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ANIMAL GENETICS

Allozyme Variation of the Pygmy Wood Mouse *Apodemus uralensis* (Rodenita, Muridae) in the Ural Region

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Abstract—Variation of 17 allozyme loci was examined in 530 *Apodemus uralensis* individuals caught in the Ural region from 2005 to 2007. In the populations examined, the mean value of the genetic differentiation index F_{ST} constituted 0.169. It was demonstrated that F_{ST} values for the samples obtained from the 1-km^2 plot in different years, as well as for the samples trapped at a distance from 0.3 to 5 km during one year, could be remarkably higher than the mean value, pointing to their high, statistically significant differentiation. It seems likely that this differentiation was caused by spatial population subdivision, associated with the mice migrations, temporal change of the population structure, and the gene drift. Population of *A. uralensis* from radioactively contaminated zone displayed no specificities in the allozyme set and frequencies, which could basically distinguish these animals from the other Ural populations.

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INTRODUCTION

Populations of pigmy wood mouse *Apodemus uralensis* Pall., 1811 are often used as the models for investigation of the biota of anthropogenously disturbed territories. The studies performed on the territory of East Ural radioactive trace (EURT) present an example of such investigations [1, 2]. This study area appeared in 1957 as a result of a nuclear accident occurred at the Mayak Production Association. This region was additionally polluted with radionuclides in 1967, due to the spread of radioactive sediment from the banks of Karachay Lake [3]. It was suggested that in the populations of pigmy wood mouse from the EURT zone, the gene pool change due to mutation increase [4, 5] and natural selection of most radioactively-resistant mice [1], took place. Comprehensive genetic analysis of these populations will provide better understanding of the distant consequences of chronic irradiation. However, in performance of population genetic investigations in the zones of radioactive contamination it should be taken into account that in many rodent species allele and genotype frequencies may be highly variable in space and time (successive generations) [6–8].

The present study was focused on analysis of allozyme variation in *Apodemus uralensis*, caused by spatial and temporal factors, as well as by habitat radioactive contamination.

MATERIALS AND METHODS

The region examined. Animals were live trapped from 2005 to 2007 on the territory of Middle and Southern Ural (Fig. 1). The Bor site (57°20′N; 64°33′E) is located on the territory of the Pripyshminskie Bory national park. The trap line was arranged at the border between a pine forest and a small agrocoenosis, organized for winter supplementary feeding of the ungulates. The Garden site (55°47′N, 60°36′E) is located in southeastern part of the city of Ekaterinburg, on the territory of the Botanical Garden of the Ural Branch of the Russian Academy of Sciences. The garden is about 0.5 km^2 in size. The localities Serga 1 to Serga 4 are located in the Olenji Ruchji national park: Serga 1 and Serga 2 (56°30′N, 59°15′E), in the floodplain of similarly named river, near the Dyrovatyi Kamen rock; Serga 3 (56°29′N, 59°18′E), at the flood bed of a stream, near the Bol'shoi Proval natural monument; Serga 4 (56°31′N, 59°13′E), in the shrubbery near the railroad embankment (Fig. 1a). The r. Uy site (54°01′N, 60°59′E) is located in the floodplain of the Uy River. The Sysert' site (56°36′N, 61°01′E) is located near the settlement of Fomino and includes the meadow, fallow land, and pine forest (Fig. 2).

The Berdenish (55°46′N, 60°52′E) and Uruskul' (55°49′N, 60°55′E) localities are located on the territory of EURT zone, and the Metlino site (55°48′N, 60°00′E) flanks the EURT eastern border (Fig. 1b). Contemporary radioecological characteristic of these localities is presented in Table 1. In the Berdenish site, the animals were trapped in the herb meadow with grass domination; in the Uruskul' site, at the edge of birch forest and in aspen forest; in the Metlino site, in the forest belt separating the road from the field. More detailed description of the gounds is presented in the previous studies [2, 9, 10].

