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# A Synergetic Approach to Analysis of Probabilistic and Deterministic Components of Seasonal and Long-Term Dynamics of European Bank Voles in the Areal Center

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**Abstract**—A comprehensive description and analysis of the probabilistic and deterministic components of the seasonal and long-term dynamics of the bank vole in the center of the range were carried out. It was noted that in the first half of the breeding season, the long-term total of the probabilities of implementation of the population numbers is described by an asymmetrical lognormal distribution, and the process of its formation is to the continuous time Markov branching process. In the second half, several homogeneous groups of probability distributions were distinguished that were separated from each another by the minimum points. It was found that the phenomenon described is a stochastic analog of the structurally stable Hopf bifurcation. It was revealed that the oscillations from the equilibrium state of a population that appear under the influence of external disturbances can be assimilated by it, becoming a source of improvement of the regulator mechanisms.

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## INTRODUCTION

The processes taking place in animal populations are, on the one hand, closely linked to the environmental conditions (climate, soil, vegetation, predators, forage, etc.); on the other hand, they are determined by the biological characteristics of the population itself (species status, socio-demographic population system, type of diet, sex and age composition, intensity of reproduction, population dynamics, density-dependent feedback, etc.). The endogenous and exogenous factors affecting a population can cause changes both in the phase portrait of the population's behavior and the intensity of the processes occurring in it. The interaction of external and internal factors affecting the population introduces an element of chance and can cause a complex behavior that determines the type of seasonal and long-term dynamics of the population, whereas the existence of self-organization allows us to consider it as a complex nonequilibrium system (Nikolis and Prigogine, 1989; Prigogine and Kondepudi, 1998; Loskutov and Mikhailov, 2007).

Different types of animal interactions with the environment have developed historically in the process of evolution and ultimately reflect the optimum way of using the entire complex of environmental conditions with an equally full implementation of the population's capacities. So far, the issue of what processes

most significantly determine the population dynamics remains controversial, despite the existence of significant data on the demographic and spatial structure of the populations of several species of small mammals. One of the main reasons for the lack of a rigorous scientific theory in population regulation is the paucity of long-term stationary observations of different species. Moreover, studies carried out in different landscapes and geographical areas, which would record not only the number and the demographic structure of the population, but the external factors as well, are also scarce (Schwartz et al., 1976, 1977; Zhigal'skii and Bernshtein, 1986; Krebs, 1996; Zhigal'skii, 2002, 2012, 2014; Getz, 2005; Mikheeva et al., 2006; Bobretsov, 2009; Dobrinskii, 2011, 2015; Litvinov et al., 2013; Lukyanova, 2013; Zhigal'skii and Mamina, 2015).

However, it is clear that, within the deterministic approach, only the problem of the origin and existence of population dynamics cannot be solved. Analysis of the causes of variability of the demographic and spatial structure of a population of small mammals can be carried out only using the theory of complex systems, which can reveal the common patterns of phenomena and processes in complex nonequilibrium population systems taking into account their principles of self-organization. Another reason consists in that nonequilibrium population systems are capable of bifurca-

**Table 1.** Characterization of the material used

Station	Coordinates		Study period/number of years	Capture effort, tr./n.	Animals captured
	N	E			
Kenskii forest	56°41′	53°19′	1973–2001/29	41 151	10 398
Varaksino	56°52′	53°10′	1974–2001/28	31 330	8 136
Yak-Bod’inskii	56°54′	53°20′	1974–2001/28	30 436	8 359

tion transitions to new states, thereby ensuring the viability of the population. After the transition to every new trajectory, the relative stability of the most probable states needs to be assessed, as well as the time spent by the system close to them. This problem can also be solved only in the framework of an extended description that takes into account the effect of disturbances. However, for a wide class of dynamical population systems, random behavior can also occur as a result of bifurcation of unstable regimes, leading, for example, to chaotic attractors. For this reason, the probabilistic description becomes a valuable complement to the deterministic approach, allowing, for example, determination of the frequency of visits to the different areas of the chaotic attractor and the time after which the memory of a particular initial state begins to fade (Nicolis and Prigogine, 1989; Prigogine and Kondepudi, 1998; Loskutov and Mikhailov, 2007).

