International Journal of Engineering and Manufacturing, **2026, 3, 125-144**
Published Online on June 8, 2026 by MECS Press (http://www.mecs-press.org/)
DOI: 10.5815/ijem.2026.03.09

Mathematical Model of Subpopulation Dynamics in Case of Different Niches for Subpopulations

O. Kuzenkov
Dept. of Calculating Mathematics and Mathematical Cybernetics, Oles Honchar Dnipro National University, Dnipro, Ukraine
E-mail: kuzenkov1986@gmail.com
ORCID iD: https://orcid.org/0000-0002-6378-7993

M. Tryputen
Dept. of Cyberphysical and Information-Measuring Systems, Faculty of Electrical Engineering, Institute of Power Engineering, Dnipro University of Technology, Dnipro, Ukraine
E-mail: nikolay.triputen@gmail.com
ORCID iD: https://orcid.org/0000-0003-4523-927X

V. Kuznetsov*
Dept. of Electrical Engineering, Ukrainian State University of Science and Technologies, Dnipro, Ukraine
E-mail: witjane20002014@gmail.com
ORCID iD: https://orcid.org/0000-0002-8169-4598
*Corresponding Author

O. Huliesha
Dept. of Electronics and Computer Engineering, Dniprovsky State Tehnical University, Kamianske, Ukraine
E-mail: e.gulesha@gmail.com
ORCID iD: https://orcid.org/0000-0002-7512-5671

V. Artemchuk
Dept. of Electrical Engineering, Ukrainian State University of Science and Technologies, Dnipro, Ukraine
E-mail: art_vv@ukr.net
ORCID iD: https://orcid.org/0000-0002-6056-5834

Received: 23 January, 2026; Revised: 22 March, 2026; Accepted: 05 May, 2026; Published: 08 June, 2026

Abstract: The article presents a model of dynamic processes occurring in non-isolated populations that differ in their habitat and mode of nutrition. The results of theoretical studies carried out on the basis of this model show the decisive influence of the ratio of the coefficients of inter-subpopulation competition on qualitative changes in the behavior of the system and individual subpopulations. This ratio is also the main factor influencing the formation of the dominant subpopulation in the system. It has been shown that the system-wide dynamics of subpopulation processes significantly depends on the reproductive potential of all subpopulations and on the mass fraction of individuals that, according to their phenotypic properties, are related to the parents. In this case, the mass fractions of individuals (transition coefficients) must correspond to the condition of closed system and be in specified intervals. It has been established that subpopulations in real life can exchange descendants, which, in turn, can significantly affect the numerical and qualitative aspects of the dynamics. Using the example of a two-dimensional system, the relationship between the sum of the main elements of the transition coefficient matrix and the mutual dependence of subpopulations, as well as their transition to qualitatively different levels, is shown. The bifurcation properties of the model of subpopulation dynamics with a Lotka–Voltaire type function in basic quality have been studied. An approximate justification of possible bifurcations of the system allows us to evaluate the factors that qualitatively influence the dynamics of the system and develop a number of recommendations to prevent the occurrence of catastrophes and collapses in the system.

Index Terms: Subpopulation; Reproduction; Phase space; Characteristic equation; Singular points; Phase portrait; Jacobian matrix; Attractor; Repeller; Bifurcation; Hypersurface

1. Introduction

In recent decades, the study of nonlinear dynamical systems has become one of the most important directions of applied mathematics and interdisciplinary research. Population systems characterized by complex interactions between heterogeneous groups are widely encountered in ecology, biology, economics, sociology, and demographic analysis. Under real-world conditions, populations are rarely homogeneous, since different subgroups may occupy distinct ecological niches, consume different resources, possess unequal reproductive potential, and demonstrate different levels of adaptability to environmental changes. At the same time, these groups are not completely isolated, because migration and the exchange of descendants between subpopulations significantly influence the long-term dynamics of the entire system.

The classical Lotka–Volterra approach and its modifications remain among the most effective mathematical tools for describing competitive interactions in population systems. Nevertheless, many existing models are primarily focused on isolated populations or simplified interaction mechanisms and therefore cannot fully capture the nonlinear effects arising in systems with heterogeneous subpopulations and transition processes between them. In particular, insufficient attention has been paid to the influence of inter-subpopulation competition coefficients, transition parameters, and bifurcation effects that determine qualitative changes in the structure and stability of the system.

The study of bifurcation phenomena is especially important for complex nonlinear systems, since even small variations in system parameters may lead to significant transformations of phase-space topology, changes in stability, the emergence of attractors, or the collapse of equilibrium states. Such processes are directly associated with the formation of dominant subpopulations, degradation of weaker groups, and establishment of stable coexistence regimes. Therefore, the development of mathematical approaches capable of identifying critical parameter values and predicting possible dynamical transitions remains an important scientific challenge.

In this paper, a mathematical model of subpopulation dynamics based on a modified Lotka–Volterra framework is proposed. The model takes into account heterogeneous ecological niches, differences in reproductive capacity, unequal levels of inter-subpopulation competition, and transition mechanisms between subpopulations. A qualitative analysis of equilibrium states, Jacobian matrices, characteristic equations, and bifurcation structures is carried out. In addition, numerical experiments are performed for various parameter combinations and initial conditions in order to investigate the influence of transition coefficients and competitive interactions on the global behavior of the system.

The obtained results make it possible to determine the conditions for stable coexistence of subpopulations, identify the mechanisms responsible for the emergence of dominant groups, and reveal critical regimes associated with structural instability and bifurcation transitions. The proposed approach may be useful for the analysis of ecological, socio-economic, demographic, and other complex adaptive systems characterized by nonlinear interactions between heterogeneous components.

1.1. Problem Statement

The relevance of the work is due to the importance of researching complex systems that form the basis of the functioning of most biological, economic and social processes, as well as the need to develop effective methods of managing these systems to achieve the appropriate economic or social effect. It is obvious that the correct description of real systems is quite a difficult task: there are no standard modeling methods, each class of models must have its own approaches. Quite often, research in this field is limited to the use of simple (linear) models and methods, which can be useful as a first step, allowing to give a principled description of the system and to establish general interdependencies between its parameters. At the same time, it is clear that the study of any complex systems cannot be limited to a linear description, without taking into account nonlinear effects in their functioning. In particular, this refers to the study of their bifurcation properties, that is, the possibility and nature of a qualitative change in the general behavior of the system with a continuous change in the values of its parameters. Such research is especially interesting and non-trivial for degenerate systems, i.e. systems, some parameters of which, according to the system feature, have critical (limiting) values. And if bifurcation studies are sometimes carried out for non-degenerate (robust) systems, corresponding methods have practically not been developed for degenerate systems.

1.2. Formulation of the problem in ecological interpretation

The research is based on the statement about the population as the multitude of individuals, which can be divided by n subpopulations that are genetically homogeneous, but at the same time they significantly differ from one another by one or more factors. They are not isolated reproductively, that means that there is some possibility of offspring getting from i-th subpopulation to j-th subpopulation. Let’s consider that subpopulations have certain differences in the way of life, resources and areas of life. In addition, individuals distinguish representatives of their own and other subpopulations so that the level of inter-subpopulation competition is different.

1.3. Mathematical model of the subpopulation dynamics with a function of Lotka–Volterra type used as the base

The differential model of the subpopulation dynamics system [1, 2] can be written as follows:

$$\dot{x}_i=\sum_{j=1}^{n} A_{ij}\cdot\left(a_j-c_j\cdot\sum_{k=1}^{n} x_k\right)\cdot x_j,\ i=\overline{1,n} \tag{1}$$

where x_j is the size of subpopulation with index j; a_j is the coefficient indicating the reproductive capacity of subpopulation with the index j; c_j is the coefficient determining the level of inter-subpopulation competition of subpopulation with the index j and other subpopulations of the system. This means that for each subpopulation, the external influence does not depend on whether it competes for a resource with a representative of its own or another subpopulation, but for each subpopulation this level is different. A_{ji} is the share of the i-th subpopulation offspring, that gets into the j-th; n is the total size of subpopulations. We assume that $\sum_i A_{ij}=1$, $i=\overline{1,n}$. Subpopulations can differ in reproduction coefficients a_i, transition coefficients λ_i (part of the growth that will belong to the "parent"), and initial size. Next, for ease of writing the formulas, we will accept $A_{ii}=\lambda_i$.

The following tasks were set in the paper:

1. Conduct a qualitative study of the studied mathematical model;
2. Perform a numerical experiment for different sets of parameters and initial conditions;
3. Compare the results of the numerical experiment with the results of qualitative research of the mathematical model;
4. Conduct a retrospective analysis of the obtained results to confirm the reliability of the model.

2. Related Work

The modern process of improving mathematical methods of research is primarily aimed at obtaining complex indicators of the system and some of its qualitative characteristics. Among the main studies on mathematical modeling of complex systems, it is necessary to highlight the works of such authors as N. Perestyuk [3]; V. Matsenko [4]; S.V. Chernyshenko [5], [6], [7]; V.Ye. Belozyorov [8], as well as foreign ones – Bossel [9], Hannon [10], etc.

Today, issues of mathematical modeling of subpopulation dynamics are becoming more and more popular, and the scope of their research covers mostly applied problems. Thus, some principles of determining the boundaries of subpopulations are laid down in the work of A.-S. Malaspinas, M. Slatkin, Yun S. Song [11].

In the work [12] of T. Doko, H.Fukui, A.Kooiman, A.G.Toxopeus, T.Ichinose, W.Chen, A.K.Skidmore, the main results of modeling the dynamics of Asian black bear subpopulations on the territory of Japan are highlighted.

As established by J.P. Kritzer, C.R. Davies [13], ecological heterogeneity can provoke spatial differences in the growth properties of subpopulations, and this can lead to a number of interpopulation differences, including in reproductive opportunities, primarily for those individuals in which reproductive properties directly depend on the received energy.

In the population interpretation of differential models, as a rule, only the dynamics between conditionally isolated groups are considered. A large number of fundamental monographs and articles are devoted to the issue of the interaction of isolated groups: N. Bailey [14], J. Hofbauer, K. Sugmund [15], R.M. May [16] et al.

Much less attention is now paid to the issue of intergroup interactions. At the same time, in most cases, the most important processes (evolution, reproduction, social and psychological development) take place precisely against the background of one group and are based on the mutual relations of homogeneous individuals among themselves. In this case, the system-wide trends are completely different, based on other subject principles. Note that the groups into which the system is conditionally divided are not isolated, so there is a possibility that a certain proportion of the descendants of one group will belong to another group by some properties. The effects of intergroup dynamics have their own unique structure. Models proposed in the works of V. Volter [17]-[18]; R. Haberman [19] and others.

3. Equilibrium points of the system

System (1) is a special case of the well-known Lotka–Voltaire model [20], [21], [22], [23]. The peculiarity of system (1) is that the coefficients of intra-subpopulation competition and inter-subpopulation competition for each subpopulation are equal. From the objective point of view, this fact is explained by the lack of priorities among individuals when they interact with each other. But the difference of this coefficient for each subpopulation reflects the main essence of the model, namely the difference between subpopulations in the degree of perception of external influence.

Further research will be carried out in accordance with the classical methodology of the study of equilibrium states according to Lyapunov.

In case if $\sum_{i=1}^{n} A_{ij}=1$, $j=\overline{1,n}, A_{ij}\in[0;1]$ system is closed. But, if the number of equations is less than the actual number of subpopulations, then the equal sign can change to a less sign and the system becomes not closed.