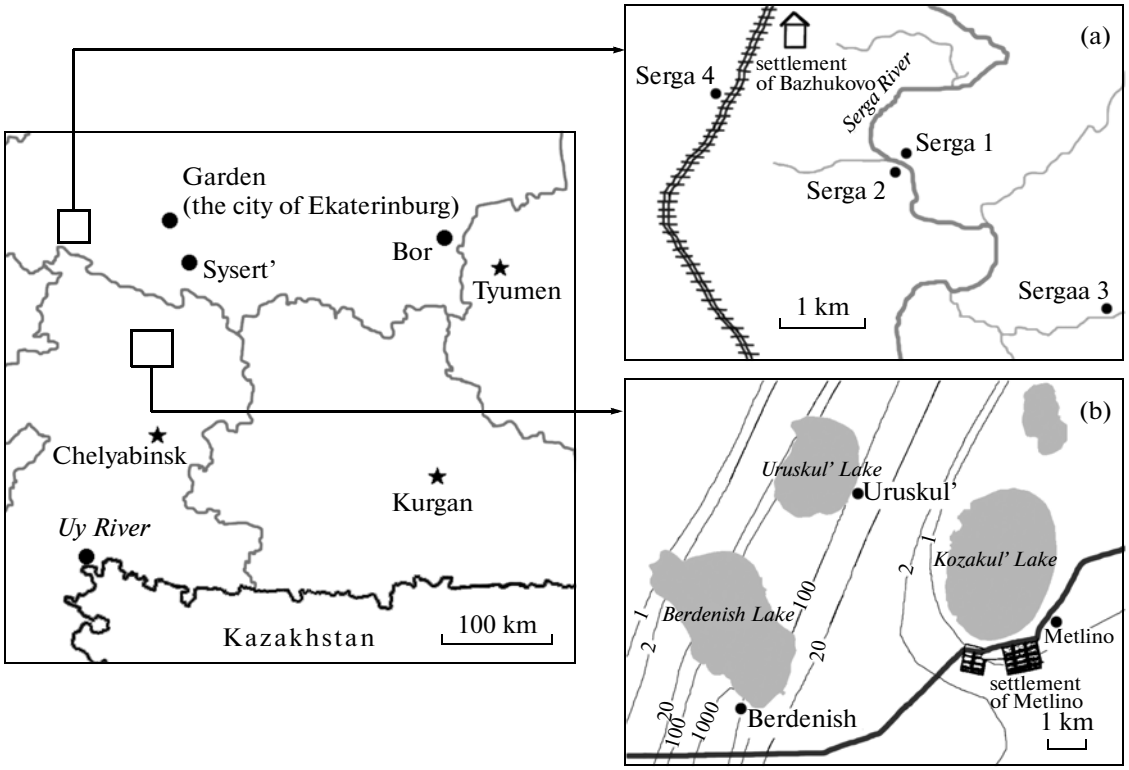

Fig. 1. Schematic presentation of the *A. uralensis* sampling sites: a, in national park "Olenji Ruchji"; b, in the EURT region (the isolines designate soil contamination with ^{90}Sr Ci/km^2). Regional centers of RF are designated with asterisks.

A total of 530 *A. uralensis* mice were trapped and tested. The animals were sacrificed before dissection. Within 15 min after sacrificing, the mouse kidneys were frozen in liquid nitrogen. On the return to the laboratory and until the performance of allozyme analysis, kidney preparations were stored in a deep freezer at –80°C.

Allozyme analysis. Electrophoresis of 11 enzymatic systems, including EST-color (E.C. 3.1.1.1.), 6-PGDH (E.C. 1.1.1.44), GPDH (E.C. 1.1.1.8), AAT (E.C. 2.6.1.1), G-PDH (E.C. 1.1.1.49), LDH (E.C. 1.1.1.27), SOD (E.C. 1.15.11) DIA (E.C. 1.6.99.1), ME (E.C. 1.1.1.40), MDH (E.C. 1.1.1.37), PGM (E.C. 2.5.7.1) was carried out in 6.4% PAAG using a Tris–EDTA borate system [11, 12]. Histochemical staining of the proteins was carried out according to a standard method [11, 13]. Alleles and isoenzymes were designated by the figures according to the descending anodic mobility. Most of the enzyme systems, including AAT (2 loci), G-6PDH (1 locus), LDH (2 loci), SOD (2 loci), DIA (2 loci), ME (2 loci), MDH (1 locus), and PGM (2 loci) showed no variation upon the analysis of the animals caught in 2005. In further analysis, electrophoresis of these systems was not performed, although, upon computation of the genetic diversity indices, these loci were scored as invariable. In the EST system, only the isoenzyme with the lowest gel mobility was interpreted.

Standard variation indices were computed as follows: proportion of polymorphic loci at the 95% confidence level ($P_{95\%}$); allele frequencies; effective (N_e) and mean (N_a) numbers of alleles per locus; expected and observed heterozygosity (H_e and H_o), and fixation index (F). Upon evaluation of sample genetic partition (F_{ST}), the calculated index value was compared to zero. Genetic differentiation among the samples was considered as statistically significant at $P < 0.05$.

