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Functional Structure in Populations of Small Mammals (Radiobiological Aspect)

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Abstract—Two alternative types of ontogenetic development commonly occurring in populations of small mammals were analyzed as a manifestation of the polyvariant developmental potential using the functional approach at the level of functional physiological groups (FPG). An example of bank vole (*Clethrionomys glareolus*) was used to demonstrate that rodents of two developmental types significantly differ in radioresistance, i.e., in the survival rate and response of their hemopoietic system to acute total irradiation regarded as an anthropogenic damaging factor. A forecast is made concerning the possible response of a population to two successive damaging factors, of which the first has already resulted in adaptive structural modifications.

INTRODUCTION

Studying structural and functional organization of the populations of small mammals is of a great theoretical and practical interest. On the one hand, many researchers considered the diversity of population response to adverse factors in connection with population heterogeneity; on the other, studies showed that animal radiosensitivity depends on age, sex, and biochemical and other features of individuals (Graevskaya, 1972). However, the response of a natural rodent population to ionizing radiation has previously been studied without taking into account the functional state of individual animals. To analyze the dynamics of key population parameters, we developed the functional approach originally intended for the zoological studies (Olenev, 1981, 1989). This gave rise to the analysis of fine age structure (Olenev, 1982) and various aspects of studying populations with reference to their structure (Kryazhimskii, 1989; Bezel' and Olenev, 1989; Testov, 1993; Luk'yanov, 1997).

The essence of the functional approach is that the main criterion for distinguishing intrapopulation structural units is the functional unity of individuals in the groups corresponding to two ontogenetic types. The groups are distinguished on the basis of functional status (the functional state of animals associated with growth pattern, development, and reproductive state) and the synchronism of its temporal changes. For convenience, we distinguished three functional physiological groups (FPG). Each group usually consisted of animals originating from several adjacent cohorts (Fig. 1) and combined into a functional unit of population reproduction (for more detail, see Olenev, 1989).

Note that studies on the characteristics of so-called seasonal generations (Shvarts, 1969) provided the basis for the concept concerning the functional population structure. We regard our investigations as their continuation and development.

BRIEF CHARACTERIZATION OF TWO ONTOGENETIC TYPES

The first type of ontogenetic development (FPG 3) is characterized by juveniles participating in reproduction during the first year of life. They predominantly belong to the first cohorts (usually, 70–90%), grow rapidly, reach the body weight of overwintered animals (25 g, on an average), and begin mating (Fig. 1). These animals are characterized by a monophasic growth (Fig. 2) and a high metabolic level; they rapidly grow old and live for three to five months. The initial stage of the tooth root formation is recorded at the age of 65–75 days. The population function of this animal group is to increase population size in the year of their birth.

The second type of ontogenetic development (FPG 2 ⟶ FPG 1). These juveniles do not mate during the first year of life. They predominantly belong to the late cohorts (Fig. 1); however, some animals of the

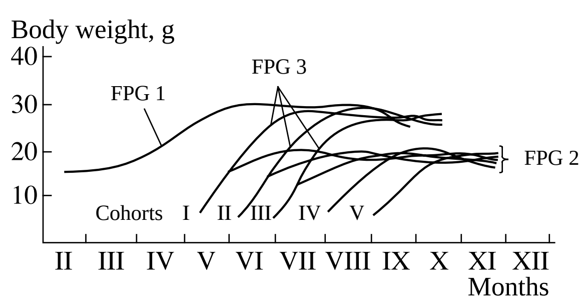

Fig. 1. Dynamics of average body weight in animals from different cohorts (I–V) of a natural population (individually marked animals).

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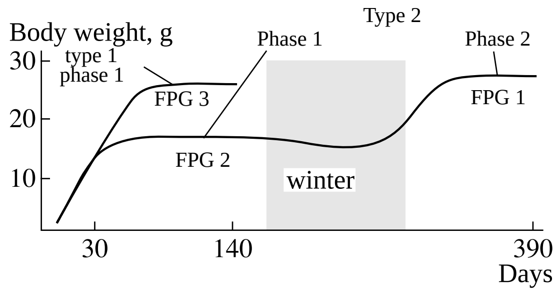

Fig. 2. The scheme of two developmental types: (FPG 3) monophasic growth and (FPG 2 ⟶ FPG 1) biphasic growth.

