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Analysis of Rodent Populations in Technogenically Transformed Areas (with Reference to *Apodemus* (*S.*) *uralensis* from the EURT Zone)

E. B. Grigorkina, G. V. Olenev, and M. V. Modorov

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia

e-mail: grigorkina@ipae.uran.ru

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Abstract—It is shown that the response of rodent populations to acute and chronic irradiation depends on its functional structure, i.e., on specific features of animals with two alternative types of ontogenetic development. Upon acute irradiation, sexually immature young of the year (animals with the second type of ontogeny) are most radioresistant. Exposure to chronic irradiation, as in the zone of the Eastern Ural Radioactive Trace (EURT), leads to an increase in the proportion of mature young of the year (animals with the first type of ontogeny), which are the most radiosensitive part of the population. The abundance and fecundity of mice in the impact zone are consistently higher than in the background zone, which improves the adaptive potential of the population. The role of species ecological specialization and configuration of the contaminated zone in the formation of migrant rodent population is emphasized. It is concluded that a high migration activity allows the pigmy wood mouse (a radiosensitive species) to avoid long-term radiation exposure.

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Key words: rodents, species diversity, population dynamics, population structure, functional approach, EURT, configuration of contaminated zone, species specialization.

The Kyshtym radiation accident in the Southern Urals (1957) resulted in the formation of the Eastern Ural Radioactive Trace (EURT). In the 1990s, the scope of the radiation safety problem expanded to protection of biotic components of the environment, including plant and animal communities as well as ecosystems as a whole (Aleksakhin, 2006). It was proposed to change from the anthropocentric principle of biota protection to the ecocentric principle (Pentreath, 1999). In radioecology, the problem of radiation resistance and the closely related but poorly studied problem of adaptive biodiversity remain highly relevant. It is known that small mammal species markedly differ in radioresistance, which may lead to the disturbance of interpopulation relationships and simplification of community structure. At present, ecological systems of different structural levels, from the organism–environment system to the biota–nonliving nature (biosphere) system are generally considered homeostatic (Bolshakov and Kryazhimskii, 2001). There is no doubt that adaptation to unfavorable environmental conditions is achieved via supraorganismic complexes such as populations and biocenoses. However, population mechanisms of such processes remain obscure because of the absence of adequate methods for analyzing responses of natural ecosystems to radioactive pollution. At the same time, poor knowledge of population responses proper implies the importance of studies based on regular monitoring of the populations long living in radioactively contaminated areas.

This paper, in which we systematized and generalized published data and the results of our own studies, is devoted to comparative analysis of the species composition of rodents, the abundance and structural–functional organization of colonies of pigmy wood mice (*Apodemus* (*S.*) *uralensis* Pallas, 1811), and resistance of these animals to acute and chronic (in the EURT zone) irradiation.

MATERIALS AND METHODS

Our field studies in plots with different levels of radioactive contamination were performed between 2002 and 2006. The impact plot lies on the EURT axis 13 km from the explosion epicenter. The background γ-radiation level at the soil surface varies from 22 to 76 μR/h, averaging 50 μR/h; the β-radiation count varies from 90 to 942 cpm/cm^2, averaging 380 cpm/cm^2. Soil contamination density (^{90}Sr) in the EURT zone varies from 6740 to 16 690 kBq/m^2, compared to 44 kBq/m^2 in the background area (Pozolotina et al., 2005). The impact plot comprises different types of biotopes: a mixed herb–nettle association (17 plant species), mixed herb–reed grass birch forest of a park type (32 species), mixed herb–grass birch forest of a park type (45 species), mixed herb–grass meadow, and ecotonal habitats (Grigorkina et al., 2006). The background plot is beyond the Eastern Ural Reserve, 10 km from the impact site and 2 km northeast of the village of Metlino. It accommodates a mixed herb–nettle association and mixed herb–grass birch forest of a park type (22 plant species). The background γ-radiation level is 12 μR/h, and the β-radiation count is 12 cpm/cm^2.

