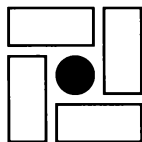# RUSSIAN JOURNAL OF ECOLOGY

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Phenetic Monitoring of Populations
of the Northern Red-backed Vole (*Clethrionomys rutilus* Pall.) in the Zone of the Eastern Ural Radioactive Trace

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Abstract—Monitoring of populations of the northern red-backed vole, carried out in the Kamenskii raion, Sverdlovskaya oblast, over two years (1992 and 1993) revealed that increased morphological diversity accounted for by an increase in the number of small morphogenetic aberrations and malformations in the skull structure steadily manifested itself in the exposed territory (along the axis of the Eastern Ural Radioactive Trace—EURT). It is revealed that the exposed sample has a steady undirectional deviation from the control ones, located outside the EURT zone, with respect to the frequencies of the phenes of nonmetric cranial traits, which do not depend on annual conditions and testifies to the genetic nature of the distinctions. It is assumed that these differences are accounted for by the chronic effects of small radiation doses on the processes of individual development in the northern red-backed vole and the accumulation of small genetic aberrations leading to the manifestation of an increased concentration of phenotypic malformations in the EURT zone.

INTRODUCTION

After the catastrophe at the Chernobyl Nuclear Power Station, the study of ecological, genetic, and morphogenetic effects of the pollution of ecosystems by radionuclides is considered one of the most urgent ecological tasks. One of the first catastrophes of this type occurred in 1957 in the southern Urals near the city of Kyshtym, where, as a result of an accidental emission (up to 2 million Ci), the Eastern Ural Radioactive Trace (EURT) was formed. In the most contaminated area, located along the trace axis, the density of pollution with ^{137}Cs and ^{90}Sr is 1.7–3.2 and 7–40 times higher, respectively, than in the control (Yushkov *et al.*, 1993).

It is known that, upon elevated ^{90}Sr contamination in animal skeletons, the process of ossification of cartilaginous tissues is depressed up to the point of the emergence of strontium rickets (Korzinkin, 1962; Il'enko, 1974; Il'enko and Krapivko, 1993). Such disturbances may manifest themselves as different deformations in the skeletons of rodents and the prolapse of fragments of bones, particularly integumentary ones, in animals dwelling in the area contaminated by radioactive fission products and may affect the occurrence of nonmetric skeletal traits. The analysis of large and small morphological aberrations (phenes of nonmetric traits) of the skeleton are often used in studying the effects of different environmental factors, including radioactive pollution, on the individual development of organisms in populations (Timofeev-Resovskii *et al.*, 1973; Il'enko, 1974; Zakharov, 1987; Yablokov, 1987; Grüneberg, 1964; Palmer and Strobeck, 1986; Parsons,

1992). Therefore, in determining the ecological state of populations, methods based on the occurrence of different disturbances in morphogenesis, as well as on the evaluation of the stability of individual development by the manifestation of the fluctuating asymmetry of bilateral structures, may be useful (Zakharov and Klark, 1993).

On the basis of the data of Il'enko and Krapivko (1993), we may assume that, in populations of small mammals subjected to chronic radiation, general resistance increases from generation to generation, possibly accompanied by change in the genotypic composition of the population.

The aim of this study was to look for possible delayed effects of chronic low radiation on the process of morphogenesis in populations of the red-backed vole (*Clethrionomys rutilus* Pall.), a model radiophore species dwelling in the EURT zone contaminated with radionuclides, by means of phenetic analysis of nonmetric traits, thereby permitting a genetic interpretation of any distinctions found.