Allele frequencies in different samples were compared using the correspondence analysis. Analysis of

Table 1. Contemporary soil contamination density with radionuclides and the gamma exposure rate on the localities of the EURT zone

Site	Soil contamination density, kBq/m^2*			Gamma exposure rate at the surface level, μR/h**
	^{90}Sr	^{137}Cs	$^{239, 240}$Pu	
Berdenish	6700–16700	200–700	25–62	50 ± 3.4 (27–76)
Uruskul'	7000–8100	213–230	21	20 ± 0.8 (15–25)
Metlino	190	128	1.3	12 ± 0.5 (9–16)

Notes: * The data are taken from earlier published studies [9, 10].
** The mean values and their standard errors are demonstrated; minimum and maximum values are shown in brackets.

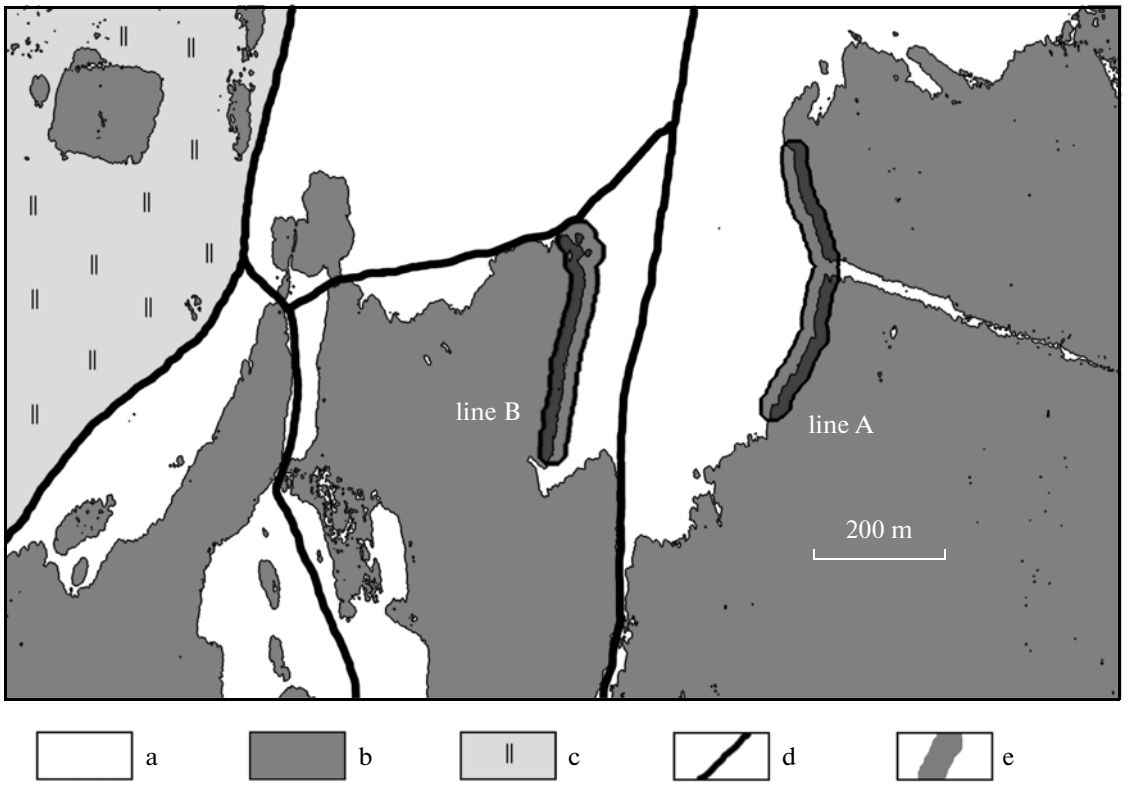

Fig. 2. Schematic presentation of the Sysert' site. a, meadow; b, pine forest; c, fallow land; d, soil roads; e, sampling sites in 2006.

the 2 × 2 tables was performed using two-way Fisher's exact test, and analysis of large data sets was performed using χ^2 test. Statistical treatment of the data was performed using the GenAlex 6.1 [14] and STATISTICA 6.0 software packages.

RESULTS AND DISCUSSION

In the populations of *A. uralensis* from the Middle and South Ural, variation was observed at three out of 17 loci analyzed (*6-Pgdh, Gpdh,* and *Est*). The indices of allozyme variation in the samples are demonstrated without sexual and age subdivision of the animals, because in the preliminary analysis, the absence of genetic differentiation between animals of different sex and age was demonstrated [15].

