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ANIMAL GENETICS

Analysis of Microsatellite DNA in Rodents from Eastern Urals Radioactive Trace Zone and Contiguous Territories

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Abstract—The variability of four microsatellite loci of rodents, caught from the head part of Eastern Urals Radioactive Trace (EURT), along with the rodents inhabiting contiguous zone with background radiation level and distant reference territory, was analyzed for the first time. Differences in the parameters of genetic diversity between northern red-backed voles from the EURT zone and from the reference population were detected. An increase in some indices of genetic diversity in animals from a contiguous to the EURT zone was found; this is probably associated with animal migration and configuration of the area of pollution. A transfer of radiation-induced effects to the contiguous territories and a decrease in the possibility of fixation of adaptations in a series of generations of mobile rodent species in the area of local radioactive pollution are consequences of migrations. The results of the study make it possible to recommend microsatellite markers for the analysis of radiation-induced effects in rodents as model objects of radioecological monitoring.

Keywords: microsatellite DNA, Eastern Urals Radioactive Trace (EURT), rodents, migrations

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INTRODUCTION

The Eastern Urals Radioactive Trace (EURT) is a result of Kyshtym radiation accident at the Mayak Production Association in 1957 (Chelyabinsk oblast, Southern Urals) and is a unique "natural laboratory" for the study of radionuclide accumulation and long-term ecological and genetic consequences of chronic radiation effects in plant and animal populations. The EURT zone is specific not only due to its spectrum, number of radionuclides and ecosystem structure, but also because of its configuration and dimensions (Fig. 1). This is a narrow extended territory with a sharply falling radioactive pollution gradient (which is one of its main peculiarities and problem no. 1 in conducting ecological and genetic studies on small rodents). Owing to the small transverse size of the cloud, radioactive fallout was focused along the axis of its movement, where the specific density of the surface pollution was maximal because of a small dispersion of radioactive substances by the atmosphere at a long distance [1]. Therefore, in the research area, the width of the test range with the density of ^{90}Sr pollution corresponding to 1000, 500, 250, and 50 Ci/km^2, accounted for 800, 1400, 1580 and 1800 m, respectively. In this regard, the EURT zone can be without exaggeration considered as a unique planetary formation and an equally unique scientific test range.

Microsatellite DNA (microsatellites), or short tandem repeats (STR) loci, are DNA fragments with a large amount (up to hundreds and more) of tandemly repeated identical "motifs" that are usually called "repeats": short sequences out of several (as usually considered from 1 to 6) nucleotide pairs. The alleles of microsatellite loci differ from each other in length (mainly owing to the different number of repeats that they contain). Microsatellites are in large amounts distributed throughout the genome of eukaryotes and are localized both in noncoding and coding (much less frequently) genome regions [2–4]. The overwhelming proportion of mutations in microsatellite loci arises because of a specific error of DNA replication in the microsatellite region (DNA polymerase slippage along the homopolymer sequence by the number of nucleotides divisible by the repeat length) [5]. In addition to changes in the number of repeats occurring as a result of the chain slippage during the time of replication, point mutations and deletions/insertions (not divisible by the nucleotide number in the repeat) are also possible within microsatellites [6]. Microsatellite loci are highly polymorphic; for example, the number of alleles in 66 studied loci of the bank vole (*Clethrionomys glareolus*) from Central Finland varied from 6 to 38 per locus [7]. Such high microsatellite variability is explained by their higher mutation rates as compared with mutability of the remaining genomic DNA [3, 8, 9]. Therefore, they can serve as efficient markers for the study of genetic and demographic processes in mammalian populations. In the most works, these processes are studied in relation to the spatial organization of popu-