MATERIALS AND METHODS

We monitored populations of the red-backed vole in the Middle Urals near the city of Kamensk-Ural'skii, Sverdlovskaya oblast, over two years (1992 and 1993). The choice of the model type was accounted for by the fact that populations of the red-backed vole are numerous and synchronated with forest ecosystems highly contaminated with radionuclides and are marked by a sedentary, burrowing mode of life, i.e., they are
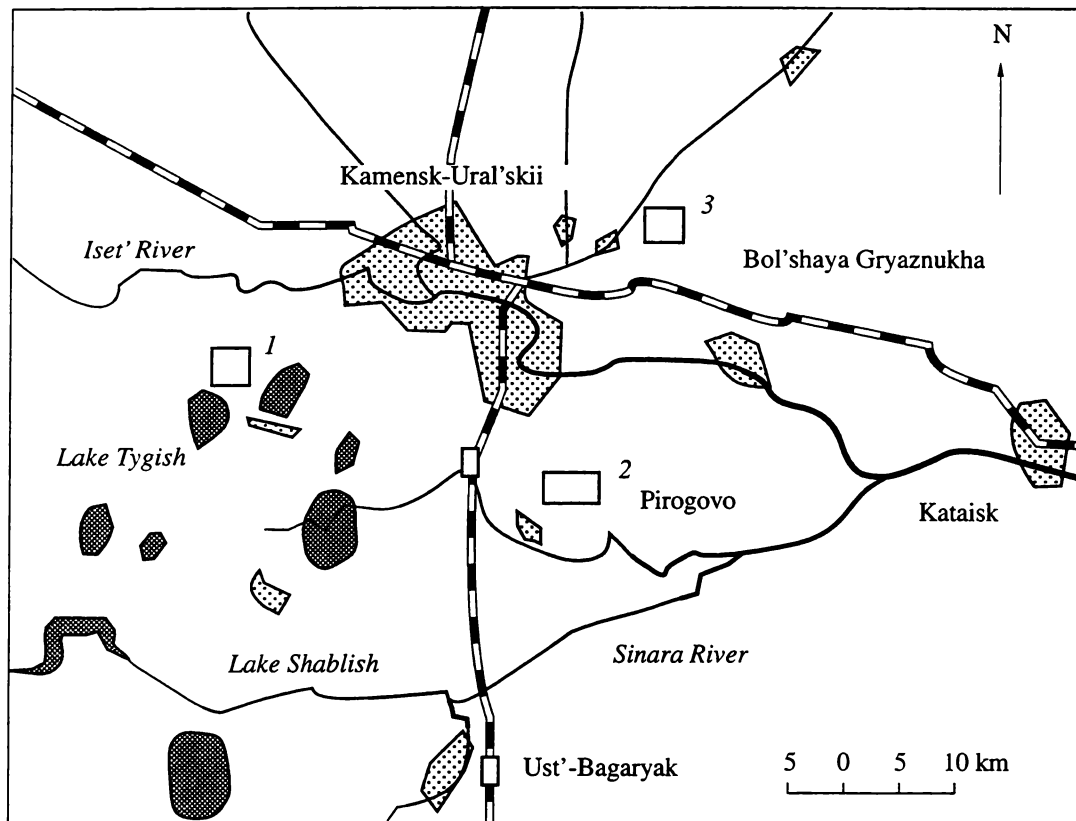
Fig. 1. Map–scheme of the location of the studied territories (marked by rectangles) in the middle Urals near the city of Kamensk-Ural'skii. Populations: (*1*) exposed; (*2*) control-1; (*3*) control-2.

exposed to direct and prolonged radioactive pollution in large territories (over at least 100 generations from the moment of the Chernobyl catastrophe), whereas the species itself is considered a radiophore (Il'enko and Krapivko, 1993).

Plots for catching rodents were located in similar climatic and biotopic conditions and were equally spaced apart (from 22 to 30 km). All the points chosen for collecting material in different years strictly coincided to enable reliable comparisons of allochronous samples. To standardize the habitats, we selected plots of birch–aspen herb–grass forest as a basic biotope. Plots for catching animals are shown in the map–scheme (Fig. 1).

We studied three basic plots: *1*—environs of Lake Tygish within the borders of the EURT zone with an initial level of radioactive pollution of about 5 Ci/km² (exposed population); *2*—environs of the village of Pirogovo (control 1), and *3*—environs of the village of Bol'shaya Gryaznukha (control 2). In the two control plots near the EURT zone (20–25 km away from the first plot), the initial levels of pollution were almost 0.1 Ci/km². An additional study was made of a control plot in the Visimskii Reserve (150 km away from the EURT zone). The latter sample represents a collection of skulls of red-backed voles (21 specimens) from the

Zoological Museum of the Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, which were captured by K.I. Berdyugin in 1977. In total, we studied 262 individual red-backed voles captured during the summers of 1992 and 1993.

