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ZOOLOGY

The Variability of Allozyme and Microsatellite Loci of the Narrow-Headed Vole *Lasiopodomys gregalis* from the Southern Urals and Trans-Urals

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Abstract—The variability of 12 allozyme and 5 microsatellite loci in narrow-headed voles captured in Chelyabinsk and Kurgan oblasts was analyzed. The low genetic differentiation of the samplings was shown. The results of comparison of the genotypes of the narrow-headed vole mothers and embryos revealed multiple paternity and polygyny. It was shown that in some cases, an analysis of microsatellite loci allows researchers to differentiate the animals that belong to different colonies.

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INTRODUCTION

Interest in the biology and ecology of narrow-headed voles *Lasiopodomys gregalis* Pallas, 1779, is associated with the fact that these animals are convenient models for studying the systems of family relationships in rodents (Zadubrovskaya, 2011; Potapov et al., 2014), microevolution (Shvarts, 1963), and paleoreconstructions (Petrova et al., 2015), as well as the fact that they carry zoonotic diseases (Mal'kova et al., 2004). In our opinion, the narrow-headed vole is a promising model object for solving certain issues in both general ecology and the ecology of polluted territories, which is due to the colonial structure of habitation of this species (Mal'kova et al., 2004; Zadubrovskaya, 2011; Potapov et al., 2014). On one hand, the animals that inhabit one colony are exposed to identical impact of environmental factors (microclimate, level of pollution of the area, influence of ectoparasites, etc.) and are closely related, i.e., genetically identical. Owing to this, individuals from one colony represent a sufficiently homogeneous sampling, for which the variability of the parameters that interest the researcher, which is determined by the sex and age of the animal and its reproductive and hierarchical status, can be evaluated. On the other hand, comparing the characteristics of a migrant from a family and those of a resident, we can estimate the influence of environmental factors on genetically similar individuals, whereas, when comparing the samplings from closely located colonies (families), we can analyze the effect of the genetic component of variability.

At present, there is no consensus on the composition of colonies of narrow-headed voles. A number of authors assume that the colonies are represented by family groups (Mal'kova et al., 2004; Potapov et al., 2014). According to Zadubrovskaya (2011), the narrow-headed vole colonies can be represented by three types: true colonies, which comprise several reproducing individuals and their offspring; simple families, which comprise an adult female (in some cases, a male, as well) and the offspring of the latest generation; and colonies of adult males.

In natural conditions, use of the advantages of the narrow-headed vole as a model species is possible if a method is available that would allow us to identify a specific family or colony, to which the animal belongs. In our opinion, a suitable tool for this is analyzing the variability of genetic markers. The aim of this work is to assess the prospects of this method by solving the following tasks: obtaining data on the variability of genetic markers that can be used for differentiation of families or colonies of narrow-headed voles; comparing the genotypes of the mother and the embryos, which is necessary for estimating the number of animals breeding in one colony; and testing the selected genetic marker in order to differentiate various families (colonies) of narrow-headed voles.

As the obtained materials will later serve as a basis for estimating the state of the rodent populations in areas with radioactive contamination, part of the animals were captured in the East Ural Radioactive Trace (EURT) area situated in the north of Chelyabinsk oblast (*Ekologicheskie...*, 1993; *UNSCEAR...*, 1996). In addition, samples collected in the areas of Kurgan oblast with a background level of radioactive contamination were used. These areas are located at a distance of 250–400 km from the EURT.

MATERIALS AND METHODS

The animals were captured during the snowless periods of 2009–2014, using mainly the method of line traps (10–50 traps were placed at a distance of 5 m from each other). The animals were not returned to nature. In Chelyabinsk oblast, samplings were carried out on eight plots located on the southwestern bank of Lake Uruskul' in the EURT area (55°49′ N, 60°54′–56′ E). The modern level of contamination with ^{90}Sr in this area constitutes 3.3–22 MBq/m^2, which exceeds the background level 1000—70000 times (*Atlas...*, 2013; Molchanova et al., 2014). In recent years, the radiation doses that the mouselike rodents inhabiting this territory have been exposed to do not exceed 0.1 mGy/day (Malinovsky et al., 2014). This value is lower than the reference range of the dose intensity accepted by the International Commission on Radiological Protection (ICRP) for rats; i.e., from the viewpoint of ICRP, the probability of injurious effects of ionizing radiation on rats at this dose intensity is absent (*ICRP...*, 2008).

