

Evolutionary Ecological Analysis of Adaptation Strategies of Rodent Populations under Extreme Conditions

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Abstract—Adaptive strategies of cyclomorphic rodent populations (Rodentia) under extreme conditions of droughts (in 1975 and 2010) have been analyzed on the basis of functional–ontogenetic approach. The following features of these strategies have been revealed: minimization of metabolic processes, block of sexual maturation, intergenerational crossing, prolongation of breeding period, and species-specific features in the dynamics of intrapopulation processes. Profound changes in the level of long-term oscillations of abundance after the drought have been noted in different species. Evidence is provided for the possibility of extremely rapid population rearrangements on an evolutionary scale that are fixed in a series of generations.

Keywords: evolutionary ecology, rodents, functional–ontogenetic approach, abundance, intergenerational crossing, drought, adaptive strategies

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In general, the development of the biota and the biosphere as a whole proceeds in the regime of coevolution of living and nonliving matter, with the normal course of development being occasionally interrupted by crises and rearrangements (Moiseev, 2001). Analysis of responses of animal communities and populations to different biotic and abiotic factors in order to reveal the mechanisms of their adaptation to changing environmental conditions is a current problem in modern ecology. Of special interest in this context are years with extreme conditions, which, in Glotov's (1983) terms, create a contrasting background that provides for especially clear manifestation of adaptive changes in animals at different organizational levels. Droughts, particularly those in the forest zone, may be justly regarded as an extreme factor that can have a destructive impact on ecosystems and, in particular, on rodents, which cannot leave the zone of drought, unlike ungulates that seasonally migrate in the savannas of Africa (Akimushkin, 1965; Blon, 1982).

The main factor affecting rodents during droughts is the deficit of succulent forage conditioned by low precipitation or its absence and high temperatures. Droughts are known to have an aftereffect on their populations, which manifests itself in the first year or two after the drought (Polyakov, 1954; Golenishchev, 1958; Olenev, 1979). However, it will be shown below that they also cause changes in population dynamics on a long time scale (tens of years). Factors responsible for such long-term changes and their phenomenol-

ogy have been poorly studied, which is explained by insufficient observation periods, on the one hand, and the rarity of extreme events entailing serious changes in population dynamics.

Droughts in arid zones are common and occur regularly. It has been shown that they have a differential effect on reproductive contributions of older and younger individuals, retarding maturation of the young (Polyakov, 1954; Golenishchev, 1958; Gladkina and Mokeeva, 1969). Rodents in arid zones are characterized by decreased abundance and fecundity, relatively narrow range of tolerable environmental conditions, shifts in the rhythms of diurnal activity (Shuai et al., 2014) and the timing of emergence from the nest, redistribution of resources expended for different life activities (e.g., foraging and mating) (Smith et al., 2014), and change in body size (Ohlberger et al., 2013).

Droughts in the forest and forest–steppe zones (the Ural region, 1975 and 2010) occur much more rarely and differ in duration from those in arid zones. A drought such as in 1975 had never been recorded over the previous 50-year history of meteorological observations in the Urals: there was no rain from April throughout summer, and even some trees aged over 80 years were damaged or died off.

The summer drought of 2010, named the Great Russian Drought (Shmakin et al., 2013), had an impact on not only national but also on global scale (Barriopedro et al., 2011; Shmakin et al., 2013). Com-

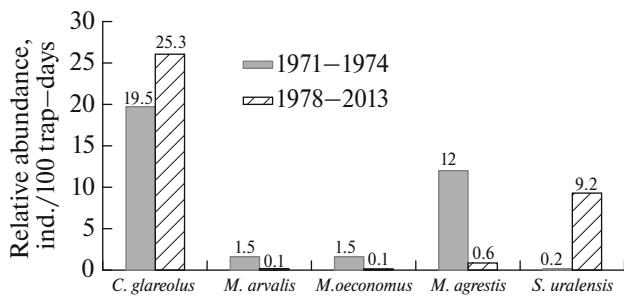


Fig. 1. Comparative data on relative abundance of rodents in the Ilmen Nature Reserve before and after the 1975 drought (long-term average values).

pared to the unusually long 1975 drought, it was shorter in duration—from mid-June to mid-August (Cherenkova et al., 2015)—but marked by extremely high temperatures (with monthly average values being 5–7°C above normal) and low precipitation throughout European Russia and in some neighboring territories. The exceptionally hot summer of 2010 exceeded the amplitude and spatial extent of the previous heat wave in western Europe in the summer of 2003. Because of this drought, the emergency situation regime was declared in 13 districts of Chelyabinsk oblast.