The purpose of this study is to conduct a comprehensive description and analysis of the probabilistic and deterministic components of the seasonal and long-term dynamics of a population of the European bank vole *Clethrionomys glareolus* Shreber, 1780, living in the heart of its species range in the zone of contact of the southern taiga and broadleaf–coniferous forests based on the principles of the synergetic approach.

## MATERIALS AND METHODS

This research was based on the results of many years of studying the population dynamics of the European bank vole collected by the members of the Central State Sanitary Epidemiological Control of the Republic of Udmurtia and the Institute of Poliomyelitis and Viral Encephalitis and put at our disposal. The material was collected by standard trap-lines (Kucheruk, 1952). Trappings were performed four times a year (April, June, August, and October) on the three stationary parts of the green area of Izhevsk, located at a distance of 5–25 km from one another. The stations are situated in the contact zone of the southern taiga and broadleaf–coniferous forests. The materials used in the work are presented in Table 1.

Geobotanically, all the studied stations are located in an area where the southern taiga and broadleaf–coniferous forests have contact in the optimum area at the center of the bank vole habitat. The woody tier consists of both conifer and deciduous species: spruce,

fir, linden, Norway maple, European white and elms. Linden occurs together with spruce and fir in the first tier and is the main component of the second tier. The rest of the broadleaf species form the second tier and undergrowth, but as a rule, they are few. In the grassy tier, broadleaf and taiga forest species grow together (Priroda..., 1972; Zavyalovskii..., 2000). The moss cover is slight. The forest is highly cluttered with fallen trees, firewood, etc.

To estimate the abundance, we used the “number of animals per 100 trap-nights (tr./n.)” parameter. The animals were caught using break-back traps. Pieces of bread soaked in sunflower oil were used as bait. The small mammals were counted on fixed lines of 50 traps located at a distance of 5 m from one another. In parallel, in each habitat, from 2 to 5 lines were placed with a spacing of 50 m. The age of animals was determined by the method by Tupikova et al. (Tupikova et al., 1970), and the reproduction intensity of populations of small mammals was assessed according to the method of Tupikova (Tupikova, 1964).

To assess the significance of differences (similarity) of the long-term seasonal population dynamics, we used the Friedman ANOVA nonparametric analysis of variance, the Wilcoxon matched pairs test, and the method of fitting continuous distributions with reliability assessment of the description by the statistics  $\chi^2$  from the STATISTICA V. 5 package.

## RESULTS

The bank vole *C. glareolus* Shreber, 1780, dominates among the small mammals at all stations. In different months of the breeding season, the proportion of the species for the three stations ranges from 54 to 75.4%. Changes in the degree of dominance in the different years of observations are probably related to the weather and foraging characteristics of each of them.

It is not always appropriate to use the average and median values of abundance and their statistical characteristics given in Table 2 for testing the statistical hypotheses using standard methods of descriptive statistics, which is associated with the specific properties of probability distributions of the monthly appearance of a number of animals. But they can be useful for qualitative evaluation of the results. To test the statistical hypotheses, we used nonparametric methods of analysis.

**Table 2.** Descriptive statistics of the long-term population abundance of the European bank vole in the different months of the breeding season for each particular distribution (number of animals per 100 tr./n.)

Month	Distribution limits	Numbers of observations	Mean	Median	Standard deviation
April	0.3–43	85	9.2	6.6	8.1
June	1.5–77	85	17.6	13.2	15.8
August	<29.5	46	15.7	15.4	7.9
"	29.5–58	26	41.8	42.8	8.6
"	>58	13	71.8	74	9.2
October	<29.7	63	12.5	11.4	7.8
"	>30.5	22	39.6	36.8	8.4

For August and October, the descriptive statistics for each particular distribution are given according to Figs. 2c–2g.