In September 2014, more detailed studies of the mobility of voles were carried out on one of the EURT plots. The animals were captured over an area 80 × 100 m^2 in size. Seventy-nine traps were installed at a distance of 10 m from each other over the course of 4 days. The captured animals were marked by severing their toes and released. The toes were fixed in ethanol for subsequent genotyping.

In Kurgan oblast, capturing was performed in the environs of the villages of Zverinogolovskoe (54°26′ N, 64°45′ E), Proryvnoe (54°22′ N, 64°29′ E), Sovetskoe (54°36′ N, 64°27′ E), and Golovnoe (55°20′ N, 66°50′ E) and the town of Makushino (55°17′ N, 67°17′ E). Owing to the inconsiderable number of animals captured and the proximity of some plots, the individuals from the first three sites were united into the Kurgan-1 sampling, and those from the last two sites, into Kurgan-2.

The variability of 11 enzyme systems in 80 adult individuals was analyzed: 6PGDH (EC 1.1.1.44), GPDH (EC 1.1.1.8), GOT (EC 2.6.1.1), G6PDH (EC 1.1.1.49), LDH (EC 1.1.1.27)–2 loci, SOD (EC 1.15.1.1), PGM (EC 2.5.7.1), PGI (EC 5.3.1.9), XDH (EC 1.1.1.204), MDH (EC 1.1.1.37), ME (EC 1.1.1.40). The procedure for obtaining the samples and performing electrophoresis was described earlier by us (Modorov and Pozolotina, 2011).

DNA was isolated by using a DNA-extran-2 kit (Sintol, Russia) according to the protocol of the manufacturer. Muscles fixed in 96° ethanol were used, or muscles were frozen in liquid nitrogen and stored at –80°C. Apart from this, DNA was isolated from the toes of animals captured in the EURT zone in September 2014. In embryos, DNA was isolated from the rear paw. The allele composition of five microsatellite loci described earlier (Ruda et al., 2009) was determined. The primers were synthesized (Sintol), and the 5'-end of the F-primer was marked with a fluorescent label: *Mar12* (FAM label), *MSMoe02* (TAMRA), *Mar49* (R6G), *Mar80* (TAMRA), and *MSMM2* (FAM).

The polymerase chain reaction (PCR) was performed using Mas^{CFE}TaqMIX-2025 (Dialat Ltd., Russia) in 10 μL of the mixture, and the concentration of $MgCl_2$ was increased to 3 mM. The PCR conditions were as follows: denaturation at 95°C for 15 min; 35 cycles of amplification: 94°C for 30 s, 57°C for 90 s, 72°C for 60 s; a final elongation at 72°C for 10 min. A MyCycler Thermal Cycler (BioRad, United States) was used. The lengths of the amplified fragments were determined using the Genetic Analyzer 3130 (Applied Biosystems, United States) in the presence of an S-450 marker of molecular mass (Sintol). The chromatograms were deciphered in the GeneMapper v. 4.0 program.

A comparison of the alleles of microsatellite loci in mother–embryo groups was performed using the loci *MSMoe02*, *Mar49*, *Mar80* and *MSMM2*. Eight females were analyzed. Females nos. 1–6 were captured in the environs of the village of Sovetskoe. The pairs of females nos. 1 and 2 and nos. 5 and 6 were captured in the same colony (i.e., by traps set near one group of burrows). Females nos. 7 and 8 were obtained in July 2011 in the EURT area in various colonies.

The following indicators of genetic variability were calculated: the allele occurrence frequency, the effective (N_e) and average (N_a) number of alleles per locus. When assessing the genetic subdivision of the samples (F_{ST}), the calculated value of the parameter was compared to zero, and the genetic differentiation was considered significant at $p < 0.05$. The GenAlex 6.501 program was used (Peakall and Smouse, 2006, 2012).