Murine rodents were caught by the trap-line method. Crush traps with standard bait (110 traps per plot) were set 5 m apart for three days. The relative abundance of rodents was estimated from the first-day catch per 100 trap–days. The total amount of field work reached 7803 trap–days, and 1476 small rodents of 10 species were caught (876 ind. in the EURT zone and 600 ind. in the control area). Among them, 546 animals (319 from the impact and 227 from the control plot) were identified as *A.* (*S.*) *uralensis*.

For estimating species diversity, we used two types of indices: the Margalef index of species richness D_{Mg} (Magurran, 1992) and the μ and *h* indices based on the relative abundance of species (Zhivotovsky, 1980). The species diversity index μ (most informative for analyzing community structure) was calculated on the basis of the proportional contribution of each species. The index *h* that characterizes the proportion of rare species in the community was calculated as follows: $h = 1 - \mu/m$, where *m* is the number of species.

The population structure of *A.* (*S.*) *uralensis* was studied using the functional–ontogenetic approach (Olenev, 2002). Its essence is that the main criterion for identifying intrapopulation structural units is the functional unity of individuals in groups corresponding to two alternative types of ontogenetic development. The function of animals representing the first type of ontogeny (mature young of the year) is to increase population abundance by breeding in the year of birth. The function of individuals with the second type of ontogeny (the young that fail to mature in the year of birth) is to preserve the corresponding part of the population until the next spring with the smallest possible losses and, in the status of overwintered adults, to begin the cycle of population renewal. The functional status of animals was determined by a set of external and internal characters, and their age was estimated from the degree of upper molar wear (Kolcheva, 1992). In analyzing age structure, three functional groups of animals were distinguished.

Mature young of the year (the first type of ontogeny) are individuals that continue their growth and development. Males have well-developed testes with distinct, usually filled epididymises. Characteristic of females are open vagina, vaginal plugs, thickened uterus, embryos, placental spots, suckling spots, yellow bodies, and enlarged adrenal glands. The second upper molars (M^2) have cuspidate crowns, but the tips of cusps are often already blunt. By August, some animals (mainly females) have M^2 with cusps worn down almost completely and dentin exposed in no more than 60% of the uneven masticatory surface.

Immature young of the year (the second type of ontogeny, the first phase) are individuals that fail to mature in the year of birth. Their growth becomes retarded after they leave the group of juveniles. Males have undeveloped testes; females, closed vagina and filamentous uterus. M^2 has a cuspidate crown, but M^3 may be noticeably worn down.

Overwintered animals (the second type of ontogeny, the second phase) remain immature until spring. After maturation, their body weight reaches definitive values. Male and female generative characters are similar to those in mature young of the year. In late spring, M^2 look the same as in females with the first type of ontogeny. In August, M^3 are worn down completely; in M^2, dentin is exposed in more than 70–80% of the masticatory surface.

Special attention should be paid to the group of **juveniles**, young animals (age no more than 30–45 days, body weight no more than 12 g) that have not yet diverged with respect to the type of ontogeny. They continue growing and have a high metabolic rate. Although morphophysiological parameters may indicate the beginning of maturation (enlarged testes, thickened uterus), these animals cannot yet be assigned to the first type of ontogeny, but assigning them to the second type by formal criteria would be also erroneous. The enamel of molars in most individuals is worn insignificantly.

The ratio of functional groups was estimated from annual data for June and July. Comparative analysis of morphophysiological indices at the level of functional groups was performed by the standard method. Data were processed statistically with the EXCEL 6.0 and STATISTICA 5.0 program packages.

RESULTS AND DISCUSSION

Faunistic diversity of rodents. The species lists consists of ten species (Table 1), most of them being widespread. The riparian meadow is inhabited by root, field, narrow-skulled, and water voles; the birch forest, by northern red-backed voles. Mice are common to all types of biotopes, being highly abundant in ecotonal habitats and in sites occupied by the mixed herb–nettle association. Pigmy wood mice numerically dominate in both plots (from 40 to 60% according to data on catches in different years); therefore, the data presented below concerns mainly this species. Striped field mice rank second by numbers; the remaining species are scarce and occur sporadically.

