The Elementary Chorological Structure of a Species Population as Exemplified by Voles

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Abstract—The results of 25-year monitoring have been used to develop a local approach to analysis of the spatiotemporal population dynamics of rodents. The main processes of the formation of the rodent population structure in a heterogeneous environment have been considered on the basis of experimental quantitative estimates obtained under natural conditions. The possibility of real-time identification of elementary chorological units of a species population has been substantiated. It has been found that complete cycles of vital activity of a model rodent species are usually no longer than 18 months. The strategy of the regional population functioning in species with short individual life cycles is considered at a new angle.

Key words: population, species population, rodents, population dynamic cycles, elementary units of the species population.

An animal species population is traditionally considered in terms of local populations and population structure of the species, with a local population regarded as an elementary unit of evolution in the framework of the neo-Darwinian evolutionary paradigm (Mayr, 1968; Timofeeff-Ressovsky et al., 1973; Timofeeff-Ressovsky and Yablokov, 1974; Shvarts, 1980; Vasil'ev and Bol'shakov, 1994; etc.). The scientific basis and original principles of another line of research in species populations, an equally important one dealing with the real-time scale (in contrast to the evolutionary dimension), have not been sufficiently developed thus far. The characteristic times of the existence of a population as an elementary evolutionary unit, on the one hand, and a system of actual spatial groups or elementary territorial settlements, on the other hand, are fundamentally different. I believe that the elementary principle of classification of biochorological units (Timofeeff-Ressovskii and Tyuryukanov, 1966) should be used in real-time studies on the spatial structure of a species population. An actual population of any species always and everywhere exists in the real-time dimension (it is no longer in the past and is not yet in the future); therefore, it seems reasonable to continue the search for the original basic forms of the organization and functioning of a species population based on the principle of elementariness (in Timofeeff-Ressovsky's terms) as "further indivisibility without loosing the current properties."

Below, the results of long-term experimental studies on a rodent population dynamics under the conditions of the Middle Ural southern taiga zone are summarized on the assumption that there is an elementary chorological structure of a local species population.

MATERIALS AND METHODS

The study was based on the results of 25-year monitoring of the rodent population dynamics in the Middle Urals. The original field material consisted of the results of irreversible removal of animals on standard transects and the results of tagging and recapture of rodents in 0.5- to 1.5-ha stationary unfenced plots. We used Naumov's (1951) method of tagging, which ensures the most accurate and detailed results in intensive studies on rodent populations of relatively small areas. For repeated animal capture, we used wooden box traps with a swing ladder, set at the corners of a square grid with 8-m sides throughout the period of the study. Animals were trapped in 4-day or 5-day series, with the traps checked twice a day (in the morning and in the evening). Two to five series of trapping were performed every year in the period from April to December. Between the series, all traps were left unbaited, with their back doors open, and were protected from atmospheric precipitations with special covers.

Settlements of bank, northern redbacked, large-toothed redbacked, common, and tundra voles, as well as two species of mice, were found in the areas surveyed. All these species exhibited similar patterns of population formation and functioning. Therefore, the

bank vole (the most abundant species) was used as a model object. More than 3200 bank voles were trapped, and 12000 cases of them entering the traps were recorded in the stationary plots between the years 1983 and 2008.

The Jolly–Seber stochastic method (Jolly, 1965; Seber, 1965) based on a probabilistic approach was used for statistical analysis of the census data. In addition, we used the most complete results of total trapping corresponding to the absolute numbers of voles in the study area within specified time intervals. We considered this approach to be justified because practically all resident rodents and those regularly visiting the plots are trapped within four to five days if the trapping is performed strictly according to the protocol. Therefore, analysis of the results encompasses all the animals inhabiting the census area in the given period.

Year-round field experiments using supplementary food supply were performed in Shalinskii raion of Sverdlovsk oblast (the Middle Urals) from the autumn of 1983 to the summer of 1985. One of two plots of equal sizes (1 ha) served as a control area. In the other plot, which was located 0.7 km away in a similar biotope, 100 special feeders with oats were set. They were designed so that the food was reliably protected from atmospheric precipitation and was accessible only to small rodents. A total of 300 kg of oats was used during the experiments.