*Start of the breeding season (April).* The long-term changes in the population numbers of the bank vole in April at the three stations have similar dynamics (Fig. 1a) and are not statistically different (Friedman ANOVA  $\chi^2$  ( $N = 28$ ,  $df = 2$ ) = 5.5,  $p = 0.07$ , where  $N$  is the number of observations,  $df$  is the number of degrees of freedom, and  $p$  is the significance level). In addition, the abundance oscillations of the bank vole at the three stations studied in April can be considered synchronous as the Spearman correlation coefficients were statistically significant between all pairs of stations and reached 0.71–0.91. The similar population dynamics and their synchronous oscillations made it possible to combine the data of observations at each of the three stations into one summary series, thereby increasing the number of observations and, hence, the quality of the statistical inference.

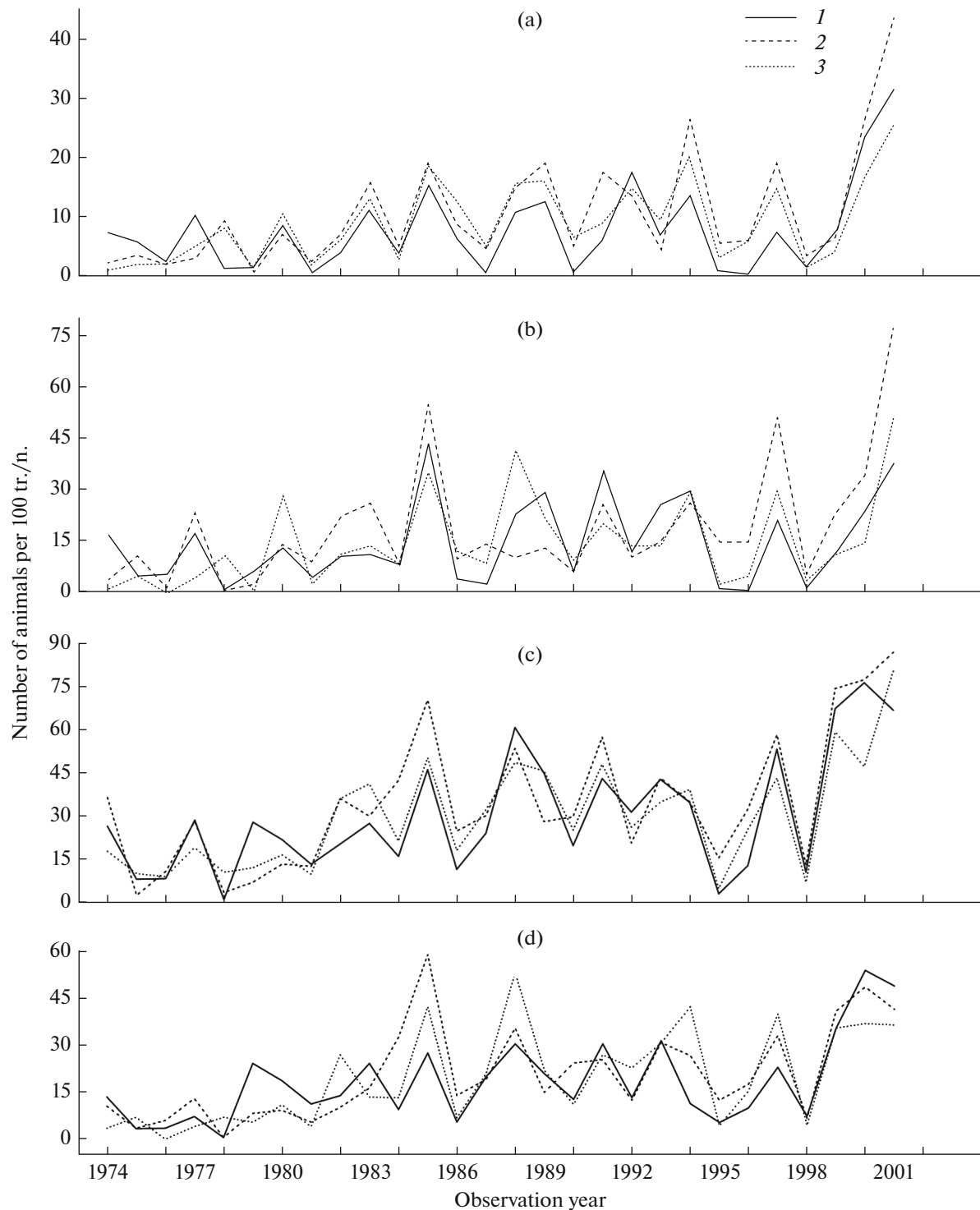
The bank vole that inhabits Udmurtia is characterized by a pronounced confinedness of the reproductive cycle to the spring–summer season, but in some years, winter (nival) reproduction is observed (Zhigal'skii, 2012). Therefore, the population numbers in April could be expected to vary within a wide range (Fig. 1a). The bank vole abundance at the three stations in April over 29 years of observations ranged from 0.3 to 43 animals per 100 tr./n. The majority (Fig. 2a) of values (at 76.8%) are in a fairly narrow range of low abundance (0.3–15 animals per 100 tr./n.). The long-term cumulative probability of realization of a certain spring population number for the total of three stations is statistically significant ( $\chi^2 = 5.8$ ,  $df = 4$ ,  $p = 0.21$ ) described by the asymmetric lognormal distribution shifted to the low abundance values (Fig. 2a). Such interval distributions are usually characterized by series with occasional random events (in our case, with high abundances of the spring numbers). Therefore, the dynamics of the studied population, which is a sequence of seasonal transitions of the population states, can be considered stochastic and the respective process, the continuous time Markov branching process, as the time spent by the animals in each state is a random continuous value (Gikhman and Skorokhod,

