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UDC 591.25-932.3+574.34

TERRITORIAL ACTIVITY AND LOCAL CHOROLOGICAL STRUCTURE OF THE FOREST RODENT POPULATION

SUMMARY. In the context of modernizing population ecology of animals, the concept of elementary chorological structure of the rodent population is developed. The central object of the research includes the integral territorial cells of the species population having the functional unity and the ability to an independent existence, at least, during several consecutive generations. As a result, we offer the local approach to the detailed analysis of the rodent population on plots from one to several hectares. The regularities of forming spatial structure of local vole settlements are established on the basis of the profound study of territorial animal activity in the conditions of long field experiments with the use of strictly dosed supplementary feeding in various climatic zones. It is stated that the trophic factor is statistically significant and influences the territorial activity and structure of the forest rodent population. The results of field experiments allow concluding that the stable spatial structure of animal population which functions on the basis of direct territorial contacts of individuals from different age and sexual groups is formed under the influence of the trophic factor. The discovered regularities see the role of winter «survival reservations» in a new light: when a great part of viable rodent population concentrates around accessible and discretely disposed nutritive resources. Basing on the analysis of the direct factual data, the special discrete phase of forming the chorological structure of the species rodent population is determined in the annual cycle of the vole population functioning. The results obtained have an important practical value for managing the population of rodents — forest and agricultural pests — and for extermination of dangerous zoonotic pesthole infections.

KEY WORDS. Spatial structure, rodents, territorial activity.

The spatial organization of the rodent population is largely determined by the ways the individuals use a territory and interact in the conditions of seasonal dynamics of environmental factors. At present, the problems of structuring and spatiotemporal arrangement of the species population remain controversial. Earlier we offered [1] the concept of elementary chorologic structure of the species population by the example of voles which differs from the ideas of metapopulation ecology [2-3]. Choruses are territorial cells of the species population having the functional unity and ability to an independent existence, at least, during several consecutive generations. As the central object of the concept, they are considered on relatively small areas. Such elementary (only in the sense of further indivisibility without losing fundamental properties) chorological structural units of population, correspond to the local unit of the metapopulation model. However, unlike local populations, choruses are characterized by a certain set of well-defined properties. In this context, it should be noted that such widely known concepts as biotype, ecoelement, temporal

population, Mendelian population, dem, parcel, merus, micropopulation, and elementary population characterize other aspects of the species super-body systems. Within the offered concept, local approach to the analysis of the rodent population in the areas from one to several hectares is developed. The results of the long continuous monitoring of the local rodent settlements from 1983 to 2011 were used to test this local approach in natural biogeocenoses. Monitoring provided re-analyzing the data of the production experiments with feeding animals from new positions. These experiments were organized in natural conditions at the initial stage of our long-term research. The choice of year-round field experiments with supplementary feeding is caused by the fact that the trophic factor is one of principal environmental parameters. Within studying the elementary chorologic organization of the rodent population, the purpose of this paper was to consider the regularities of forming the territorial structure of local vole settlements, basing on the analysis of territorial activity of animals in the conditions of experimental feeding, taking into account seasonal dynamics in various climatic zones. This paper continues our earlier research [1].

The data for study and methods of the research. Field experiments with the use of strictly dosed supplementary feeding were conducted in the south of Yamal Peninsula, in the area of the middle current of the Hadyta River, and in the Middle Urals in the Shalinsky District of the Sverdlovsk Region. For precise control of the oats consumed by rodents, we used special feeders, which in different variants of experiments were placed either on unfenced experimental plots (0.5ha) of the stationary discount areas or on the separate open areas of 1 ha. In the latter variant separate unfenced reference areas of the same size were the control ones. Total amount of grain oats used in each region was 300 kg. Wooden box traps with a swinging floor were always set in the open territories, in the corners of a square grid with a side of 8 m. Trapping was arranged in a series of 4-5 days, with an interval of 1-3 months, in the snowless period in the Southern Yamal, and all the year round in the Middle Urals. In the intervals between the series, baits and supplementary feeding were not used, the back covers of all traps were left open, and all the traps were covered with special lids protecting against precipitation.

