SHORT COMMUNICATIONS

Ecological Mechanisms Maintaining the Demographic and Spatial Structure of Small Mammal Populations

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The dynamics of abundance is an integrated indicator of its state and reflects the outcome of its interaction with the environment. The breeding cycles of animals are timed to the spring–summer season, which may be regarded as a major factor responsible for the delayed response of a population to changes in environmental conditions. This delay, the high reproductive potential of small mammals, density dependent regulation of animal breeding and mortality, the amount and quality of food resources, and many other factors may cause changes in the demographic and spatial structure of the population (Shilov, 1967; Shvarts, 1980; Bol'shakov and Kubantsev, 1984; Bol'shakov et al., 1986; Krebs, 1996; Zhigalski, 2002, 2012; Lukyanova, 2013).

The question concerning the causes underlying the variability of population phenomena is far from being resolved. The growing amount of data based on long-term observations on mammals living in different geographic zones makes it increasingly clear that the level of variation in population processes is determined not only by the geographic component: it also depends on the quality and holding capacity of the environment, its heterogeneity, productivity of plant communities, the state of the population in the current and previous moments of time, the hierarchical status of species in the community, and other factors (Shilov, 1967; Shvarts, 1980; Zhigalski, 1992; Krebs, 1996; Ivanter and Zhigalski, 2000; Zhigalski, 2002, 2012).

The significance and relevance of the materials presented here consist in evaluation of the roles of intrapopulation and external factors in the formation of mechanisms for maintaining the demographic and spatial structure of small mammal populations in the center and at the periphery of the range.

Studies were performed in two permanent test plots established in locations selected in accordance with the purposes of studies on the geographic aspects of population dynamics in the bank vole (*Clethrionomys glareolus* Schreber, 1780). Both plots were in the boreal zone. The Udmurt plot was in the subzone of linden–fir–spruce subtaiga forests in the center of the bank vole range, where conditions were optimal for the species. The Karelian plot was in the middle taiga forest subzone at the periphery of the bank vole range. The bank vole was dominant in both plots and accounted for 70.4% of the total number of trapped animals.

The material was collected by the standard trap line method (Karaseva et al., 2008) four times a year (in April, June, August, and October). This work over the study period amounted to more than 103000 trap–days, and 26 893 small mammals were trapped. The data were processed statistically by univariate and multivariate spectral analysis and ANOVA. Differences were considered significant at $p < 0.05$.

As yet, there is no accepted opinion concerning the relative roles of random and regular components in the long-term population dynamics of voles. To obtain quantitative estimates providing a basis for coming to an adequate conclusion as to whether fluctuations of animal abundance are random or follow a certain pattern, a spectral analysis was performed of long-term data series on the abundance of bank voles in the two geographically distant test areas.

The spectrograms of data series on both populations were found to have a distinct density peak corresponding to a period of 2–5 years and another strong peak with a period of 1 year (a seasonal peak). This may be regarded as evidence that the observed changes in the abundance of bank vole populations reflect a complex, regular process accounted for by the sum of two oscillations (i.e., of the seasonal and long-term components). Four phases of the population cycle and, in addition, repeated transitions from one phase to another were revealed in both populations, with the
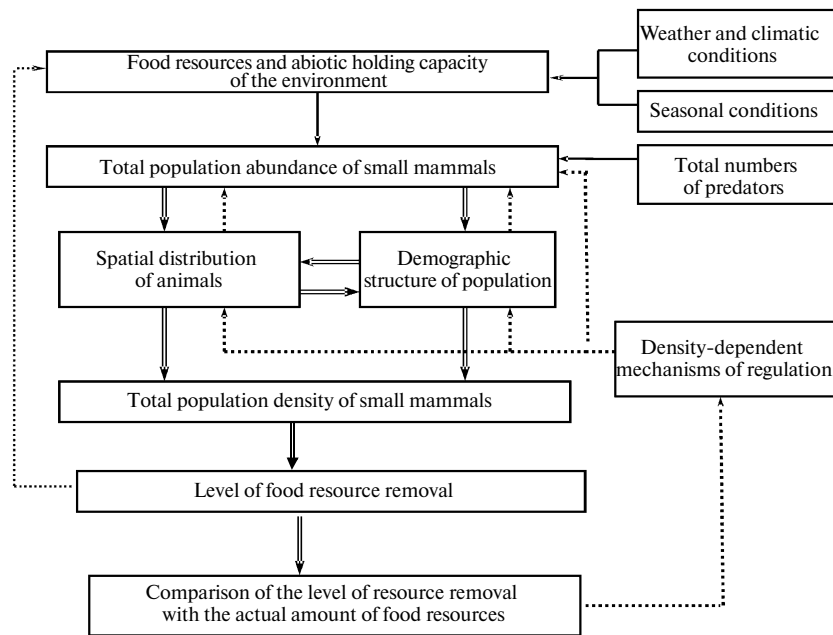
Scheme of the functioning of mechanisms maintaining demographic and spatial structure of small mammal populations. *Solid lines* indicate direct action of external factors; *broken lines*, feedback loops; *double lines*, transitions from one structural—functional group to another.

structure of these transitions was unique for each population. The population cycle was 2—4 years long in the Udmurt plot (in the center of the range) and 2—5 years long in the Karelian plot (at the range periphery).