Interannual Allozyme Variation in the Populations of A. uralensis

Statistically significant differences in the allele frequencies between the samples caught on one territory in different years were observed in the Berdenish site in 2005 through 2006, at the *6-Pgdh* locus ($P = 0.02$); in the Sysert' site in 2006 through 2007, at the *Est* locus ($P < 0.01$); in the Garden site in 2005 and 2007, at the *Gpdh* ($P < 0.01$) and *Est* ($P < 0.03$) loci, and in 2006 through 2007 at the *Gpdh* ($P < 0.02$) and *Est* ($P < 0.01$) loci.

The proportions of polymorphic loci and the mean number of alleles per locus in the samples trapped on one site in different years were similar, enabling pooling of the samples of different years and calculation of the mean values of the indices of interest (Table 3). Standard errors of the heterozygosity indices, fixation index, and effective allele number per locus were high. Hence, accurate index comparison in the samples of different years was impossible.

Genetic differentiation of the samples trapped in the Uruskul', Metlino, and Serga 1 localities in different years was not expressed; the value of F_{ST} index was not significantly different from zero. Interannual differentiation of the populations from the localities Garden, Berdenish, and Sysert' constituted $F_{ST} = 0.040$ to 0.273 ($P < 0.05$) (Table 2). Thus, grouping of the animals trapped in different years on each of these localities in one sample would be incorrect. For this reason, comparison of the samples collected on different localities was carried out using the animals trapped during one calendar year. It should be noted that this was true for the populations from the EURT zone, as well as for the populations from the territories with the background contamination level.

Interannual genetic differentiation in the sampes of *A. uralensis* of different years can be explained by gene drift, mice migrations, and natural selection [16, 17]. In rodent populations, genetic drift is traditionally

Table 2. Allele frequencies in the samples of *A. uralensis* of different years and the levels of genetic differentiation of the samples trapped on one site in different years

Sampling site	Year	*N*	Allele frequencies							F_{ST}	*p*
			6-Pgdh		*Gpdh*		*Est*				
			2	3	1	2	1	2	3		
Berdenish	2005	34	0.40	0.60	1	0	0.38	0.62	0	0.040	0.04*
	2006	29	0.62	0.38	1	0	0.31	0.69	0		
Uruskul'	2005	14	0.46	0.57	1	0	0.68	0.32	0	<0.01	0.56
	2006	15	0.47	0.53	1	0	0.83	0.17	0		
Metlino	2005	11	0.41	0.59	1	0	0.59	0.41	0	<0.01+	0.20
	2006	24	0.50	0.50	1	0	0.73	0.27	0		
	2007	51	0.60	0.40	1	0	0.73	0.27	0		
Garden	2005	16	0.56	0.44	0.66	0.34	0.75	0.25	0	0.048+	0.01*
	2006	19	0.37	0.63	0.74	0.26	0.47	0.53	0		
	2007	28	0.50	0.50	0.93	0.07	0.50	0.50	0		
Bor	2005	28	0.71	0.29	1	0	0.30	0.70	0		
Serga 1	2005	13	0.69	0.31	0.73	0.27	0.04	0.96	0	<0.01+	0.41
	2006	49	0.58	0.42	0.69	0.31	0.05	0.95	0		
	2007	38	0.62	0.38	0.80	0.20	0.08	0.92	0		
Serga 2	2006	24	0.77	0.23	0.85	0.15	0.15	0.83	0.02		
Serga 3	2007	15	0.70	0.30	0.87	0.13	0.13	0.87	0		
Serga 4	2007	15	0.43	0.57	0.73	0.27	0.27	0.70	0.03		
Uy River	2006	48	0.39	0.61	0.72	0.28	0.24	0.76	0		
Sysert'	2006	37	0.19	0.81	1	0	0.80	0.20	0	0.273	0.01*
	2007	22	0.14	0.86	1	0	0.30	0.70	0		
Total sample		530	0.50	0.50	0.88	0.12	0.40	0.60	0.002		

Note: *N*, sample size.

* Differenses are statistically significant.