The average values of the Margalef index of species richness (D_{Mg}) in both plots are similar: 1.12 in the

Table 1. Average data on species composition of rodents (%) and indices of their species diversity in test plots

Species	Years									
	EURT					control				
	2002	2003	2004	2005	2006	2002	2003	2004	2005	2006
A. uralensis	40.6	39.5	53.4	37.6	41.1	57.6	34.7	38.4	61.4	22.8
A. agrarius	23.3	14.3	17.5	56.7	21.8	16.4	28.1	6.2	19.7	60.6
M. oeconomus	25.6	38.5	26.2	1.2	16.5		3.7	7.7		1.3
Cl. rutilus		3.3		1.2	6.5	26.0	25.2	15.4	14.8	9.4
A. terrestris	9.3	1.1			10.0					
M. arvalis		1.1		1.2	0.6		5.6	27.7	3.3	3.4
M. agrestis		1.1		0.5			0.9	4.6		2.1
M. gregalis				1.4	2.9				0.8	0.4
S. betulina	1.2	1.1	2.9	0.2	0.6		0.9			
M. minutus							0.9			
Total, ind.	86	91	103	426	170	73	107	65	122	233
Number of species	5	8	4	8	8	3	8	6	5	7
D_{Mg}	0.90	1.55	0.65	1.16	1.36	0.47	1.50	1.20	0.83	1.10
Index of species diversity (μ)	4.2 ± 0.2	5.0 ± 0.2	3.4 ± 0.2	3.7 ± 0.2	5.8 ± 0.3	2.8 ± 0.1	5.5 ± 0.4	5.2 ± 0.3	3.6 ± 0.2	4.3 ± 0.2
Proportion of rare species (*h*)	0.17	0.17	0.16	0.54	0.27	0.07	0.32	0.13	0.29	0.39

EURT and 1.02 in the control ($t = 0.44$, $df = 8$, $p = 0.67$). They are also close to those for murine rodent communities of anthropogenically disturbed areas of Chelyabinsk oblast (Nurtdinova, 2005). The values of index μ based on the relative abundance of species (μ) are also similar: 4.40 in the EURT and 4.26 in the control ($t = 0.20$, $df = 8$, $p = 0.85$); the same applies to the proportions of rare species (*h*): 0.26 in the EURT and 0.24 in the control ($t = 0.23$, $f = 8$, $p = 0.82$). No significant differences in the indices of species diversity were recorded in the Chernobyl zone (Baker et al., 1996) and in the EURT zone with a contamination level of 1000 Ci/km^2 (Chibiryak and Krashaninina, 2007). Note that the structural index μ in the EURT zone is comparable to that determined by Lukyanova and Lukyanov (2004) for small mammal communities of the Visim Biosphere Reserve (the Middle Urals) before the impact of destabilizing factors such as windfall and fire (μ = 3.86). Therefore, recent levels of radioactive contamination do not cause any decrease in species diversity of murine rodents in the Eastern Ural Reserve.

Morphophysiological characteristics of the pigmy wood mouse. A comparison of indices between territorial groups of mice (EURT and control) revealed differences in some characters (Table 2). Overwintered males from the impact plot were larger, but the kidney, adrenal, and spleen indices proved to be significantly smaller in overwintered females. In groups of mature young of the year from the EURT, the heart index in males was lower and the adrenal index in females was higher than in the control group. In the group of immature young of the year (due to the absence of sex-related differences, males and females were pooled), indices did not differ from those in the control. Changes in most morphophysiological parameters showed no distinct trends: some parameters were higher in control animals, while others were higher in animals from the impact zone. A direct comparison revealed similar variability of indices in both samples. At the same time, indices calculated for animals of different functional groups from the impact zone are close to those in *A.* (*S.*) *uralensis* inhabiting collective gardens in Chelyabinsk oblast (Nurtdinova and Pyastolova, 2006). A distinctive feature of animals in all functional groups from the EURT zone is a low spleen index. The spleen as one of the most radiosensitive organs is highly sensitive to irradiation.