System (1) has n+1 isolated equilibrium points, with coordinates $\begin{pmatrix} a_1/c_1 \\ 0 \\ \dots \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ a_2/c_2 \\ \dots \\ 0 \end{pmatrix}, \dots, \begin{pmatrix} 0 \\ 0 \\ \dots \\ a_n/c_n \end{pmatrix}$, That is, one point is the origin of the coordinates, and the others belong to different axes of the phase space and are located at a distance of $\frac{a_j}{c_j}, j=\overline{1,n}$ from the origin.

For case when n=2, the system (1) has the following form:

$$\begin{cases} \&\dot{x}_1=\lambda_1[a_1-c_1(x_1+x_2)]x_1+(1-\lambda_2)[a_2-c_2(x_1+x_2)]x_2 \\ \&\dot{x}_2=(1-\lambda_1)[a_1-c_1(x_1+x_2)]x_1+\lambda_2[a_2-c_2(x_1+x_2)]x_2 \end{cases} \tag{2}$$

At the origin, the Jacobian matrix of the system (2) will take the form:
$J|_{(0;0)}=\begin{pmatrix} \lambda_1\cdot a_1 & (1-\lambda_2)\cdot a_2 \\ (1-\lambda_1)\cdot a_1 & \lambda_2\cdot a_2 \end{pmatrix}$, at singular points $(a_1/c_1\,;0)$ and $(0;a_2/c_2)$ it will take the following form
$J|_{(a_1/c_1;0)}=\begin{pmatrix} -\lambda_1 a_1 & (1-\lambda_2)(a_2-a_1c_2/c_1)-\lambda_1 a_1 \\ -(1-\lambda_1)a_1 & \lambda_2(a_2-a_1c_2/c_1)+a_1(\lambda_1-1) \end{pmatrix}$,
$J|_{(0;a_2/c_2)}=\begin{pmatrix} \lambda_1(a_1-a_2c_1/c_2)+a_2(\lambda_2-1) & -(1-\lambda_2)a_2 \\ (1-\lambda_1)(a_1-a_2c_1/c_2)-\lambda_2 a_2 & -\lambda_2 a_2 \end{pmatrix}$
accordingly. The characteristic equation of system (2) takes the following form $t^2-Tr(J)+Det(J)=0$

4. Bifurcation analysis of the system in the two-dimensional case

The components of the Jacobian matrix of the system (1) are generally as follows: $J_{ij}=\sum_{j=1}^{n}\left[A_{ij}\left(a_j-c_j\sum_{k=1}^{n}x_k\right)-c_jx_j\right]$; when n=2 we have

$$\begin{gathered} J_{11}=\lambda_1\left(a_1-c_1(2x_1+x_2)\right)+c_2x_2(\lambda_2-1) \\ J_{12}=(1-\lambda_2)\left(a_2-c_2(2x_2+x_1)\right)-\lambda_1c_1x_1 \\ J_{21}=(1-\lambda_1)\left(a_1-c_1(2x_1+x_2)\right)-\lambda_2c_2x_2 \\ J_{22}=\lambda_2\left(a_2-c_2(2x_2+x_1)\right)+c_1x_1(\lambda_1-1) \end{gathered} \tag{3}$$

Table 1 presents the coefficients of characteristic polynomial of the Jacobian matrix for three equilibrium points of system (2).

Table 1. Coefficients of the characteristic polynomial of the Jacobian matrix of the system (2)

Point	$b=-Tr(J)$	$c=Det(J)$
(0;0)	$-(\lambda_1a_1+\lambda_2a_2)$	$a_1a_2(\lambda_1+\lambda_2-1)$
$(a_1/c_1\,;0)$	$a_1-\lambda_2(a_2-c_2a_1/c_1)$	$a_1(1-\lambda_1-\lambda_2)(a_2-c_2a_1/c_1)$
$(0;a_2/c_2)$	$a_2-\lambda_1(a_1-c_1a_2/c_2)$	$a_2(1-\lambda_1-\lambda_2)(a_1-c_1a_2/c_2)$

Theorem 1: the system (2) is degenerate in the vicinity of a singular point (origin) when $a_1=0\cup a_2=0\cup\lambda_1+\lambda_2=1\cup\begin{cases} \&a_1a_2(\lambda_1+\lambda_2-1)>0 \\ \&\lambda_1a_1+\lambda_2a_2=0 \end{cases}$.

Proof: it can be easily seen that the origin is a singular point of system (2). Based on (3), it is obvious that the Jacobian matrix of the system (2) at a singular point (origin) is as follows:

$$J|_{(0;0)}=\begin{pmatrix} \lambda_1\cdot a_1 & (1-\lambda_2)\cdot a_2 \\ (1-\lambda_1)\cdot a_1 & \lambda_2\cdot a_2 \end{pmatrix} \tag{4}$$

The determinant of the characteristic matrix of the system (2) at the origin has the following form $Det(J)=a_1a_2(\lambda_1+\lambda_2-1)$ and within the theorem conditions $a_1=0\cup a_2=0\cup\lambda_1+\lambda_2-1=0$ it reaches zero value.

The roots of the characteristic equation are complex under the condition $Tr^2(J)-4Det(J)<0$, and the condition of equality of their real part of the zero value in the notation of the system is as follows: $Tr(J)=\lambda_1a_1+\lambda_2a_2=0$. Therefore, the real part of the pair of complex roots of the characteristic equation of the Jacobian matrix of the system (2) is zero if $\begin{cases} \&a_1a_2(\lambda_1+\lambda_2-1)>0 \\ \&\lambda_1a_1+\lambda_2a_2=0 \end{cases}$.

The theorem has been proven.

Theorem 2: the system (2) in the vicinity of a singular point (origin) has the saddle type under the condition that $a_1a_2(\lambda_1+\lambda_2-1)<0$. If $0<a_1a_2(\lambda_1+\lambda_2-1)<\frac{(\lambda_1a_1+\lambda_2a_2)^2}{4}$, a singular point (origin) is a node, and if $a_1a_2(\lambda_1+\lambda_2-1)>\frac{(\lambda_1a_1+\lambda_2a_2)^2}{4}$ – it is a focus. In the last two cases, the point is stable if $\lambda_1a_1+\lambda_2a_2<0$ and unstable if $\lambda_1a_1+\lambda_2a_2>0$.

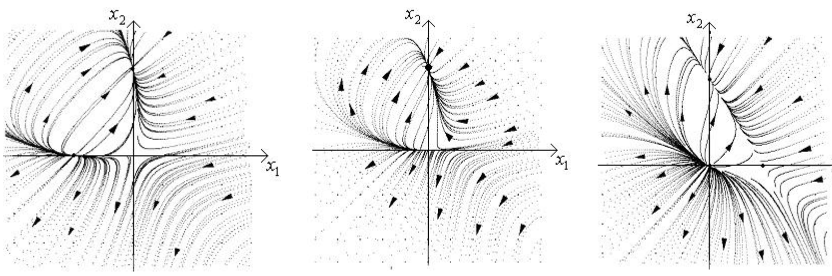
Proof: the Jacobian matrix of the system (2) at a singular point (origin) has the form (4), and its characteristic equation is $t^2-(\lambda_1a_1+\lambda_2a_2)t+a_1a_2(\lambda_1+\lambda_2-1)=0$. It is obvious that under following condition $Det(J)=a_1a_2(\lambda_1+\lambda_2-1)<0$ the discriminant of the characteristic equation (which has the general form $D(J)=Tr(J)^2-4Det(J)$) is greater than zero, and the product of the roots of the characteristic equation (according to Vieta's formulas) is less than zero. Therefore, a singular point (origin) has a saddle type by definition. Further, we will assume that $Det(J)>0$.

The discriminant $D(J)$ of the characteristic equation has the following form – $D(J)=(\lambda_1a_1+\lambda_2a_2)^2-4a_1a_2(\lambda_1+\lambda_2-1)$. It is obvious that under the condition that $a_1a_2(\lambda_1+\lambda_2-1)>\frac{(\lambda_1a_1+\lambda_2a_2)^2}{4}$ – the singular point (origin) is elliptic, and the real part of a pair of complex roots has the form $\lambda_1a_1+\lambda_2a_2$. So, if $\lambda_1a_1+\lambda_2a_2<0$the singular point (origin) has a stable focus type, and if $\lambda_1a_1+\lambda_2a_2>0$ – an unstable focus type. If $a_1a_2(\lambda_1+\lambda_2-1)<\frac{(\lambda_1a_1+\lambda_2a_2)^2}{4}$, the singular point (origin) is hyperbolic. According to the assumption – $Det(J)>0$; therefore, the roots of the characteristic equation (as a consequence of Vieta's formulas) have the same sign, which means that if the $\lambda_1a_1+\lambda_2a_2<0$ singular point (origin) has the type of stable node, and if $\lambda_1a_1+\lambda_2a_2>0$ – an unstable node.

The theorem has been proven.

As it was shown above, the analytical condition for the occurrence of bifurcation in the system is the equality of the real part of at least one of the eigenvalues of the Jacobian matrix to zero. Also, it is proposed to distinguish the bifurcation transition from the node to the focus. The first bifurcation, of the general form $Det(J)=0$, can occur in the system when one of the reproductive parameters a_i passes through the zero value. In this case, in addition to the change of the phase space topology, the quarter in which the corresponding equilibrium point is located also changes. Note that the change of parameters a_1 and a_2 leads to symmetric bifurcations, so we will consider such a bifurcation only on the example of the parameter a_1.

$$\lambda_1=0{,}8;c_1=0{,}01;\lambda_2=0{,}75;a_2=1{,}5;c_2=0{,}01 \tag{5}$$



a b c

Fig. 1. Phase portrait of the system (2) with parameters (5) and a) a_1=-1; b) a_1=0); c) a_1=1

The bifurcation structure is quite clear. When the reproductive coefficient a_1 passes through the zero value, a singular point on the axis of the corresponding subpopulation goes beyond the first quarter, that is, with a negative reproductive potential of one of the subpopulations, it does not have a non-zero equilibrium state in the first quarter (which is the range of real values of the sizes of subpopulations). Such a bifurcation is "saddle-node", the topological structure of the phase space around the stationary point of origin has a degenerate structure. The behavior of the system in the vicinity of a non-zero singular point on the other axis does not undergo changes. Let us emphasize that, along with the saddle-node structure of such a bifurcation, it has the properties of a transcritical bifurcation, i.e., under the condition that $a_i=0$ – non-zero singular point located on the corresponding axis coincides with the origin, becoming unstable at the same time.

Theorem 3: the system (3.2) under following conditions $a_1=0\cup(1-\lambda_1-\lambda_2)==0\cup(a_2-c_2a_1/c_1)=0\cup\begin{cases}\&a_1(1-\lambda_1-\lambda_2)(a_2-c_2a_1/c_1)>0\\ \&\lambda_2(a_2-c_2a_1/c_1)-a_1=0\end{cases}$ is degenerate around a singular point $(a_1/c_1;0)$.