Since the animals were trapped in all seasons of the year, traps set on the ground at each trapping site were covered in winter with waterproof cardboard cylinders with sheet metal lids, 80 cm in diameter and 120 cm in height, to protect them from snow.

RESULTS AND DISCUSSION

Voles are the most typical ephemeral species and r-strategists among mammals (MacArthur and Wilson, 1967; Stearns, 1992). Therefore, the main functional characteristic of their population is that the constituent individuals tend to completely fulfill their reproductive potential (utilizing available environmental resources) during the short breeding season to compensate for the high mortality rate and survive through winters in the state of the reproductive pause. During these relatively longer periods, mass mortality takes place without any population recruitment. As a result, a species population concentrated in relatively small, discrete "surviving stations" by the beginning of the next breeding season (Naumov, 1948). Thus, elementary aggregations of the adult population are formed (Naumov, 1965, 1971; Shvarts, 1960), which are likely to play the key role in maintaining the vital activity of the rodent population.

We put forward the following hypothesis: an elementary aggregation of rodents that have survived through winter may occupy an area no larger than 1 ha, the trophic factor playing the main role in the formation of such aggregations. This hypothesis was repeatedly confirmed by field experiments involving supplementary food supply (Dobrinskii et al., 1988; Dobrinskii, 1990). An isolated "island" of the vole population with a relatively large local population density normally functioned in the experimental plot (1 ha) for two consecutive years, against a background of considerable population depression in the surrounding area (Fig. 1). This "island" remained isolated even in summer, because there were no other neighboring aggregations of mature voles in spring. If there are enough such aggregations, young of the year from different "surviving stations" usually mix with each other, forming a more or less heterogeneous population continuum. However, by the start of each breeding season, the rodent population is concentrated again in discrete territorial units where the food resources are rich enough to last them during winter. Under heterogeneous environmental conditions, these units always form a complex mosaic pattern, the inevitable annual changes in the "biogeocenotic matrix" of the environment leading to substantial changes in the sizes, shapes, and arrangement of individual units and their combinations. What remains invariable is that the regional population is concentrated again in discrete foci (which formed in the places where food is sufficient) every year at the beginning of the breeding season. In all other parts of the region, a considerable proportion of the animals (usually, all of them) die during the long autumn–winter periods. Therefore, these are the animals from the elementary territorial units completely formed by spring that "relay the baton of life" to subsequent generations. The patterns of the formation and functioning of the population units are considered elsewhere (Dobrinskii, 2007).

Because of their small body size, rodents have a limited capacity for traveling over long distances. Therefore, elementary units of their populations occupy small areas (from one to several hectares). This is a necessary condition for each unit to function as a single whole on the basis of close interaction between individual animals.