1973). In this case, the Markov process can be described using a system of ordinary differential equations, in which the probability functions of the population states are known, having been obtained experimentally (Vatutin and Zubkov, 1985).

*The seasonal population growth stage (June).* In June, the total number increased 1.91-fold and its variability increased 1.95-fold (Table 2). As in April, during the seasonal growth phase, the long-term changes in the population numbers have similar dynamics (Fig. 1b) and do not differ statistically (Friedman ANOVA  $\chi^2$  ( $N = 28$ ,  $df = 2$ ) = 5.42,  $p = 0.07$ ). In addition, a spatial and temporal coherence in the changes of the population numbers is observed at all stations. The nonparametric Spearman correlation coefficients in June are lower than in April, but the differences between all the stations were not statistically significant (0.6–0.72). As in April, the observation data at each of the three stations in June were combined into one summary series. The bank vole abundance at the three stations in June over 29 years of observations ranged from 1.5 to 77 animals per 100 tr./n. (Table 2), however up to 76.2% of the abundance values are in the range of 1.3–25 animals per 100 tr./n.) (Fig. 2b). The long-term cumulative probability of realization of a certain population number in June for the total of three stations is also statistically significant ( $\chi^2 = 5.2$ ,  $df = 3$ ,  $p = 0.16$ ) and is described by the asymmetric lognormal distribution shifted to the lower end of abundance values (Fig. 2b).

For this type of distribution, the state of the population is mainly determined by its spatial and demographic structure in April. This population process is also a continuous time Markov branching process with a countable set of states. The actual population abundance at the stage of the seasonal growth shapes the population dynamics in the following months.