Proof: it is easy to see that the point $(a_1/c_1;0)$ is a singular point of the system (2). The Jacobian matrix of the system (2) at a singular point $(a_1/c_1;0)$ has the following form

$$J|_{(a_1/c_1;0)}=\begin{pmatrix} -\lambda_1 a_1 & (1-\lambda_2)\left(a_2-\frac{a_1c_2}{c_1}\right)-\lambda_1 a_1 \\ -(1-\lambda_1)a_1 & \lambda_2\left(a_2-\frac{a_1c_2}{c_1}\right)+a_1(\lambda_1-1) \end{pmatrix} \tag{6}$$

The system is degenerate in the vicinity of a singular point under the condition that the real part of at least one of the roots of the characteristic equation is equal to zero. It is obvious that the determinant of the characteristic matrix of system (2), which in the notation of the system has following form $Det(J)=a_1(1-\lambda_1-\lambda_2)(a_2-c_2a_1/c_1)$, under the conditions of the theorem $a_1=0\cup(1-\lambda_1-\lambda_2)=0\cup\ \cup(a_2-c_2a_1/c_1)=0$ reaches zero value. Similarly, the roots of the characteristic equation are complex under the condition $Tr^2(J)-4Det(J)<0$, and the condition of equality of their real part of the zero value in the notation of the system has the form $Tr(J)=\lambda_2(a_2-c_2a_1/c_1)-a_1=0$. Therefore, system (2) is degenerate at a singular point $(a_1/c_1\,;0)$ under the condition $\begin{cases} a_1(1-\lambda_1-\lambda_2)(a_2-c_2a_1/c_1)>0 \\ \lambda_2(a_2-c_2a_1/c_1)-a_1=0 \end{cases}$.

The theorem has been proven.

Theorem 4: singular point $(a_1/c_1\,;0)$ of the system (2) is of saddle type under the following condition $a_1(1-\lambda_1-\lambda_2)(a_2-c_2a_1/c_1)<0$. If $0<a_1(1-\lambda_1-\lambda_2)\cdot(a_2-c_2a_1/c_1)<\frac{(\lambda_2(a_2-c_2a_1/c_1)-a_1)^2}{4}$, a singular point $(a_1/c_1\,;0)$ is a node, and under the condition $a_1(1-\lambda_1-\lambda_2)\cdot(a_2-c_2a_1/c_1)>\frac{(\lambda_2(a_2-c_2a_1/c_1)-a_1)^2}{4}$ – it is a focus. In the last two cases, the point is stable if $\lambda_2(a_2-c_2a_1/c_1)-a_1<0$, and it is unstable if $\lambda_2(a_2-c_2a_1/c_1)-a_1>0$.

Proof: Jacobian matrix of the systems (2) at a singular point $(a_1/c_1\,;0)$ has the form (6), and its characteristic equation is $t^2-(\lambda_2(a_2-c_2a_1/c_1)-a_1)\cdot t++a_1(1-\lambda_1-\lambda_2)\cdot(a_2-c_2a_1/c_1)=0$. It is obvious that under following condition $Det(J)=a_1(1-\lambda_1-\lambda_2)\cdot(a_2-c_2a_1/c_1)<0$ that the discriminant of the characteristic equation $D(J)=Tr(J)^2-4Det(J)$ is greater than zero; and the product of the roots of the characteristic equation (according to Vieta's formulas) is less than zero. So, the singular point $(a_1/c_1\,;0)$ is of saddle type. Next, we will assume that $Det(J)>0$. The discriminant $D(J)$ of the characteristic equation has the following form $-D(J)=(\lambda_2(a_2-c_2a_1/c_1)-a_1)^2-4a_1(1-\lambda_1-\lambda_2)\cdot(a_2-c_2a_1/c_1)$. It is obvious that under the condition $a_1(1-\lambda_1-\lambda_2)\cdot(a_2-c_2a_1/c_1)>\frac{(\lambda_2(a_2-c_2a_1/c_1)-a_1)^2}{4}$ – the singular point $(a_1/c_1\,;0)$ is elliptic; and the real part of a pair of complex roots has the form $\lambda_2(a_2-c_2a_1/c_1)-a_1$. Thus, if $\lambda_2(a_2-c_2a_1/c_1)-a_1<0$the singular point $(a_1/c_1\,;0)$ is a stable focus, and if $\lambda_2(a_2-c_2a_1/c_1)-a_1>0$ – it is an unstable focus. If $a_1(1-\lambda_1-\lambda_2)\cdot(a_2-c_2a_1/c_1)<\frac{(\lambda_2(a_2-c_2a_1/c_1)-a_1)^2}{4}$, the singular point $(a_1/c_1\,;0)$ is hyperbolic. According to the assumption $Det(J)>0$; therefore, the roots of the characteristic equation (as a consequence of Vieta's formulas) have the same sign, and hence, if $\lambda_2(a_2-c_2a_1/c_1)-a_1<0$ than singular point $(a_1/c_1\,;0)$ is a stable node, and if $\lambda_2(a_2-c_2a_1/c_1)-a_1>0$than it is an unstable node.

The theorem has been proven.

Except the considered cases, another type of bifurcation can occur when $(\lambda_1+\lambda_2-1)a_1a_2>0$. In this case, the critical value of the parameters is determined by following equality

$$\lambda_1a_1+\lambda_2a_2=0 \tag{7}$$

It is obvious that in the vicinity of the point (7) the discriminant of the characteristic equation is negative, i.e. the singular point is a focus. Bifurcation in this case is a change of a stable focus to an unstable one or vice versa. Fig.2 shows the case of such a bifurcation when the parameter λ_1 passes through the critical value 0. Other parameters are selected as follows:

$$a_1=1{,}00;c_1=0{,}01;\lambda_2=0{,}20;a_2=-2{,}00;c_2=0{,}01; \tag{8}$$

The bifurcation (that was presented above) occurs if the size of one subpopulation decreases, and the other compensates the shortage in the first one. When passing through the bifurcation value, the system changes the growth trend from positive to negative or vice versa. Thus, either the developing subpopulation manages to compensate the losses of the declining subpopulation (Fig.2, c); or due to the part that goes to the dying subgroup, the sizes of both subgroups approach zero over time (Fig.2, a). It should be noted that the stability of a singular point of origin is sufficiently local. Thus, with a slight deviation from the origin, the topology of the phase space changes (Fig.2, a) and the phase trajectories go to $-\infty$.

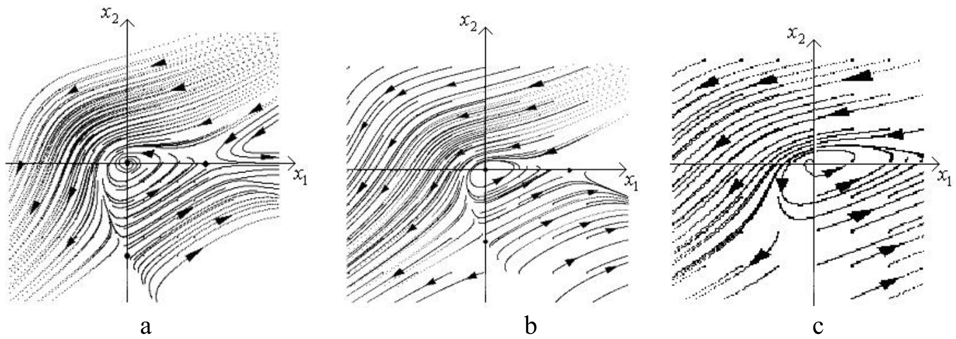


Fig. 2. Phase portrait of the system (2) with parameters (8) and a) λ_1=0,3; b) λ_1=0,4; c) λ_1=0,5

Theorem 5: the system (2) under the following condition $a_2=0 \cup (1-\lambda_1-\lambda_2)==0 \cup (a_1-c_1 a_2/c_2)=0 \cup \begin{cases} \& a_2(1-\lambda_1-\lambda_2)\cdot\ (a_1-c_1a_2/c_2)>0 \\ \& \lambda_1(a_1-c_1a_2/c_2)-a_2=0 \end{cases}$ is degenerate at a singular point $(0;a_2/c_2)$.

Proof: it is easy to see that the point $(0;a_2/c_2)$ is a singular point of the system (2). The Jacobian matrix of the system (2) at a singular point $(0;a_2/c_2)$ has following form

$$J|_{(0;a_2/c_2)}=\begin{pmatrix} \lambda_1\left(a_1-\dfrac{a_2c_1}{c_2}\right)+a_2(\lambda_2-1) & -(1-\lambda_2)a_2 \\ (1-\lambda_1)\left(a_1-\dfrac{a_2c_1}{c_2}\right)-\lambda_2a_2 & -\lambda_2a_2 \end{pmatrix} \tag{9}$$

The system is degenerate at a certain point under the condition that the real part of at least one of the roots of the characteristic equation is equal to zero. It is obvious that the determinant of the characteristic matrix of the system (2), which in the notation of the system has the form $Det(J)=a_2(1-\lambda_1-\lambda_2)(a_1-c_1a_2/c_2)$, under the conditions of the theorem $a_2=0 \cup (1-\lambda_1-\lambda_2)=0 \cup (a_1-c_1a_2/c_2)=0$ acquires a zero value. Similarly, the roots of the characteristic equation are complex under the condition $Tr^2(J)-4Det(J)<0$; and the condition of equality of their real part to zero in the notation of the system has the form $Tr(J)=\lambda_1(a_1-c_1a_2/c_2)-a_2=0$ Therefore, the system (2) is degenerate at a singular point $(0;a_2/c_2)$ under the following condition $\begin{cases} \& a_2(1-\lambda_1-\lambda_2)(a_1-c_1a_2/c_2)>0 \\ \& \lambda_1(a_1-c_1a_2/c_2)-a_2=0 \end{cases}$.

The theorem has been proven.

Theorem 6: the singular point $(0;a_2/c_2)$ of the system (2) is of saddle type under following condition $a_2(1-\lambda_1-\lambda_2)(a_1-c_1a_2/c_2)<0$. If $0<a_2(1-\lambda_1-\lambda_2)\cdot\ (a_1-c_1a_2/c_2)<\frac{(\lambda_1(a_1-c_1a_2/c_2)-a_2)^2}{4}$, the point $(0;a_2/c_2)$ is a node; and if $a_2(1-\lambda_1-\lambda_2)\cdot\ (a_1-c_1a_2/c_2)>\frac{(\lambda_1(a_1-c_1a_2/c_2)-a_2)^2}{4}$ – it is a focus. In the last two cases, the point is stable if $\lambda_1(a_1-c_1a_2/c_2)-a_2<0$ and it is unstable if $\lambda_1(a_1-c_1a_2/c_2)-a_2>0$.

Proof: the Jacobian matrix of the system (2) at a singular point $(0;a_2/c_2)$ has the form (9), and its characteristic equation is $t^2-(\lambda_1(a_1-c_1a_2/c_2)-a_2)t+\ +a_2(1-\lambda_1-\lambda_2)(a_1-c_1a_2/c_2)=0$. It is obvious that under the condition $Det(J)=a_2(1-\lambda_1-\lambda_2)(a_1-c_1a_2/c_2)<0$ the discriminant of the characteristic equation, which has the general form $D(J)=Tr(J)^2-4Det(J)$, is greater than zero; and the product of the roots of the characteristic equation (according to Vieta's formulas) is less than zero, and therefore the singular point $(0;a_2/c_2)$ is a saddle point. Further, we will assume that $Det(J)>0$. The discriminant $D(J)$ of the characteristic equation has the form $D(J)=(\lambda_1(a_1-c_1a_2/c_2)-a_2)^2-4a_2(1-\lambda_1-\lambda_2)\cdot\ (a_1-c_1a_2/c_2)$. It is obvious that under the condition $a_2(1-\lambda_1-\lambda_2)\cdot\ (a_1-c_1a_2/c_2)>\frac{(\lambda_1(a_1-c_1a_2/c_2)-a_2)^2}{4}$ the singular point $(0;a_2/c_2)$ is elliptic, and the real part of a pair of complex roots has the following form $\lambda_1(a_1-c_1a_2/c_2)-a_2$. Whence, if $\lambda_1(a_1-c_1a_2/c_2)-a_2<0$ – the singular point $(0;a_2/c_2)$ is a stable focus, and if $\lambda_1(a_1-c_1a_2/c_2)-a_2>0$ – it is an unstable focus. If $a_2(1-\lambda_1-\lambda_2)\cdot\ (a_1-c_1a_2/c_2)<\frac{(\lambda_1(a_1-c_1a_2/c_2)-a_2)^2}{4}$, the singular point $(0;a_2/c_2)$ is hyperbolic. According to the assumption – $Det(J)>0$, then the roots of the characteristic equation (as a consequence of V Vieta's formulas) have the same sign, hence if $\lambda_1(a_1-c_1a_2/c_2)-a_2<0$ then the singular point $(0;a_2/c_2)$ is a stable node, and if $\lambda_1(a_1-c_1a_2/c_2)-a_2>0$ – it is an unstable node.