Having available a 43-year long series of continuous observations, we could perform an up-to-date analysis of the impact of the 1975 and 2010 droughts on the communities and populations of murine rodents (Rodentia) in the southern taiga subzone and Transural forest–steppe. The relevance and significance of the data presented below lie in providing an insight into the adaptive strategies of widespread rodent species under extreme conditions of drought and its remote consequences for rodent cenoses and populations.

MATERIAL AND METHODS

Analysis was performed on the basis of field data collected in two test areas in the Southern Urals (Chelyabinsk oblast), with emphasis of the extreme drought years 1975 and 2010. The effects of the 1975 drought were studied using the material from the Ilmen Nature Reserve obtained between 1971 and 2014¹. The reserve lies in the pine–birch forest band of the Southern Ural pre-forest–steppe (Gorchakovskii, 1968), the total amount of material was more than 10000 ind. The data on the 2010 drought were collected in the zone of the Eastern Ural Radioactive Trace (EURT) over the period from 2002 to 2014 (more than 3000 ind.). According to forest and Geobotanical zoning, the EURT zone lies in the Transural forest–steppe and is characterized by alternation of meadow–steppe areas,

¹ Data on the years 1971–1973 were taken from Gashev (1975).

birch or birch–aspen forest outliers, and (less frequently) pine forests (Gorchakovskii, 1968; Koleznikov, 1960).

From year to year, rodents were trapped in the same biotopes to exclude the effect of biotope preference on the results of catches. Both traditional and original methods of field research were used, including capture–mark–recapture (CMR) (ind./ha), irreversible removal (ind./100 trap–days), the method of morphophysiological indicators, and methods for determining the absolute age of animals. The age–sex structure of rodent communities was analyzed on the basis of functional–ontogenetic approach (Olenev, 2002), which implies identification of structural units within a population based on the functional status of individuals (i.e., specific features of growth, development, and involvement in reproduction). The animals were attributed to intrapopulation functional groups (corresponding to different types of ontogeny, or life history patterns) with regard to a complex of exterior and interior traits characterizing the state of their reproductive system, taking into account age markers. Thus, three groups were distinguished: reproductive young of the year (ontogeny type 1); nonreproductive young of the year, i.e., those that fail to mature in the year of birth (ontogeny type 2, phase 1); and overwintered animals (ontogeny type 2, phase 2).

The results were processed statistically using MS Excel 2007 and STATISTICA 6.0 programs.

RESULTS AND DISCUSSION

In the Ilmen Nature Reserve, six rodent species were recorded: the bank vole (*Clethrionomys glareolus* Schreb., 1780), northern red-backed vole (*Cl. rutilus* Pall., 1779), pygmy wood mouse (*Sylvaemus uralensis* Pall., 1811), field vole (*Microtus agrestis* Linnaeus, 1761), common vole (*M. arvalis* Pall., 1779), and root vole (*M. oeconomus* Pall., 1776). The data on their relative abundance in the rodent cenosis before and after the drought are shown in Fig. 1. The impact of the drought was refracted through the lens of specific consequences for individual genera (species), which are considered below.

Population Strategies of Clethrionomys Voles

The response to drought in both species of this genus (*Cl. glareolus* and *Cl. rutilus*) proved to be identical. Therefore, the results of analysis are described using the example of bank vole, which is the absolute dominant in the study region. The spring of 1975 started 1 month earlier than usual, and the same was true of breeding season in these rodents. An increase in body size was noted as early as in late February; an increase in the size of testes, in early March; and mass emergence of the young was observed in April (usually, this occurs during the first 10 days of May). The subsequent course of breeding was unusual. Overwintered animals ceased to mate in early July, and all

young of the year (100%) remained nonreproductive, i.e., belonged to the group with ontogeny type 2 (Olenev, 1979, 1981). All cohorts consisted only of the young born to overwintered parents; i.e., animals with ontogeny type 1 were absent, which resulted in an atypical population structure: a whole generation was missing! Young of the year failed to breed not only in dry but also in sufficiently moist biotopes, and their morphophysiological parameters remained low until the next spring, providing evidence for a low rate of metabolic processes. The state of overwintered animals did not differ from normal, and it is only this group that accounted for population growth. The sex ratio was equal among both overwintered animals and young of the year (Olenev and Grigorkina, 2011).