Further studies (after supplementary feeding was terminated in the year 1985) showed that one more substantial increase in the food supply to voles, compared to the maximum level that would have been possible under usual conditions, took place after the disastrous windfall in the Middle Urals (including the study region) in 1995, which could be regarded as a spontaneous large-scale "experiment" in nature. In addition to food supply, the windfall areas offered considerably better protection to rodents, because the number of available shelters became many times greater. The interaction between these two leading environmental factors had a combined effect that was essentially similar to, but considerably stronger than, that considered above. Probably, this is why the phenomenon of synergism was detected (Dobrinskii, 2005).
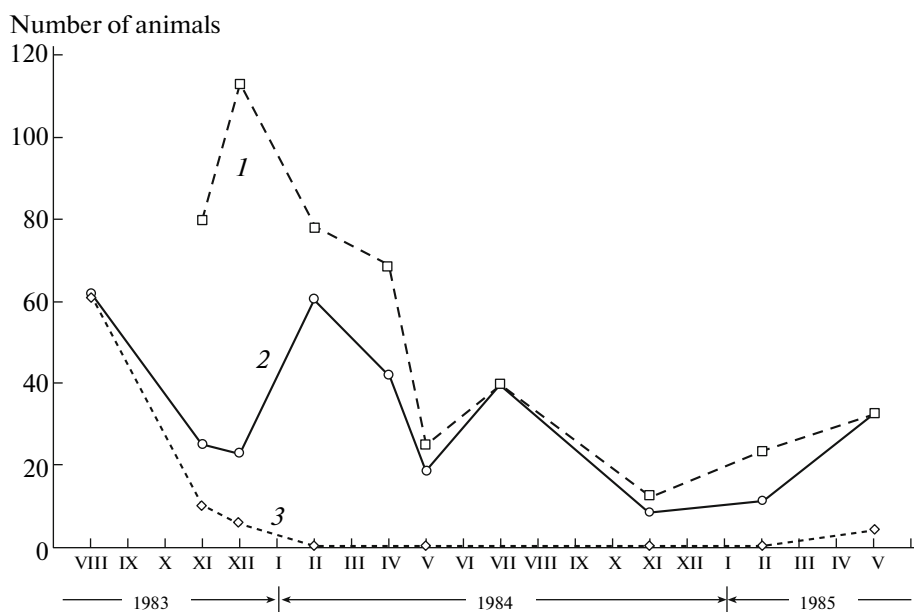
Number of animals

Fig. 1. Bank vole population dynamics in the experimental (0.5 ha) and control (0.5 ha) tagging plots in Shalinskii raion of Sverdlovsk oblast (the Middle Urals): (*1*) population size estimated by the Jolly–Seber method, (*2*) absolute population size in the experiment, and (*3*) absolute population size in the control are shown. Here and in Figs. 2 and 3, Roman numerals refer to months of the year.

It is especially important that, owing to the combined effect of the two leading ecological factors, the rodent population switched to a special functional mode without long-term oscillations of the resultant population size in summer. This effect is clearly illustrated by the data obtained in the period from 1998 to 2004. The absolute numbers of voles when the reproduction had been completed were unusually uniform, falling within the range of 63–69 animals per 0.5-ha tagging plot (Fig. 2). Only in 2002 was the postbreeding population size relatively small (25 animals). This corresponded to the mean rodent population density under normal conditions (50 ind./ha). This was because trapping in 2002 was carried out later than usual. When this outlier was excluded from analysis, the absolute numbers of bank voles averaged over six years proved to be 66.7 ± 0.8 ind.; i.e., there was no substantial long-term variation in the postbreeding population size of bank voles.

After the disastrous windfall, surviving climax taiga biogeocenoses with a stable carrying capacity of the environment and tagging plots located in them became surrounded with dramatically transformed "donor" habitats that were very favorable for rodents (Hansson, 1977; Sadykov and Benenson, 1992). Irrespective of the specific conditions of each year, these animals always utilized the carrying capacity of the plots as completely as possible by the end of summer. In terms of our approach, this means that rodents in these plots formed viable, saturated, functionally complete open superorganismal biological systems

(primary population units) capable of long-term self-sustainable existence.