The theorem has been proven.

Theorem 7: points of conditional stationary hyperplane

$$\sum_{j=1}^{n} x_j = \frac{a_1}{c_1} \tag{10}$$

of the system (2), arising under an additional condition

$$\frac{a_i}{c_i} = \frac{a_j}{c_j}, \quad i,j = \overline{1,n}, \tag{11}$$

are degenerate, and the determinant of the Jacobian matrix of the system at these points is zero.

Proof: the general view of the *ij*-th element of the Jacobian matrix (2) can be represented as follows:

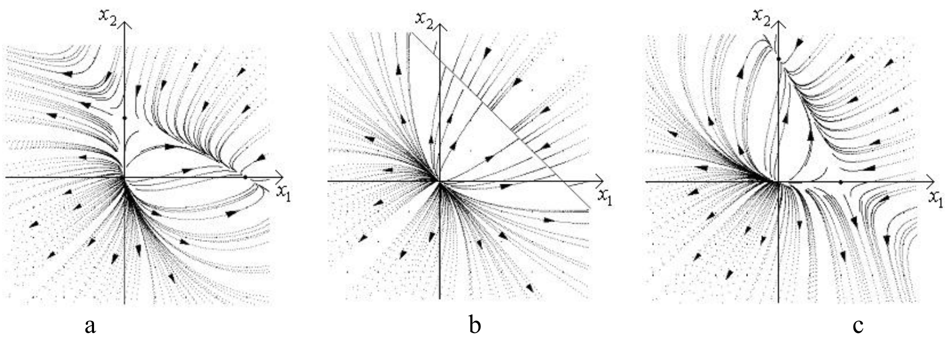
$$J_{ij} = \sum_{j=1}^{n} \left[a_j A_{ij} \left(1 - \frac{c_j}{a_j} \sum_{k=1}^{n} x_k \right) - c_j x_j \right] \tag{12}$$

Taking into account (12), the general form of the ij-th element of the Jacobian matrix of system (2) on the conditional stationary hyperplane (10), (11) is as follows: $J_{ij} = \sum_{j=1}^{n} \left(-c_j \cdot x_j \right)$. Based on the fact that J_{ij} does not directly depend on i, we must assert that $J_{pi} = J_{hi}$, $p,h = \overline{1,n}$, and therefore vectors of the Jacobian matrix columns are linearly dependent, i.e. $det\,(J) = 0$.

The theorem has been proven.

The analytical condition of the next bifurcation, in which an attractor appears in the phase space, includes the coefficients of intersubpopulation competition c_i. In this case, the critical value of the parameters is determined by the equality $\frac{a_1}{c_1} = \frac{a_2}{c_2}$, other parameters were chosen as follows:

$$\lambda_1 = 0{,}80; c_1 = c_2 = 0{,}01; \lambda_2 = 0{,}80; a_2 = 2{,}00 \tag{13}$$



a b c

Fig. 3. Phase portrait of the system (2) with parameters (13) and a) $a_1=3$; b) $a_1=2$; c) $a_1=1$

The case of the attractor existence in the system of subpopulation dynamics is considered in more detail in [54]. It should be noted that the structure of the system is sufficiently degenerate and occurs in nature only if the level of intersubpopulation competition of all subpopulations of the system is equal. But from another point of view, it reflects the symmetrical nature of subpopulation processes. When such a bifurcation occurs in the system, a conditional stationary hyperplane appears in the phase space, all points of which are degenerate, and the stability is determined by a nonzero eigenvalue, which in the notation of the system has the form $\lambda_1 a_1 + \lambda_2 a_2$. In the bifurcation state, a certain equilibrium is established between the increase in the size of subpopulations, which allows the coexistence of subpopulations in certain ratios (depending on the initial conditions). At the same time, the stationary line consists of two parts of attractive and repulsive rays.

Theorem 8: the degenerate stationary straight line (10), (11) of the system (2) consists of the points of the attracting ray (attractor) of the general form $\frac{c_1 x_1 (a_2 - a_1)}{a_1} - a_2 < 0$ and the points of the repelling ray (repeller) of the general form

$\frac{c_1 x_1 (a_2 - a_1)}{a_1} - a_2 > 0$. The composite singular point connecting the attractor and repeller has coordinates $\left(\frac{a_1 a_2}{c_1 (a_2 - a_1)}; \frac{a_1^2}{c_1 (a_1 - a_2)}\right)$ and the root of the characteristic equation of the Jacobian matrix equal to zero; and the multiplicity of which is equal to two.

Proof: according to Theorem (7), the system (2) is degenerate around the points of the stationary line (10), (11). At these points, the Jacobian matrix of the system (2) has the form

$$J = \begin{pmatrix} -(\lambda_1 a_1 x_1 + (1-\lambda_2) a_2 x_2) \frac{c_1}{a_1} & -(\lambda_1 a_1 x_1 + (1-\lambda_2) a_2 x_2) \frac{c_1}{a_1} \\ -((1-\lambda_1) a_1 x_1 + \lambda_2 a_2 x_2) \frac{c_1}{a_1} & -((1-\lambda_1) a_1 x_1 + \lambda_2 a_2 x_2) \frac{c_1}{a_1} \end{pmatrix}$$

and its characteristic equation is $t^2 - Tr(J) t + Det(J) = 0$, where $Det(J) = 0$, and $Tr(J) = \frac{-c_1 (a_1 x_1 + a_2 x_2)}{a_1}$ due to the degeneracy (according to Theorem 7) of the characteristic matrix, therefore $t_1 = 0$, $t_2 = \frac{-c_1 (a_1 x_1 + a_2 x_2)}{a_1}$. Considering the fact that at the points of the conditional stationary line $x_2 = \frac{c_1}{a_1} - x_1$, the non-zero root of the characteristic equation of the system at the points of this line will have the form: $t_2 = \frac{c_1 x_1 (a_2 - a_1)}{a_1} - a_2$, so if $\frac{c_1 x_1 (a_2 - a_1)}{a_1} < 0$ the points of the stationary straight line are attractive, and under the condition $\frac{c_1 x_1 (a_2 - a_1)}{a_1} > 0$ they are repulsive. It is obvious that these two rays will be combined at a point whose coordinates satisfy the following conditions $\begin{cases} \& \frac{c_1 x_1 (a_2 - a_1)}{a_1} - a_2 = 0 \\ \& x_1 + x_2 = \frac{a_1}{c_1}, \ \frac{a_i}{c_i} = \frac{a_j}{c_j}, i,j = \overline{1,n} \end{cases}$, so its coordinates have the form $\left(\frac{a_1 a_2}{c_1 (a_2 - a_1)}; \frac{a_1^2}{c_1 (a_1 - a_2)}\right)$, at this point, according to the condition $\frac{c_1 x_1 (a_2 - a_1)}{a_1} - a_2 = 0$, the root of the characteristic equation is $t_2 = 0$.

The theorem has been proven.

The next bifurcation of the type $Det(J) = 0$ occurs when the parameters pass through the critical value defined by the equality $\lambda_1 + \lambda_2 = 1$, and other parameters have been chosen.

$$\lambda_1 = 0{,}6; a_1 = 10{,}0; c_1 = 0{,}1; a_2 = 10{,}0; c_2 = 0{,}2 \tag{14}$$

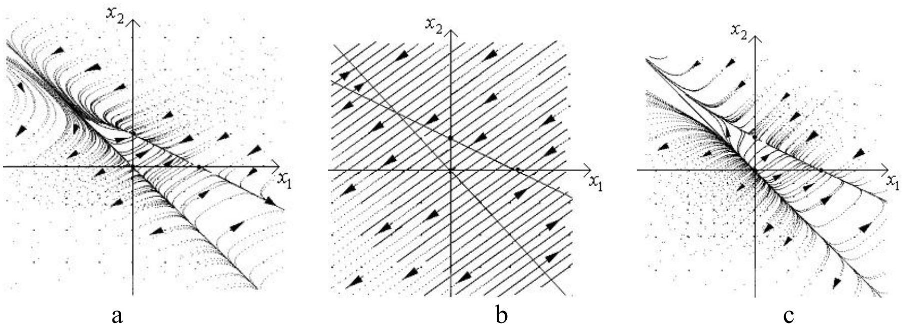


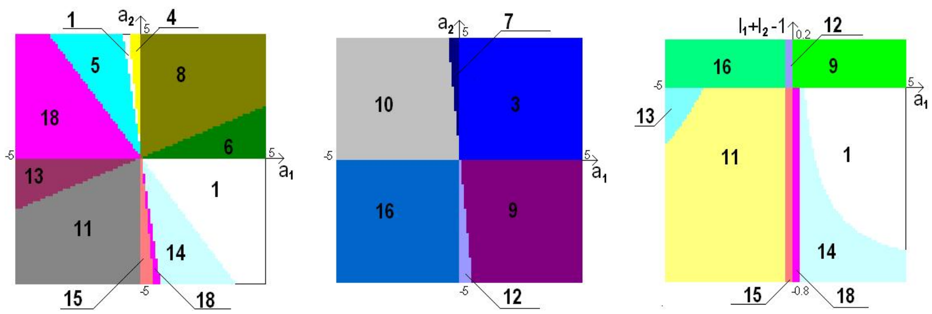
Fig. 4. Phase portrait of the system (2) with parameters (14) and a) $\lambda_1 = 0{,}3$; b) $\lambda_1 = 0{,}4$; c) $\lambda_1 = 0{,}5$

Such a bifurcation leads to the existence of an infinite number of equilibrium points. The transcriticality of such bifurcation consists in the loss of stability of the non-zero equilibrium point belonging to the axis x_2 and in the formation of a stable node in the non-zero singular point of the system, which is located on the axis x_1. From an objective point of view, this state is caused by the balance between the level of reproduction of two subpopulations. Taking this into account, a certain ratio arises in which there is no dynamics in the system.