\+ Genetic distances were calculated for the samples over period of three years.

explained in terms of association with the abundance dynamics. Nevertheless, according to our observations, in 2005 to 2007, the size of the Serga 1 population, having experienced the 16-fold fluctuations, constituted in July of each year 9, 16, and 1 individuals, respectively, per 100 traps per day. At the same time, allele frequencies in the samples remained unchanged. On the contrary, in the population of Berdenish, allele frequencies at the *6-Pgdh* locus statistically significantly changed, despite the fact that annual average population size in the investigation period in 2005 to 2007 was similar [2, 15]. It seems likely, that genetic drift is the reason for statistically significant changes of the allele frequencies in the samples from the Garden population, which was isolated from the other populations by motor roads and small effective population size.

Evaluation of the influence of such factor as natural selection requires special research, considering the high number of environmental influences, characteristics of the population itself, and the allele properties. These issues were beyond the tasks of present investigation. Because of this, identification of the contribution of natural selection to interannual genetic differentiation of the samples of *A. uralensis*, based on experimental data obtained, was impossible.

Gene drift can serve as determining factor of interannual genetic differentiation of the samples of *A. uralensis* in case that populations are spatially subdivided [16]. In some studies [18, 19], such subdivision of the populations of pigmy wood mice from Ural was demonstrated. The animals were characterized by the existence of survival stations and dispersal stations.

Table 3. Indices of genetic variation in the samples

Sampling site	N	Variation indices					
		$H_o \pm SE$	$H_e \pm SE$*	F	$P_{95\%}$	N_a	N_e
Berdenish	63	0.051 ± 0.036	0.057 ± 0.039	0.09	11.8	1.12	1.11
Uruskul'	29	0.043 ± 0.030	0.052 ± 0.036	0.17	11.8	1.12	1.09
Metlino	86	0.059 ± 0.041	0.054 ± 0.037	–0.10	11.8	1.12	1.10
Garden	63	0.066 ± 0.037	0.078 ± 0.043	0.15	17.6	1.18	1.14
Bory	28	0.053 ± 0.037	0.050 ± 0.034	–0.07	11.8	1.12	1.08
Serga 1	100	0.067 ± 0.041	0.058 ± 0.035	–0.15	17.6	1.18	1.10
Serga 2	24	0.044 ± 0.026	0.053 ± 0.029	0.17	17.6	1.24	1.07
Serga 3	15	0.067 ± 0.040	0.054 ± 0.031	–0.25	17.6	1.18	1.08
Serga 4	15	0.086 ± 0.047	0.080 ± 0.044	–0.10	17.6	1.24	1.14
Uy River	48	0.080 ± 0.044	0.074 ± 0.040	–0.09	17.6	1.18	1.13
Sysert'	59	0.040 ± 0.028	0.045 ± 0.032	0.09	11.8	1.12	1.08
Total sample	530	0.060 ± 0.011	0.059 ± 0.011	–0.02	17.6	1.16	1.10

* Unbiased estimate (UH_e) is demonstrated.

In the first stations, the mice are present during the whole year, while in the second stations, only during warm seasons. In summer, mice migrate to the dispersal stations, fix on certain territories [20], and start reproduction. In case that the station size is small, and subpopulation is formed by a small number of animals, the allele frequencies in such grouping will be largely determined by the genetic drift (specifically, by the founder effect). In addition, in each year, the role of founder will be played by different mice, and substantial differences of these mice in allozymes can be the reason for interannual differentiation of the samples. In the fall period, during reverse migrations into survival stations [19], the gene pools of different subpopulations will mix, losing their specificity. The contribution of migration to the interannual dynamics of the allele frequencies are analyzed below.

Spatial Allozyme Variation

Based on the data on maximum day run of pigmy wood mice, which constitutes about 1.5 km [15], it can be suggested that the gene pools of subpopulations living at a small distance from one another (in our study the distance varied from 0.3 to 10 km) can experience mutual, or one-way change, as a result of gene flow. The hypothesis on the legitimacy of grouping the samples trapped at a distance up to 10 km from one another is analyzed below.

Table 4. The *6-Pgdh* and *Est* allele frequencies in the samples trapped in 2006, in the Sysert' site

Line	N	*6-Pgdh*		*Est*	
		2	*3*	*1*	*2*
A	17	0.029	0.971	1.000	0
B	20	0.325	0.675	0.625	0.375

The data on local allozyme variation were obtained from the Sysert' site. In 2006, trappings were performed along the two trapping lines, A and B. The lines were arranged at a distance of about 300 m from one another (Fig. 2). The samples collected in these lines demonstrated statistically significant differences ($P < 0.01$) in allele frequencies (Table 4), $F_{ST} = 0.498$ ($P < 0.01$). The concepts on the population partition [16–19] serve as an explanation for the high genetic differentiation of the samples observed. For instance, most of the mice trapped were associated with *Rosa canina* L., sporadically growing at the border between the meadow and pine forest (lines A and B). In the forest, the number of mice was small, and they were absent from the meadow. It can be suggested that the differences in allele frequencies in such small "istland" mouse settlements could be initially determined by the gene drift [16]. Later, these differences were "inherited" by the closely relative descendants of the subpopulation founders.