As noted above, the leading principle of the functioning of a rodent species population is to fulfill as much of the reproductive potential as possible, at the given duration of the breeding season (which is relatively short) and the available amount environmental resources, to compensate for the population depression during the considerably longer winter periods. As a result, the integrated population dynamics of (in the given case) bank voles fits a characteristic undulating curve shown in Fig. 2. Note that the inflexion points of the curve strictly correspond to the quantitative data on the tagging plot. Not only does the shape of the integrated curve reflect the natural, so-called seasonal variation of the population size, but its trajectory always shows regular ascents and descents. Every spring, the curve more or less steeply ascended, peaked within about four months, and more gradually descended to a relatively low level within the next eight months. In other words, the so-called annual cycles, or regular seasonal variations, of the vole numbers (Zhigal'skii and Kshnyasev, 2003) always occurred within approximately 12-month intervals. The second half of the descending segments of the population dynamic curve in Fig. 2 reflects the mortality of wintering animals and the subsequent ascending segments show the appearance of young of the year. Technically, therefore, the animals that have survived through winter are included into the group of young of the year. In other words, the biological sense of the traditional
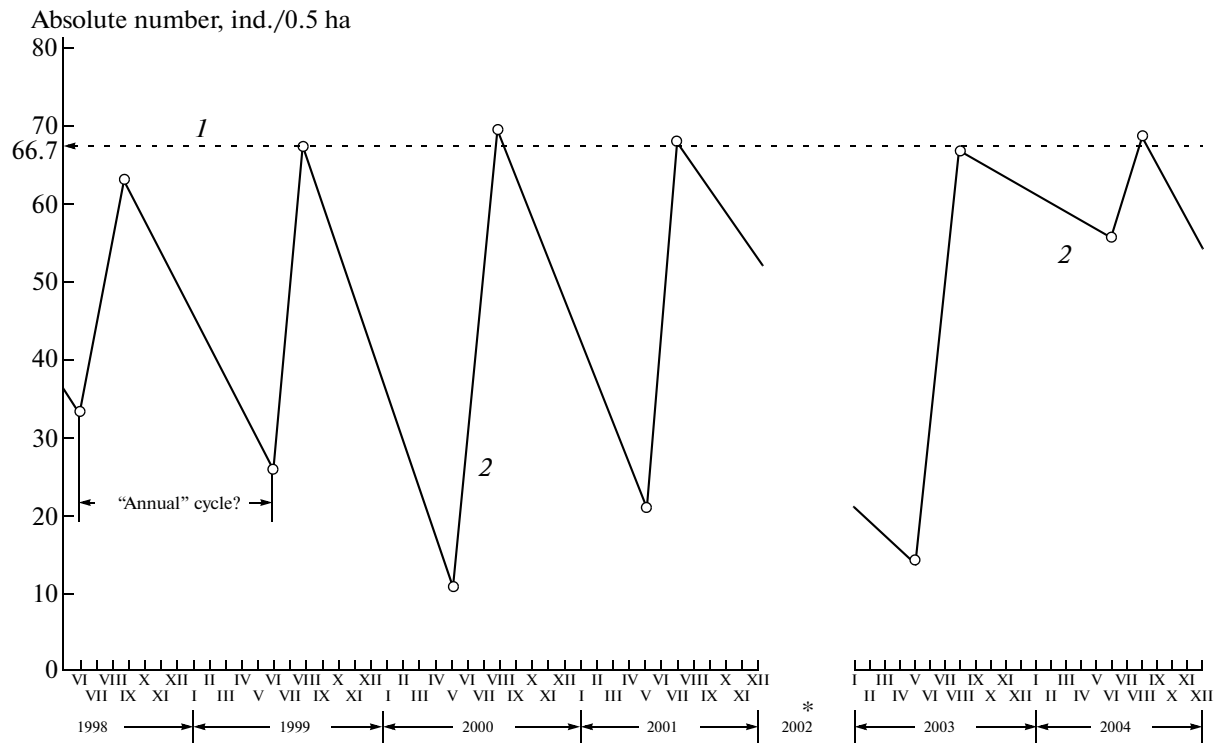
Absolute number, ind./0.5 ha

Fig. 2. The traditional graphic presentation of data on the rodent population dynamics as exemplified by a series of captures of bank voles in the tagging plot (0.5 ha) in the Middle Urals: (*1*), the numbers of bank voles (including the animals that had survived through winter and young of the year) averaged over six years of censuses (66.7 ind./0.5 ha); (*2*), the bank vole population dynamic curve. *The data on the year 2002 have been excluded (see the text for explanations).

graphic presentation of the population dynamics is essentially self-contradictory.