Fig. 5 – 7 show the bifurcation diagrams of the system (2) in its various parametric spaces. The designations used in Figs. 5 – 7 are given in Table 2:

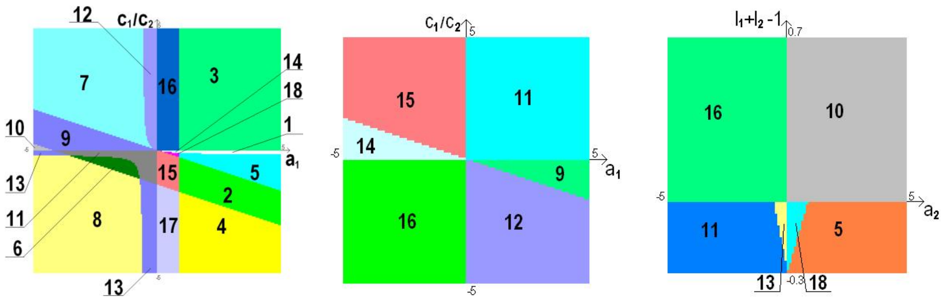
Table 2. The topology of the phase space of the system (2) for the values of parameters shown in Fig. 5 – 7

Designation	**Type of equilibrium point(0;0)**	**Type of equilibrium point(a_1/c_1;0)**	**Type of equilibrium point(0;a_2/c_2)**
1	Stable	Stable	Saddle
2	Stable	Saddle	Stable
3	Stable	Saddle	Saddle
4	Stable	Saddle	Unstable
5	Stable	Unstable	Saddle
6	Saddle	Stable	Stable
7	Saddle	Stable	Saddle
8	Saddle	Stable	Unstable
9	Saddle	Saddle	Stable
10	Saddle	Saddle	Unstable
11	Saddle	Unstable	Stable
12	Saddle	Unstable	Saddle
13	Saddle	Unstable	Unstable
14	Unstable	Stable	Saddle
15	Unstable	Saddle	Stable
16	Unstable	Saddle	Saddle
17	Unstable	Saddle	Unstable
18	Unstable	Unstable	Saddle



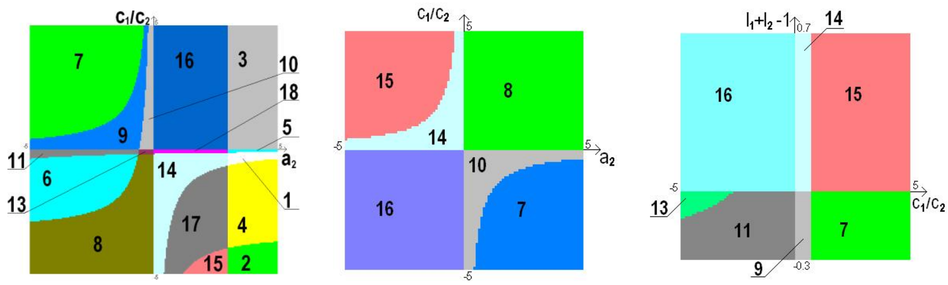
a b c

Fig. 5. The bifurcation diagram of the system (2) with the designations given in Table 2, and parameters a) λ_1=0.7; λ_2=0.2; c_1/c_2=−0.1; b) λ_1=0.7; λ_2=0.8; c_1/c_2=−0.1; c) a_2=−3; c_1/c_2=−0.1



a b c

Fig. 6. The bifurcation diagram of the system (2) with the designations given in Table 2, and parameters a) a_2=3; λ_1=0.7; λ_2=0.2; b) a_2=3; λ_1=0.7; λ_2=0.8; c) a_1=1; c_1/c_2=−0.1



a b c

Fig. 7. The bifurcation diagram of the system (2) with the designations given in Table 2, and parameters a) a_1=1; λ_1=0.7; λ_2=0.2; b) a_1=2; c_1/c_2=−0.1; λ_1=0.7; λ_2=0.8; c) a_1=1; a_2=−3

Based on the general appearance of the coefficients of the characteristic equation of the system (2), we can see that at its three special points their sign depends on the value of four parameters a_1, a_2, $(\lambda_1+\lambda_2-1)$ and $\frac{c_1}{c_2}$, In turn, the sign of these points will determine whether the point will be stable. At the same time, we are interested in the states of the system with positive and negative values of the parameters a_1, a_2, $(\lambda_1+\lambda_2-1)$, and also when the value of the parameter $\frac{c_1}{c_2}$ is less than zero, belongs to the interval from 0 to 1 and is greater than one. The number of phase portraits of the system is equal to 3×3×3=27. As a result of analytical studies, it was established that only 18 types of phase portraits are compatible, and 9 (Table 3) are incompatible, respectively.

Table 3. Topologies of the phase space of the system (2), which are incompatible

No	Point type(0;0)	Point type(a_1/c_1;0)	Point type(0;a_2/c_2)
1	Stable	Stable	Stable
2	Stable	Stable	Unstable
3	Stable	Unstable	Stable
4	Stable	Unstable	Unstable
5	Saddle	Saddle	Saddle
6	Unstable	Stable	Stable
7	Unstable	Stable	Unstable
8	Unstable	Unstable	Stable
9	Unstable	Unstable	Unstable

Based on the symmetry of singular points $(a_1/c_1;0)$, $(0;a_2/c_2)$it was established that 11 types of non-equivalent phase spaces are possible for system (3) (Table 4).

Table 4. Non-equivalent topologies of the phase space of the system (2) taking into account the symmetry of non-zero singular points

No	Point type(0;0)	Point type(a_1/c_1;0)	Point type(0;a_2/c_2)
1	Stable	Stable	Saddle
2	Stable	Saddle	Unstable
3	Stable	Saddle	Saddle
4	Saddle	Stable	Stable
5	Saddle	Stable	Saddle
6	Saddle	Stable	Unstable
7	Saddle	Saddle	Unstable
8	Saddle	Unstable	Unstable
9	Unstable	Stable	Saddle
10	Unstable	Saddle	Saddle
11	Unstable	Saddle	Unstable

5. Bifurcations of the codimensional system >1

Usually, the degenerate states of the system are determined by the critical values of its parameters. It is known that such states can occur when *Det*(*J*)=0 and *Tr*(*J*)=0. As it was shown in the previous subsections, in case of the systems that are considered in this work, the analytical form of invariant *Det*(*J*) and *Tr*(*J*) is represented as a product of several (linear) terms. It is obvious that along with simple bifurcations, complex bifurcations may exist, in which critical values are taken by several invariants of the system at once. Such cases are distinguished by more complex topologies of the phase space, such as: "focus – saddle", "node – center", "stable node – unstable node", etc.

Theorem 9: the system (2) can undergo the following complex bifurcations of codimensionality >1:

a) under the condition that $\left[\begin{array}{l}\&a_1=0\\ \&a_2=0\end{array}\right.$ – the system (2) undergoes a complex bifurcation of *the second* type, characterized by bifurcations of codimensionality 1 at its *two* singular points.
b) under the condition that $\lambda_1+\lambda_2=1$ – the system (2) undergoes a complex bifurcation of *the third* type, which is characterized by bifurcations of codimensionality 1 at its *three* singular points.
c) under the condition that $\left\{\begin{array}{l}\&a_1=0\\ \&a_2=0\end{array}\right.$ – the system (2) undergoes bifurcation of *the third* type of codimensionality 2, which is characterized by the bifurcation of codimensionality 2 of the system at its *three* singular points.

Proof: it is usually considered that the analytical condition for the occurrence of bifurcation in the system is the equality of the real part of at least one of the roots of the characteristic equation to zero. The equilibrium points of the system (2) are points (0;0), $(a_1/c_1;0)$ and $(0;a_2/c_2)$. The Jacobian matrix of the system (2) at a singular point (origin) has the form (4), at a singular point $(a_1/c_1;0)$ – it has the form (6), and at a singular point $(0;a_2/c_2)$ – it has the form (9). Therefore, the general form of the coefficients of the characteristic equation $t^2-Tr(J)t+Det(J)=0$ at special points of the system (2) is as follows:

$$\begin{gathered}Tr(J)_{(0;0)}=\lambda_1 a_1+\lambda_2 a_2\\ Det(J)_{(0;0)}=a_1 a_2(\lambda_1+\lambda_2-1)\end{gathered} \tag{15}$$

$$\begin{gathered}Tr(J)_{(a_1/c_1;0)}=\lambda_2(a_2-c_2 a_1/c_1)-a_1\\ Det(J)_{(a_1/c_1;0)}=a_1(1-\lambda_1-\lambda_2)(a_2-c_2 a_1/c_1)\end{gathered} \tag{16}$$

$$\begin{gathered}Tr(J)_{(0;a_2/c_2)}=\lambda_1(a_1-c_1 a_2/c_2)-a_2\\ Det(J)_{(0;a_2/c_2)}=a_2(1-\lambda_1-\lambda_2)(a_1-c_1 a_2/c_2)\end{gathered} \tag{17}$$

If $a_1=0$ the system $\begin{cases}Det(J)_{(0;0)}=0\\ Det(J)_{(a_1/c_1;0)}=0\end{cases}$ is fair, and if $a_2=0$ the system $\begin{cases}Det(J)_{(0;0)}=0\\ Det(J)_{(0;a_2/c_2)}=0\end{cases}$ is fair. Thus, the bifurcation arising in the system is a bifurcation of codimensionality 1, but at the same time the system undergoes such a bifurcation at its two singular points. Clause A of the theorem has been proven.

It is easy to see that if $\lambda_1+\lambda_2=1$ – the system $\begin{cases}Det(J)_{(0;0)}=0\\ Det(J)_{(a_1/c_1;0)}=0\\ Det(J)_{(0;a_2/c_2)}=0\end{cases}$ is fair and therefore the system undergoes a bifurcation at all three equilibrium points. Clause B of the theorem has been proven.

From the general form of the coefficients of the characteristic equation (15)–(17), it is clear that under the condition $\begin{cases}a_1=0\\ a_2=0\end{cases}$ – the system $\begin{cases}Det(J)_{(0;0)}=0\\ Det(J)_{(a_1/c_1;0)}=0\\ Det(J)_{(0;a_2/c_2)}=0\end{cases}$ is fair. So, under such conditions, the system (2) undergoes bifurcation of the third type of codimensionality 2, which is characterized by the bifurcation of codimensionality 2 of the system in all its three singular points. Clause C of the theorem has been proven.

The theorem has been proven.

