GENERAL BIOLOGY

Multimode Phenomenon in the Population Dynamics of Animals with Short Live Cycles

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Fluctuation of animal populations continues to be one of the most interesting and mysterious ecological phenomena. A lot of evidence available to date suggests not only regular changes in population abundance, but also clear cycling of various dynamic modes in biological populations.

The most striking and well-known examples of changes in animal population dynamics are transitions between stable and cyclic phases in the lemming (*Lemmus lemmus*) populations all over southern Norway [1] and in the red-gray vole (*Clethrionomys rufocanus*) populations in Finland [2]. The reverse situation can be also observed, when small fluctuations around the equilibrium state are replaced by either oscillatory or chaotic modes. For example, a trend of the snow goose population (*Chen caerulescens*) in the New York state (United States) to grow up monotonously for a long time has changed to irregular oscillations, probably, because of exceeding the ecological capacity of the environment [3]. Another type of disturbed population dynamics is related to variation in the lengths of cycles. In particular, in Canada and the northern United States, there was a transition from two- to three-year oscillations in the evening grosbeak (*Coccothraustes vespertinus*) population [4]. Note that similar phenomena were observed in the populations of lemming and some vole species, because the cycles with lengths of 2, 3, and 4 are characteristic of them [5, 6]. Moreover, there are situations when non-interacting, practically identical populations of the same species display different dynamics. In particular, the laboratory experiments have demonstrated that, at the same initial population size and under similar conditions, two different anti-phased periodic modes may be observed in the flour beetle (*Tribolium castaneum*) populations [7].

Thus, there are situations when local populations have different (and sometimes radically different) modes of population dynamics at the same values of demographic parameters. This phenomenon of the dynamic mode dependence on initial conditions is referred to as multistability in the theory of dynamic systems [8]. Appearance of several different dynamic modes is possible when a system has several stable attractors, each serving as a stable point or being involved into a limiting set of attractors (e.g., an invariant curve). Hence, the term "multistability" is somewhat misleading in this context and, to our opinion, it is more convenient to use a new notion of "multimode" to reflect the essence of the phenomenon occurring in real objects (different population dynamics depending on the initial conditions). Note that a natural change of dynamic regimes can be readily explained as a multimode phenomenon because the modifying influence of external factors can be regarded, in particular, as modification of initial conditions.

At present, the study of mechanisms responsible for switching of the population dynamic modes is of great interest. None of the numerous concepts and hypotheses proposed to explain the emergence and disappearance of fluctuations in population size is universally accepted.

In this study, the multimode phenomenon has been identified and analyzed using a simple mathematical model of an animal species population with a short life cycle (rapid maturation of the juveniles). To illustrate the adequacy of the model dynamic modes they were compared with real dynamics of the bank vole (*Myodes glareolus*) population. We used the data obtained by Bernstein and Khvorenkov using the long-term monitoring of the relative total numbers of animals in an Udmurt station.

Equations of dynamics. There are the following stages in the life cycle of most murine rodents: in

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spring, the overwintered animals come out from under the snow and their reproduction begins to provide several litters for the spring–summer period. Late in autumn the population "goes under the snow" for the whole winter. Under favorable condition, reproduction of mature animals, mostly the young of the current year, continues in winter; i.e., a transition is observed from the seasonal to year-round reproduction [5, 9, 10]. Immature underyearlings attain maturity during winter. Hence, by the beginning of the next breeding season, when the snow melts, the population is represented by two age groups: the underyearlings born under the snow and the mature overwintered animals.

For this life cycle, the following equation of the dynamics can be written, which links the initial population sizes of the adjacent generations:

$$x_{n+1} = R_1 x_n + R_2 y_n,$$
$$y_{n+1} = s \cdot x_n + v \cdot y_n, \tag{1}$$

where n is the breeding season number; x is the number of animals born under the snow (mature underyearlings), y is the number of overwintered mature animals; R_1 and R_2 are the reproductive indexes of mature groups taking into account survival of the young, s and v are the animal survival in different age groups.