We distinguished four age groups on the basis of the degree of the maturity of the teeth roots (Tupikova *et al.*, 1968): 1—*juvenis* (up to 1 month); 2—*subadultus* (1.5–2 months); 3—*adultus* (2.5–5 months); and 4—*senex* (over 8 months). The last group included overwintered animals. In subsequent analysis, the group of the youngest animals was not used.

Basic phenetic analysis was performed on the series including 241 skulls of red-backed voles aged from 1.5 to 5 months—those of *subadultus* and *adultus*. Phenes of nonmetric cranial traits may be broadly considered morphogenetic aberrations. Altogether, we studied 28 phenes of nonmetric cranial traits. The lack of a generally accepted Latin nomenclature of nonmetric threshold traits of the skull and their stable discrete states, i.e. phenes, forced us to restrict ourselves to working names. Some traits were described earlier (Vasil'ev, 1984), whereas those that were revealed for the first time are homologous to traits described by other authors for other species. A complete list of nonmetric traits is given in Fig. 2. The numbering of the
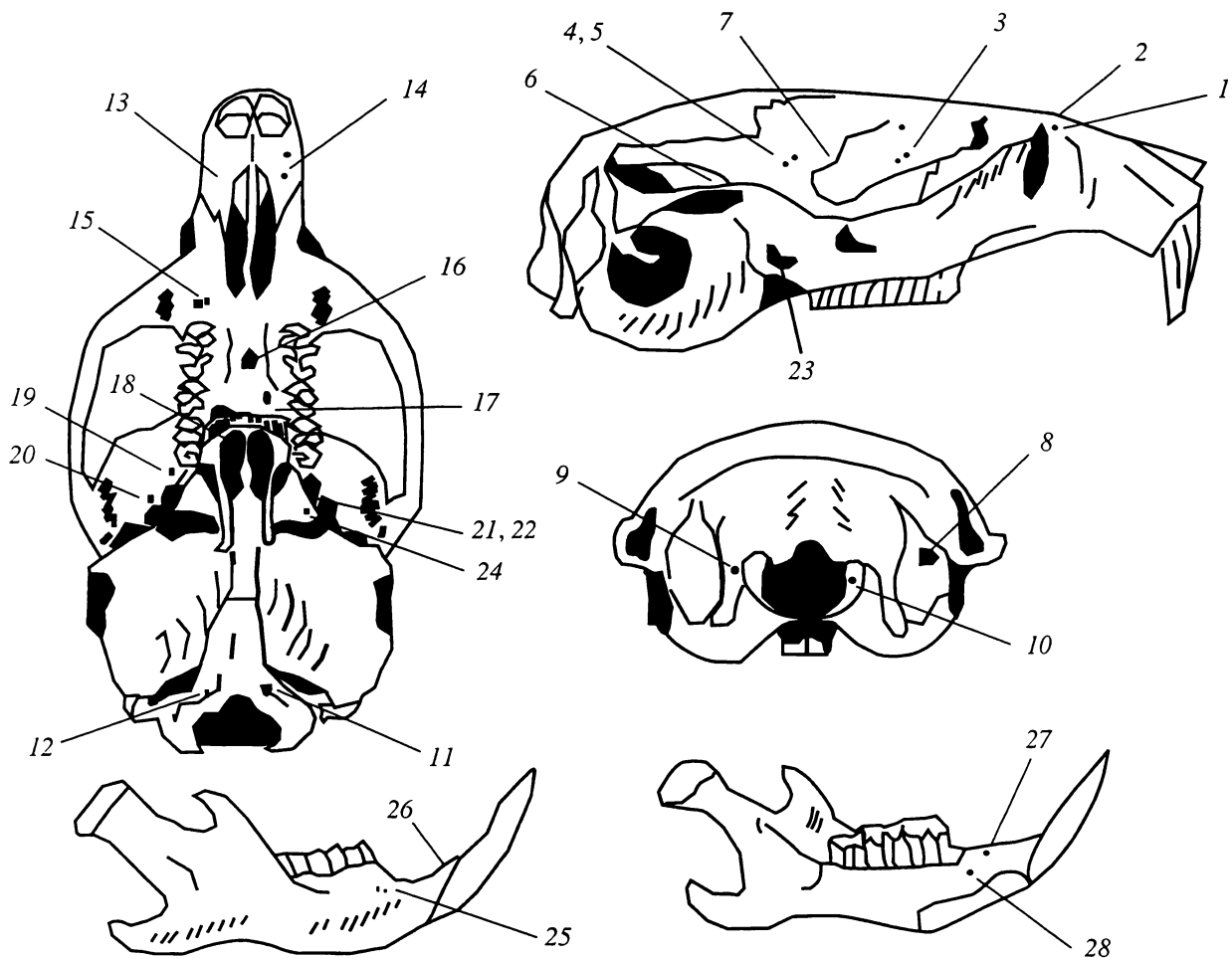