As model objects, we used the local settlements of dominant species, such as the red-backed vole in the Southern Yamal, and the red vole in the Middle Urals. To obtain the most complete and accurate results during the intensive work with the rodent population, we used the technique of life branding [4]. For all trapped animals, we determined weight, sex, reproductive status, and age according to the branding data. If a rodent died during the trapping, it was dissected in the laboratory. From 1983 to 1987 in the sub-Arctic intrazonal forest biotopes, 694 red-backed voles were caught and branded; and in the conditions of the southern taiga, 525 red voles were trapped. 2,247 and 1,539 calls in traps were registered for the animals of the two model species, respectively.

For the statistical data analysis we applied Leslie regression method [5] modified by Heine [6] and conventional statistical criteria. For the comparative analysis of the territorial activity of the voles in the experiment and control conditions and for the detailed analysis of the dynamics of spatial rodent distribution, we used the statistical method based on the calculation of radii of individual territorial animal activity ("home range sigma") [7]. The accuracy of the size difference in the average radius of the territorial activity between the gender and age groups of voles was

determined by Fisher F-criterion. The number of degrees of freedom was calculated with the formula df = 2 (N - n), where N is the total number of the animals caught; n is the number of individuals.

Since the animals in the Middle Urals were caught in all seasons, at the stationary branding sites in the trapping points, we installed vertical waterproof cardboard cylinders 80 cm in diameter, 120 cm high. From above they were closed by metal lids. During the winter period, the traps were installed inside the cylinders on the soil to be protected from snow.

Results and discussion. In 1983, in the Southern Yamal, in the period of low baseline abundance of forest voles (20 individuals/ha), at the end of the reproduction season, mature males and females concentrated mainly in areas with supplementary feeding. Adult males in these areas had a truly smaller average radius of territorial activity, compared with the directly bordering control ($F = 1.9$; $p = 0.05$).

The changes in the territorial activity of mature individuals are caused by both reproductive processes and domination-subordination relationships [8]. Therefore, the dependence of the radius size of the vole territorial activity on feed supply is the most evident for underyearlings, not involved in reproduction. In 1984, the re-introduction of supplementary feeding (already in the conditions of baseline abundance of voles) resulted in a significant reduction of the average radii of territorial activity (Table 1) for immature males and females, compared to the control ($F = 1.3$; $p < 0.05$ and $F = 1.5$; $p < 0.05$, respectively). Moreover, this decrease was registered with a lower density of red voles, on a separate site with feeding (64 individuals/ha compared to 83 individuals/ha in the control). Consequently, the significant reduction in rodent relocation values in the experiment is connected with a decrease in feed-obtaining activity on the site with an increased amount of preferred feed available to animals.

Table 1

Average radii of territorial activity (R, m) of red voles of different sex and age groups on experimental plot No. 1 (with supplementary feeding) and on separate control plot No. 3 (without feeding). Southern Yamal, autumn of 1984

Age groups	Males			Females		
	n	K	R, m	n	K	R, m
Over-wintered	5	29	24.0	7	40	17.6
	—	—	—	—	—	—
	0	–	–	3	25	16
Underyearlings of the first cohorts involved in reproduction				2	16	7.5
				—	—	—
				3	18	18.9
Underyearlings not involved in reproduction	16	87	13.1	26	109	13.5
	—	—	—	—	—	—
	33	131	16.8	11	60	20.6
Underyearlings of the last cohorts weighing up to 10 g	0	–	–	1	3	— *
	—	—	—	—	—	—
	1	4	— *	3	7	26.1

The end of Table 1

Age groups	Males			Females		
	n	K	R, m	n	K	R, m
Over-wintered	5	29	24.0	7	40	17.6
	—	—	—	—	—	—
	0	–	–	3	25	16
Underyearlings of the first cohorts involved in reproduction				2	16	7.5
				—	—	—
				3	18	18.9
Underyearlings not involved in reproduction	16	87	13.1	26	109	13.5
	—	—	—	—	—	—
	33	131	16.8	11	60	20.6
Underyearlings of the last cohorts weighing up to 10 g	0	–	–	1	3	— *
	—	—	—	—	—	—
	1	4	— *	3	7	26.1

Note. The numerator shows the data from experimental plot No. 1; the denominator shows the data from separate control plot No. 3; n is the number of voles; K is the number of repeated vole catches, * means that the animals were caught only in one and the same trap.