Abundance of the murine populations is often believed to be mainly regulated via the limiting of birth rate [5, 9, 10], which is always reduced at high population numbers. In particular, with increasing population size, the immature animal puberty is slowing down, while among sexually mature animal, the intervals between successive pregnancies are increased. In addition, the death rate of mainly young animals grows up. With this in mind, we assume that, as in Ricker's model [11], R_1 and R_2 are functions of the age group sizes, and we write them as

$$R_1 = r_1 e^{-\beta \cdot x - \gamma \cdot y} \quad \text{and} \quad R_2 = r_2 e^{-\beta \cdot x - \gamma \cdot y}.$$

The r_1 and r_2 parameters correspond to the reproductive potentials of mature groups; β and γ coefficients of limitation which reveal the influence of competition between mature individuals of different age in the birth rate and survival juveniles. To reduce the number of parameters, it is assumed that β and γ are the same in both adult groups. Then, the dynamics Eq. (1) looks like

$$x_{n+1} = (r_1 x_n + r_2 y_n) e^{-\beta \cdot x_n - \gamma \cdot y_n},$$
$$y_{n+1} = s \cdot x_n + v \cdot y_n. \tag{2}$$

Simple substitutions of the variables $s\gamma \cdot x \to x$, $\gamma \cdot y \to y$, $a_1 = r_1$, $a_2 = sr_2$, $\rho = \beta/(s\gamma)$ makes it possible to reduce model (2) to the four-parametric model

$$x_{n+1} = (a_1 x_n + a_2 y_n) e^{-\rho \cdot x_n - y_n},$$
$$y_{n+1} = x_n + v \cdot y_n, \tag{3}$$

where $a_1 > 0$, $a_2 > 0$, $\rho \geq 0$, $0 < v \leq 1$.

System (3) has a unique nontrivial fixed point

$$\bar{x} = \frac{1-v}{1+\rho(1-v)} \ln\left(\frac{a_1 + a_2 - a_1 v}{1-v}\right),$$
$$\bar{y} = \frac{1}{1+\rho(1-v)} \ln\left(\frac{a_1 + a_2 - a_1 v}{1-v}\right) \tag{4}$$

under the conditions of existence $\rho \geq 0$, $0 \leq v < 1$, $a_2/(1-v) + a_1 > 1$.

We investigated the stability of solution (4) and examined various scenarios of the transition from stable fixed point to fluctuations and irregular dynamics. Figure 1 shows changes in stability region in the space of parameters a_1 and a_2 at different ρ and v values, as well as possible scenarios of transition to fluctuations and chaotic dynamics.

Studying the boundaries of the stability region showed that a loss of stability depends on the ratio of parameters ρ and v. If $\rho < 1$ (because of a change in the model parameters and crossing the boundary of the stability region), then a loss of stability occurs according to the Neimark–Sacker scenario: population dynamics of the age classes becomes quasi-periodic. When $\rho > \rho^* = (3 + v)/(v^2 + 2v + 1)$, a loss of stability of the fixed point is going on Feigenbaum's scenario: persistent fluctuations occur in the number of population. When $1 \leq \rho \leq \rho^* = (3 + v)/(v^2 + 2v + 1)$, both of the above scenarios are possible.

Afterwards, we focused on detailed analysis of the possible dynamic modes in the zone of equilibrium and outside this zone.

Possible dynamic modes: numerical study and emergence of the cycle with a length of 3. In numerical experiments, it has been found out unexpectedly that, within the region of parameters where the stationary solution is stable, there is a subregion where other stable attractors appear in addition to this equilibrium. When $\rho < 1$, the cycle of the length 3 (or 3-cycle) is such a stable attractor. This means that, at the same values of the model parameters, the population of a certain initial size comes to a stable equilibrium while in a population of another initial size a transition occurs to stable 3-year oscillations. Coexistence of different dynamic modes at similar parameter values is well known for the attractors that appear in a region of irregular dynamics. The effects of this kind can be when a system has several stable equilibriums (e.g., bistability). However, in the given case, the model has a unique non-trivial fixed point and a variety of dynamic modes arises at the demographic parameter values from the stability region of the stationary solution.