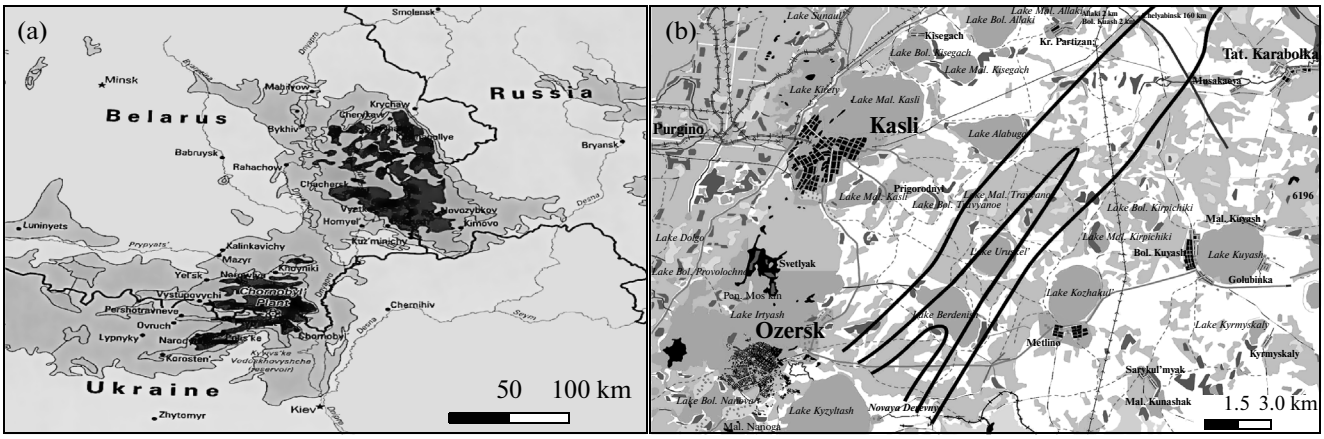

Fig. 1. Sizes and configuration of radioactive pollution zones. (a) Chernobyl zone; (b) Eastern Urals Radioactive Trace. Areas highlighted by isolines: central (EURT epicenter, 500 Ci/km^2); average (100 Ci/km^2); periphery (20 Ci/km^2).

lations and cyclic fluctuations of the number of rodents [10–12]. Microsatellite DNA variability in mammals and other vertebrates under the influence of anthropogenic environmental pollution was studied to a much lesser extent. In these cases, both the direct effect of toxicants or physical factors (for example, ionizing radiation) on DNA structure and the indirect effect through the damage of correct replication and timely reparation occur; finally, directed molecular processes of higher level (which can have an adaptive significance or be a consequence of weakening of the protective features of cells) can occur [13]. The ambiguity of data obtained during the study of microsatellite DNA variability in different vertebrate species under the influence of the anthropogenic effect indicates the complexity of the problem. Thus, according to some studies employing microsatellite markers analysis, the pollution of habitats by heavy metals (chromium, nickel, arsenic, cadmium, lead) does not always have a significant effect on indices of genetic diversity in bank voles (*Cl. glareolus*) [14, 15], estimated according to microsatellite markers, however, such an association is quite likely in the case of the wood mouse [16]. Ambiguous results in such studies were also obtained for radioactive pollutants [17–20].

The present study is focused on the analysis of genetic diversity of microsatellite markers in the northern red-backed vole (*Clethrionomys rutilus* Pallas, 1779) in the zone of EURT influence and the role of rodent migrations in the variability of microsatellites of voles inhabiting contiguous territories.

MATERIALS AND METHODS

Characterization of the object of study and sites of rodent capture. Northern red-backed voles caught in 2006 are the object of the study. The northern red-backed vole is a widespread species in the Ural region. This is one of the background species of the rodent taxocene in the EURT zone; however, the number of animals of this species in faunal collections was always low. It should be noted that a "great" drought in 2010 [21] resulted in the transformation of the rodentocenosis toward its simplification (a decrease in the species diversity); a single species (small wood mouse (*Sylvaemus uralensis* Pall., 1811) remained among rodents [22]. The remaining species (ten species were registered before 2010), including the northern red-backed vole, were hardly found in the radioactive pollution zone after that. The rodents were caught in animal traps in three sites (impact, contiguous background, and reference). The impact site (Berdenish) is located in the head part of the EURT zone in the vicinity of Lake Berdenish (55°46′ N, 60°53′ E) 13 km from the epicenter of the accident; the initial density of the soil pollution by ^{90}Sr was 500 Ci/km^2 (6740–16690 kBq/m^2). The gamma background at the soil level varied from 22 to 76 μR/h (on average, 50 μR/h); the β-radiation count was 90–942 cpm/cm^2 (on average, 380 cpm/cm^2). The contiguous background site, Metlino (55°48′ N, 61°00′ E), is located outside of the radiation reserve in the vicinity of Lake Kozhakul', at a distance of 9–10 km from the impact site: gamma background, 12 μR/h; β-radiation count, 12 cpm/cm^2; density of soil pollution by ^{90}Sr, 2 Ci/km^2 (44 kBq/m^2). The samples from the neighborhood of Shigaevo village (Sverdlovsk oblast, 57°20′ N, 58°40′ E) located 220 km from the other two sites were a geographically distant control (reference group); the pollution level there is within the regional norm [23].