The group identification of the individuals was analyzed in the Structure v. 2.3.4 program, which allows us to cluster the sampling on the basis of the data on the genotypes of individuals (Pritchard et al., 2000; Falush et al., 2003). Data on the variability of four polymorph microsatellite loci were used. The analysis included the individuals for which all alleles of the selected loci were characterized. The number of repeat tests is 100000, and the first 10000 tests were not taken into account. The first analysis united the animals from three subpopulations (EURT, $N = 76$; Kurgan-1, $N = 17$; Kurgan-2, $N = 5$, where N is the size of the sampling), and the second analysis included the animals captured in the EURT zone at the site of marking in September 2014 ($N = 36$). The admixture model and allele frequencies correlated settings were used, the choice of which was based on the assumption that a certain fraction of the genome of each individual is inherited from k of various populations. It is convenient to visualize the results of the analysis in a diagram, in which each individual is represented as a vertical column divided into K of variously colored sections. The size of the sections is proportionate to the

Table 1. Frequencies of alleles of allozyme loci and parameters of genetic diversity in the samples of *L. gregalis*

Locus	Allele	Sample			All animals
		EURT	Kurgan-1	Kurgan-2	
Gpdh	1	0.989	1	0.937	0.987
	2	0.011	0	0.063	0.013
Me	1	0.511	0.333	0.438	0.444
	2	0.067	0	0	0.037
	3	0.378	0.574	0.438	0.45
	4	0	0.093	0.124	0.044
	5	0.044	0	0	0.025
6Pgdh	1	1	0.981	1	0.994
	2	0	0.019	0	0.006
Got	1	0.111	0	0	0.063
	2	0.889	1	1	0.937
	N	45	27	8	80
	N_a	1.42 ± 0.26	1.25 ± 0.18	1.25 ± 0.18	1.58 ± 0.34
	N_e	1.14 ± 0.12	1.11 ± 0.1	1.14 ± 0.13	1.14 ± 0.12

(N) Size of the sampes ind., (N_a) average number of alleles per locus, (N_e) effective number of alleles per locus; for Tables 1 and 2.

share of the genome that the individual obtained from each of k of ancestor groups. The hypotheses were tested, according to which the number of various groups of animals constitutes from 2 to 10 ($K = 2–10$). An optimum number of groups was chosen in the Structure harvest program (Earl and von Holdt, 2012), which implements the method suggested by Evanno et al. (Evanno et al., 2005).

RESULTS

The allozyme loci *Ldh-1*, *Ldh-2*, *Sod*, *Pgi*, *G6p*, *Mdh*, *Pgm*, and *Xdh* did not manifest any variability. The data on the variability of the remaining loci are given in Table 1. The genetic subdivision of the three samplings compared does not significantly differ from zero.

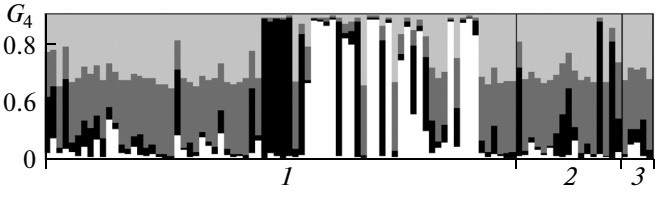

Fig. 1. Group identification of narrow-headed voles captured at the (*1*) EURT sites, (*2*) Kurgan-1, and (*3*) Kurgan-2. Each individual is represented as a vertical column divided into four differently colored sections. G_4 is the proportion of the genome that the individual obtained from each of the four ancestor groups.

The locus *Mar12* did not manifest variability in the analysis of 100 individuals (the size of the fragment was 68 bp) and was excluded from the analysis. Data on the variability of polymorph loci are given in Table 2. The genetic subdivision of the compared samplings was $F_{ST} = 0.013$ ($p = 0.001$).

To separate the paternal and maternal alleles in the embryos, a comparison of the genotypes of each descendant and mother was conducted. Then, the number of various paternal alleles in each loci was calculated for each group of embryos. The embryos of female no. 3 captured at Kurgan-1 at the end of May 2009 had more than two different paternal alleles per locus, which can be explained by multiple paternity. In the remaining seven females, the number of paternal alleles per locus did not exceed two. The explanation for this can be one father for all embryos of one female or the close kinship of several fathers of one female's offspring.