Fig. 2. Scheme of the location of phenes of nonmetric traits on the skull of the red-backed vole. (*1–28*) are trait numbers: (*1*) doubled *foramen praeorbitale*; (*2*) *forma acuminata os nasale*—the aboral end of the nasal bones is sharpened (nonbilateral trait); (*3*) doubled *foramen ethmoidale*; (*4*) lack of *foramen temporale*; (*5*) doubled *foramen temporale*; (*6*) lack of *meatus temporale*; (*7*) *foramen squamosum*; (*8*) *fenestra flocculi*; (*9*) singular *foramen occipitale*; (*10*) presence of the condylar orifice; (*11*) singular inner *foramen hypoglossi*; (*12*) additional inner *foramen hypoglossi*; (*13*) lack of *foramen praemaxillare*; (*14*) doubled *foramen praemaxillare*; (*15*) doubled *foramen maxillare* I; (*16*) *fenestra palatina* (nonbilateral trait); (*17*) closed-type posterior palate end; (*18*) *foramen sphenoidale laterale*; (*19*) additional *foramen rotundum*; (*20*) additional *foramen ovale*; (*21*) additional longitudinal septum *foramen ovale*; (*22*) additional transverse septum *foramen ovale*; (*23*) fusion of the *foramen rotundum* and *foramen ovale*; (*24*) presence of an opening at the ventral surface of the lateral plate *processus pterigoidaeus*; (*25*) doubled *foramen mentale*; (*26*) *foramen mentale anterior*; (*27*) predental opening; (*28*) inner predental opening.