Analysis of microsatellite DNA variability. Variability of four microsatellite loci (*MSCg4, MSCg9, MSCg15, LIST-3-003*) consisting of dinucleotide repeats was analyzed [24, 25]. Total DNA was isolated from the muscle tissue by a salt extraction method [26]. Microsatellite DNA amplification was conducted according to recommendations stated in the work by Gockel et al. [24] with some modifications. Polymerase chain reaction was carried out in 10 μL of the reaction mix-

ture at the following regimes: 3 min at 94°C, then 35 cycles (94°C, 20 s; 58°C, 20 s; 72°C, 20 s), and final elongation at 72°C for 3 min. Per one reaction, 30–60 ng total DNA, 0.1 units *Taq*-polymerase (SibEnzyme, Russia), single SE buffer (60 mM Tris-HCl (pH 8.5), 1.5 mM $MgCl_2$, 25 mM KCl, 10 mM 2-mercaptoethanol, 0.1% triton X-100 (SibEnzyme, Russia)), 0.1 mM of each deoxyribonucleotide, 1.5 mM $MgCl_2$, and 0.2 μM forward and reverse primers were used. The allele size was determined in denaturing polyacrylamide gel on an automatic ALFexpress-II gel sequencer (Amersham Biosciences) by means of the Alfwin Fragment Analyser 1.03 program. Data were processed using the following software packages: Arlequin 3.5, Fstat 2.9.3.2, Micro-Checker 2.2.3, Genepop on the Web, GenAlEx 6.5, and Microsatellite Tools for Excel. Sixty-seven northern red-backed voles were used for the analysis of microsatellite DNA variability.

Estimation of rodent migrations. The rodent migrations in the zone of the EURT effect were studied by a method of small mammal group marking by tetracycline (2002–2005, 973 animals), which was performed according to recommendations [27]. The bait with tetracycline was laid on the ground in a homogeneous biotope at a distance of 3 m from each other in areas 30 × 300 m in size located in different years at the epicenter of the radioactive pollution zone or at the periphery of the trace (for more details, see [28]). The rodents were caught by crush traps (Gero construction) with a trap–line method at different times at different distances from the labeling site. The presence of the label was determined by yellow illumination in ultraviolet light in upper incisors [27]. Tasting the bait with tetracycline one time, the rodents of different ecological specialization are identified according to yellow illumination in the teeth in ultraviolet light. We verified this fact [28] in our own vivarium experiments conducted directly before labeling the animal population in nature. ^{90}Sr deposited in the bone tissue is a quantitative marker of the animal staying in the EURT zone. However, the question regarding the time of the small animal being in the radiation biocenosis (required for registration of the radiometric amount of ^{90}Sr) remains unresolved, since it is not possible to compare the amount of radionuclide obtained in nature with food with that in the experiments.

Radiometric studies. Determination of the specific activity of ^{90}Sr in the rodent skeleton (thighbones) was performed by O.V. Tarasov (Candidate of Biology) at the Mayak Production Association. The samples were prepared by a method of damp ignition. The sample preparation method was described previously [22]. The measurements of the specific activity of ^{90}Sr were carried out by the β-spectrophotometric method using a BS-1 spectrometer (Ozersk, Russia); the measurement error was no more than 8%. The specific activity of radionuclides in the bone tissues was calculated per 1 g of dry mass of the substance (Bq/g). Data were analyzed after checking the character of their distribution; mean, maximum, and minimum values were used. Data processing was conducted using PSP EXCEL 6.0 and STATISTICA 5.0.

RESULTS

Specific Activity of Strontium-90 in Rodent Bone Tissues

^{90}Sr, which is accumulated in the bone tissue of vertebrates and is a source of internal irradiation, is the main pollutant in the EURT zone [1]. The specific β activity of ^{90}Sr in the northern red-backed vole organism from the reference territory did not exceed 0.5 Bq/g or in rodents from the sites, contiguous to the EURT zone, which corresponds to the background level of radionuclide content in small mammals inhabiting uncontaminated territories. The mean value of specific activity of ^{90}Sr deposited in the bone tissue of rodents in the impact site was 105.5 ± 92.1 Bq/g. The maximum and minimum values differed by 41 times (329 and 7.94 Bq/g, respectively). Such a pronounced degree of differences in accumulation of radionuclides in northern red-backed voles is significantly caused by configuration of the EURT zone (Fig. 1), unevenness of the pollution of the territory, and rodent migrations.