Numbers, structure, and dynamics of demographic parameters. The observation period covered different phases of rodent population dynamics (Fig. 1). The total animal abundance varied by years with a three- to fourfold amplitude: In the EURT, from 16.6 to 54 ind./100 trap–days; in the control, from 16.1 to 51.5 ind./100 trap–days. Note that the abundance of mice in the EURT zone was also consistently higher than in the control plot: 7.6–28.1 vs. 5.6–18.4 ind./100 trap–days, respectively; it changed in both plots synchronously and reached the highest values in 2005 and

Table 2. Morphophysiological characteristics of *Apodemus* (*S.*) *uralensis* mice with different types of ontogeny (2002–2006)

Index, ‰	Sex	EURT				Control				*p*
		N	$\bar{X}$	*StD*	*Me*	*N*	$\bar{X}$	*StD*	*Me*	
Ontogeny type I (mature young of the year)										
Body weight, g	♀	7	22.63	2.93	23.00	12	20.89	2.97	21.19	0.23
	♂	12	18.15	3.79	16.80	11	18.57	3.32	19.40	0.64
Heart	♀	7	8.29	2.55	8.00	12	7.81	1.12	7.64	0.61
	♂	12	6.99	1.57	7.37	11	8.23	1.09	8.32	0.04
Liver	♀	7	68.65	11.28	65.79	11	67.97	13.79	67.62	0.91
	♂	12	58.06	8.25	59.35	11	66.13	15.10	63.92	0.12
Kidney	♀	7	9.42	1.81	9.87	12	9.08	1.40	9.02	0.66
	♂	12	9.14	2.69	8.73	11	9.68	1.69	9.66	0.31
Adrenal gland	♀	7	0.36	0.11	0.35	11	0.24	0.08	0.26	0.02
	♂	12	0.27	0.08	0.27	10	0.38	0.15	0.38	0.06
Spleen	♀	7	2.94	1.95	2.17	12	3.24	2.01	3.19	0.74
	♂	12	3.14	1.50	2.70	11	4.05	1.92	3.94	0.16
Testis	♂	12	11.23	1.47	11.12	11	12.01	2.64	11.23	0.38
Ontogeny type II (phase 1, immature young of the year)										
Body weight, g		69	17.67	1.95	17.4	32	16.05	1.36	15.9	$\ll$0.01
Heart		68	8.17	1.43	8.18	32	8.04	0.89	7.76	0.54
Liver		68	51.96	8.37	52.56	32	54.06	7.86	54.55	0.23
Kidney		69	7.75	1.22	7.72	31	7.74	1.57	7.22	0.53
Adrenal gland		69	0.34	0.12	0.32	31	0.31	0.08	0.28	0.10
Spleen		65	2.29	1.01	2.17	31	3.40	1.60	3.13	$\ll$0.01
Ontogeny type II (phase 2, overwintered animals)										
Body weight, g	♀	23	22.44	2.51	22.90	8	22.26	3.74	22.50	0.88
	♂	30	24.94	1.94	24.76	23	22.89	2.16	23.40	<0.01
Heart	♀	23	7.22	1.64	6.87	8	8.13	1.73	8.03	0.11
	♂	30	7.54	1.45	7.75	23	8.10	1.21	8.29	0.14
Liver	♀	23	65.43	9.92	68.97	8	72.37	17.43	86.35	0.42
	♂	30	60.47	10.72	58.79	20	57.78	10.18	57.29	0.38
Kidney	♀	23	8.31	1.48	8.19	8	9.90	2.04	9.97	0.02
	♂	30	8.50	2.02	8.28	23	8.62	1.48	8.81	0.81
Adrenal gland	♀	23	0.25	0.09	0.26	7	0.37	0.12	0.35	0.01
	♂	30	0.24	0.07	0.22	23	0.26	0.10	0.25	0.30
Spleen	♀	22	3.17	1.43	2.92	8	4.77	1.89	4.97	0.03
	♂	29	5.07	2.47	4.19	23	5.28	2.35	4.44	0.50
Testis	♂	30	11.16	1.32	10.88	23	11.67	2.01	11.06	0.42

2006. The lowest abundance of all murine rodents in both plots (18 and 16 ind./100 trap–days) was recorded in 2004. This could be due in part to destabilization of the environment: in May 2004, the entire territory of the Eastern Ural Reserve was engulfed in fire, and rodent abundance recorded one month later remained at the spring level (5 ind./100 trap–days). The control plot was simultaneously damaged by agricultural machines, which also affected animal abundance (3 ind./100 trap–days).