A combination of the analytical and numerical studies of model (3) suggests that 3-cycle appears as a result of fold bifurcation. The curves in Fig. 2, which
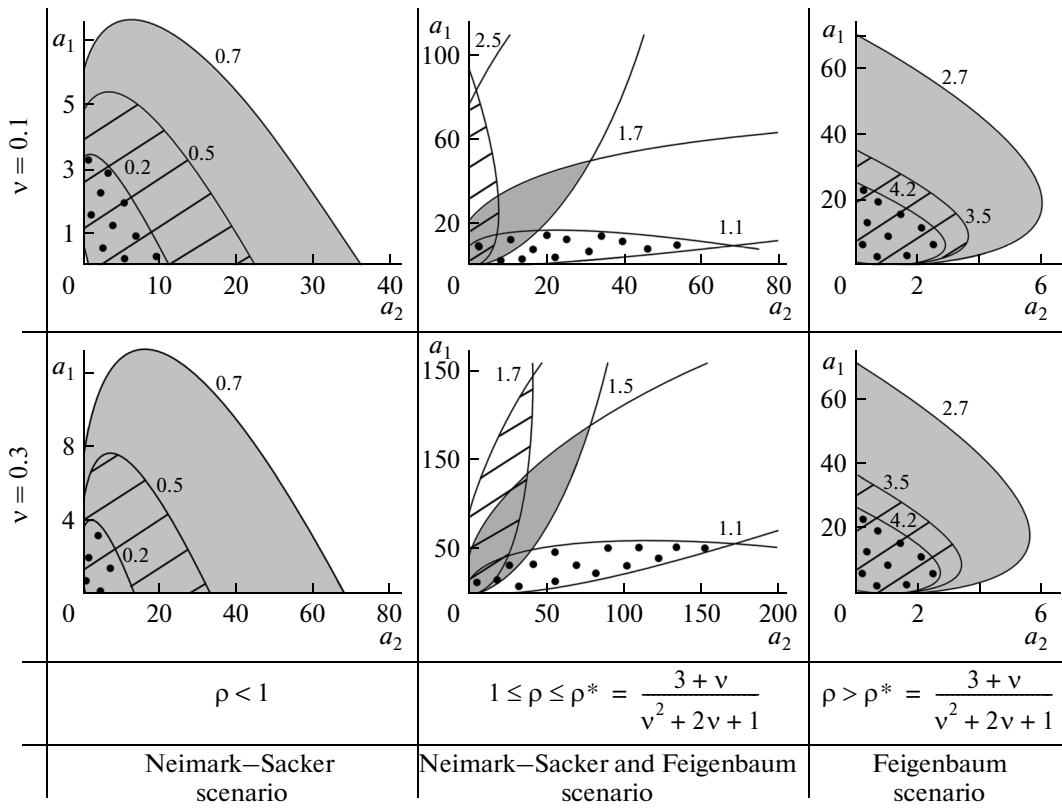
Fig. 1. Stability region of nontrivial fixed point (4) of system (3). Figures on the graphs correspond to the values of the ρ parameter.

are constructed by scanning [12], describe the three-fold iterated model equations (3). Intersections of these curves correspond to three fixed points of operator (3) as applied threefold: stable equilibrium, three points of the stable 3-cycle, and three points of the unstable 3-cycle. Furthermore, Fig. 2 shows the basins of attraction (the initial value areas) from which the system tends to stable equilibrium (this area is marked with gray and 1) and to the stable 3-cycle (three white areas and 3). Note that the unstable 3-cycle is located at the boundaries of the basins of attraction, while the stable 3-cycle is "within" its own basin of attraction at a distance from the basin of attraction of stable equilibrium.

When $1 \leq \rho \leq \rho^*$ and loss of stability occurs according to the Neimark−Sacker scenario in zones of both regular and irregular dynamics, not only the length-3 cycle, but also a "periodicity window" may exist which corresponds to the attracting cycle of the length 4. Hence, the basins of attraction for the cycles of the lengths 1, 3, and 4 coexist in the phase space of system (3) (Fig. 3).

