 - \gamma x_1 & 0 & 0 \\ -\beta x_2 - \gamma x_1 & B_{22} & 0 & 0 \\ 0 & 0 & B_{33} & 0 \\ 0 & 0 & 0 & B_{44} \end{bmatrix},
 \end{aligned}$$

where $B_{11} = a_1x_1 + p_{11}x_1^2 + q_{13}x_1x_3 + q_{14}x_1x_4 + \beta x_2 + \gamma x_1$, $B_{22} = a_2x_2 + p_{22}x_2^2 + \beta x_2 + \gamma x_1$, $B_{33} = c_3x_3 + p_{33}x_3^2 + q_{34}x_3x_4 + d_{13}x_1x_3$, $B_{44} = c_4x_4 + p_{44}x_4^2 + d_{34}x_3x_4 + d_{14}x_1x_4$.

Thus, using the software package the construction of the “prey–migration area–predator–superpredator” model is constructed for both stochastic and deterministic cases. After constructing the models other modules of the software package can be applied for the numerical investigation of the system based on Runge–Kutta methods [12].

The results of the numerical experiments are presented in Fig. 5. The same parameter values are used as those for the numerical solution of the SDE with additive and multiplicative noise. The plots show the dynamics of the phase variables (population densities) x_1 , x_2 , x_3 , x_4 , respectively.

Based on the results of the numerical experiments it can be concluded that the self-consistent stochastic model exhibits a different qualitative behavior. The solutions of the SDE also reach a stationary regime. However, for this model the introduction of stochasticity in the described manner leads to the extinction of both predators populations while the prey continues to exist in both the main habitat and the refuge.

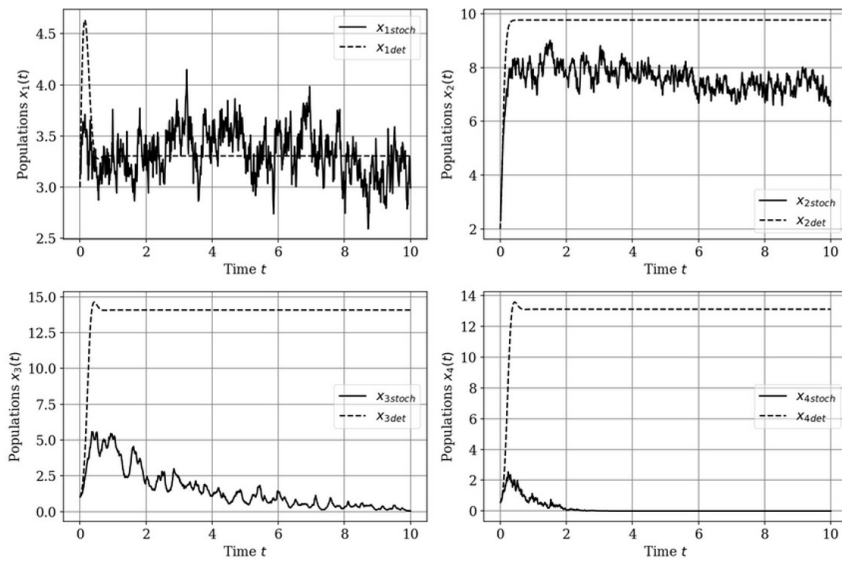


Figure 5. Visualization of the numerical solution

4. Discussion

In this paper a four-dimensional dynamic population model of the “prey-migration area-predator-superpredator” type which accounts for complex trophic interactions, intraspecific and interspecific competition as well as prey migration to a refuge are investigated. For the model with complex trophic interactions and migration flows, stochastization are performed using various approaches: the approach with additive and multiplicative noises, the approach involving stochastic parametric perturbations and the approach based on constructing self-consistent one-step models.

Using the scheme of stages of applying the differential evolution algorithm presented in Fig. 2 for the study of model (1), a parameter set ensuring the coexistence of populations in the main habitat and the survival of the prey population in the refuge is obtained. It is worth noting the universal nature of the developed algorithm which can be applied to various types of dynamic models.

According to Fig. 3 the introduction of additive noise has a minor effect on the behavior of the model. Adding a random process to the migration parameters significantly affects not only the population density of prey that can migrate to the refuge but also the population densities of predator and superpredator in the main habitat. The introduction of multiplicative noise influences the trajectory dynamics; however, this influence is less significant compared to the stochastization of migration parameters. The solution trajectories of the system of stochastic differential equations reach a stationary regime. According to Fig. 5 the introduction of stochasticity using the method of constructing self-consistent one-step models leads to the extinction of both predator populations while the prey continues to exist in both the main habitat and the refuge.

Figure 6 shows a diagram illustrating the types of stochastization of a deterministic dynamic population model with migration flows.