In 2007, we continued trapping on the Sysert' site. It was demonstrated that the highest number of the mice inhabited fallow land (Fig. 2), while on the lines A and B, only sporadic individuals were found. High

interannual differentiation of the samples collected on the site mentioned (see above) can be explained by the fact that in 2006 and 2007, the trapped animals were from different subpopulations, characterized by different allele frequencies. Therefore, the processes determining the allele frequency dynamics in the samples in space and time, are closely linked to each other. A survey of genetic subdivision of populations within certain territory should take into account the chronogenic variation.

Analysis of subpopulations from the Olenji Ruchji national park revealed statistically significant differences in allele frequencies between the Serga 1 and Serga 2 samples, trapped in 2006 in similar biotopes located on different banks of the about 20-m wide Serga River, $F_{ST} = 0.057$ ($P = 0.01$). In 2007, comparison of the Serga 1, Serga 3, and Serga 4 subpopulations was carried out. Genetic differentiation of the Serga 1 and Serga 3 samples was not statistically significantly different from zero ($F_{ST} < 0.001$; $P = 0.49$). At the same time, differentiation between each of these samples and the Serga 4 sample appeared to be statistically significant ($F_{ST} = 0.053$ to 0.066; $P = 0.03$).

Analysis of subpopulations from the EURT zone showed that genetic differentiation of the Uruskul' and Metlino samples in 2005 and 2006, as well as of the Berdenish and Metlino samples in 2005, was statistically significantly indifferent from zero ($P = 0.22$ to 0.36). The coefficient of genetic differentiation F_{ST} for the Berdenish and Uruskul' samples in 2005 was 0.061 ($P = 0.03$), in 2006 – 0.239 ($P = 0.001$). The value of this index for the Berdenish and Metlino samples in 2006 was 0.161 ($P < 0.01$). Thus, genetic subdivision of the two subpopulations of pigmy wood mice, living along the longitudinal EURT transect was found to be high. On the contrary, the Uruskul' and Metlino samples trapped on the territories, which were the orders of magnitude different in the levels of ^{90}Sr contamination, demonstrated similar allele frequencies during the period of two years.

The results presented above suggest that radioactive contamination is not the leading ecological factor, determining the differences in allele frequencies in the populations of *A. uralensis* from EURT zone. We think that the reason for differentiation in this case also lies in the gene drift, and the reason for subpopulation similarity, in intense migration flows between them. No insurmountable isolation barriers between the localities were observed. However, the biocoenoses separating them were different. For instance, the Berdenish site is separated from the two others by the birch forest, where the number of mice is low [2, 15]. At the same time, between the Uruskul' and Metlino localities there are fallow lands and forest edges, full of earth roads, where the number of mice is relatively high.

Comparison of Allozyme Variation in the Ural Populations

High variability of the allele frequencies between the groupings examined shows that one *A. uralensis* sample cannot characterize the whole population. Such estimate requires grouping of several subpopulation samples. Because of this, for the comparison of the allozyme sets and frequencies in the Ural populations, we grouped the mice trapped in closely located localities in different years. Thus, comparisons were performed using the Serga 1, Serga 2, Serga 3, Serga 4, r. Uy, Sysert', Garden, Bor, and EURT samples. The latter sample included animals from the Metlino, Berdenish, and Uruskul' localities.

In the samples tested the value of the genetic differentiation index F_{ST} constituted 0.169. In other words, in *A. uralensis* from Urals, about 83% of allozyme variation was found within the populations, and 17%, between the populations. Note that inclusion in analysis of only one (the largest in size) subpopulation from each population produced a similar index value ($F_{ST} = 0.197$).

The observed (H_o) and expected (H_e) heterozygosity for the Ural populations varied from 0.040 to 0.086. However, the errors of these values were high, making difficult the data interpretation. It should be noted that there was no tendency towards the prevalence of either homo- or heterozygous genotypes in the samples from EURT zone, which was indicated by the fixation index F (Table 3).