phenes of nonmetric traits is identical to the one listed in the tables. Phenes were calculated on the left and right side of the skull, whereas the frequencies of occurrence for each trait were calculated on the basis of the total number of studied sides (Hartman, 1980). Coefficients of the Spearman rank correlation between the occurrence of different traits and between the frequencies of traits and body sizes were calculated. The dependence of the manifestation of phenes on sex and age was assessed by means of the *G* criterion. Multiple comparisons of samples for particular traits were performed by the *G* criterion (Sokal and Rohlf, 1981).

Phenetic distances (*MMD*) between samples and their standard deviations (*MSD*) were calculated by the Smith formula (Sjøvold, 1977). Differences were sta-

tistically significant at a level of $p < 0.05$ at $MMD > 2MSD$. The measure of uniqueness (*MU*) for each sample was calculated as the sum of all *MMD*s (Berry, 1964).

The average population index of fluctuating asymmetry FA_{nm} was calculated as the average portion of bilateral asymmetrical manifestations of the phene per trait in different individuals (see, for instance, Markowski, 1993). The significance of differences between samples by this index was evaluated by the Kruskal–Wallace method of nonparametric statistics, which is similar to single factor analysis of variance.

In assessing the intrapopulation phenetic diversity, we used the index μ—the average number of trait variations in the sample (Zhivotovsky, 1991).

Statistical treatment was performed with the applied software packages ECOSTAT and PHEN (Version 3.0), which were developed by O.A. Zhigal'skii, A.G. Vasil'ev, and O.A. Luk'yanov at the Institute of Plant and Animal Ecology, as well as with the help of an NTSYS PC (Version 1.4) (Rohlf, 1988).

RESULTS AND DISCUSSION

Analysis revealed that traits 10 (condylar orifice) and 17 (closed-type posterior end of the palate) are sex-related, i.e., they may be accidental in nature, since they makes up only 7% of the traits. The sex ratio in the samples was nearly the same; hence, we decided not to exclude these traits from subsequent analysis and neglect their small effect on the final result of the comparison. The relationship between the occurrence of traits and age was assessed while comparing animals of two different age groups, i.e., the brood of the current year (*subadultus* + *adultus*) and overwintered animals (*senex*). Significant age differences were revealed with respect to five traits (traits 8, 11, 12, 15, and 17), which does not allow us to unite the groups of the brood of the current year and overwintered animals; hence, these age groups were subsequently analyzed as separate samples. Basic comparisons were performed on the group of the brood of the current year. Significant correlations between nonmetric traits and size (length of

Table 1. Frequencies of phenes of nonmetric cranial traits in the exposed and two control populations of the red-backed vole (the material for 1992 and 1993 is consolidated)

Trait number	Control-1		Control-2		Exposed		Multiple *G*-criterion
	K/N	%	*K/N*	%	*K/N*	%	
1	4/231	1.7	1/78	1.3	4/171	2.3	
2	43/116	37.1	16/39	41.0	22/84	26.2	
3	10/229	4.4	0/75	0	11/171	6.4	*
4	1/221	0.5	0/74	0	0/169	0	
5	8/221	3.6	0/74	0	3/169	1.8	
6	36/218	16.5	18/74	24.3	20/170	11.8	
7	25/220	11.4	6/73	8.2	11/170	6.5	
8	40/230	17.4	14/76	18.4	37/168	22.0	
9	70/218	32.1	23/74	31.1	45/166	27.1	
10	56/218	25.7	15/74	20.3	43/164	26.2	
11	48/218	22.0	12/73	16.4	20/164	12.2	*
12	27/219	12.3	11/74	14.9	46/164	28.0	***
13	22/231	9.5	13/78	16.7	47/172	27.3	***
14	46/231	19.9	14/78	17.9	15/172	8.7	**
15	101/231	43.9	30/78	38.5	53/172	30.8	*
16	3/113	3.0	0/37	0	12/85	14.1	**
17	14/224	6.3	7/74	9.5	21/168	12.5	
18	137/220	62.3	43/73	58.9	124/169	73.4	*
19	15/221	6.8	11/70	15.7	16/170	9.4	
20	28/221	12.7	9/72	12.5	47/170	27.6	***
21	5/220	2.3	2/72	2.8	1/170	0.6	
22	11/220	5.0	9/72	12.5	12/170	7.1	
23	3/220	1.4	1/73	1.4	8/170	4.7	
24	90/222	40.5	14/72	19.4	70/170	41.2	**
25	20/232	8.6	6/77	7.8	13/169	7.7	
26	61/231	26.4	24/77	31.2	30/168	17.9	*
27	27/232	11.6	11/77	14.3	28/169	16.6	
28	42/232	18.1	9/77	11.7	17/169	10.1	

Note: Distinctions are statistically significant: *—$p < 0.05$; **—$p < 0.01$; ***—$p < 0.001$; *K* is the number of sides on which the phene occurred, and *N* is the number of the studied sides.

the body) were found in neither the brood of the current year nor overwintered animals. Significant differences in the occurrence of traits on the left and right sides were absent.

Calculation of the coefficients of the Spearman rank correlation between all pairs of nonmetric traits was performed on the group of the brood of the current year. The number of small, but statistically significant, correlations made up 4.2%, which did not exceed the level of random ones (5%). For this reason, none of the traits were excluded from the analysis.