The bifurcation, during which the conditional stationary hyperplane loses its stability, is a bifurcation of codimensionality 2. At such a bifurcation, the parameters a_1 and a_2 reach critical values. Bifurcation is characterized by a change in both parameters, while not only the stability of the stationary hyperplane changes, but also its location. Mostly, the degrees of freedom are represented, if not natural, then at least by positive values, which limit the domain of definition to the first quarter. But for the completeness of the bifurcation study, we emphasize that the double bifurcation is a bifurcation of a higher order, representing a qualitative change in the topology of the phase portrait as a whole, and not its individual part. This case is realistic from the point of view of ecology, because with a negative reproductive potential of both subpopulations in the quarter I, there are no equilibrium states, i.e. the only scenario for the development of subpopulations is the decline of both subpopulations. Phase portraits corresponding to such a bifurcation are presented in Fig. 8. As mentioned above, parameters a_1 and a_2 pass through, other parameters are selected as follows:

$$\lambda_1=0{,}60; c_1=c_2=0{,}01; \lambda_2=0{,}90 \tag{18}$$

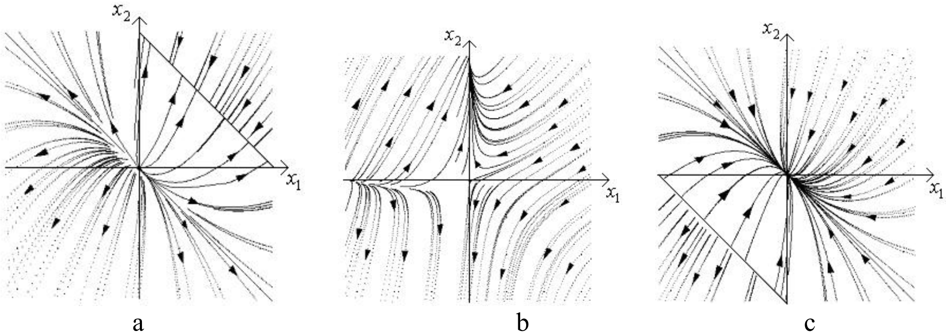
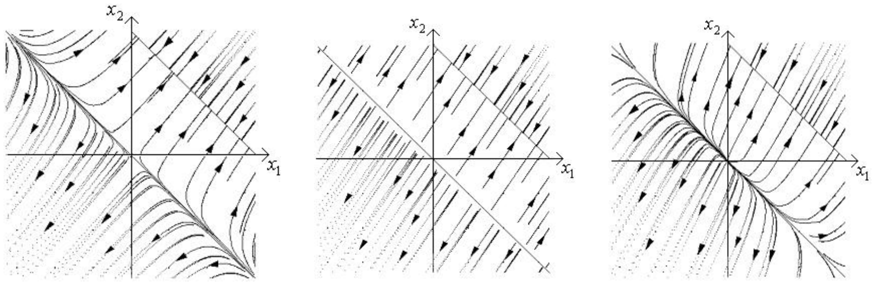


Fig. 8. Phase portrait of the system (2) with parameters (18) and a) $a_1=a_2=2$; b) $a_1=-2$, $a_2=2$; c) $a_1=a_2=-20$

A similar bifurcation of codimensionality 2 occurs when the conditions $\begin{cases}\lambda_1+\lambda_2=1\\ a_1/c_1=a_2/c_2\end{cases}$ are fulfilled simultaneously. From practical point of view, with such a bifurcation, there are no significant changes in dynamics, but qualitative changes definitely exist. It should be noted that the separatrixes of the origin are placed at a certain angle to the axes, but do not coincide with them. During such a transcritical bifurcation, the topological structure of the phase portrait around the origin undergoes a transformation from a node to a saddle.

$$\lambda_1=0{,}40;a_1=a_2=2{,}00;c_1=c_2=0{,}01 \tag{19}$$



a b c

Fig. 9. Phase portrait of the system (2) with parameters (19) and a) λ_2=0,5; b λ_2=0,6; c) λ_2=0,7

6. Investigation of Nonlinear Properties of Bifurcation Hypersurfaces on Two- and Three-Dimensional Parametric Spaces of a Two-Dimensional Model

The Jacobian matrix of the system (2) at the singular point of the origin coincides with the Jacobian matrix of the system (4), so we will classify bifurcation hypersurfaces only for non-zero singular points $(a_1/c_1;0)$, $(0;a_2/c_2)$.

According to the coefficients of the characteristic equation presented in Table 3.1, a bifurcation of the node-saddle type at a point $(a_1/c_1;0)$ occurs under the conditions (20) – (22):

$$a_1=0 \tag{20}$$

$$\lambda_1+\lambda_2=1 \tag{21}$$

$$a_1/c_1=a_2/c_2 \tag{22}$$

The bifurcation hyperplane (20) exists only on two-dimensional bifurcation diagrams a_1:0:a_2, λ_i:0:a_1, c_i:0:a_1, and on them it coincides with the axis a_2, λ_i and c_i respectively.

The node-saddle bifurcation arising under the analytical condition (21) is present only on bifurcation diagrams of the general form λ_1:0:λ_2, λ_i:0:a_i, λ_i:0:a_j, λ_i:0:c_i, λ_i:0:c_j. In these diagrams, the bifurcation curves are straight lines, and in the parametric spaces λ_i:0:a_i, λ_i:0:a_j, λ_i:0:c_i, λ_i:0:c_j this line is perpendicular to the axis λ_i, and in the parametric space λ_1:0:λ_2 it will pass through the points $(0;1)$ and $(1;0)$.

In most cases, bifurcation hyperplanes are nonlinear. The results of the study of the bifurcation hyperplane represented by equality (22) are shown in Table 5.

Table 5. Constants of equation (22), reduced to the canonical form (16)

Param. space	b_{ij}	I_2	I_3	Curve type
a_1:0:λ_2	A curve of the third order			
a_1:0:λ_2	A curve of the third order			
a_1:0:c_2	A curve of the third order			
λ_1:0:λ_2	$b_{11}=b_{22}=b_{12}=0$	0	0	A pair of parallel lines
	$b_{33}=a_1a_2-\dfrac{a_1^2c_2}{c_1}$			
	$b_{13}=-\dfrac{a_1a_2}{2}+\dfrac{a_1^2c_2}{2c_1}$			
	$b_{23}=-\dfrac{a_1a_2}{2}+\dfrac{a_1^2c_2}{2c_1}$			
λ_1:0:c_2	$b_{11}=b_{22}=0$	$-\dfrac{a_1^4}{4c_1^2}$	0	Real intersecting lines
	$b_{33}=a_1a_2(1-\lambda_2)$			
	$b_{23}=-a_1^2(1-\lambda_2)/2c_1$			
	$b_{13}=-a_1a_2/2$			
	$b_{12}=a_1^2/2c_1$			
λ_2:0:c_2	$b_{11}=b_{22}=0$	$-\dfrac{a_1^4}{4c_1^2}$	0	Real intersecting lines
	$b_{33}=a_1a_2(1-\lambda_1)$			
	$b=-\dfrac{a_1^2(1-\lambda_1)}{2c_1}$			

	$b_{13}=-\frac{a_1 a_2}{2}$			
	$b_{12}=\frac{a_1^2}{2c_1}$			
a_1:0:a_2	$b_{13}=b_{22}=b_{23}=b_{33}=0$	$(1-\lambda_1-\lambda_2)^2$	0	Imaginary intersecting lines
	$b_{11}=\frac{c_2(\lambda_1+\lambda_2-1)}{2c_1}$			
	$b_{11}=b_{22}=0$			
	$b_{13}=\frac{a_1(1-\lambda_2)}{2}$			
	$b_{33}=\frac{a_1^2 c_2(\lambda_2-1)}{c_1}$			
	$b_{12}=-\frac{a_1^2}{4}$			
	$b_{23}=\frac{a_1^2 c_2}{2c_1}$			
	$b_{11}=b_{22}=0$			
a_2:0:λ_1	$b_{13}=\frac{a_1(1-\lambda_1)}{2}$	$-\frac{a_1^2}{4}$	≠0	Hyperbole
	$b_{33}=\frac{a_1^2 c_2(\lambda_1-1)}{c_1}$			
	$b_{12}=-\frac{a_1}{2}$			
	$b_{23}=\frac{a_1^2 c_2}{2c_1}$			
	$b_{11}=b_{22}=b_{12}=b_{33}=0$			
	$b_{13}=a_1(1-\lambda_1-\lambda_2)/2$			
	$b_{23}=-a_1^2(1-\lambda_1-\lambda_2)/2c_1$			

On other parametric fields, the corresponding bifurcation curve is presented in the form of a graph, which is not a second-order curve.

The analytical condition for the occurrence of a node-focus bifurcation transition at a point $(a_1/c_1\,;0)$ is as follows:

$$a_1^2+\lambda_2^2\left(a_2-\frac{c_2 a_1}{c_1}\right)^2-4a_1\left(1-\lambda_1-\frac{1}{2}\lambda_2\right)\left(a_2-\frac{c_2 a_1}{c_1}\right)=0 \tag{23}$$

The classification of the corresponding bifurcation curves is presented in Table 6.

Table 6. Constants of equation (22), reduced to the canonical form (16)

Field	b_{ij}	I_2	I_3	Curve type
	$b_{11}=b_{12}=0$			
	$b_{13}=2a_1(a_2-c_2 a_1/c_1)$			
	$b_{22}=(a_2-c_2 a_1/c_1)^2$			
λ_1:0:λ_2	$b_{23}=a_1(a_2-c_2 a_1/c_1)$	0	$4a_1^2\left(a_2-\frac{c_2 a_1}{c_1}\right)^4$	Parabola
	$b_{33}=a_1^2-4(a_2-c_2 a_1/c_1)$			
λ_1:0:a_1	A curve of the third order			
	$b_{11}=0$			
	$b_{12}=2a_1$			
	$b_{13}=-2c_2 a_1^2/c_1$			
	$b_{22}=\lambda_2^2$			
λ_1:0:a_2	$b_{23}=-2a_1+a_1\lambda_2-\frac{\lambda_2^2 c_2 a_1}{c_1}$	$-4a_1^2$	≠0	Hyperbole
	$b_{33}=a_1^2-2\frac{\lambda_2 c_2 a_1^2}{c_1}-$ $-4\frac{c_2 a_1^2}{c_1}+\lambda_2^2\frac{c_2^2 a_1^2}{c_1^2}$			
λ_2:0:a_1	A curve of the fourth order			
λ_2:0:a_2	A curve of the fourth order			
λ_2:0:c_2	A curve of the fourth order			
a_1:0:c_2	A curve of the fourth order			
λ_1:0:c_2	$b_{11}=0$	$\lambda_2^4 a_1^4$	≠0	Hyperbole

	$b_{22}=\lambda_2^2 a_1^2/c_1^2$ $b_{12}=-2\,a_1^2/c_1$ $b_{13}=2a_1a_2$ $b_{23}=-\frac{\lambda_2^2 a_1 a_2}{c_1}-2\frac{a_1^2}{c_1}-\frac{\lambda_2 a_1^2}{c_1}$ $b_{33}=(a_1+\lambda_2 a_2)^2-4a_1a_2$			
a_2:0:c_2	$b_{11}=\lambda_2^2$ $b_{12}=-\lambda_2^2 a_1/c_1$ $b_{13}=-2a_1+2a_1\lambda_1+a_1\lambda_2$ $b_{22}=\lambda_2^2 a_1^2/c_1^2$ $b_{23}=-2\,a_1^2/c_1-2\,\lambda_1 a_1^2/c_1-$ $-\lambda_2 a_1^2/c_1$ $b_{33}=a_1^2$	0	$\neq 0$	Parabola
a_1:0:a_2	$b_{13}=b_{23}=b_{33}=0$ $b_{11}=1+\lambda_2^2\cdot\left(\frac{c_2}{c_1}\right)^2-4\frac{c_2}{c_1}\times$ $\times(2+2\lambda_1+2\lambda_2)$ $b_{12}=-\lambda_2^2\frac{c_2}{c_1}-2+2\lambda_1+\lambda_2$ $b_{22}=\lambda_2^2$	Unsigned	0	Straight lines

On other parametric fields, the corresponding bifurcation curve is presented as a graph, which is not a second-order curve.