Microsatellite DNA Variability

All loci that we studied were highly polymorphic, which is typical of rodents [4] (from 8 alleles in *MSCg9* to 14 in *MSCg4*). The allele sizes varied from 104 to 134 bp in the *MSCg4* locus, from 145 to 167 in the case of *MSCg9*, from 113 to 133 in *MSCg15*, and from 212 to 236 in *LIST-3-003*. The genotype frequencies for separate loci did not deviate significantly from Hardy–Weinberg equilibrium (the probabilities were determined using the Bonferroni procedure). The special analysis demonstrated the absence of detection errors and null alleles.

The indices of genetic diversity averaged over four microsatellite loci in three northern red-backed vole samples are presented in Table 1. The mean observed heterozygosity was the largest in voles from the EURT zone. In the remaining samples, it was also high and close to the values previously observed in other rodent species [7, 15, 16]. For example, the mean observed heterozygosity in the close species (bank vole from the zone of the effect of Middle Urals copper smelting plant (56°50′ N, 59°51′ E) varied from 0.719 to 0.829 [14]. The mean values of the observed heterozygosity in all studied populations were higher as compared with the mean values of expected heterozygosity. A negative value of Wright's fixation index (F_{IS}) indicating the excess of heterozygotes also is evidence of this. It has a value closest to 0 (1.5%) in the reference sample, indicating that this population is in the state the closest to equilibrium. The excess of heterozygotes in the impact population is 3 times larger (4.6%) as com-

Table 1. Indices of genetic diversity in three northern red-backed vole samples averaged over four microsatellite loci

Index	Locality		
	EURT (Berdenish)	Metlino	Shigaevo
Number of animals	24	15	28
H_E	0.867	0.849	0.845
H_O	0.906	0.867	0.857
F_{IS}	–0.046	–0.022	–0.015
Average number of alleles per locus	10	9.25	9.25
Number of unique alleles	1	3	1
Allelic diversity	9.07	9.25	8.46
Garza–Williamson index	0.51343	0.38762	0.46981

H_E, mean expected heterozygosity; H_O, mean observed heterozygosity; F_{IS}, Wright's fixation index.

pared with the reference, and it has an intermediate value (2.2%) on the territory contiguous to EURT.

The Garza–Williamson index (ratio of the number of alleles to the range of their sizes) was the largest in voles from the EURT zone. The values of this index indicate the preservation of genetic diversity in populations in spite of the possible "bottleneck" effect [29]. We recall that the northern red-backed vole is not numerous in the EURT zone and is registered in catchings not every year; therefore, the phenomenon mentioned above can take place. At the same time, the number of unique alleles (i.e., present in a single copy only in one of all studied samples) and the allelic richness index (which takes into account the sample sizes) were the largest in animals of the contiguous site (Metlino).

Interpopulation genetic differentiation was estimated on the basis of the variance of allele frequencies of microsatellite loci (AMOVA, F_{st}). The analysis of molecular variability (AMOVA) demonstrated small levels of interpopulation differentiation; the portion of variance determined by it was 1.34% ($P = 0.005$). The level of pairwise differentiation between samples in F_{st} values for all microsatellite loci changed from 0.01147 to 0.01549 (Table 2). It was found that the genetic structure of impact (EURT) and reference (Shigaevo) groups differs significantly. At the same time, differences between the group from the EURT zone and from the vicinity of the village of Metlino were at the border of 5% level of significance. The background and reference samples (Metlino and Shigaevo) displayed no significant interpopulation differentiation (in spite of significant distance between them (220 km)).

In order to estimate a possible influence of osteotropic radionuclides on the rate of microsatellite mutation origin at the individual level, the analysis of association between specific activity of ^{90}Sr in the bone tissue of voles from the EURT zone and heterozygosity for microsatellite loci was conducted. A tendency toward a positive association between these parameters ($R_s = 0.21$, $N = 24$, $P = 0.33$) was found. It is known that a certain set of allelic variants for the overwhelming majority of microsatellite loci remains throughout the entire life in somatic tissues of individuals with the absence of clearly pronounced pathology. Therefore, we register both spontaneous and radiation-induced genome instability for microsatellite loci transmissible through the parental sexual cells in the progeny somatic tissues. In this connection, it is logical to expect an increase in the genome instability (including by microsatellite DNA loci) in residents living for several generations under conditions of the radiation pollution and in their descendants as compared with individuals from the reference zones. However, high migration activity of rodents (both in the pollution zone and outside) apparently significantly contributes to the observed correlation between the specific activity of ^{90}Sr in the bone tissues of voles and the level of heterozygosity for microsatellite loci. The stability of this correlation will be confirmed (or disproved) in further studies.