early cohorts (usually 10–30%) do not mate during the first year of life. These animals are characterized by a biphasic growth (Fig. 2) and a low metabolic level. They cease growing at the age of approximately one month and body weight of 16–18 g, irrespective of the season, thus completing the first ontogenetic phase. The initial stage of the tooth root formation is recorded at the age of 120–130 days. These animals grow old two times slower than the animals of FPG 3, and they live for 13–14 months (taking into account the period corresponding to FPG 1). In the next spring, the "conservation" period is completed by a short-term growth and maturation within two to three weeks. The animals reach definitive size at the body weight of 24–27 g. Almost all overwintered animals (FPG 1) maturate. The activity of metabolic processes is similar to that in the animals of FPG 3, although the absolute age of these overwintered animals is substantially greater. The animals of FPG 2 form the population reserve, become FPG 1, and begin a cycle of population renewal. The scheme and reasons for animal divergence (the trigger mechanism resulting in two developmental pathways) were discussed previously (Olenev, 1994).

POTENTIALITY OF THE FUNCTIONAL APPROACH AND ADDITIONAL CHARACTERISTICS OF TWO ONTOGENETIC TYPES

The functional approach is promising for a detailed analysis of a wide range of basic biological parameters. Cyclomorphic animals (rodents) characterized by two alternative ontogenetic types of growth and development (monophasic and biphasic growth) were used to demonstrate that the dynamics of many biological parameters is determined functionally.

At the organism level, substantial differences were revealed in the following parameters: metabolism intensity (morphophysiological parameters), the rate of aging (age markers), and life span (Olenev, 1981, 1991); significant differences in the mitotic index (Olenev *et al.*, 1983); biochemical distinctions (specific changes in the electrophoretic pattern of transferrins) (Gulyaeva and Olenev, 1979); differences in the accumulation of heavy metals in bone tissue (Bezel' and Olenev, 1989); and changes in proliferation rate (in the corneal epithelium) under technogenic pollution (Gatiyatullina *et al.*, 1988). The rate of changes in age markers (age-related changes in teeth) also strictly depended on the ontogenetic type to which an individual belonged; in particular, this allowed us to determine the age of rhizodont voles with twice greater accuracy (Olenev, 1989).

At the population level, substantial changes in the ratio between animals of the first and second developmental types were revealed against the background of a universal adaptive response to a wide range of adverse factors, both natural (drought or high population density) (Olenev, 1981; Olenev and Kolcheva, 1987) and anthropogenic.

This study deals with the radiobiological aspect of the functional population structure. We consider the radiation effect as a powerful deleterious anthropogenic factor frequently affecting natural associations and humans. Previously, we considered this topic briefly (Grigorkina and Olenev, 1987, 1996). The purpose of this study was to estimate radioresistance of animals differing in their functional status (FPG 2 and FPG 3) by criteria of average semilethal dose ($LD_{50/30}$) and response of the hemopoietic system.

MATERIALS AND METHODS

We performed laboratory experiments using animals from a natural bank vole population (*Clethrionomys glareolus* Schreb.) captured in Il'menskii Nature Reserve (the Southern Urals). After preliminary maintenance in a vivarium for ten days, animals were exposed to gamma radiation emitted by ^{137}Cs at a dose of 9.0 to 15.0 Gy (at 0.5-Gy intervals) to obtain a dose–effect curve for each FPG and to determine $LD_{50/30}$. We examined two animal groups belonging to two developmental types, i.e., reproductive juveniles from the first spring and summer cohorts (FPG 3) and nonreproductive juveniles, mainly from the late autumn cohorts (FPG 2). Irradiated animals were kept on a standard diet and observed daily for 30 days.

To exclude possible effect of vivarium conditions and the diet on radiosensitivity, we determined $LD_{50/30}$ in voles of the vivarium colony (using FPG 2 as an example). We estimated lethality, average life span, and the response of the hemopoietic system after irradiation at a dose of 12.7 Gy using seven animals for each time point in both functional groups under study. Nonirradiated animals from the same natural sample and functional groups served as controls. A total of 177 animals from FPG 2, 130 from FPG 3, and 63 individuals of FPG 2 bred in the laboratory were used. The data on animal mortality after irradiation were processed by the probit method and traditional statistical methods.