The seasonal dynamics of population structure and abundance in the pigmy wood mouse (Fig. 2) were of the same type. The abundance of overwintered animals (the initial number of spawners) at the beginning of the breeding season in all years did not exceed 5 ind./100 trap–days. Pygmy wood mice, which are

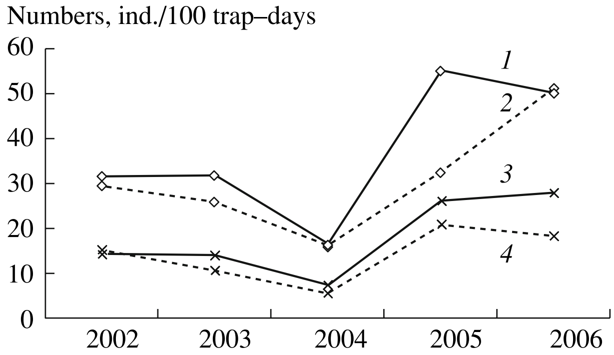

Fig. 1. Rodent population dynamics from 2002 to 2006 (annual average values): (*1*, *2*) rodents in the EURT and control areas; (*3*, *4*), *Apodemus* (*S.*) *uralensis* in the EURT and control areas, respectively.

highly mobile, concentrated in spring mainly in ecotonal habitats and birch forest with suitable food and shelter conditions. The initial state of the population at the beginning of the breeding season largely determines subsequent abundance. A comparative analysis of the abundance ratio between groups with different types of ontogeny (Fig. 3) provides evidence for the important role of overwintered animals in the reproductive part of the EURT population. Their proportion in years of medium (2002–2003) and high (2006) abundance reached 60–80%, compared to 40% in the control population. However, the proportion of mature young of the year involved in reproduction is also substantial. In 2005, for instance, the population increment in both plots was accounted for mainly by young of the year, which produced two litters by mid-June; in overwintered females, three groups of spots were recorded. The seasonal peak of abundance in September 2005 (Fig. 2) and successful wintering provided a reliable basis for population growth in 2006 (in May, the abundance of mice was 40 ind./100 trap–days in the EURT zone and 10 ind./100 trap–days in the control), with the role of overwintered animals being most significant. Previously, an inverse relationship was revealed between the durations of breeding period in overwintered animals and in young of the year: in years when this period is long in overwintered animals, young of the year reproduce poorly, and vice versa (Olenev, 2002). A change in the age structure of the population leads to a change in its genetic structure (Shvarts, 1969).

The results of long-term monitoring of rodent populations (Olenev, 2002) show that the age composition of the overwintered group is highly variable: even in extreme years (drought), when sexual maturation of young of the year is blocked, animals of all generations born in the previous year are already present in the population, which is especially important under unfavor-