Data from the ealier works on the allele sets and frequencies in *A. uralensis* from different regions of Eurasia [22–25] shows that Ural population of pigmy wood mouse was mostly similar to the populations of Eastern Europe.

CONCLUSIONS

It was demonstrated that differentiation of the samples of *A. uralensis* trapped in one site in different years, or of the samples collected at the same time close to one another, could vary in a wide range ($F_{ST} = 0$–0.498).

In our investigation, population of *A. uralensis* from radioactively contaminated zone (EURT) displayed no specificities in the allozyme set and frequencies, which could basically distinguish these animals from the other Ural populations. Specifically, no rare alleles, marking the genetic load, were identified, albeit the frequency of chromosomal aberrations in the bone marrow cells of pigmy wood mice from the EURT zone (including the mice used in our analysis) was increased [4, 5]. As already mentioned, literature data indicated that in EURT population, selection of the mice most adapted to the conditions of chronic irradiation took place [1]. The selection effect in the populations of irradiated animals could be manifested as shifts in either allele or genotype frequencies. However, analysis carried out in the present study demon-

strated that these frequencies were rather determined by the gene drift and migration, than by the factor of radiation.

It could be suggested that protein changes actually took place in pigmy wood mice from EURT zone, and the reason for the failure to detect these changes lay in the insufficient number of loci examined, along with the lethality of the mutant alleles. However, the use of more sensitive techniques (the mtDNA D loop sequencing) [8] upon genetic monitoring of natural vole populations from the vicinity of the Chernobyl Nuclear Power Plant led to the conclusion that the differences in the genetic diversity indices observed could be rather explained by historical reasons and geographic variation then by the radioactive contamination. At the same time, the level of chromosomal aberrations in these animals was also increased [26].

The existence of basic differences between the data sets obtained with the use of different markers is evident. At the current step of investigation, we can only suggest that the radiation-caused genetic damages took place in individual cells. Multilevel protection systems of the organisms limit the transmission of mutations to the progeny, providing stable existence of the population.