A different periodization may be introduced on the basis of the exact definition of the cycle, the principle of population size cycles, and the contributions of different structural and functional groups of voles (animals that have survived through winter and young of the year that have or have not reproduced) to reproduction. In my opinion, this would be reasonable because, according to the data reported by Olenev (1991, 2002) and our long-term observations, a considerable part of any vole species population lives longer than one year (by 1.5−4.5 months). Obviously, the life cycles of individual animals cannot be longer than the cycles of superorganismal systems, namely the population groups to which they belong. This problem can be solved as follows.

It is reasonable to shift the descending segments of the undulating population dynamic curve of voles to the zero mark, because the loss of the animals that have survived through winter continues after the beginning of the breeding season and is rather rapid throughout summer. At the same time, the ascending segments of the curve should also begin from zero values, because there are no young of the year in populations until the breeding season. This is graphically shown in Fig. 3, which is based on the exact quantitative data for the tagging plot.

These transformations reveal new conceptual aspects of the pattern of dynamic processes of rodent population renewal. First of all, it becomes possible to distinguish specific transitional periods when a regional population contains both wintering voles and their offspring (young of the year). This is a period of intense transmission of the hereditary material to the next generation. In addition, this is when the new generation can receive, via direct contacts and behavioral stereotypes, important additional (nonhereditary) information. Every year, the completion of these transitional periods is followed by the formation of new local groups (superorganismal systems) that continue the previous succession of such system but are not identical to them. They no longer contain voles born in the previous year; i.e., they are 100% new and, hence, possess new properties. Because of local heterogeneity (patchiness) of natural landscapes (within areas from 0.5 ha to several hectares), each of these new, small settlements acquire numerous unique characteristics in which it differs from the surrounding elementary settlements. Moreover, since the ecological conditions of each year are unique, the local rodent population formed in each particular year has specific local characteristics in which it differs from all previous and all subsequent elementary groups. This may be also favored by the fact that all ontogenetic develop-
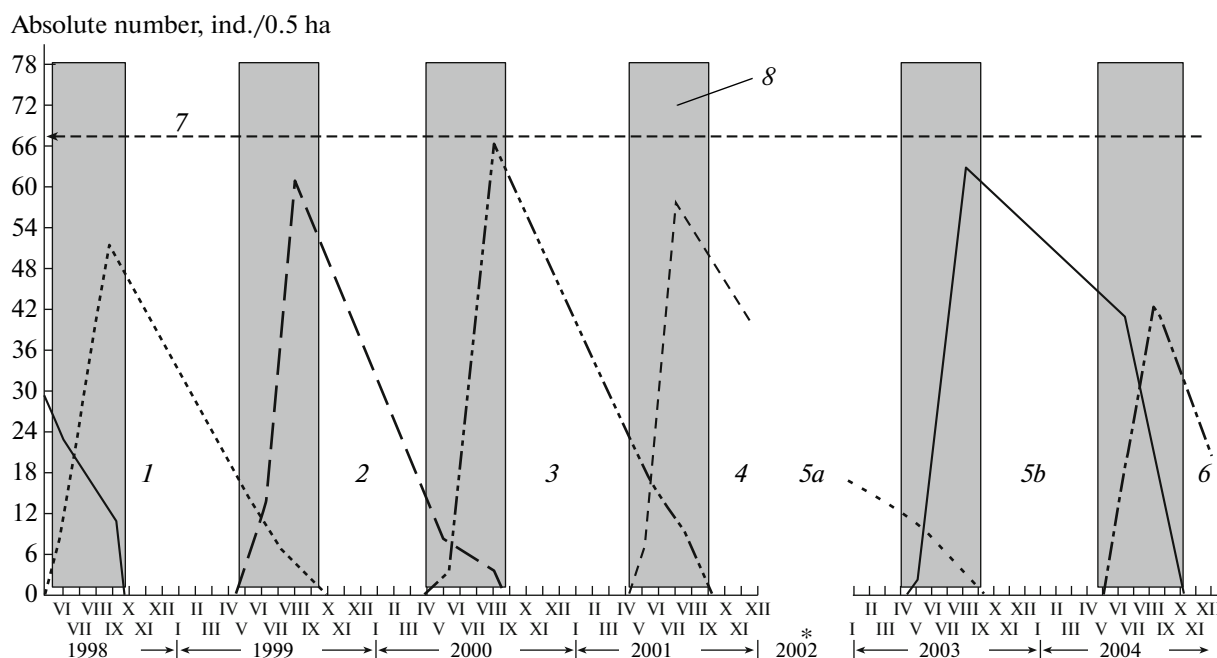
Absolute number, ind./0.5 ha