The consequences of drought for the population were as follows:

(1) The autumn–winter period of 1975–1976 was marked by significant animal mortality. According to CMR data, the absolute population density dropped by spring to 2.1 ind./ha, with the overwintered group having a simplified age structure (Olenev, 1981). The animals matured and started breeding 1 month later than usual. This may be regarded as an aftereffect typical of rodents in arid zones (Polyakov, 1954; Golenishchev, 1958, Olenev, 1979).

(2) Population growth in 1976 was achieved due to a prolonged breeding period of overwintered females (5.5 months vs. usual 3.5 months), which lived for an average of 16 months and produced 5–6 litters each (compared to 12–13 months and 3–4 litters). This was interpreted as an adaptive response of the population (specific physiological state of animals related to the conditions of growth and development in the previous season) providing for the maximum utilization of possibilities for population growth. The breeding of overwintered animals could be prolonged due not only to abiotic conditions in the year of their birth but also to the quality and amount of food. The role of the food factor is confirmed by the results of experiments on reducing the amount and caloric value of food, which show that this helps to increase the life span and reproductive period of rodents (McCay, 1952; Comfort, 1960; Lynch and Ennis, 1983).

(3) Overwintered females mated with overwintered males until midsummer and then, when the latter died, with male young of the year from the first cohorts (the proportion of female young of the year was small). Thus, intergenerational crossing was noted in *Cl. glareolus* in the next year after the drought, against the background of increase in life span and reproductive period (Olenev, 1982), and this phenomenon is known to help in maintaining heterogeneity of the population.

The pattern of population processes was recovered in 1977. The overwintered group successfully survived the autumn–winter season (1976–1977). The life span of individual cohorts in 1977 was the shortest, the

abundance of animals increased due to active breeding of young of the year (ontogeny type 1), and the population cycle was completed with its peak. Thus, the adaptive strategy of the bank vole population under the extreme conditions of drought proved to completely coincide with the strategy that is observed from year to year in wintering individuals (Olenev et al., 1980; Olenev, 1981). The survival of animals under these conditions was achieved due to the same adaptation mechanisms aimed at reducing energy expenditures to a minimum through cessation of growth, retardation of sexual development, and minimization of metabolic processes. It was most important for the population to preserve the young rather than to increase its size by involving young of the year in breeding.

Population Strategies of Microtus Voles

The response of *M. oeconomus*, *M. arvalis*, and *M. agrestis* voles to the 1975 drought was principally different from that of *Clethrionomys* voles. In addition to overwintered animals, young of the year from the first and second cohort matured and were involved in breeding (ontogeny type 1). The proportion of males was significantly greater among both overwintered and young voles (Olenev and Grigorkina, 2011), and both these groups contributed to the formation of population size; i.e., the situation was close to long-term average. However, the consequences for the populations of all *Microtus* species were disastrous: their abundance dropped abruptly because of mass mortality among yearlings in the autumn–winter season of 1975–1976, and the level of its oscillations has become significantly lower and remained so since 1977 (Fig. 2). These processes also had certain species-specific features concerning mainly the levels of abundance before and after the drought.

The abundance of *M. oeconomus* in the period before the drought was at the lowest level. It reached 1.5 ind./ha in the drought year but dropped by more than half in 1976, which was followed by deep population depression in 1977 (Fig. 2). Since then, the relative abundance of this species has remained very low, increasing to about 1.0 ind./100 trap–days only in some years.

The abundance of *M. arvalis* prior to the drought was comparable to that of *M. oeconomus*. It then increased to 8 ind./ha in 1975, decreased to 0.4 ind./ha in 1976, and slightly increased again in 1977 (to 2 ind./ha). Thereafter, the general level of abundance dropped to 0.56 ind./100 trap–days and has remained low (Fig. 2).