To evaluate the magnitude of possible shifts in phenetic assessments made in different years due to climatic and phenological characteristics, we compared the frequencies of the occurrence of phenes between samples of 1992 and 1993 separately in the exposed and control (environs of the village of Pirogovo) populations. Year-to-year differences were statistically significant for only one trait in the control population and two in the exposed one. Chronographic shift in the frequencies of traits was insignificant and is probably random in nature. Phenetic distances (*MMD*) between samples of different years in the exposed and control populations were extremely small and statistically insignificant (0. 0097 ± 0. 0083 and −0.0050 ± 0.0070, respectively). This permits us to unite corresponding samples of different years and perform all basic calculations on the consolidated material (Table 1).

In the exposed population, we found a specific windowlike prolapse of the fragment of the palatine bone, as well as a large opening in the parietal bone, which are associated with a slowing down of the process of skull ossification. Analogous effects were found by other authors at elevated concentrations of ^{90}Sr in the skeletons of animals (Il'enko and Krapivko, 1989). Single cases of ossification of the fragment of the palatine bone were also discovered in the control population in the environs of the village of Pirogovo in 1993.

Multiple comparison, performed by the *G* criterion, revealed statistically significant differences between the three samples under comparison in the frequencies of 11 phenes (Table 1).

The subsequent aspect of research entailed the evaluation of the level of intrapopulation "phenetic" diversity based on the index μ. Values of the index μ, which characterizes the average number of phenes per trait, are listed separately in Fig. 3 for the brood of the current year and overwintered animals in the four populations under comparison. Similar results were revealed in both age groups. The magnitude of "phenetic" diversity in both the brood of the current year and overwintered animals in the exposed population was significantly higher than in each control population, including the additional sample from the Visimskii Reserve.

To assess the probable effect of the epigenetic deviation of the exposed population from the control ones, we calculated phenetic distances (*MMD*) and the measure of uniqueness (*MU*) of populations in different
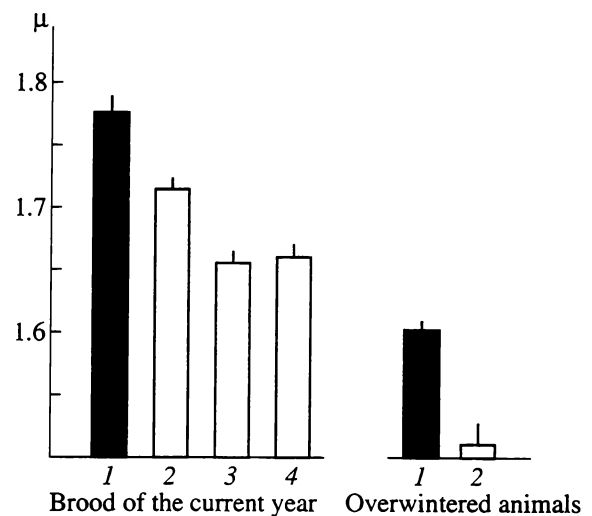

Fig. 3. Levels of "phenetic diversity" (μ) in the brood of the current year of the red-backed vole in exposed and control populations. (*1*) EURT, Lake Tygish; (*2–4*) control; (*2*) Pirogovo; (*3*) B. Gryaznukha; (*4*) Visimskii Reserve.

years (Table 2). It is evident that, in 1992 and 1993, the control groups were similar, and differences between them were statistically insignificant. Conversely, the exposed sample phenetically differs from both control ones almost equally, the differences in both cases being statistically significant (*p* < 0.05). The consolidated material for the two years reveals almost the same pattern of intersample relationship. The value of the measure of uniqueness (*MU*) of the samples from the exposed population (Lake Tygish) in all the three cases is almost three times higher than in the control ones. These distinctions remained steady in both years.

The magnitude of *MMD* between overwintered animals from the exposed and the first control population made up 0.1232 ± 0.0103, whereas the differences between the broods of the current year from these populations were three times smaller (0.0400 ± 0.0031). Unfortunately, the sample of overwintered animals from Bol'shaya Gryaznukha (control 2) turned out to be extremely small and was not used in the comparisons.