It should be emphasized that, in this system, the length-4 cycle, as well as the length-3 cycle, appears as a result of tangent bifurcation. Moreover, division of the phase space on the 3-cycle and 4-cycle basins of

attraction is especially remarkable, because both the 3- and 4-year oscillations are observed in small rodent populations [5, 6, 9, 13].

When $\rho > \rho^*$, the birth rate is reduced mostly when the number of underyearlings grows up and a loss of stability happens according to Feigenbaum's scenario, i.e., the two-year oscillations occur. Note that the two-year cycle of some vole species takes place in nature [5, 6, 9, 13]. When $\rho > \rho^*$, as before, the length-3 cycle arises in a region of stable nontrivial equilibrium as a result of fold bifurcation. But the basins of attraction differ significantly from those when $\rho < 1$. The system (3) phase space represents a set of basins of attractions of various stable modes and resembles a "zebra". The regions from where the system tends to a stable point alternate with the regions from where it tends to the stable length-3 cycle.

The use of the model to describe the population dynamics of the bank vole (Myodes glareolus). At the next step of our study, we verified the model on data of real population size. The model parameters were estimated using the materials of many years of monitoring for the relative total numbers of bank voles (the number of individuals per 100 trap−days) in the Udmurt station in the boreal zone of the linden−fir−spruce subtaiga (57°20′ N, 52° E). The model coefficients
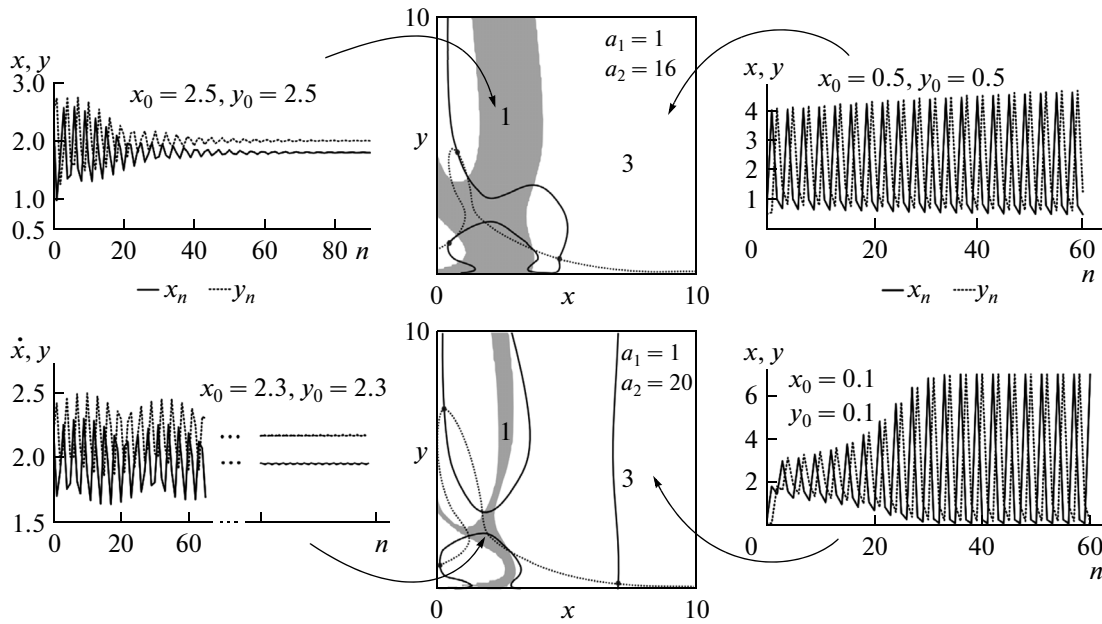
Fig. 2. The fixed points of the system of threefold iterated equations (3) and the basins of attraction of the model (3) with $\nu = 0.1$ and $\rho = 0.5$.
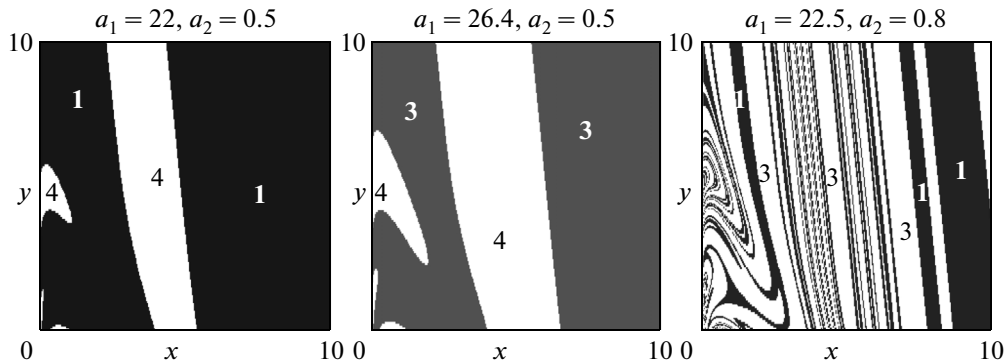