Polymorphism for evenness/oddness of the number of nucleotide pairs in the *MSCg15* locus (found in all three studied northern red-backed vole samples) deserves special attention. Deletions, insertions, and translocations are quite frequently found in the spectrum of dislocations registered in microsatellite DNA loci of the progeny of parents (both spontaneous and induced by the effect of radiation and chemical mutagens). They are registered as a change in the length of alleles of simple tandem repeats as a result of

Table 2. Estimates of genetic differentiation (F_{st}-statistics) of northern red-backed vole samples according to four microsatellite loci

Locality	EURT (Berdenish)	Metlino	Shigaevo
EURT (Berdenish)	–	0.052	**0.010**
Metlino	0.01189	–	0.073
Shigaevo	0.01549	0.01147	–

Values of F_{st} statistics are given below the diagonal; values of probability are given above the diagonal.

functioning of different processes involving DNA of sexual cells carrying nonlethal damages. It is assumed that microsatellites can contain "hot spots" or sites according to which recombination and conversion events are realized [30]. The alleles with an even number of nucleotide pairs prevailed in all samples that we studied; the remaining allelic variants were represented by an odd number of base pairs; the largest number of them were observed in the impact group (25%); the smallest, in the contiguous site (13.3%). It is possible that odd alleles in the *MSCg15* locus arose as a result of insertion or deletion of odd number of nucleotide pairs. This can be due to both radiation effect on rodents in the EURT zone and peculiarities of the mutation process for this locus, since odd alleles in smaller amounts were also found in voles from the reference group (21.4%).

Rodent Migrations

Figure 1 illustrates the types of configurations of radioactive pollution zones generated as a result of the accident at the Chernobyl Nuclear Power Plant in 1986 (vast territory) and Kyshtym radiation accident in 1957 (narrow extensive territory) (see scales).

The rodent migrations in the zone of EURT effect were studied on the basis of a large amount of statistical material (973 animals) obtained during 4 years of massive animal population labeling by tetracycline label [28]. The results indicate a high migration mobility of rodents, the presence of active animal movements both in the pollution zone and outside the radiation reserve (i.e., a flowing population, a population with constantly changing composition). The portion of migrants from the EURT zone to the background site in different years and seasons varied from 5 to 30% [28]. Rodents of different ecological specialization were registered among migrants. Labeled animals (wood and field mice, as well as northern red-backed voles) were caught at a rather significant distance (9 km) from areas where the bait with tetracycline was placed (including outside the radiation reserve, which is convincing evidence of the absence of animal population isolation in the EURT zone). According to radioactive (^{90}Sr) self-labeling of rodents in the EURT zone, the portion of migrants in the samples of different years and seasons varied from 17 to 40% [28]. Long-term field studies of the small mammal population in the EURT zone also indicate the presence of seasonal interbiotopic migrations of small wood and field mice [22].

DISCUSSION

The most significant differences in indices of genetic diversity are observed between northern red-backed voles from the reference population (Shigaevo), experiencing only a global anthropogenic effect, and voles from the EURT zone, in the bone tissues of which osteotropic radionuclides, which can induce an increased instability of microsatellite loci, are accumulated. The samples from the EURT zone (Berdenish) and contiguous site (Metlino) are significantly closer to each other than to animals from Shigaevo. The isolation by distance is excluded in the EURT and Metlino sites, since it is only 9–10 km. It is logical to assume that the observed effects are first of all associated with rodent migrations and peculiarities of configuration of the pollution zone. It follows from the labeling data that both labels (quantitative (tetracycline) and qualitative (^{90}Sr)) provide similar results on the portion of migrants and convincingly prove the absence of animal population isolation in the local radioactive pollution zone.

The transfer of radiation-induced effects to contiguous territories (where it is possible to expect an increase in the genetic diversity induced by *de novo* mutations) is a consequence of animal migrations. This is demonstrated by the results of this study obtained on the basis of the analysis of microsatellite DNA, in which an increase in the allelic diversity index and in the amount of unique alleles in the northern red-backed vole sample from the contiguous site was found as compared with these parameters in rodents from the EURT zone and geographically distant control (Table 1). Similar results (more expressed differences in the genetic diversity indices) were observed during the comparative study of microsatellite DNA variability between bank voles from the region of Middle Urals copper smelting plant (Sverdlovsk oblast), in the liver of which the content of mutagenic pollutants (arsenic, cadmium, lead, chromium, nickel) was increased, and animals from the reference population (located at a distance of 90 km) [14]. At the same time, an increase in some indices of genetic diversity (the number of private alleles, mean number of alleles per locus) was detected in the peripheral zone (20–30 km from the source of emission), where the degree of mutagenic pollution is lower than in the impact zone. It is likely that rodent migrations played their determinative role here.