In the summer of 1985, the next year after the supplementary feeding cessation, the after-effect was found in the territorial activity of voles. It was expressed in the reduction of territorial activity of mature males on former experimental plot No. 1, in comparison with control plot No. 3. The phenomenon outwardly similar to it was registered in 1983, in the conditions of direct feeding influence. However, various behavioural reactions are the reasons of the homotypic reductions of territorial activity of adult voles in each of the above-mentioned cases. In the initial period of the research (1983), in the conditions of low abundance of rodents, there was a disturbance of uniform spatial distribution of sex-and-age groups of voles, after the supplementary feeding application on the experimental territory. Later, the manifestation of the supplementary feeding after-effect was caused, most probably, by the long maintenance of the territorial structure of the vole population developed earlier (in the conditions of artificially excessive feed provision). The latter circumstance, most probably, helped to regulate the communicative relationships of animals and the maintenance of the developed spatial structure of the over-wintered voles. This is confirmed by the fact that the mature males living for a long time (since the autumn of the previous year) in the conditions of artificially high feed provision on plot No. 1, in the spring of the next year, at the baseline level of feed supply in the same habitats, had a significantly lower rate of territorial activity, in comparison with the animals settled in later (14.7 vs. 19.7; $F = 1.3$; $p = 0.05$).

In the conditions of the Middle Urals, at the initial stage, 60 kg of supplementary feeding was placed evenly on the territory of the branding site (1 ha), in the period from August, 18 to September, 20, 1983. During trapping No. 3 (29.10 — 1.11.1983), the average radius of the territorial activity (R) of males and females of the red bank vole had no significant differences, with an average abundance of rodents

(27.1 ± 0.2 individuals in the experiment and 33.4 ± 2.2 individuals in the control on both halves of the branding site. Later (after trapping No. 3) the supplementary feeding was always placed only on the experimental half of the site. During trapping No. 4 (6-10.12.1983), in the conditions of the typical seasonal decrease in the abundance of rodents, the average radius of the territorial activity (due to small number of repeated trappings) was calculated only for immature red vole females on the control site. According to this index (R = 9.8 m), they did not differ significantly from the immature males and females registered in the previous autumn catching. Trapping No. 5 (21-26.02.1984) was carried out in the conditions of the sharp increase in the abundance of red voles, on the branding plot half with the supplementary feeding up to 92.2±20.7 individuals, as a result of migration. Besides, in the population composition, we registered 6 voles weighing from 10 to 13 g, which is the evidence of the winter sub-snow breeding of rodents in the conditions of sufficient supplementary feeding available to the animals. Despite the increased population density, during trapping No. 5 we did not register a significant reduction of the territorial activity radius of adult males (R = 7 m) and females (R = 8.9 m) from the experimental site, in comparison with the voles caught in the autumn of 1983 (R = 9.8 m). Probably, it is connected with the atypically early beginning of sub-snow reproduction of rodents consuming supplementary feeding.