In addition, it can be noted that in females nos. 1 and 2 captured on May 31, 2009, in one colony in the native territory, the paternal alleles coincide. Judging by the degree of formedness of the skull, the high body mass, and absence of a thymus, these females can be considered wintered animals. These females had no common alleles. This evidences that they, most likely, are not sisters. The mass of one embryo in both females constituted 1.25 g, which indicates close terms of fertilization.

The coincidence of "paternal" alleles was also observed for females nos. 5 and 6, captured in Kurgan oblast in the same colony on May 28 and 29, 2010. Female no. 5 had a large thymus and unformed skull,

Table 2. Parameters of genetic diversity of microsatellite loci of *L. gregalis* samples

Site	Parameter	Locus*				
		MSMM2 (159–201)	*MSMoe02* (160–186)	*Mar80* (216–249)	*Mar49* (209–269)	All loci
EURT	N	92	103	115	112	92–115
	N_a	20	12	18	30	20 ± 3.7
	N_e	11.8	7.0	10.0	14.6	10.9 ± 1.6
Kurgan-1	N	22	24	20	27	20–27
	N_a	12	12	14	20	14.5 ± 1.9
	N_e	7	8.3	11.3	13.3	10 ± 1.4
Kurgan-2	N	7	11	10	9	7–11
	N_a	9	9	10	9	9.3 ± 0.3
	N_e	6.5	5.6	7.1	6.5	6.5 ± 0.3
All animals	N	121	138	145	148	121–148
	N_a	20	15	19	35	22.3 ± 4.3
	N_e	11.3	7.6	11.4	16.1	11.6 ± 1.7

* The numbers in parentheses are the sizes of the fragments, bp.

on the basis of which it can be attributed to the underyearlings. Female no. 6 was attributed to the overwintered individuals. The weight of one embryo produced by females no. 5 and 6 was 0.3 and 0.76 g, respectively, which indicates different timing of fertilization.

On the basis of the principle put forward by Evanno et al. (Evanno et al., 2005), the generalized sampling was divided into four groups. Figure 1 shows them in different colors: black, white, light gray, and dark gray. The method did not enable us to distinguish vole subpopulations. However, part of the animals were attributed to one of the groups with a reliability >0.75. The group marked by black included two individuals captured on the native territory in the environs of the village of Proryvnoe, as well as nine individuals obtained at the marking site in the EURT zone. The group marked white was represented by 15 individuals captured at the marking site. The rest have mixed genotypes, in which the alleles of two groups prevail, shown in dark gray and light gray. It is possible that information about the variability of four loci is insufficient for their differentiation.

The sampling of animals obtained at the marking site (EURT) in September 2014 was divided into three groups (Fig. 2). The individuals from clusters A, C, and E have a genotype of one of these groups with a significance >0.8. Such clusters are designated by capital letters. Individuals from clusters b, d, f, and g have a mixed genotype of ancestor populations, and they were designated by lowercase letters.

Data on the identification of individuals with the clusters were plotted onto a map of places of capture of the animals at the marking site in the EURT zone (Fig. 3). Based on the data on the place of capture and group identification of the animals, the narrow-headed vole population of the studied plot can be characterized. Individuals from clusters A, C, and E correspond to the broods of three various founder pairs, which possibly include parents, whereas animals from clusters b and d correspond to one brood produced by one of the founders of broods A and C or their closest relatives. The animals from each of the clusters A, C, E, and b form an aggregation at the plot of 30–60 m^2. The minimum distance between the aggregation is 10 m. Approximately a third of the animals from each brood can be found at a distance from their aggregation, including in an aggregation of other genetic groups.