The most vivid picture of “population crash,” with transition to a lower level of oscillations in abundance, was revealed in *M. agrestis*. Prior to 1975, this species was codominant with the bank vole, and the level of oscillations in its abundance was consistently high, as in the latter. In the drought year, mass mortality among

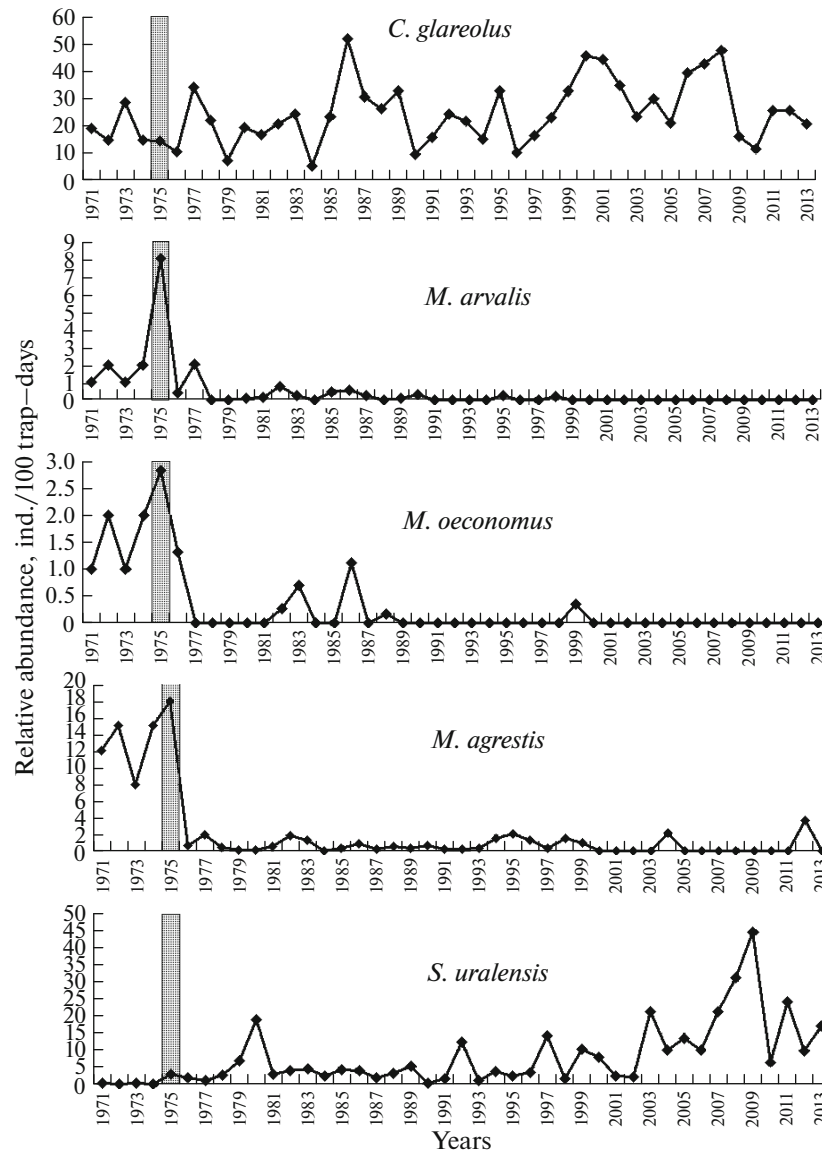


Fig. 2. Dynamics of abundance of five rodent species in the Ilmen nature Reserve before the 1975 drought (1971–1974) and after it (1976–2013). The drought year is indicated by hatched bar.

young of the year took place, and population abundance dropped by autumn by more than an order of magnitude, from 18 to 1 ind./100 trap–days. Today, 40 years later, this parameter is about 0.1–2 ind./100 trap–days (Fig. 2).

It should be emphasized that the new levels of oscillations in the abundance of all the three *Microtus* vole species proved to be fixed in time.

Population Strategy of the Pygmy Wood Mouse (Genus Sylvaemus)

The response to drought in *S. uralensis* and its consequences for the population of this species proved to differ from those in *Clethrionomys* and *Microtus* voles.

Individuals of this species rarely occurred in catches prior to the drought, but their abundance increased to 2.0 ind./ha in the drought year (Fig. 2). The results of long-term studies on small mammals in the Ilmen Nature Reserve show that *S. uralensis* during the subsequent period has become codominant with *Cl. glareolus*, replacing *M. agrestis* in this role, and proved to be the only species that has changed over to a higher level of population oscillations. The abundance of *S. uralensis* has shown a tendency to increase in recent years (see Fig. 2).