RESULTS AND DISCUSSION

Survival rate is an integral parameter of radioresistance commonly used in studies on organisms of various constitution. The most valid parameter is the dose causing 50% mortality of irradiated animals, as its use reduces the effect of individual variation of this parameter in the population.

Average Semilethal Dose and Survival Rate

Animals of FPG 2 proved to be significantly more radioresistant ($LD_{50/30}$ = 13.2 ± 0.1 Gy) than voles of FPG 3 ($LD_{50/30}$ = 12.7 ± 0.2 Gy, $p \leq 0.05$). A comparative study of tolerance to radiation in voles of FPG 2 from the natural population and the laboratory colony (born in the vivarium in late August–early September of the same year and examined simultaneously with animals captured in nature) revealed no significant differences between corresponding average semilethal doses. Thus, for animals of the same functional status from the laboratory colony and the natural population, $LD_{50/30}$ were 13.1 ± 0.1 and 13.2 ± 0.1 Gy, respectively. Ogryzov (1970) reported that radiosensitivity of great and Mongolian gerbils substantially increased when they were kept on the laboratory diet, which was attributed to the presence of plants with a distinct radioprotective effect in the natural diet.

When determining the average semilethal dose, we compared the mortality of animals from different functional status after irradiation at a dose of 12.7 Gy. Thus, mortality among juveniles mating in the year of birth (FPG 3) was almost three times higher than among FPG 2 juveniles (table).

Average Life Span

The average duration of life within a certain period of observation after animal exposure to radiation is also a criterion of radiation effect and is inversely proportional to the irradiation dose (Luchnik, 1957). Comparative analysis (at a dose of 12.7 Gy) revealed significant differences between the examined groups in life span (table) and time of animal death (Fig. 3).

Differences between voles from different functional groups were also manifested in the progression of acute radiation sickness after irradiation at this dose. Clinical manifestations (dyspepsia, refusal to eat, decrease in motor activity, and conjunctivitis) were expressed to a greater extent in rodents of FPG 3. Moreover, these manifestations ranged from the partial presence of individual symptoms to distinctly expressed radiation damage. In animals of FPG 2, symptoms of radiation sickness were weakly expressed.

Response of the Hemopoietic System

Radioresistance in mammals depends on radiation damage to radiosensitive systems, including the hemopoietic system. Actively proliferating bone marrow cells are extremely radiosensitive, and this fact is responsible for death of the bone marrow syndrome (*Effects...*, 1992). A key parameter characterizing the severity of radiation damage and the completeness of regeneration in the hemopoietic system is the total leukocyte count. Animals of different functional status substantially differed in the hemopoietic cell kinetics. In animals of FPG 2, the number of leukocytes decreased after irradiation to a significantly lesser extent and the degree of hemopoiesis restoration was greater than in representatives of FPG 3. We think that changes in bone marrow of irradiated rodents is of essential interest, as the degree and pattern of damage in animals from different intrapopulation groups did not differ significantly (Fig. 4). However, the rates of bone marrow regeneration differed: by the end of observation, the number of bone marrow cells in animals from FPG 3 and FPG 2 reached 70 and 100% of the initial number, respectively.

We found that cell dynamics in the spleen (a decrease in number and regeneration rate) was similar to that in bone marrow. However, this parameter was generally inadequate for characterizing radiation damage in wild rodents because of a high variation of weight and cell number in this organ. Parameters of the spleen in wild rodents were shown to be a highly variable interior trait serving as an indicator of the state of population (Ivanter *et al.*, 1985).

Thus, parameters of cell dynamics in the hemopoietic tissue (a radiosensitive and critical system of organism) showed that animals of different developmental

Mortality and average life span of animals from different functional groups irradiated at a dose of 12.7 Gy

Parameter	Group	
	FPG 2	FPG 3
Number of animals, ind.	34	41
Number of dead animals, ind.	6	22
Mortality, %	17.6	53.7
Average life span, days	9.8 ± 1.0	13.5 ± 0.7

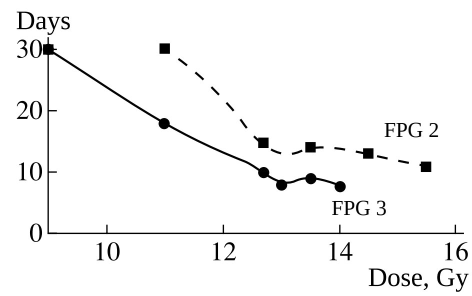

Fig. 3. Time of death after irradiation at different doses in voles from two FPG.