Fig. 3. The basins of attraction of the model (3) with $\nu = 0.1$ and $\rho = 0.5$. Figures indicate lengths of the observed cycles.

were found by selecting the values with which the sum of the model population numbers of both age classes had the best fit to the known sequence of estimated size of the bank vole population at the beginning of the breeding season. To estimate the parameters, the minimum of residual function was found using the Leven-berg–Marquardt method [14], as in the MathCAD 14 software, and the penalty method [12].

The model trajectory at the estimated parameters describes the dynamics trend satisfactorily, but it does not catch the main peaks of the bank vole population size. The coefficient of determination, which characterizes the quality of approximation, was $R^2 = 0.681$. The estimated parameter values are in the zone of irregular dynamics in the case when the loss of stability occurs through invariant curve formation; i.e., the

bank vole population numbers undergo quasi-periodic oscillations. We believe that discrepancy between the observed and model data is caused by the influence of external factors. To take into account the effect of external factors, the functions $R_i = (x, y)$ were modified as follows:

$$R_i(x_n, y_n) = r_i e^{-\beta \cdot x_n - \gamma \cdot y_n + b S_n}, \tag{5}$$

where b is the coefficient which characterizes the intensity of the external factor effect on winter reproduction of the bank vole, S_n is the average value of Selyaninov's hydrothermal coefficient [15] for the period April–July of the year n. This coefficient characterizes the ambient humidity (moisture of soil) in the vegetative period. This index has been chosen because it characterizes indirectly food abundance in
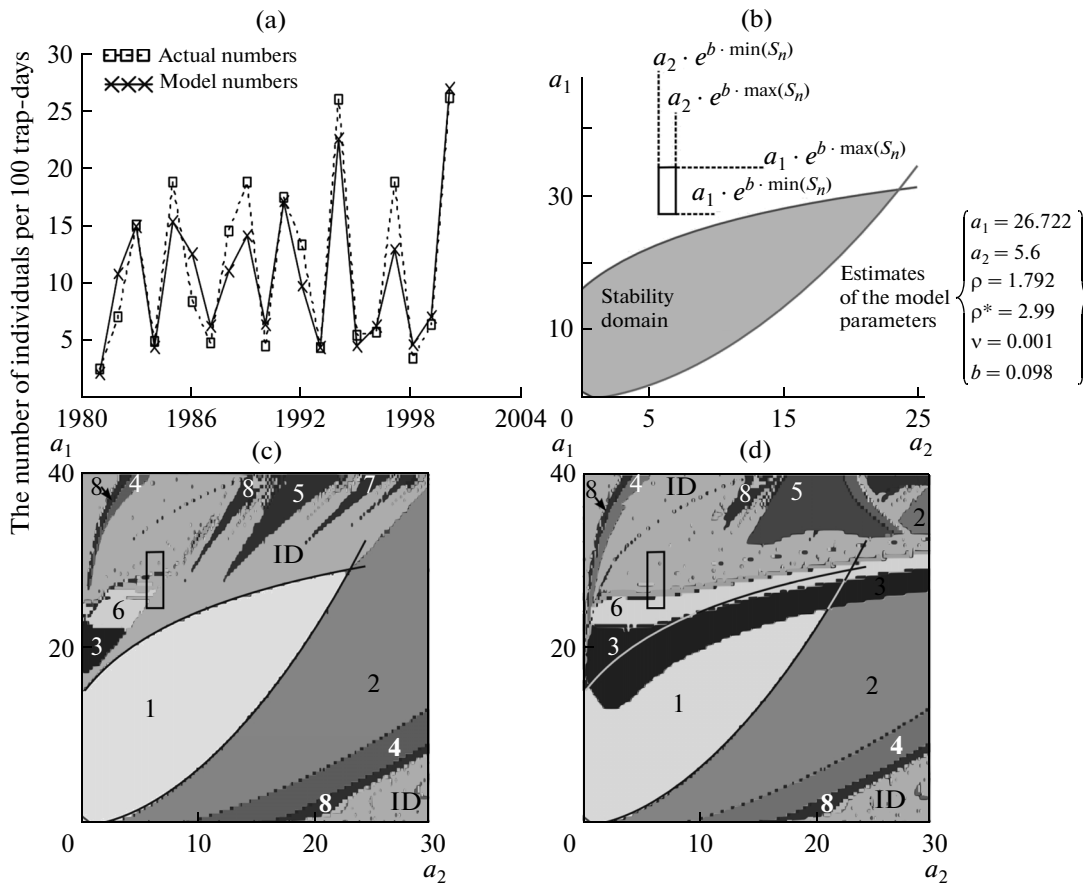
Fig. 4. (a) Dynamics of the bank vole population; (b) the parametric portreit corresponding to the estimates obtained; (c, d) the maps of possible dynamic modes at these parameters as dependent on the initial level. In map (c), starting conditions belongs to the basin of attraction of the fixed point; in map (d), starting condition belongs to the basin of attraction of the stable 3-cycle. Figures indicate the lengths of cycles; ID is irregular dynamics.

winter, which is a factor having a significant effect on the dynamics of bank vole population.