Fig. 3. The proposed graphic interpretation of rodent population cycles as exemplified by long-term results of bank vole capture in the tagging plot (0.5 ha) in the Middle Urals: (*1*) the population dynamics of the TES formed in the year 1998; (*2*) the same for the TES of the year 1999; (*3*) the same for the TES of the year 2000; (*4*) the same for the TES of the year 2001; (*5a*), a part of the descending arm of the population dynamics of the TES formed in 2002; (*5b*) the population dynamics of the TES formed in 2003; (*6*) the same for the TES of the year 2004; (*7*) the numbers of bank voles (including the animals that had survived through winter and young of the year) averaged over six years of censuses (66.7 animals per 0.5 ha), excluding the data on the year 2002 (see the text for explanations); (*8*) transitional periods.

mental processes in animals from every new elementary unit of a given year occur under unique environmental conditions.

Finally, in terms of the approach presented here, the complete life cycle of elementary chorological structures of rodents falls within an interval of 16–18 months, rather than one year or several years. In other words, the complete cycle is always substantially longer than a year but almost never exceeds 1.5 years, which agrees with the data obtained by Olenev (2004). Therefore, in rodents, the apparently continuous "waves of life" (Chetverikov, 1905) actually prove to consist of partly overlapping discrete "surges"; each of them, however, contains a continuous wave component.

Thus, an adequate time interval of vital activity corresponds to the local spatial scale of elementary units of a rodent species population. Therefore, fundamental differences between species with the *r*- and *K*-strategies of life cycles at the individual level may be preserved at the population level.

In my opinion, the aforementioned fundamental properties of primary structural units of a species population suggest that they serve as the basis for the integrated ecological process of maintaining the necessary species population size at the local level in the real-time mode. Therefore, a special term should be intro-

duced to denote the elementary aggregations that are real-time structural units of a regional species population. I believe that this is necessary because none of the widely known terms, concepts, and definitions for population-level biosystems encompasses the entire diversity of primary chorological elements of a species population or sufficiently corresponds to their essence and/or status. In addition, not all classical concepts applied to the population level offer clear criteria for them to be reliably and objectively distinguished in actual biogeocenoses. In this connection, it should be emphasized that invention of one more term to supplement the list that is already long is by no means my purpose. The novelty of the approach proposed here is entirely opposite. It is rather an attempt at correctly unifying all more or less widely known definitions of biological systems applied to the elementary level of organization of a species population. This unification has led me to the conclusion (which available data seem to substantiate) that one general definition would be possible and sufficient as applied to the elementary level of organization of a species population. The proposed general term is intended for noncontradictory unification of all terms corresponding to the given organizational level. The strictest and most concise definition of this unifying term may be formulated as follows:

An elementary chorological structural unit, or horus, is an integral, indivisible (or not divisible without the loss of its essential properties) territorial spatial cell of a species population characterized by functional integrity, genetic uniqueness, and capacity for autonomous existence for at least several successive generations.

The terms deme, merus, micropopulation, parcelle, and local population (Hanski, 1996; Hanski and Gaggiotti, 2004) apply to other aspects of the superorganismal level of life. The term *demion* and the expressions *territorial (spatial) elementary structure* (TES) and *territorial (spatial) elementary unit* (TEU) may be recommended as synonyms substitutable for *horus* (elementary chorological structural unit of a species population).