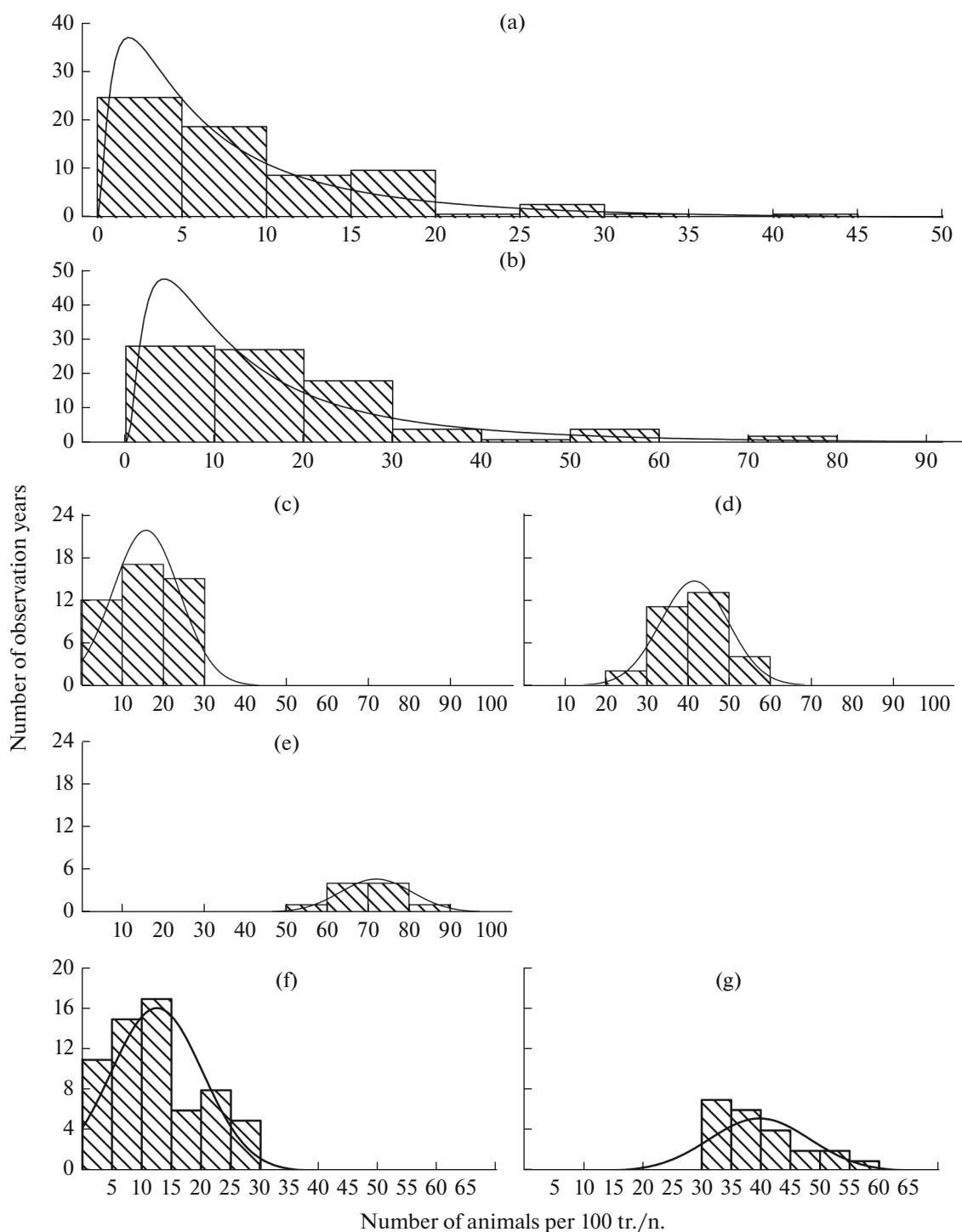
*The seasonal population peak stage (August).* In August, the total abundance of the bank vole significantly increased, reaching a seasonal peak in various years, while its variability remained the same as in April and June. The long-term population dynamics at



**Fig. 1.** Long-term population abundances of the bank vole at the stations (number of animals per 100 tr./n.). (1) Kenskii forest, (2) Varaksino, and (3) Yak-Bod'inskii. (a–d) April, June, August, and October, respectively.

the three stations (Fig. 1c) did not differ statistically (Friedman  $\chi^2$  ( $N=28$ ,  $df=2$ ) = 5.4,  $p=0.067$ ). At the same time, the changes in the abundance of voles occur synchronously as the nonparametric correlations are reliable and vary from 0.78 to 0.87. As in

June, the data of observations at each of the three stations are combined into one summary series. Each year in August, at all the stations, the bank vole numbers vary from 1 to 86.5 animals per 100 tr./n. (Fig. 1c). In contrast to the previous months, the probability distri-



**Fig. 2.** Distribution of the probabilities of abundances in total for the three stations in a long-term series of observations. (a) April, (b) June. Abundance ranges in August: (c–e) <29.5, 29.5–58, >58 animals per 100 tr./n., respectively. Abundance ranges in October: (f and g) <29.7, >30.5 animals per 100 tr./n., respectively.

butions of certain abundances in a long-term series are divided into three homogeneous groups (Figs. 2c–2e) separated by the minimum points, each of which is described by a normal distribution ( $\chi^2 = 5.2$ ,  $df = 4$ ,  $p = 0.27$ ). The average values of each particular distri-

bution statistically differ from others (Table 2). Therefore, in August, the population can choose one of three ways of development, which allows it to compensate for the external influences, while retaining a high viability of the population. For each asymptoti-

cally stable path of development of the population, the population values fluctuate around the mean value, which is significantly lower than the deterministic ones (Table 2). This phenomenon is nothing other than a stochastic analog of bifurcation. Even in a multimodal mode, when the spread around the mean value is considerable, the dispersion next to each of the peaks remains small (Table 2).