The significance of the migration factor in the development of genetic diversity in the kangaroo rat (*Dipodomis merriami*) population inhabiting the regions exposed to radioactive pollution in Nevada (United States) and the contiguous territories is reported [31]. The absence of clear geographical confinement of the mtDNA control region haplotype distribution to radioactively polluted or reference sites was demonstrated, and it was possible to explain the topology of the constructed phylogenetic tree only taking into account the rodent migrations. Finally, from the position of the determinative effect of the rodent dispersions on the results of cytogenetic and molecular genetic studies, the authors logically concluded that the migration processes (1) mask genotoxic effects of the radiation influence in residents on radioactively polluted sites [31] and (2) decrease the

frequency of unique alleles in residents (which is an efficient indicator of genetic exchange) [32]. Apparently, our results are a consequence of the migration processes, which cause "diffusion" of statistical effects during pairwise comparison of samples from the EURT zone and the contiguous and background territories. The results documented during the study of genomic instability at the chromosomal level in the bone marrow cells of the common vole (*Microtus arvalis*) caught in the territory, contiguous to EURT (Metlino site) [33] also support this fact; mutant karyotypes and increased level of aberrant chromosomes were found in them as compared with the voles from EURT zone. Data on the influence of microsatellite DNA on the development of chromatin and expression of mutator genes [4] make it possible to expect that variability in microsatellite loci can to a certain extent modify the frequency of chromosomal mutations in the rodent somatic cells and be positively correlated with it (being a marker of general genomic mutation background in the organism).

The materials that we presented confirm the conclusion [33] that the territories adjacent to the Eastern Urals radiation reserve are at present a unique test range (the zone of EURT effect) for estimation of the role of increased mutation frequency in the processes of natural population microevolution. Their mutational pool is expanded owing to gene flows from Eastern Urals reserve. An individual visiting the EURT zone carries away the consequences of the radiation effect (including to significantly distant contiguous territories). It is possible that genetic instability inherited from migrants from the pollution zone can be another source of its completion. A territory with the population carrying the consequences of contact with the pollutant (some kind of continuation of the zone at the level of biological effects) is created around the EURT zone. Migrations in the narrow and extended EURT territory considerably decrease the possibility of transmission and fixation of adaptations in a series of generations in mobile rodent species [28]. Considerable changes in hematopoietic and immune systems that we detected [34], as well as a higher level of chromosomal instability and increased frequency of micronuclei in the bone marrow cells [35] in rodents from the EURT zone, indicate this. The study of allozyme variability demonstrated the absence of differences in the set and frequency of allozymes in northern red-backed voles from the EURT zone and contiguous territories [36].

On the contrary, small mammals living in a huge area of the Chernobyl pollution (Fig. 1a) are exposed to the effect of ionizing radiation in a series of generations (in spite of migrations). This time is sufficient not only for the development of different biological effects but also for their fixation in the genome [37]. At the same time, the processes similar to those in the EURT zone, occur at the borders of the Chernobyl zone. The EURT zone strictly (Fig. 1b) is another type of configuration (narrow extended radioactively polluted territory); biological effects are pronounced [28, 34, 35] but are subjected to constant "diffusion" owing to a change in the population composition.

Summarizing the data obtained, one can conclude that the rodent samples from the head part of the EURT zone and from distant control site differ with respect to indices of microsatellite DNA locus variability. And an increase in a number of parameters of intrapopulation genetic diversity in the site contiguous to the EURT zone (where the level of radioactive pollution corresponds to those in the territories permitted for residence of the population and economic activity) was found. This contradiction at first sight, which is most probably associated with the migration activity of rodents and peculiarities of the configuration of the radioactive pollution zone, requires further study with an increase in the number of microsatellite DNA loci and size of analyzed samples. In this regard, the necessity of considering the migration factor in a wide spectrum of investigations during the study of long-term effects in small mammals in the zones of local anthropogenic pollution should also be highlighted. The results of the study give all grounds to recommend microsatellite markers for the analysis of radiation-induced effects in rodents as model objects of radioecological monitoring.

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