CONCLUSIONS

Different points of view on the term "population" can be integrated in the framework of a unifying concept. An elementary chorological structural and functional unit, which I propose to term a horus or a *territorial elementary unit* (TEU), is of basic importance in a species population on the real-time scale. It is presumable that the fundamental differences at the individual level between species with the *r*- and *K*-strategies of life cycles are still observed at a higher (population) level. Therefore, the original forms of self-organization of mammalian species populations with short life cycles of individual animals also have short, strictly determined cycles of functioning, i.e., they comply with the *r*-strategy.

Another important consequence follows from the existence of territorial elementary units of a species population. Under natural conditions, natural selection may occur not only at the level of individuals and their groups, but also at the level of elementary chorological units of species population, or horuses. Since the formation of these elementary units under natural conditions is based on self-organization, it is conceivable that the animals themselves perform the necessary selection activity by intensively interacting with one another within integral and relatively autonomous population units. In other words, this situation may be called self-selection (autoselection), with individual animals themselves as parts of close functional integral units at the elementary level serving as the "acting force" of natural selection.

In the case of artificial selection, humans provide the objects of selection (concentrated to artificially form elementary population units) with food and the necessary shelter. The concentration of suitable selection material at the local level is a necessary condition for efficient artificial selection. In the case of natural selection, animals themselves form elementary units only where the necessary trophic resources and protective environmental conditions are available. Less "fit" (less viable) individuals that have been left outside the elementary chorological structures are under worse conditions and are the first to die when exposed to adverse environmental factors. The effect of adverse environmental conditions on animals in the units is weaker, and their mortality rate is considerably lower. Since the most part of the "fittest" (viable) species population is concentrated in the elementary chorological structural units (horuses), the genetic material of these animals forms the basis of the gene pool and is mostly transmitted through successive generations. Apparently, the differential contribution of genetic material to the future generations postulated by Fisher (1930) takes place in this case. Thus, the concept of the elementary chorological structural and functional unit of a regional species population can be used for further development of the views on the modes of natural selection at the population level.

REFERENCES

Chetverikov, S.S., The Waves of Life: From Lepidopterological Observations in the Summer of 1903, *Dnevn. Zool. Otd. Imp. O−va Lyubitelei Estestvozn. Etnogr. Mosk. Univ.*, 1905, vol. 3, no. 6, pp. 106−110.

Dobrinskii, N.L., An Experimental Study on the Role of Trophic Factor in the Formation of Population Structure and Dynamics in Voles of the Genus *Clethrionomys, Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Sverdlovsk: Inst. Plant Anim. Ecol., Ural Div., USSR Acad. Sci., 1990.

Dobrinskii, N.L., Specific Features of Vole Population Dynamics after Disastrous Windfall in Forests of the Middle Urals, *Mlekopitayush*chie *gornykh territorii: Mat-ly Mezhd. soveshch.* (Proc. Int. Conf. on Mammals in Mountain Areas), Moscow: KMK, 2005, pp. 57−61.

Dobrinskii, N.L., Trophic Factor and Population Dynamics of Voles of the Genus *Clethrionomys* in Low-Mountain Landscapes of the Middle Urals, *Mlekopitayushchie gornykh territorii: Mat-ly Mezhd. soveshch.* (Proc. Int. Conf. on Mammals in Mountain Areas), Moscow: KMK, 2007, pp. 101−107.

Dobrinskii, N.L., Kryazhimskii, F.V., and Malafeev, Yu.M., Dependence of Population Dynamics on Food Supply in Voles of the Genus *Clethrionomys*: Results of Field Experiments, in *Gryzuny* (Rodents), Nalchik, 1988, vol. 2, pp. 80−81.

Fisher, R.A., *The Genetical Theory of Natural Selection*, Oxford: Clarendon, 1930.

Hanski, I., Metapopulation Ecology, in *Population Dynamics in Ecological Space and Time*, Chicago: Univ. of Chicago Press, 1996, pp. 13−43.

Hanski. I. and Gaggiotti, O., *Ecology, Genetics and Evolution of Metapopulations*, San Diego: Elsevier, 2004.

Hansson, L., Spatial Dynamics of Field Voles *Microtus agrestis* in Heterogeneous Landscapes, *Oikos*, 1977, vol. 29, pp. 539−544.