The values of probability that the number of voles in a particular year will be in the neighborhood of an unstable state are small and decrease exponentially with an increase in the population size. This means that, for a significant part of its development, the population is close to a stable state and the time of transition between the peaks is extremely large (Fig. 2c–e, Table 2). A typical chaotic attractor has none of these properties. In this case, population abundance takes on values differing from one another with a time interval comparable to the deterministic time scales and indicates that the amplitude of deviation from the mean is comparable to the mean itself (Table 2).

*Seasonal depression stage (October).* In October, the total abundance of the population naturally decreases (Table 2), which is due to the almost complete cessation of puberty of the young animals and significant loss of the voles that had already reproduced. If in June the proportion of the breeding females was 43.5% and in August 12.5%, in October, only a few pregnant females (their share does not exceed 3%) were found. The population numbers change synchronously at all the stations, and the Spearman rank correlation coefficients for various pairs of stations range from 0.69 to 0.82. The long-term changes in the numbers at the three stations were not statistically different (Friedman ANOVA  $\chi^2$  ( $N = 28$ ,  $df = 2$ ) = 0.71,  $p = 0.7$ ), so the probability distribution of abundance by years was also drawn for the total sampling, including all three stations. The population in different years varied from 2.5 to 86.1 per 100 tr./n. (Fig. 1d). The total abundance in October is statistically reliably described by two distributions ( $\chi^2 = 5.3$ ,  $df = 4$ ,  $p = 0.29$ ): the first one (2.5–29.7 animals per 100 tr./n.) (Fig. 2f) is described by a normal distribution, and the second one (>29.7 animals per 100 tr./n.) (Fig. 2g) is described by a lognormal distribution. Most of the periods are characterized by low numbers not exceeding 29.7 animals per 100 tr./n., and in only 2.2% of the years did they amount to more than 39.6 animals per 100 animals per 100 tr./n. (Table 2).

The bank vole belongs to cyclomorph species, so the seasonal dynamics of its population in the following year is largely determined by the state of the population in the preceding year (the demographic structure in the fall of the previous year, winter survival, abundance of winter forage, weather conditions in the winter, spring numbers, etc.). That could be the reason why, in October, two alternative groups of abundance distributions exist in the population, each of which

may be implemented depending on the winter conditions. In October, as in August, a bifurcation is observed, but in contrast to August, the population can evolve in only two trajectories.

## DISCUSSION

The seasonal and long-term dynamics of the bank vole population are a sequence of events from the state of the population in spring (the size, age, and sex structure) to the generation of seasonal reproductive cycles accompanied by the formation of a new spatial and demographic organization at every temporal stage of development. In addition, voles are found in an environment, the state of which under certain conditions can contribute to population growth, while under others, can inhibit it mainly due to changes in the reproductive potential of individuals and an increase in the mortality of young animals. In response to changes in the intrapopulation and external factors, the population creates a new spatial and demographic structure, allowing it to react flexibly to these changes. The mechanism of adjustment of the spatial and demographic structure of the population consists in the regulatory density-dependent relationships between the animals, which bring the size and structure of the population into compliance with the current conditions (Zhigal'skii and Bernshtein, 1986; Ivanter and Zhigal'skii, 2000; Zhigal'skii, 2002, 2014; Getz, 2005; Bobretsov, 2009; Lukyanova, 2013; Zhigal'skii and Mamina, 2015).

Earlier, using a model of the population size dynamics built on the basis of the characteristics of an existing population of the bank vole with a simple age structure, we revealed the multimodality of the population abundance, which consisted in the possibility of existence of several stable dynamic modes at the same parameters of the model, the transition to which is determined by the initial values of the abundance and the fluctuations of the external factors (Frisman et al., 2014, 2015). Importantly, this effect occurs in a model with several qualitatively different attractors: the equilibrium position, limit cycles, and chaotic attractor.