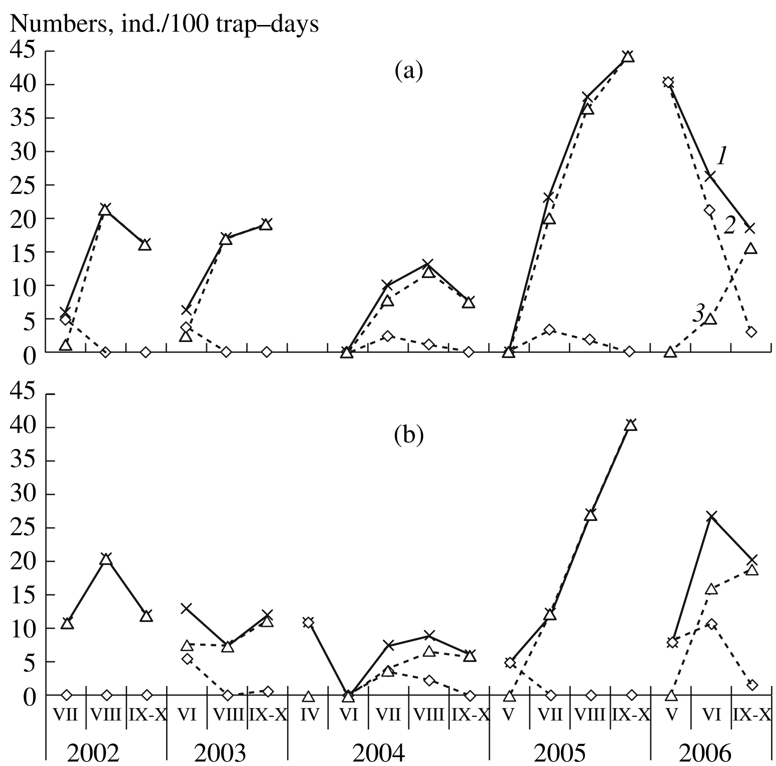

Fig. 2. Seasonal dynamics and structure of *Apodemus* (*S.*) *uralensis* population (a) in the EURT and (b) in the control: (*1*) overwintered animals and young of the year; (*2*) overwintered animals; (*3*) young of the year. Roman numerals indicate months.

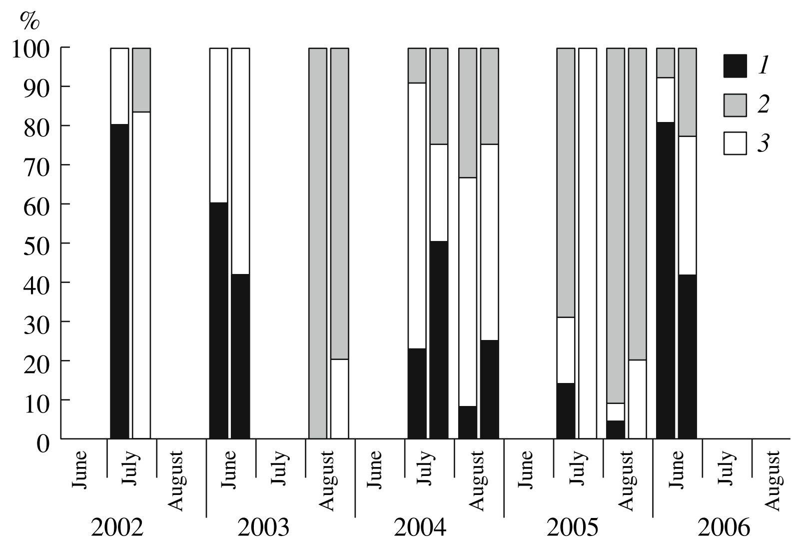

Fig. 3. Ratio of ontogeny types in *Apodemus* (*S.*) *uralensis* by functional groups: (*1*) overwintered animals, (*2*) immature young of the year, (*3*) mature young of the year (left bars, EURT; right bars, control).

able environmental conditions. The higher the proportion of overwintered individuals, the higher the potential for transgeneration transmission of genetic information (see below). As follows from Fig. 3, the proportion of overwintered individuals in the EURT zone markedly varied during the observation period. Trends revealed in the impact territory agree in part with data on long-term dynamics of pygmy wood mouse population structure and abundance in a river floodplain fluvial plain (Orenburg oblast), where optimal habitat conditions are disturbed in the period of spring flood (Kolcheva, 2002).

Radiosensitivity to acute and chronic irradiation in the pigmy wood mouse. Note that *A.* (*S.*) *uralensis* is a radiosensitive species: the integrated index of radioresistance $LD_{50/30}$ is only 7.0 ± 0.4 Gy (Grigorkina and Pashnina, 2007) and does not differ in animals from the impact and control samples equalized with respect to functional status. Our previous study on bank voles (*Clethrionomys glareolus* Schreber, 1780) from the natural population showed that individuals differing in the functional status also differ significantly in $LD_{50/30}$, life span, and the response of the hematopoietic system to acute irradiation at the same dose (Olenev and Grigorkina, 1998). For instance, mortality among mature young of the year was 53.6%, compared to 17.6% among immature young of the year. This phenomenon is based on differences in the rate of metabolic processes. In a natural population, acute irradiation may affect the ratio of its reproducing and nonreproducing parts and, as a result, its abundance. Since the ratio of individuals with different types of ontogeny considerably differs by seasons and by years, the total damaging impact on the population will also be different. If these structural changes (an increase in the proportion of resistant individuals) are preadaptive, it is logical to suppose that, in case of exposure to another damaging factor (for instance, radiation) in this period, the total damaging effect should be considerably weaker. It was found that the response of the population to unfavorable factors (for instance, drought or very high population density) is expressed in a decrease in the proportion of individuals with the first type of ontogeny (most sensitive) and an increase in the proportion of individuals with the second type of ontogeny (most resistant) (Olenev, 1981). This is a general, nonspecific adaptive response of the population to regular (common) autumn–winter–spring conditions that has developed in the course of evolution.