Phenetic distances (*MMD*) between these age groups from the two populations were analyzed by Kruskal's nonmetric multidimensional scaling method (1964). Multidimensional scaling was performed by the NTSYS statistical program (Rohlf, 1988). Ultimately, coordinates of the initial samples in a two-dimensional space were derived (Fig. 4). It is clearly seen that intrapopulation differences emerged along the first axis, and age distinctions appeared along the second. The trends of age variation in both populations were different. Age variation was more clearly pronounced in the control population. In the exposed population, differences between the brood of the current year and overwintered animals were considerably less pronounced. It can be assumed that threshold intensifi-
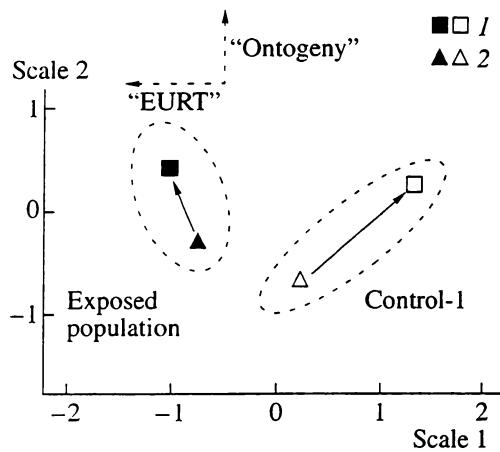
Fig. 4. Phenetic relations between samples of (*1*) the brood of the current year and (*2*) overwintered animals from the control and exposed populations. Ordination was performed by means of multidimensional nonmetric scaling by Kruskal's minimum "stress" method (1964).

cation of interpopulation differences in overwintered animals as compared to the brood of the current year, as well as a different trend of "ontogenetic" alterations in these populations, according to the frequencies of nonmetric traits, reflect epigenetic transfomations in the exposed population, which had been dwelling for a long time in the EURT zone.

The assessment of the average index of fluctuating asymmetry (FA_{nm}) for nonmetric traits as the average population portion of asymmetrical bilateral compositions of phenes per trait was performed separately for the brood of the current year and the overwintered animals in the three populations according to materials from 1992 (Table 3). Using the Kruskal–Wallace test, we established that differences between these groups were statistically significant ($p < 0.01$). Relatively greater values of FA_{nm} were revealed in all groups of the

brood of the current year as compared to overwintered animals. Distinctions in the indices of FA_{nm} between the samples of different populations, when comparing them within one age group, were not statistically significant.

Thus, phenetic monitoring of the red-backed vole, carried out over two years on the EURT-effected territories of the Sverdlovskaya oblast, revealed higher phenetic diversity among animals dwelling on the exposed territory (environs of Lake Tygish), which was accompanied by a steady reliable increase in the proportion of small morphogenetic aberrations (phenes) during skull formation in this group. All the populations compared were nearly equally spaced (about 25 km apart); therefore, *a priori*, their phenetic distances during comparison in pairs should have coincided by level. However, in both 1992 and 1993, the phenetic distances between the two control samples (the environs of the villages Pirogovo and Bol'shaya Gryaznukha) by the frequencies of phenes turned out to be extremely small and statistically insignificant, whereas the sample from the exposed population (environs of Lake Tygish) showed a statistically significant deviation from them. This deviation steadily recurred in different years. It can be assumed that this was due to the chronic effect of small doses of radiation in the EURT zone on the processes of the development of individual red-backed voles, potentially inducing the accumulation of small genetic aberrations and mutations leading to an elevated concentration of phenotypic deformities in the EURT zone. The persistence of the phenetic deviations of animals from the EURT zone in years differing with respect to their ecological conditions testifies to the genetic nature of the deviations. Analysis revealed that the *MMD* between the control and exposed samples of overwintered animals from these populations was three times greater than between the samples of the brood of the current year. The level of differences between the overwintered animals in this case was comparable to that of