The presence of several asymptotically stable attractors in August and October identified by us in the dynamics of the bank vole population studied indicates that, as the model population, it possesses the property of multimodality because the modifying effect of the external factors can be considered, in particular, as a modification of the initial conditions.

In April and June, the population abundance gradually increases and is mainly determined by the reproductive activity of the animals. The probability of a certain population number in a given year in these months is described by a unimodal asymmetrical lognormal distribution shifted toward lower abundance values (Figs. 2a, 2b).

In August (during the seasonal peak in numbers), over the years of observing the development of the population, three directions were identified, each of which is implemented according to the specific conditions of the year (Figs. 2c–2e). The attractor with low numbers (15.7 animals per 100 tr./n.) was manifested the most frequently (in 54.8% of the years of observation). The average number values corresponded to 41.8% of the years of observations (31 animals per 100 tr./n.). And only in 14.3% of cases did the population reach 71.8 animals per 100 tr./n. The manifestation of a particular attractor is mainly associated with the different ratios of the action of the density-dependent population regulation mechanisms and the external factors (Zhigal'skii, 2002, 2014).

After each breeding season, a specific population of wintering animals is formed, the fate of which is determined by the processes that occurred during the spring–summer period. After the seasonal peak in number, in 70% of the years of observation, the population comes to the stage of seasonal depression (October) with low abundance and in 30% with rather high abundance for this time. The two modes of the dynamics available in October allow the population to implement the optimal strategy of behavior in the winter and provide a high viability of the next year's population. Depending on a number of wintering conditions, the spring abundance will be either low or high, which largely determines the dynamics of the population in the following year (Zhigal'skii, 2012).

The revealed patterns can be described by a simple equation, which admits an exact solution by standard methods (Nikolis and Prigogine, 1989):

$$dx/dt = f(x, \lambda) = -x^3 + \lambda x. \quad (1)$$

This system contains a single control parameter  $\lambda$ , and the rate of change of  $x$ , denoted as a function  $f$ , depends on this parameter strictly linearly. First of all, consider the fixed points (stationary states):

$$-x_s^3 + \lambda x_s = 0.$$

With a negative value of  $\lambda$ , this equation has an imaginary solution, which cannot reflect any real situation. However, with the positive values of  $\lambda$ , it allows for the following two solutions:

$$x_{\pm} = \pm\sqrt{\lambda}.$$

These solutions merge with  $x_0$  at  $\lambda = 0$  and branch off from it at  $\lambda > 0$  (Nikolis and Prigogine, 1989). This is the so-called bifurcation phenomenon that was observed during the seasonal peak and the stage of seasonal depression.

The proposed solution implies only two ways of development of the population dynamics, which is probably due to the absence in Eq. (1) of one more mandatory variable, including the structure of the population. It is equally important to include the non-linearity parameters associated with regulatory pro-

cesses in Eq. (1): the density-dependent changes in the reproductive capacity of the population and mortality of different demographic groups, adjusting the population number to the possibilities of the environment.

Under the influence of permanent or temporary impacts of different external disturbances, no detailed balance exists in the nonequilibrium state. As a result, small (not going beyond the limits of stability) deviations from the equilibrium state are not necessarily destroyed by the constantly arising actions against the population: they can be absorbed by it, becoming a source of improvement of regulatory mechanisms. This property is the basis of the ability of nonequilibrium population systems to carry out bifurcation transitions to new states, ensuring the viability of the population, and makes the nonequilibrium state unlike any equilibrium. The fundamental property of such systems is manifested in the ability to move to an ordered state through fluctuations. However, the period and amplitude of the oscillations in the number of the population are its own properties and depend only on the parameters of the demographic structure, so we can assume that such Hopf bifurcation is a structural and sustainable process. This phenomenon is common in populations subjected to the impact of external factors, which creates certain difficulties in predicting the behavior of the system. Moreover, it follows that the number and demographic structure of the population is unpredictable as they possess the basics property of chaotic dynamics: a significant dependence on the initial conditions.

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