Jolly, G.M., Explicit Estimates from Capture−Recapture Data with both Death and Immigration: Stochastic Model, *Biometrika*, 1965, vol. 52, pp. 225−247.

MacArthur, R.H. and Wilson, E.O., *The Theory of Island Biogeography*, Princeton: Princeton Univ. Press, 1967.

Mayr, E., *Animal Species and Evolution*, Cambridge: Harvard Univ. Press, 1963. Translated under the title *Zoologicheskii vid i evolyutsiya*, Moscow: Mir, 1968.

Naumov, N.P., *Ocherki sravnitel'noi ekologii myshevidnykh gryzunov* (Essays on Comparative Ecology of Murine Rodents), Moscow: Akad. Nauk SSSR, 1948.

Naumov, N.P., A New Method for Studying the Ecology of Small Forest Rodents, in *Fauna i ekologiya gryzunov* (Fauna and Ecology of Rodents), Moscow, 1951, vol. 4, pp. 3–21.

Naumov, N.P., Specific Spatial Features and Mechanisms of Population Dynamics in Terrestrial Vertebrates, *Zh. Obshch. Biol.*, 1965, vol. 26, no. 6, pp. 625–633.

Naumov, N.P., Spatial Structure of the Species in Mammals, *Zool. Zh.*, 1971, vol. 50, no. 7, pp. 965–980.

Olenev, G.V., The Role of Structural–Functional Groups in the Dynamics of Basic Population Parameters in Rodents, in *Razvitie idei akademika S.S.Shvartsa v sovremennoi ekologii* (The Development of Academician S.S. Shvarts' Ideas in Modern Ecology), Moscow: Nauka, 1991, pp. 92–108.

Olenev, G.V., Alternative Types of Ontogeny in Cyclomorphic Rodents and Their Role in Population Dynamics: An Ecological Analysis, *Ekologiya,* 2002, vol. 33, no. 5, pp. 341–350.

Olenev, G.V., Functional–Ontogenetic Approach to Studies on Populations of Cyclomorphic Mammals, *Extended Abstract of Doctoral (Biol.) Dissertation,* Yekaterinburg: Inst. Anim. Ecol. Evol., Ural Div., Russ. Acad. Sci., 2004.

Sadykov, O.F. and Benenson, I.E., *Dinamika chislennosti melkikh mlekopitayushchikh: Kontseptsii, gipotezy, modeli* (Population Dynamics of Small Mammals: Concepts, Hypotheses, and Models), Moscow: Nauka, 1992.

Seber, G.A., A Note on the Multiple-Recapture Census, *Biometrika*, 1965, vol. 52, pp. 249–259.

Shvarts, S.S., Principles and Methods of Modern Animal Ecology, *Tr. Inst. Biol. Ural. Fil. Akad. Nauk SSSR*, 1960, no. 21.

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

Stearns, S.C., *The Evolution of Life Histories,* New York: Oxford Univ. Press, 1992.

Timofeeff-Ressovskii, N.V. and Tyuryukanov, A.N., On Elementary Biochorological Divisions of the Biosphere, *Byull. Mosk. O–va Ispyt. Prir., Otd. Biol.*, 1966, no. 1, pp. 123–132.

Timofeeff-Ressovskii, N.V. and Yablokov, A.V., *Mikroevolyutsiya* (Microevolution), Moscow: Znanie, 1974.

Timofeeff-Ressovskii, N.V., Yablokov, A.V., and Glotov, N.V., *Ocherk ucheniya o populyatsii* (An Essay on Population Theory), Moscow: Nauka, 1973.

Vasil'ev, A.G. and Bol'shakov, V.N., A View on Population Ecology: Yesterday and Today, *Ekologiya*, 1994, no. 3, pp. 4–15.

Zhigalskii, O.A. and Kshnyasev, I.A., Population Cycles of the Bank Vole in the Range Optimum, *Ekologiya*, 2000, no. 5, pp. 383–390.