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REFERENCES

1. Il'enko, A.I. and Krapivko, T.P., *Ekologiya zhivotnykh v radiatsionnom biotsenoze* (The Ecology of Animals in Radiation Biocenosis), Moscow: Nauka, 1989.
2. Grigorkina, E.B., Olenev, G.V., and Modorov, M.V., Analysis of Rodent Populations in Technogenically Transformed Areas (with Reference to *Apodemus (S.) uralensis* from the EURT Zone), *Russ. J. Ecol.*, 2008, no. 4, pp. 284–291.
3. Conclusion of the Commission for Evaluating the Ecological Situation in the Sphere of Influence of the Industrial Plant (IP) of the Ministry of Atomic Energy of the USSR, Ordered by the Presidium of the USSR Academy of Sciences no. 1140–501, 12.06.1990, *Radiobiologiya*, 1991, vol. 31, no. 3, pp. 436–452.
4. Dubinin, N.P., Shevchenko, A.V., Alekseenok, A.Ya., et al., Genetic Processes in Chronically Irradiated Populations, *Usp. Sovrem. Genet.*, 1972, no. 4, pp. 170–205.
5. Yalkovskaya, L.E. and Grigorkina, E.B., Chromose Instability in *Apodemus (S.) uralensis* in the Eastern Urals Radioactive Trace Zone, in *Biologicheskie effekty malykh doz ioniziruyushchei radiatsii i radioaktivnoe zagryaznenie sredy* (Biological Effects of Low Doses of Ionizing Radiation and the Radioactive Contamination of Environment), Syktyvkar: Izd. Komi Nauchn. Tsentra Uralskogo Otdelenia Ross. Akad. Nauk, 2009, pp. 295–297.
6. Gaines, M.S., McClenaghan, L.R., Jr., and Rose, R.K., Temporal Patterns of Allozymic Variation in Fluctuating Populations of *Microtus ochrogaster, Evolution*, 1978, vol. 34, no. 4, pp. 723–739.
7. Booth, W., Montgomery, W.I., and Prodohl, P.A., Spatial Genetic Structuring in a Vagile Species, the European Wood Mouse, *J. Zool.*, 2009, vol. 279, pp. 219–228.
8. Meeks, H.N., Chesser, R.K., Rodgers, B.E., et al., Understanding the Genetic Consequences of Environmental Toxicant Exposure: Chernobyl as a Model System, *Environ. Toxicol. Chem.*, 2009, vol. 28, no. 9, pp. 1982–1994.
9. Pozolotina, V.N., Molchanova, I.V., Karavaeva, E.N., et al., *Sovremennoe sostoyanie nazemnykh ekosistem Vostochno-Ural'skogo radioaktivnogo sleda: urovni zagryazneniya, biologicheskie effekty* (Current State of Terrestrial Ecosystems in the Eastern Urals Radioactive Trace Zone: Contamination Levels and Biological Effects), Yekaterinburg: Goshchitskii, 2008.
10. Molchanova, I., Pozolotina, V., Karavaeva, E., et al., Radioactive Inventories within the East Ural Radioactive State Reserve on the Southern Urals, *Radioprotection,* 2009, vol. 44, no. 5, pp. 747–757.
11. Korochkin, L.I., Serov, O.L., and Maichenko, G.P., *Genetika izofermentov* (Genetics of Isozymes), Moscow: Nauka, 1977.
12. Maurer, H.R., Disc Electrophoresis and Related Techniques of Polyacrylamide Gel Electrophoresis, New York: de Gruyter, 1971, 2nd ed.
13. Hillis, D.M. and Moritz, C., *Molecular Systematics*, Sunderland: Sinauer, 1990.
14. Peakall, R. and Smouse, P.E., GenAlex 6: Genetic Analysis in Excel. Population Genetic Software for Teaching and Research, *Mol. Ecol. Notes*, 2006, vol. 6, pp. 288–295.
15. Modorov, M.V., Ecological Genetic Characteristics of *Apodemus uralensis* from the Eastern Urals Radioactive Trace Zone, *Cand. Sci. (Biol.) Dissertation*, Yekaterinburg: Institute of Plant and Animal Ecology, 2009, p. 171.
16. Hedrick, P.W., *Genetics of Populations*, Boston: Jones and Bartlett, 2003.
17. *Dinamika populyatsionnykh genofondov pri antropogennykh vozdeistviyakh* (Dynamics of Population Gene Pools under Anthropogenic Impact), Altukhov, Yu.P., Ed., Moscow: Nauka, 2004.
18. Nurtdinova, D.V. and Pyastolova, O.A., Distribution and Abundance of *Apodemus uralensis* (Pallas, 1811) in Allotment Gardens in a Large Urban Agglomeration, *Povolzhskii Ekol. Zh.*, 2006, no. 1, pp. 23–31.
19. Shvarts, S.S., Population Structure of Species, *Zool. Zh.*, 1967, vol. 46, no. 10, pp. 1456–1469.
20. Gromov, V.S., *Prostranstvenno-etologicheskaya struktura populyatsii gryzunov* (Spatial Ethological Structure of Populations of Rodents), Moscow: KMK, 2008.
21. Karulin, B.E., Nikitina, N.A., Khlyap, L.A., et al., Diurnal Activity and Territory Utilization of Common Field Mice (*Apodemus sylvaticus*) According to Obser-

vations of Animals Marked by Cobalt-60, *Zool. Zh.*, 1976, vol. 55, no. 1, pp. 112–121.

22. Mezhzherin, S.V., Allozyme Variability and Genetic Divergence in Wood Mice of Subgenus *Sylvaemus* (Ognev et Vorobiev), *Genetika* (Moscow), 1990 vol. 26, no. 6, pp. 1046–1054.

23. Bogdanov, A.S., Allozyme Variation of the Pygmy Wood Mouse *Sylvaemus uralensis* (Rodentia, Muridae) and Estimation of the Divergence of Its Chromosome Forms, *Russ. J. Genet.*, 2004, vol. 40, no. 8, pp. 897–909.

24. Filippucci, M.G., Macholan, M., and Michaux, J.R., Genetic Variation and Evolution in the Genus *Apodemus* (Muridae: Rodentia), *Biol. J. Linn. Soc.*, 2002, vol. 75, pp. 395–419.

25. Macholan, M., Filippucci, M.G., Benda, P., et al., Allozyme Variation and Systematics of the Genus *Apodemus* (Rodentia: Muridae) in Asia Minor and Iran, *J. Mammal.*, 2001, vol. 82, no. 3, pp. 799–813.

26. Goncharova, R.I. and Ryabokon', N.I., Biological Effects in Natural Populations of Small Rodents in Radioactively Contaminated Territories: Dynamics of Chromosome Aberration Frequency in a Series of Bank Vole (*Clethrionomys glareolus* Schreber) Generations, *Radiatsionnaya Biol. Radioekol.*, 1998, vol. 38, no. 5, pp. 746–753.