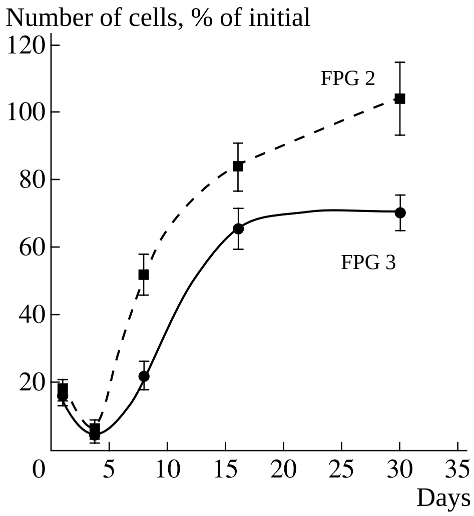

Fig. 4. Bone marrow cell dynamics in voles of different functional status after irradiation at a dose of 12.7 Gy.

types substantially differed in the response to total acute irradiation; namely, rodents of FPG 2 (a reserve for population renewal) showed a relatively greater radiation resistance. Reproductive juveniles (FPG 3) were characterized by a greater metabolic intensity and a two times higher mitotic index (the parameter characterizing the activity of tissue metabolism) than juveniles of FPG 2 (Olenev *et al.*, 1983). Radiobiological studies showed that dividing cells of actively proliferating tissues (such as hemopoietic) are extremely sensitive to the damaging effect of radiation, especially during mitosis. This is evidence that a relatively greater resistance to radiation in the animals remaining nonreproductive in the year of birth is determined by low levels of metabolism and energy consumption. This can be regarded as a general adaptive population response (similar to the adaptation syndrome proposed by H. Selye) to anthropogenic damaging effects, as well as to adverse natural effects such as drought (Olenev, 1981) and increased population density (Shilov *et al.*, 1977; Olenev and Kolcheva, 1987). This was first proposed by Olenev (1981) and corroborated by subsequent natural experiments on the damaging effect of heavy metals (Bezel' and Olenev, 1989).

The concept of two alternative ontogenetic types is applicable to small mammals belonging to cyclomorphic animals (rodents) and inhabiting regions with distinct alternation of winter and summer seasons (e.g., it was confirmed under both severe climatic conditions of the Urals and relatively mild conditions of Ukraine).

CONCLUSION

The analysis of previously published data and our experimental results confirmed that the adaptive population response to a wide range of factors (including damaging anthropogenic effects, in particular, ionizing radiation), being determined by the nature and intensity of these factors, also depends on the functional structure of the population (in this case, on the specificity of two alternative developmental types of rodents). Animals of the same individual age but different functional status significantly differ in mortality after irradiation at the same dose, 53.6% and 17.6% in the first (FPG 3) and second (FPG 2) developmental types, respectively, and in the response of the hemopoietic system. In natural populations, this can influence the ratio of reproductive and nonreproductive animals and, consequently, the population size. Similar radiosensitivity of nonreproductive juveniles (FPG 2) from natural populations and the laboratory colony suggests that the diet of bank vole lacks natural radioprotectors.

We believe that the functional approach should not be limited to the practice of radioecological studies. Its use will substantially reduce errors and provide a better methodological basis for estimating the consequences of a wide range of deleterious effects. The general damaging effect of radiation or any other factor on a population depends on differences in the sensitivity of intrapopulation groups to corresponding influences. As the ratio between animals of different developmental types substantially differs both seasonally and annually, the general damaging effect on the population should also differ. Olenev (1981) showed that the adaptive population response to adverse conditions involves a decrease in the number of the most sensitive animals of the first developmental type (FPG 3) and an increase in the proportion of the relatively more resistant animals of the second developmental type (FPG 2). If these structural changes (an increase in the proportion of resistant individuals) are preadaptive, it is logical to assume that the simultaneous exposure of the population to some other damaging factor, e.g., radiation (superposition of effects), will produce a substantially weaker total effect.

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