In both Udmurt and Karelian populations, the transition from the peak phase to the depression phase occurs regularly, regardless of continuously changing conditions in each particular year. The dynamics of the abundance and structure of the two populations appear to follow a typical scenario of transition from chaotic to steady state motion via certain intermediate states. In such a case, random fluctuations alternate with intervals characterized by regular, almost periodic oscillations.

Two qualitatively different parts of the population cycle were distinguished. The predetermined (regular) part—transition from the peak phase to the depression phase—takes place in both populations in different years and is independent of conditions in a given year and location of the population. This is possible only if demographic processes during the transition are governed mainly by intrapopulation density-dependent mechanisms, being practically independent of external factors. In both populations, this transition is accomplished within one autumn—winter—spring period and has no effect on the total duration of the population cycle.

The duration of its stochastic part varies depending on the relationship between external and intrapopulation factors and has an effect on the possibility for the

population to increase its abundance. The rate of this process depends on the weather, food supply, numbers of predators, position of the population in the species range, etc. A similar picture has also been observed in other parts of the rage of forest voles (Bernshtein et al., 1989; Krebs, 1996; Stenseth et al., 1996; Bobretsov, 2009). In general, the stochastic part of the cycle is 1—3 years long in the center and 2—4 years long at the periphery of the range.

The original scheme shown in the figure illustrates the process of regulation of small mammal abundance with account for environmental conditions, food resources, predation, and intrapopulation factors. Environmental conditions include the whole set of seasonal, weather, and climatic factors (temperature, precipitation, humidity, anthropogenic factors, etc.). The category of intrapopulation factors refers to homeostatic density-dependent mechanisms regulating the demographic and spatial structure of the population (Shilov, 1967; Shvarts, 1980; Ivanter and Zhigalski, 2000, Zhigalski, 2002, 2012).

Seasonal, weather, and climatic factors govern the formation of food reserves and abiotic holding capacity of the environment, which, in turn, determine the abundance of the population (figure). The abundance of the population is a determinant of its density and spatial demographic structure, and these parameters, depending on the amount and quality of food resources and predation pressure, can switch on or off the density-dependent mechanisms controlling animal mortality and breeding rate. An increase in animal

density within a certain area leads to thinning of vegetation and reduction in the amount of above- ad belowground phytomass. If this impact on plant communities exceeds a certain allowable threshold, their productivity deteriorates, which subsequently may cause a decline in animal abundance. Biomass transfer between the levels of primary producers and primary consumers is associated with matter and energy loss. It is considered that, on average, only about 10% of biomass and associated are transferred to the next trophic level, with the rest being expended for the maintenance of life activities, growth, and development. Food resources in forest biocenoses in summer are so great that the removal of 10% of the total phytomass cannot cause reduction in the abundance of voles, whereas a high yield of linden and spruce seeds (winter forage) in the previous autumn can stimulate winter breeding, thereby providing for high animal abundance in the next spring (Zhigalski, 2012).

It is also questionable that predation has a determining influence on the population dynamics of forest voles. Predators cannot reduce the abundance of prey animals below a certain limit; otherwise, the amount of energy received with food would not cover the energy cost of prey capture. Numerous publications provide evidence that predators have an effect on prey abundance, but this effect is insignificant. In particular, predators remove no more than 5−7% of the total biomass of vole population at the phase of its growth, and proportion is even smaller at the phase of depression (Zhigalski, 2002). Therefore, predators in forest biocenoses cannot be the factor determining population decline in small mammals (Durward, 1980; Chernyavskii and Dorogoi, 1981; Norrdahl and Korpimaki, 2002; Zhigalski, 2002; etc.).

Density-dependent mechanisms of regulation play a considerable role in the surveyed populations of forest voles: they explain up to 70% of the total variance in population processes (Zhigalski, 2002), except for the winter period and the onset of breeding season, when the contributions of endo- and exogenous factors to the maintenance of abundance are approximately equal.