The results of this paper are obtained using two software packages. One of the two software packages is developed for finding the optimal parameters of the deterministic “prey-migration area-predator-superpredator” model, constructing and analyzing the trajectory dynamics of stochastic models based on additive and multiplicative noise, as well as for building a stochastic model with

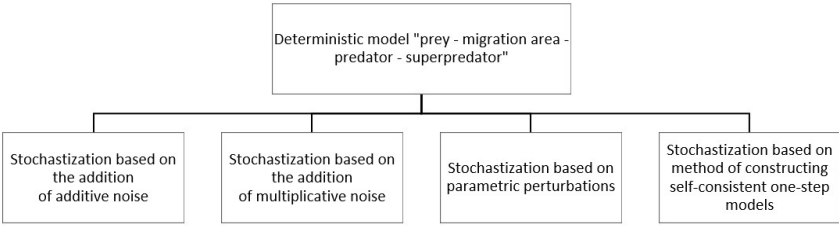


Figure 6. Stochastization directions of a deterministic dynamic population model with migration flows

random migration parameters. The other software package [12, 16] is designed for stochastization based on the method of constructing self-consistent one-step models. The study results of the “prey–migration area–predator–superpredator” model obtained using these software tools enabled a comparative analysis of the trajectory dynamics for the deterministic population system with migration flows and its corresponding stochastic variants.

5. Conclusion

The paper uses an approach to the study of population models with trophic interactions and migration flows which is based on the use of evolutionary algorithms for finding parameters, additive and multiplicative noises, the method of constructing self-consistent stochastic models and modified numerical methods for solving systems of stochastic differential equations. Solving the optimization problem using differential evolution allowed to find the optimal parameters of the “prey–migration area–predator–superpredator” model with species competition in the main habitat and prey migration to a refuge. For this model an approximate positive equilibrium state corresponding to the obtained set of parameters is found.

In this paper the use of the applied methods made it possible to construct new stochastic models of population dynamics that take into account trophic interactions, competition and bidirectional prey migration. The implementation of algorithms for the stochastization of model (1) through the introduction of additive and multiplicative noises as well as stochastization based on given interaction schemes enabled an analysis of the trajectory dynamics for the stochastic variants of the model in comparison with the deterministic model.

As directions for further research one can consider the construction of new modifications of multidimensional population models based on model (1) and the identification of parameter sets that lead to significant differences in the dynamics of deterministic and stochastic models. Additionally future research prospects include modeling complex trophic interactions involving several types of prey or predator species as well as accounting for the nonlinear nature of migration flows.

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Information about the authors

Vasilyeva, Irina I.—Assistant professor of Department of Mathematical Modeling, Computer Technologies and Information Security of Bunin Yelets State University (e-mail: irinavsl@yandex.ru, ORCID: 0000-0002-4120-2595)

Druzhinina, Olga V.—Doctor of Physical and Mathematical Sciences, Chief Researcher of Federal Research Center «Computer Science and Control» of Russian Academy of Sciences (e-mail: ovdruzh@mail.ru, ORCID: 0000-0002-9242-9730)

Masina, Olga N.—Doctor of Physical and Mathematical Sciences, Professor of Department of Mathematical Modeling, Computer Technologies and Information Security of Bunin Yelets State University (e-mail: olga121@inbox.ru, ORCID: 0000-0002-0934-7217)

Demidova, Anastasia V.—Candidate of Physical and Mathematical Sciences, Associate Professor of Department of Probability Theory and Cyber Security of RUDN University (e-mail: demidova-av@rudn.ru, ORCID: 0000-0003-1000-9650)

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Анализ стохастической модели “жертва–ареал миграции–хищник–суперхищник”

И. И. Васильева¹, О. В. Дружинина², О. Н. Масина¹, А. В. Демидова³

¹ Елецкий государственный университет им. И.А. Бунина, ул. Коммунаров, д. 28, Елец, 399770, Российская Федерация

² Федеральный исследовательский центр «Информатика и управление», Российской академии наук, ул. Вавилова, д. 44, кор. 2, Москва, 119333, Российская Федерация

³ Российский университет дружбы народов, ул. Миклухо-Маклая, д. 6, Москва, 117198, Российская Федерация

Аннотация. К актуальным направлениям исследования динамических миграционно-популяционных моделей относятся анализ траекторной динамики и решение задач параметрической оптимизации с применением компьютерных методов. В настоящей работе рассматривается популяционная модель «жертва–ареал миграции–хищник–суперхищник», которая задаётся системой четырёх дифференциальных уравнений. В модели учитываются трофические взаимодействия, внутривидовая и межвидовая конкуренция, а также миграция жертвы в убежище. С помощью дифференциальной эволюции найдены параметры, обеспечивающие сосуществование популяций жертвы, хищника и суперхищника соответственно в основном ареале обитания и существование популяции жертвы в убежище. Выполнен переход к стохастическим вариантам модели на основе аддитивных шумов, мультипликативных шумов и метода построения самосогласованных моделей. Для описания структуры стохастической модели использованы уравнения Фоккера–Планка и выполнен переход к системе уравнений в форме Ланжевена. Численное решение стохастических систем дифференциальных уравнений реализовано методом Эйлера–Маруямы. С помощью программного комплекса на языке Python проведены компьютерные эксперименты, построены траектории для детерминированного и стохастических случаев. Проведён сравнительный анализ детерминированной и соответствующих ей стохастических моделей. Результаты могут найти применение при решении задач математического моделирования биологических, экологических, физических, химических и демографических процессов.

Ключевые слова: система дифференциальных уравнений; миграционные потоки; стохастизация; метод построения самосогласованных моделей; дифференциальная эволюция