During trapping No. 6 (20-24.04.1984), the beginning of the reproductive period of the over-wintered voles was registered on the branding plot. For this reason, the males from the experimental site demonstrated significantly higher average radius of territorial activity (Table 2), in comparison with females ($F = 1.83$; $p < 0.05$), which corresponds to our earlier results [9]. According to summer trapping No. 8 (27-31.07.1984), among the adult mature animals in the experiment, there was a significant difference in the average radii of territorial activity between males and females ($F = 1.83$; $p = 0.05$). At the same time, the females involved in breeding had a significantly lower activity rate on the half with supplementary feeding ($F = 1.86$; $p < 0.05$), in the conditions of equal population density on both sides of the plot. It is also specific for immature females from the group of underyearlings (Table 2), which confirms the previously discovered in Southern Yamal phenomenon of the decrease in territorial activity of voles, in the conditions of habitats with high feed supply. Last trapping No. 11 was carried out on 20-27.05.1985, without supplementary feeding, during the period of active reproduction of rodents, when the appearance of the first underyearlings, weighing up to 10 g, was registered. In spite of the fact that the total number of voles, inhabited the former experimental half of the site, was truly large ($\chi 2 = 8.8$; $p < 0.005$), the average radius of territorial activity was not significantly different between males and females from the former experimental and control sites (Table 2). This fact, most probably, is caused by the above-mentioned feeding after-effect, which was also registered in the Southern Yamal during the summer of 1985, after the cessation of supplementary feeding in the previous year.

Table 2

Average radii of territorial activity (R, m) of red voles on the experimental (with supplementary feeding) and the control (without feeding) halves of the branding plot (1ha). The Middle Urals, the Shalinsky District of the Sverdlovsk Region

Age groups	Trapping No. 5 21-26.02.1984			Trapping No. 6 20-24.04.1984			Trapping No. 8 27-31.07.1984			Trapping No. 11 20-27.05.1985		
	n	K	R, м	n	K	R, м	n	K	R, м	n	K	R, м
Males over-wintered	11	30	7.0	10	30	12.8	4	11	16.1	5	14	9.8
	—	—	—	—	—	—	—	—	—	—	—	—
	1	2	– *	1	4	– *	3	15	15	2	5	10.2
Females over-wintered	10	23	8.9	16	53	6.8	6	33	8.8	6	19	10.2
	—	—	—	—	—	—	—	—	—	—	—	—
	0	0	–	1	6	– *	3	18	16.4	2	7	15.6
Males underyearlings	1	3	– *				1	3	– *			
	—	—	—				—	—	—			
	0	0	–				1	3	– *			
Females underyearlings							2	7	6.1			
							—	—	—			
							3	7	14.9			
Males and females weighing up to 10 g							1	2	– *			
							—	—	—			
							1	4	– *			

Note. The numerator gives the data from the experimental half of the branding plot; the denominator gives the data from the neighbouring control (without feeding) half of the branding plot; n is the number of voles, K is the number of repeated trappings of voles, * means that the animals were caught only in one and the same trap.

Thus, the trophic factor is significant; it influences the spatial population structure and the territorial activity of forest rodents during all seasons. Even during the summer vegetation period, against the background of the maximum seasonal increase in the food object biomass, the supplementary feeding causes the statistically true reduction of the radii of territorial activity of both the adult over-wintered animals, and the young underyearlings. The results of field experiments allow concluding that stable spatial structure of rodent population, which functions on the basis of direct territorial contacts of individuals from different age-and-sex groups is formed under the influence of the trophic factor. The leading role of the trophic factor in the formation of the local chorological structure of the forest rodent population is confirmed by the fact that the after-effect of feeding, registered both in the Southern Yamal and in the Middle Urals, remains the next year after the feeding cessation.

The results obtained demonstrate that the role of the tiling food resources increases during the winter period, when the natural food stocks and their availability sharply decrease in the conditions of constant snow cover. As a result of active searching "survival reservations" in unfavourable conditions [10], the considerable

part of viable forest rodent populations concentrates around accessible and discretely located nutritive resources. Moreover, the mass vole mortality in the snow period inevitably causes the sharp reduction of their population size in the conditions of the reproduction termination. Due to this, the main part of the population is concentrated in relatively small (from one to several hectares), separately located in suitable habitats, elementary territorial cells of species population or choruses [1]. Therefore, basing on the analysis of the results obtained, in the annual cycle of the vole population functioning, the specific discrete phase of forming local chorological structure of the forest rodent population is determined.

The author is grateful to L.N. Dobrinskiy, F.V. Kryazhimskiy, and Yu.M. Malafeev for their assistance in carrying out research works, and also for the active discussion of the results and useful recommendations on the choice of methods of statistical analysis.

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