Population growth is accompanied by increasing food consumption, which leads to imbalance between the actual amount of food resources and the level of their removal by animals. This imbalance is corrected mainly via selective elimination of animals and reduction of their breeding activity (figure). Thereafter, intrapopulation mechanisms provide for rearrangements in the spatial and demographic structure that adjust population processes to a new level of functioning. This may result in transition from strictly territorial to group mode of life with the establishment of a new hierarchy allowing the population to maintain its abundance at a higher level at the same resource supply (Shilov, 1967; Shvarts, 1980; Zhigalski, 1992;

Krebs, 1996; Ivanter and Zhigalski, 2000; Zhigalski, 2002, 2012).

Thus, the maximum effects of relevant exo- and endogenous factors on forest voles are separated in time: the former play a greater role in the autumn—winter period and at the onset of breeding season, whereas the latter are more important during the reproduction cycle. External factors (weather conditions, food resources, predation, etc.) determine the upper limit of the holding capacity of the environment that is optimal at a given level of animal density. The function of intrapopulation mechanisms is to bring the population size (abundance) to the level adequate to these conditions. The results presented above allow the conclusion that the population is a follow-up system that continuously modifies its spatial and demographic structure, adjusting it to changing environmental conditions.

REFERENCES

Bernshtein, A.D., Zhigalski, O.A., and Panina, T.V., Multiannual fluctuations in the size of population of bank vole in European part of the Soviet Union, *Acta Theriol.*, 1989, vol. 34, no. 30, pp. 409−438.

Bobretsov, A.V., Population dynamics of the northern red-backed vole (*Clethrionomys rutilus*, Rodentia) in the northern Cisural Region over a 50-year period, *Zool. Zh.*, 2009, vol. 88, no. 9, pp. 1115−1126.

Bol'shakov, V.N. and Kubantsev, B.S., *Polovaya struktura populyatsii mlekopitayushchikh i ee dinamika* (The Sex Structure of Mammal Populations and Its Dynamics), Moscow: Nauka, 1984.

Bol'shakov, V.N., Balakhonov, V.S., Benenson, I.E., et al., *Melkie mlekopitayushchie Ural'skikh gor (ekologiya mlekopitayushchikh Urala)* (Small Mammals of the Ural Mountains: Ecology of Ural Mammals), Sverdlovsk: Ural Nauch. Tsentr Akad. Nauk SSSR, 1986.

Chernyavskii, F.B. and Dorogoi, I.V., On the role of predators in the population dynamics of lemmings: The example of Wrangel Island, in *Ekologiya mlekopitayushchikh Severo-Vostochnoi Sibiri* (The Ecology of Mammals in Northeastern Siberia), Moscow: Nauka, 1981, pp. 32−50.

Durward, A.L., The essential roles of predation, *Nature Conserv. News*, 1980, vol. 30, no. 2, pp. 2−7.

Ivanter, E.V. and Zhigalski, O.A., Analysis of mechanisms controlling the population dynamics in the bank vole (*Clethrionomys glareolus*) at the northern part of its range, *Entomol. Rev.*, 2000, vol. 80, Suppl. 1, pp. 191−205.

Karaseva, E.V., Telitsyna, A.Yu., and Zhigalski, O.A., *Metody izucheniya gryzunov v polevykh usloviyakh* (Methods of Field Studies on Rodents), Moscow: LKI, 2008.

Krebs, C.J., Population cycles revisited, *J. Mammal.*, 1996, vol. 77, pp. 8–24.

Lukyanova, L.E., Association of Sympatric Small Mammal Species under Contrasting Environmental Conditions, *Russ. J. Ecol.*, 2013, no. 1, pp. 60–67. doi 10.7868/S0367059713010095

Norrdahl, K. and Korpimaki, E., Seasonal changes in the numerical responses of predators to cyclic vole populations, *Ecography*, 2002, vol. 25, pp. 428–438.

Shilov, I.A., On mechanisms of population homeostasis in animals, *Usp. Sovrem. Biol.*, 1967, vol. 64, no. 2 (5), pp. 333–351.

Shvarts, S.S., *Ekologicheskie zakonomernosti evolyutsii* (Ecological Patterns of Evolution), Moscow: Nauka, 1980.

Stenseth, N.C., Bjornstad, O.N., and Saitoh, T., A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan, *Proc. Roy. Soc. Lond. B: Biol. Sci.*, 1996, vol. 263, pp. 1117–1126.

Zhigalski, O.A., Factorial analysis of population dynamics in rodents, *Pol. Ecol. Stud.*, 1992, vol. 18, no. 1–2, pp. 3–158.

Zhigalski, O.A., Analysis of population dynamics of small mammals, *Entomol. Rev.*, 2002, vol. 82, Suppl. 2, pp. 320–351.

Zhigalski, O.A., Seasonal dynamics of bank vole population in Udmurtia, *Vestn. Udmurt. Gos. Univ.*, 2012, no. 4, pp. 64–70.

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