Bifurcation of the type “stable focus – unstable focus” at a point $(a_1/c_1\,;0)$ occurs under following condition:

$$a_1-\lambda_2\left(a_2-\frac{c_2a_1}{c_1}\right)=0 \tag{24}$$

When reducing equation (24) to the canonical form of the second-order curve, the invariants listed in Table 7 were obtained:

Table 7. Analysis of the properties of bifurcations of the "stable focus – unstable focus" type of the system (2) at the equilibrium point $(A_1/C_1;0)$

Field	b_{ij}	I$_2$	I$_3$	Curve type
λ_1:0:a_1 λ_1:0:a_2 λ_1:0:c_1 λ_1:0:c_2 λ_1:0:λ_2	Two parallel lines			
λ_2:0:a_1	$b_{11}=b_{22}=b_{33}=0$ $b_{12}=-0.5\cdot\ c_2/c_1$ $b_{13}=-0.5\cdot\ a_2$ $b_{23}=0.5$	$-\frac{c_2^2}{4c_1^2}$	$\frac{c_2a_2}{4c_1}$	Hyperbole
λ_2:0:a_2	$b_{11}=b_{22}=b_{23}=0$ $b_{12}=-0.5$ $b_{13}=c_2a_1/2c_1$ $b_{33}=a_1$	−0.25	$0.25\cdot\ a_1$	Hyperbole
λ_2:0:c_2	$b_{11}=b_{22}=b_{23}=0$ $b_{12}=0.5\cdot\ a_1/c_1$ $b_{13}=-0.5\cdot\ a_2$ $b_{33}=a_1$	$-\frac{a_1^2}{4c_1^2}$	$-0.25\frac{a_1^3}{c_1^2}$	Hyperbole
a_1:0:c_2	$b_{11}=b_{12}=b_{22}=0$ $b_{13}=0.5$ $b_{23}=0.5\cdot\ \lambda_2 a_1/c_1$ $b_{33}=-\lambda_2 a_2$	0	0	Two parallel lines
a_2:0:c_2	$b_{11}=b_{12}=b_{22}=0$ $b_{13}=-0.5\cdot\ \lambda_2$ $b_{23}=0.5\cdot\ \lambda_2 a_1/c_1$ $b_{33}=a_1$	0	0	Two parallel lines
a_1:0:a_2	$b_{11}=b_{12}=b_{22}=0$ $b_{13}=0.5\cdot\ (1-\lambda_2 a_1/c_1)$ $b_{23}=-0.5\cdot\ \lambda_2$	0	0	Two parallel lines

On other parametric spaces of the system (2), the corresponding bifurcation curve is represented as a graph that is not a second-order curve. Analytical conditions for the occurrence of bifurcation at points $(a_1/c_1\,;0)$, $(0;a_2/c_2)$ are symmetric, and their list of topological structures is the same, so we limit the study of bifurcation hyperplanes to the point $(a_1/c_1;0)$

7. Three-dimensional bifurcation diagrams

The analytical condition for the occurrence of bifurcation in the system (2) at the point $(a_1/c_1;0)$ is presented in the form (20)-(22). The bifurcation hyperplane (20) is present only on the planes $a_1{:}a_2{:}\lambda_i$, $a_1{:}a_2{:}c_i$, $a_1{:}\lambda_1{:}\lambda_2$, $a_1{:}\lambda_i{:}c_i$, $a_1{:}\lambda_i{:}c_j$, $a_1{:}c_1{:}c_2$ on which it is perpendicular to the axis a_1. The bifurcation hyperplane (21) exists on parametric spaces of the general form: $\lambda_1{:}\lambda_2{:}a_i$, $\lambda_1{:}\lambda_2{:}c_i$. Moreover, there it will pass through the points (1;0;0), (0;1;0) and will be parallel to the third axis. Also, the bifurcation hyperplane (21) will be present on all bifurcation diagrams, one of the variables of which is λ_1 or λ_2. On these parametric spaces, this bifurcation hyperplane will be represented by planes perpendicular to the axes λ_1 and λ_2 respectively.

Let's rewrite the bifurcation condition (22) in the following form:

$$a_2 \cdot c_1 = a_1 \cdot c_2 \tag{25}$$

Taking into account the nonlinearity of the bifurcation effects of the system, which were discovered earlier, we will conduct a full study of the possible bifurcation properties of the system.

Table 8. Analysis of the properties of the "node – saddle" bifurcation of the system (2) at the equilibrium point $(A_1/C_1;0)$

Field	b_{ij}	I_2	I_3	I_4	Curve type
$a_1{:}a_2{:}c_1$	$b_{14}=c_2/2$	−0,25	0	$(c_2/4)^2$	Hyperbolic paraboloid
	$b_{23}=-0.5$				
$a_1{:}a_2{:}c_2$	$b_{13}=0.5$	−0,25	0	$(c_1/4)^2$	Hyperbolic paraboloid
	$b_{24}=-c_1/2$				
$a_1{:}c_1{:}c_2$	$b_{13}=0.5$	−0,25	0	$(a_2/4)^2$	Hyperbolic paraboloid
	$b_{24}=-a_2/2$				
$a_2{:}c_1{:}c_2$	$b_{12}=-0.5$	−0,25	0	$(a_1/4)^2$	Hyperbolic paraboloid
	$b_{34}=a_1/2$				

Under condition (25), the bifurcation hyperplane is a hyperbolic paraboloid.

From the bifurcation condition (23), which contributes to the emergence of a node-focus type bifurcation at a non-zero singular point of the system, it can be seen that in most cases the degree of bifurcation hypersurfaces reaches three, and sometimes exceeds this value. The only exception to this rule is the bifurcation hyperplane represented by the bifurcation diagram $a_2{:}c_2{:}\lambda_1$. Table 9 presents the results of the study of bifurcation hyperplanes on possible bifurcation 3-dimentional measurement diagrams, as well as invariants.

Table 9. Bifurcation hyperplanes of the "focus - node" type of the system (2) at point $(A_1/C_1;0)$

Field	b_{ij}	I_2	I_3	I_4	Curve type
$a_1{:}a_2{:}c_2$	Hyperplane of the 4th order				
$a_1{:}a_2{:}\lambda_1$	Hyperplane of the 3rd order				
$a_1{:}a_2{:}\lambda_2$	Hyperplane of the 4th order				
$a_1{:}c_2{:}\lambda_1$	Hyperplane of the 3rd order				
$a_1{:}c_2{:}\lambda_2$	Hyperplane of the 6th order				
$a_1{:}\lambda_1{:}\lambda_2$	Hyperplane of the 4th order				
$a_2{:}c_2{:}\lambda_1$	$b_{11}=\lambda_2^2$	$4a_1^2\left(\frac{a_1^2}{c_1^2}-1\right)$	0	0	Cylinder ($a_1>c_1$ – elliptic, $a_1=c_1$ – parabolic, $a_1<c_1$ – hyperbolic)
	$b_{22}=\frac{a_1^2 \cdot \lambda_1^2}{c_1^2}$				
	$b_{44}=a_1^2$				
	$b_{12}=-\frac{a_1 \cdot \lambda_2^2}{c_1}$				
	$b_{23}=-\frac{2a_1^2}{c_1}$				
	$b_{13}=2a_1$				
	$b_{24}=\frac{a_1^2(2-\lambda_2)}{c_1}$				
	$b_{14}=a_1(\lambda_2-2)$				
	$b_{33}=b_{34}=0$				
$a_2{:}c_2{:}\lambda_2$	Hyperplane of the 4th order				
$a_2{:}\lambda_1{:}\lambda_2$	Hyperplane of the 4th order				
$c_2{:}\lambda_1{:}\lambda_2$	Hyperplane of the 4th order				

On other parametric spaces, the bifurcation surface is represented as a graph, which is not a second-order surface.

The bifurcation arising under condition (25) is characterized by several features. First, since the parameter λ_1 is not included in (25), on three-dimensional bifurcation diagrams, in which one axis is represented by the constant λ_1, the bifurcation hyperplane will have the form of a cylinder perpendicular to the axis λ_1. That is why research on the corresponding diagrams should be simplified to 2-dimentional measurement diagrams.

Table 10. Analysis of bifurcation properties of the "stable focus – unstable focus" type of the system (2) at the equilibrium point (A_1/C_1;0)

Field	b_{ij}	I_2	I_3	I_4	Curve type
a_1:a_2:c_2	$b_{13}=-0.5\lambda_2/c_1$ $b_{14}=0.5$ $b_{24}=-0.5\lambda_2$ $b_{11}=b_{12}=b_{22}=b_{23}=$ $=b_{33}=b_{34}=b_{44}=0$	$-\dfrac{\lambda_2^2}{4c_1^2}$	0	$\dfrac{\lambda_2^4}{16c_1^2}$	Hyperbolic paraboloid
a_1:a_2:λ_2	$b_{13}=-\dfrac{c_2}{2c_1}$ $b_{14}=0.5$ $b_{23}=-0.5$ $b_{11}=b_{12}=b_{22}=b_{24}=$ $=b_{33}=b_{34}=b_{44}=0$	$-\dfrac{1}{4}-\dfrac{c_2^2}{4c_1^2}$	$-\dfrac{a_1^2}{4c_1^2}$	$\dfrac{1}{16}$	Hyperbolic paraboloid
a_1:c_2:λ_2	$b_{14}=0.5$ $b_{23}=-0.5a_1/c_1$ $b_{34}=-0.5\cdot a_2$ $b_{11}=b_{12}=b_{13}=b_{22}=$ $=b_{24}=b_{33}=b_{44}=0$	$-\dfrac{a_1^2}{4c_1^2}$	0	$\dfrac{a_1^2}{16c_1^2}$	Hyperbolic paraboloid
a_2:c_2:λ_2	$b_{13}=-0{,}5$ $b_{23}=-a_1/2c_1$ $b_{44}=a_1$ $b_{11}=b_{12}=b_{14}=b_{22}=$ $=b_{24}=b_{33}=b_{34}=0$	$-\dfrac{a_1^2}{4c_1^2}-\dfrac{1}{4}$	0	0	Hyperbolic cylinder

On other parametric spaces, the corresponding bifurcation surface is represented as a hyperplane, which is not a second-order surface.

8. Discussion

The proposed model extends classical Lotka–Volterra dynamics by incorporating non-isolated subpopulations with migration and heterogeneous ecological niches. The analysis demonstrates that the ratio of competition coefficients and transition parameters critically determines system stability, dominance, and possible coexistence. Bifurcation analysis reveals that small parameter variations can trigger qualitative changes, including shifts between stable and unstable states or the emergence of attractors. These findings highlight the importance of accounting for inter-subpopulation exchange in modeling real-world biological, social, and economic systems, where ignoring such interactions may lead to oversimplified or inaccurate predictions.

9. Conclusion

Compared with previous studies, the conditions for the occurrence of bifurcations at equilibrium points (of the “node–saddle,” “node–focus,” and “stable focus–unstable focus” types) have been determined, and a complete classification of bifurcation curves and hyperplanes has been provided with respect to their nonlinearity.

From the presented results, it is clear that the model sufficiently adequately describes intra-dynamic processes that are taking place against the background of several subpopulations that are not isolated, but at the same time differ among themselves in terms of habitat and feeding method. The adequacy of the proposed model is confirmed by a large number of phase portraits and diagrams reflecting the conditions of qualitative changes in the behavior of both the system in general and individual subpopulations in particular. The results show that the key factor in the case of interaction of subpopulations with separate niches for existence is the ratio of the coefficients of intersubpopulation competition: c_1/c_2. This ratio plays one of the main roles in determining the dominant subpopulation in the system. It should be noted that the system-wide dynamics of subpopulation processes also significantly depends on the reproductive potential of all subpopulations and on intra-system dynamics, which are reflected in the transition coefficients proposed in this work. Thus, the mass fraction of individuals, which according to their phenotypic properties belong to the parent, is proposed in the work to be called transition coefficients, which, in turn, belong to the gap $[0;1]$ and must meet the condition of the closedness of the system.

It has been established that subpopulations in real life can exchange offspring, which, in turn, can significantly affect both quantitative and qualitative aspects of dynamics. For example, for a two-dimensional system, the sum of the main elements of the matrix of transition coefficients is essential. In the case where the sum is close to the size of subpopulations in the system, the subpopulations have little dependence on each other. In opposite case, the dynamics, being much more complex, can move to qualitatively different levels.