Table 2. Matrices of phenetic distances (*MMD*) between the exposed and two control populations of the red-backed vole in different years

Population	Year	Control-1	Control-2	Exposed	*MU*
Control-1	1992	–	0.012*	0.037	0.049
Control-2		0.009	–	0.036	0.048
Exposed		0.006	0.011	–	0.073
Control-1	1993	–	0.003*	0.055	0.058
Control-2		0.015	–	0.056	0.059
Exposed		0.010	0.012	–	0.111
Control-1	1992–1993	–	0.009*	0.040	0.049
Control-2		0.005	–	0.045	0.054
Exposed		0.003	0.006	–	0.085

Note: Upper triangular matrices include phenetic distances (*MMD*), whereas the bottom matrices include the values of the standard deviations (*MSD*) for each *MMD*; *MU* are measures of phenetic uniqueness: sums of *MMD* per one sample (according to Berry, 1964) are listed in the final column of the table; * means that the distinctions are not statistically significant.

Table 3. Average indices of the fluctuating asymmetry (FA_{nm}) of nonmetric traits (average portion of asymmetrically displayed traits per individual) in two age groups (brood of the current year and overwintered animals) in the exposed and two control populations of the red-backed vole (1992)

Age group	Populations			
	Control-1	Control-2	Exposed	Composite
Brood of the current year	$n = 37$ 22.0 ± 1.0	$n = 18$ 20.3 ± 2.0	$n = 23$ 20.6 ± 1.5	$n = 78$ 21.17 ± 0.77
Overwintered animals	$n = 28$ 16.0 ± 1.6	$n = 4$ 14.5 ± 3.0	$n = 22$ 15.0 ± 1.7	$n = 54$ 15.44 ± 1.09
Significance of differences between age groups	$p < 0.01$	ns	$p < 0.05$	$p < 0.001$

Note: ns means that distinctions are not statistically significant.

significant interpopulation distinctions (Vasil'ev, 1984).

It is particularly remarkable that the indices of FA_{nm} in the brood of the current year were higher than in the overwintered ones; however, within each age group, the interpopulation differences in these indices were not pronounced. With age, it seems likely that the selection of animals exhibiting traits more symmetrically on both sides of the body occurs, whereas, in all populations, individuals with a higher level of fluctuating asymmetry (FA) drop out. The fact that, in the exposed population, the effects observed are similar to those for the control ones, and the population itself does not differ from them in the FA index and "behaves normally," may indirectly indicate that the process of development in the population has already normalized. It is possible that an adaptation to low doses of radiation has already developed in this population. The emergence of new traits of development in the exposed population is confirmed by the local increase in the phenetic diversity and steadily high MMD between the exposed and control populations, as compared to the distinctions between the control ones. Since the present levels of radioactive pollution of the territory under study are relatively small, the observable specific features of the exposed population in the EURT zone can be considered the results of the delayed effects of the Kyshtym catastrophe, which have an accumulative nature.

Thus, the data obtained are in line with data of the long-term study by Il'enko and Krapivko (1993) in the southern part of the EURT zone, which is more extensively contaminated with radionuclides. We agree with their conclusion that, under these conditions, an increase in the radioresistance of the population occurs from generation to generation, accompanied by alterations in the genotypic composition of the population. Our analysis enables us to consider that, in the exposed population, stable genetic alterations in the developmental process have already emerged, whereas the process itself resembles a normal process evolving in a new epigenetic way. It may be assumed that this is simultaneously accounted for by two factors. The first

factor includes the chronic effects of small doses of radiation on the processes of the individual development of red-backed voles and the accumulation of small genetic aberrations in the population leading to the manifestation of an elevated concentration of phenotypic malformations in the EURT zone. The second factor is associated with the selection of sires most resistant to the effects of small doses of radiation, accompanied by the formation of adaptive genetic transformations of the process of development. Further monitoring may reveal whether the level of the specific nature of the exposed population becomes more pronounced or whether, during the 100 generations that have passed since the catastrophe, it has already attained a new stable adaptive state.

ACKNOWLEDGMENTS

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