DISCUSSION

The genetic differentiation of the samplings of narrow-headed voles obtained at a distance of several hundred kilometers from each other is extremely insignificant (according to the results of microsatellite

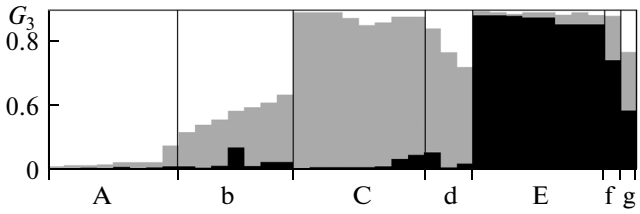

Fig. 2. Group identification of the narrow-headed voles obtained at the marking site in September 2014. The division of the sampling into clusters (A–g) was conducted by the author on the basis of an expert estimation. G_4 is the proportion of the genome that the individual obtained from each of the three ancestor groups.

(a)

				2	1					x
		x,x,x	2	x	2,2,2, 2,x				1,1	
	x	x,x			2				1,1,1	1
			2,2,2	2,2,2						x
	x		2,2				1			
									1	
								x		

(b)

				b	E					d
		C,C, C	b	d	b,b,b, b,g				E,E	
	C	C,C			b				E,E, E	f
			A,A, A	A,A, A						C
	d		A,A				E			
									E	
								C		

Fig. 3. Places of capture of narrow-headed voles attributed to different genetic groups at the marking site. Each square corresponds to a plot 10×10 m^2 in size, at the center of which the capturing device is installed. A figure or a letter indicates the individual that was captured by this trap. Repeat captures are not marked on the map. (a) Clusters distinguished according to the results of analysis of the generalized sampling. (1) Corresponds to the group marked in black; (2) group marked white (Fig. 1). (x) Animals that were not attributed to either group with a significance >0.75. (b) Clusters distinguished according to the results of analysis of individuals obtained at the marking site. The letters correspond to those in Fig. 2. Capital letters indicate individuals with a "pure" genotype of one of the "populations" of ancestors with a significance >0.8; lowercase letters indicate the individuals with a mixed genotype of ancestor populations.

loci $F_{ST} = 0.013$) or is not manifested (according to the results of analysis of allozyme loci). This corresponds to the data of Petrova et al., which showed a low level of genetic differentiation of narrow-headed voles inhabiting the territory from the South Urals to Altai, and were obtained the basis of analysis of variability of the fragment of cytochrome *b* (Petrova et al., 2015). We can assume that the data obtained by us characterize the genetic variability of the narrow-headed voles of the South Urals and Trans-Urals.

The parameters of the allozyme diversity of the analyzed narrow-headed vole sampling are not significant ($N_a = 1.58$, $N_e = 1.14$, Table 1). They are comparable to the values obtained by us earlier for the herb field mouse ($N_a = 1.16$, $N_e = 1.10$) and the red-backed vole ($N_a = 1.13–1.75$, $N_e = 1.12–1.3$) in this region (Modorov and Pozolotina, 2011; Modorov, 2014). Therefore, using the allozyme for separating various families of the narrow-headed vole is not justified. Microsatellite loci, on the contrary, demonstrate high variability. Four of five loci are represented by 15–35 alleles, so they are suitable for the intrapopulation, and, in particular, interfamily differentiation of animals.

According to the results of comparison of the alleles of microsatellite loci in the mother–embryo pairs, in one of eight cases multiple paternity was established. It is possible that in this species it is more frequent but as fathers are close relatives, it is not always revealed in an analysis similar to the one performed by us. Moreover, the simultaneous presence of several pregnant females fertilized by one male was found in the colony. This indicates that polygyny is inherent in narrow-headed voles.

Thus, in one colony of narrow-headed voles, over a short period of time, animals can be born that are descendants of at least four individuals (two females and two males). The allele set of the offspring can reach eight items per locus. All this introduces significant difficulties in determining the identification of the individual with a certain colony on the basis of the data of genetic markers, and in a number of cases makes this identification impossible.

According to the results of analysis of the variability of microsatellite loci, we divided 31 of 36 narrow-headed voles captured in September in the EURT zone in the area of ~1 ha, into four genetic groups, which correspond to the broods, possibly including the parents. This example demonstrates the effectiveness of the method used, allowing us to determine the identification of animals with a certain colony or family on the basis of analysis of the variability of microsatellite loci. At the same time, we did not manage to divide the generalized sampling of voles. A successful analysis, most likely, requires increasing the number of loci involved in the analysis and using more representative samplings of animals from one colony.

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