The bifurcation properties of the subpopulation dynamics model with a basic Lotka–Volterra type function were studied. Applied substantiation of possible bifurcations of the system makes it possible to assess the factors that will qualitatively affect the dynamics of the system, and to develop a number of recommendations to prevent the occurrence of disasters and collapses in the system.

All the Declarations and Statements

Author Contribution Statement

O. Kuzenkov – Methodology, data curation and software implementation: Handled data acquisition, data set preprocessing, and implementing the research model. Validated results using standard metrics, and benchmarked performance against existing methods. Review and Editing, and Project Management: Reviewed and edited the manuscript, ensured clarity and coherence, and helped coordinate project milestones and deadlines.
M. Tryputen – Conceptualization, Supervision: Proposed research ideas, Constructed the overall framework, and supervised project execution. Drafted the initial manuscript, contributed to the literature survey, and documented the technical background of the study.
V. Kuznetsov – Development of the mathematical model and its analytical investigation, including the derivation of equilibrium conditions, construction of the Jacobian matrix, and analysis of bifurcation properties of the system. Participated in the interpretation of theoretical results and their consistency with the proposed model assumptions.
O. Huliesha – Performed numerical simulations of the system for various parameter values and initial conditions, developed phase portraits and bifurcation diagrams, and contributed to the analysis and interpretation of computational results. Preparation of graphical materials presented in the manuscript.
V. Artemchuk – Validation of the obtained results and their comparison with existing studies. Conducted the literature review, participated in drafting and editing the manuscript, and approved the final version for publication.

All authors have read and agreed to the published version of the manuscript.

Conflict of Interest Statement

The Authors declared no conflicts of interest.

Funding Declaration

This research received no external funding.

Data Availability Statement

The data that support the findings of this study are from the corresponding author upon reasonable request.

Ethical Declarations

This study did not involve human participants or animals.

Acknowledgements

We sincerely thank the experts for their professional evaluation and valuable recommendations, which have contributed to improving the quality of the experiment and the reliability of its results.

Declaration of Generative AI in Scholarly Writing

During the preparation of the manuscript, the authors carefully reviewed the content and take full responsibility for the accuracy and integrity of the manuscript.

References

[1] Kuzenkov O., Zaitseva T. Bifurcation analysis of the differential model of subpopulation dynamics. Scientific Bulletin of the Zaporizhia National University - Zaporizhzhia, 2009. - P. 102 - 108.
[2] Chernyshenko S.V., Kuzenkov O.O. Bifurcation effects in degenerate differential models of subpopulation dynamics (2013) Proceedings - 27th European Conference on Modelling and Simulation, ECMS 2013, pp. 130 - 135, DOI: 10.7148/2013-0130
[3] Perestyuk, Nikolai A., Plotnikov, Viktor A., Samoilenko, Anatolii M. and Skripnik, Natalia V.. Differential Equations with Impulse Effects: Multivalued Right-hand Sides with Discontinuities, Berlin, Boston: De Gruyter, 2011. https://doi.org/10.1515/9783110218176

[4] Matsenko, V.H. (2003). A Nonlinear Model of Age-Dependent Population Dynamics. Nonlinear Oscillations, 6, 350-360.

[5] Belozyorov V.Ye., Chernyshenko S.V., Chernyshenko V.S. Hierarchical heterogenity of populations: Modeling by the open Eigen hypercycle (2012) Proceedings - 26th European Conference on Modelling and Simulation, ECMS 2012.DOI: 10.7148/2012-0150-0156

[6] Chernyshenko S.V., Ruzich R.V. Energy and information aspects of self-organisation of ecological systems: Mathematical models and interpretations (2015) Proceedings - 29th European Conference on Modelling and Simulation, ECMS 2015, pp. 94 - 99, DOI: 10.7148/2015-0094

[7] Chernyshenko S.V., Ruzich R.V. Bifurcation model of successions in ecosystems (2013) Proceedings - 27th European Conference on Modelling and Simulation, ECMS 2013, pp. 769 - 774, DOI: 10.7148/2013-0769

[8] Belozyorov V.Ye., Dantsev D.V. Stability of neural ordinary differential equations with power nonlinearities (2020) Journal of Optimization, Differential Equations and their Applications, 28 (2), pp. 21 - 46, DOI: 10.15421/1420O5

[9] Bossel H. Modelling and simulation. – Wellesley, MA: A. K. Peters, 1994. – 484 p.

[10] Hannon B., Ruth M. Dynamic modeling. – N.Y.:Springer, 1994. – 248 p.

[11] Anna-Sapfo Malaspinas, Montgomery Slatkin, Yun S. Song, Match probabilities in a finite, subdivided population, Theoretical Population Biology, Volume 79, Issue 3, 2011, Pages 55-63, ISSN 0040-5809, https://doi.org/10.1016/j.tpb.2011.01.003.

[12] Tomoko Doko; Wenbo Chen; Reina Uno; Hidetoshi B. Tamate; A.G. Toxopeus; A.K. Skidmore; Hiromichi Fukui Potential Ecological Corridors for Remnant Asiatic Black Bear Populations and its Subpopulations Linked to Management Units in Japan, Bears of the World (2020), p. 356. DOI:10.1017/9781108692571.026

[13] Jacob P. Kritzer, Campbell R. Davies, Demographic variation within spatially structured reef fish populations: when are larger-bodied subpopulations more important? Ecological Modelling ,Volume 182, Issue 1, 25 February 2005, Pages 49-65.

[14] Mathematical Models in Biology and Medicine . Edited by N. T. J. Bailey, B. Sendov and R. Tsanov. (Proceedings of IFIP TC4 working conference, Varna, September 6th–11th, 1972). London, North Holland ; Amsterdam, Elsevier, 1974.

[15] Hofbauer J.,Sugmund K. The theory of evolution and dynamical systems. – Berlin, Heidelberg, N.Y.:Springer – Verlag, 1988.

[16] May R. M., Oster G. F. Bifurcations and dynamic complexity in simple ecological models // American Naturalist. – 1976. – Vol. 110. – P. 573-599.

[17] Volterra V. Lecons sur la theorie mathematiqque de la lutte pour la vie. – P.:Gauthier – Villars, 1931

[18] Volterra V. Fluctuations in the abundance of a species considered mathematically / Volterra V. // Nature. - 1926. - Vol. 188. - P. 558-560.

[19] Haberman R. Mathematical Models, Prentice-Hall, Englewood Cliffs, 1977. NJ

[20] Vozmishcheva, T. (2020). The Study of the Modification of the Lotka - Volterra Model: Influence of External Factors on the Evolution of the System of Competing Processes. Intellekt. Sist. Proizv. 18. 61. 10.22213/2410-9304-2020-2-61-70.

[21] Busher, V., Chornyi, O., Kuzenkov, O., Tryputen, M., Kuznetsov, V., Rumiantsev, V. (2022). Investigation of the Bifurcation Properties of the Dynamics of a Biological Population Based on a Logistic Model. In: Hu, Z., Petoukhov, S., Yanovsky, F., He, M. (eds) Advances in Computer Science for Engineering and Manufacturing. ISEM 2021. Lecture Notes in Networks and Systems, vol 463. Springer, Cham. https://doi.org/10.1007/978-3-031-03877-8_18

[22] O. Kuzenkov, V. Kuznetsov and N. Tryputen, "Analysis of Phase Trajectories of the Third - Order Dynamic Objects," 2019 IEEE 2nd Ukraine Conference on Electrical and Computer Engineering (UKRCON), Lviv, Ukraine, 2019, pp. 1235-1243, doi: 10.1109/UKRCON.2019.8879819.

[23] O. Kuzenkov, V. Busher, O. Chornyi, A. Nikolenko, V. Kuznetsov and O. Savvin, "Nonlinear Analysis of Bifurcatory Properties of Mathematical Model of Subpopulation Dynamics in the Case of a Single Niche for Subpopulation," 2022 IEEE 3rd International Conference on System Analysis & Intelligent Computing (SAIC), Kyiv, Ukraine, 2022, pp. 1-5, doi: 10.1109/SAIC57818.2022.9923003.

Authors' Profiles

Dr. O. Kuzenkov was born in Dniepropetrovsk, Ukraine and graduated from the Dniepropetrovsk National University. Candidate of Physical and Mathematical Sciences, Associate Professor of the Department of Computational Mathematics and Mathematical Cybernetics, Oles Honchar Dnipro National University, Dnipro, Ukraine.

Dr. M. Tryputen was born in Dniepropetrovsk, Ukraine. He completed his higher education at the Dnepropetrovsk Mining Institute (now Dnipro University of Technology, National Technical University "Dnipro Polytechnic"), Dnipro, Ukraine. In 1980, he graduated with a degree in Automation and Telemechanics and obtained the qualification of electrical engineer. In 1988, he obtained the degree of Candidate of Technical Sciences (Ph.D. equivalent) in specialty 05.13.07 – Automation of Technological Processes and Production (Industry). His dissertation, titled "Development of automated crusher operating modes for a large-piece crushing process control system", was devoted to improving the efficiency of automated industrial control systems. He has many years of experience in teaching and scientific work in the field of automation and control systems. He is currently affiliated with the Department of Cyberphysical and Information-Measuring Systems at Dnipro University of Technology, where he is actively engaged in academic, methodological, and research activities. He contributes to the development of modern educational programs and supervises student and postgraduate research in the areas of automation, electromechanics, and intelligent control systems. He is the author and co-author of numerous scientific and methodological publications devoted to automation of technological processes, control theory, and modeling of complex systems. His works reflect both theoretical developments and practical applications in industrial automation. His research interests include automatic control theory, modeling and optimization of technological processes, adaptive and optimal control systems, development of performance criteria for automation systems, industrial process automation, and application of modern computational methods in control engineering.

Dr. V. Kuznetsov was born in Dniepropetrovsk, Ukraine, 1975. He received the B.S. degree in electromechanics from the Dnipropetrovsk Institute of Railway Transport (DIIT) in 1997, specializing in electric drive and automation of industrial installations and technological complexes, qualifying as an electrical engineer. He obtained the Ph.D. degree in technical sciences (electrical engineering field). He currently holds the academic title of associate professor. He is currently an Associate Professor at the Department of Electrical Engineering of the Ukrainian State University of Science and Technologies (formerly National Metallurgical Academy of Ukraine, NMetAU). He is also involved in educational program development and serves as a guarantor or member of academic program groups in the field of electrical engineering. He is the author and co-author of more than 80 scientific publications, including journal articles and conference papers indexed in international scientometric databases such as Scopus. His research work is widely focused on modern problems of electrical engineering and energy systems. His research interests include electric power engineering, electromechanics, modeling and control of induction motors, analysis of electric drive systems under conditions of poor power quality, integration of renewable energy sources, and optimization of energy conversion processes.

Mrs. O. Huliesha is candidate of pedagogical sciences, associate professor at the Department of Electronics and Electronic Communications, Dnipro State Technical University.

Dr. V. Artemchuk was born in 1975. He is currently Professor at the Department of Electrical Engineering of the Ukrainian State University of Science and Technologies (formerly National Metallurgical Academy of Ukraine, NMetAU).

How to cite this paper

O. Kuzenkov, M. Tryputen, V. Kuznetsov, O. Huliesha, V. Artemchuk, "Mathematical Model of Subpopulation Dynamics in Case of Different Niches for Subpopulations", International Journal of Engineering and Manufacturing (IJEM), Vol.16, No.3, pp.125-144, 2026. DOI:10.5815/ijem.2026.03.09