Under conditions of chronic irradiation (the EURT zone), the dominant group in the population are individuals with the first type of ontogeny, i.e., the mature children of overwintered animals, which form the second generation. The group of overwintered animals, whose members are equal physiologically (Table 2), is highly heterogeneous, since it includes representatives of all generations born in the previous year, with their proportions being variable. This provides the possibility of genetic information transmission not only via successive change of generations, but also directly from the first generation born in a given year to the first generation born in the next year of birth (transgeneration transmission). Knowledge of these aspects appears important for the practice of ecogenetic studies on rodents, since overwintered animals, being similar in morphophysiological and many another aspects, differ in origin and, in different years, may qualitatively differ in the ratio of allele frequencies. This is not only a result of successive generation change rations, but also a qualitative basis for assessing the adaptive potential of the population.

Biological effects observed in animals from the EURT zone may be conventionally divided into two groups. The first group includes the appearance of carriers of inherited chromosomal instability (Gileva et al., 1996), an increase in the proportion of morphogenetic aberrations and anomalies in cranial structure, and an elevated level of fluctuating asymmetry (Vasil'eva et al., 2003). The increased frequencies of bone marrow cells with micronuclei and peripheral leukocytes with structural anomalies in mice and voles should also be included in this group (Grigorkina and Pashnina, 2007). The second group comprises changes in physiological characteristics of animals. For instance, mice from the contaminated zone are characterized by numerous shifts in the hematopoietic system and reduced functional activity of the immune system (Pashnina, 2003). In addition, as shown in studies on reproductive characteristics of murine rodents in a radioactively contaminated biocenosis, their actual fecundity is higher, whereas embryonic mortality and the proportion of females with embryonic losses are significantly lower than in the background area (Grigorkina et al., 2006).

It is known that inherited effects play the main role in the development of pathological processes in small mammals living in radioactively contaminated areas. The total absorbed dose in the sequence of rodent generations ranges from 6.0 to 27.0 Gy (Lyubashevsky et al., 1995). Such a wide range is evidence for unceasing gene exchange that takes place due to constant fluxes of migrants from relatively clean to contaminated areas and vice versa. Therefore, the opinion concerning isolation of radiogenic groups of mice and voles in the Eastern Ural Reserve is erroneous.

Considering the possibilities of adaptation of small rodents to the technogenic environment, attention should first be paid to the configuration of contaminated zone and ecological specialization of species (Grigorkina and Olenev, 2004). According to data of specialists from the Institute of Geophysics (Ural Division, Russian Academy of Sciences), the maximum width of the trace with a ^{90}Sr soil contamination density of 1.0 Ci/km^2 is about 10 km (Utkin et al., 2001). Since the transverse size of the cloud was small, radioactive fallout concentrated along the axis of its movement. Therefore, the widths of areas with different ^{90}Sr contamination densities in the study region are as follows: 1000 Ci/km^2, 800 m; 500 Ci/km^2, 1400 m; 250 Ci/km^2, 1580 m; and 50 Ci/km^2, 1800 m. At the same time, vagility of pigmy wood mice and their specific migration pattern (seasonal interbiotopic migrations) (Kolcheva, 2002) allow them to quickly colonize large areas comparable to the width of the contaminated zone. This provides for the formation of a flowing (migrant) population (Grigorkina and Olenev, 2004), whose composition changes on account of in-migrants from clean areas and out-migrants from the impact area. However, for some animals (pregnant and lactating females, juveniles, and resident individuals), the time of staying there proves sufficient for the development of disturbances, including those of hereditary nature that may be reliably traced. Note that it is temporal residence that considerably decreases the probability that certain changes will be fixed and inherited in a series of generations. Thus, rodents of mobile species escape long-term exposure to the damaging factor (radiation), which interferes with the development of radioadaptation in these animals.

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