Involvement of the external factor enabled us to catch the main peaks of the population size (Fig. 4a). The coefficient of determination which characterizes the efficiency of fit of the actual data to the model was equal to $R^2 = 0.88$, which is related to the fact that the coefficients of reproductive potentials of individuals were not the constants in this case, but they have the values from the parametric pattern area marked as a rectangle in Fig. 4b. Furthermore, the maps of asymptotic dynamic modes demonstrate that the point estimate of the model parameters fall into a zone of the cycle of length 6, which emerged because of period doubling bifurcation of the 3-cycle . At the same time, these estimates are shifted into the zone of quasi-periodic dynamics because of the climatic factor influence (Figs. 4c, 4d).

Thus, we have developed a mathematical model of the populations with a short life cycle and density-dependent regulation of the reproduction processes. In this model of the population dynamics with a sim-

ple age structure, the multimode phenomenon has been found out, which suggests that, at the same model parameters, different stable dynamic modes are possible and the change of dynamic mode depends on initial population numbers. Hence, specific population dynamics depends significantly on the initial conditions (or current population size). It is important that this effect is observed in a model having simultaneously several qualitatively different attractors: an steady state, limit cycles, and a chaotic attractor.

Various aspects of the model dynamic behavior, which are based on the recurrence equations, are still not completely explored, but they enable the researchers to explain differences in population dynamics of some species living virtually under identical conditions. On the other hand, in a local population, in particular, in the population of murine rodents, the multimode phenomenon makes it possible to explain both the emergence of oscillations with 3- and 4-year periods and disappearance of fluctuations.

Our model displays either regular oscillations or quasi-periodic fluctuations at the parameter values

corresponding to the estimates obtained on the basis of population dynamics of the bank vole (*Myodes glareolus*) in Udmurtia. The influence of external climatic factors on the population reproduction expands noticeably the range of possible dynamic modes and leads virtually to random transitions of these modes between the basins of attraction.

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