Thus, the species composition of the rodent cenosis has remained the same after the 1975 drought, but the representation of individual species in it has drastically changed, and the majority of them have

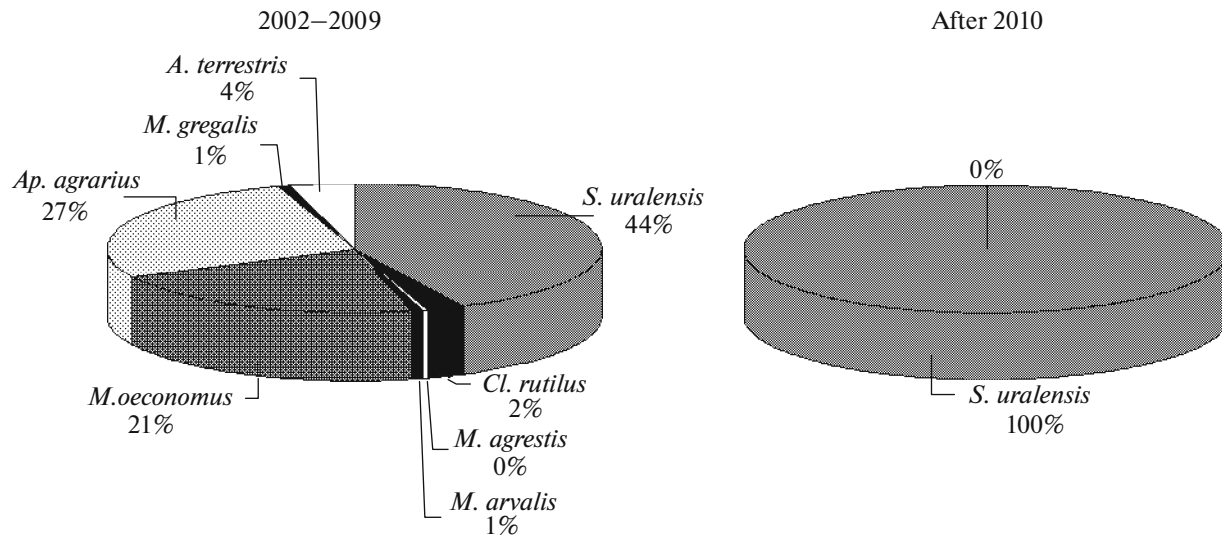


Fig. 3. Composition of rodent censuses in the Eastern Ural Radioactive Trace before the 2010 drought (2002–2009) and after it.

changed over to a different level of population oscillations.

The consequences of the 2010 drought in the EURT zone were no less serious, despite the aforementioned differences of this event from the 1975 drought. In particular, they included significant transformation of the rodent census toward simplification of its species composition (Grigorkina et al., 2013). Before the drought, the species list of rodents in this zone consisted of eight widespread species: the pygmy wood mouse (*S. uralensis*), striped field mouse (*A. agrarius*), root vole (*M. oeconomus*), northern red-backed vole (*Cl. rutilus*), European water vole (*Arvicola terrestris*), common vole (*M. arvalis*), field vole (*M. agrestis*), and narrow-skulled vole (*M. gregalis*). (Fig. 3). The pygmy wood mouse was a consistent dominant, with its proportion in catches ranging from 40 to 60%; then followed the striped field mouse (14–56%, averaging 27%) and the root vole (21%). In 2010, rodents were represented by a single species, *S. uralensis* (Fig. 3). Today, single *Microtus* voles and field mice may also sporadically occur in catches.

In the spring of 2010, the rodent breeding season in the EURT zone started 1 month earlier than the long-term average date, as did the 1975 season in the Ilmen reserve. Catches made in late April included a considerable proportion of parous females, with many others being at the latest stages of pregnancy; in May, pregnant young of the year appeared. As calculated from the results of monthly catches, the annual average abundance of rodents (represented exclusively by *S. uralensis*) was 45 ind./100 trap–days. The seasonal peak of abundance (65 ind./100 trap–days) was recorded in September.

A detailed analysis of age–sex structure of *S. uralensis* population based on samples taken in summer

(June–July), when all functional groups are represented in it, provided evidence for intergenerational crossing (Grigorkina et al., 2013). The essence of this phenomenon is that breeding pairs are formed by animals of different ages, generations, and functional groups. According to Shvarts (1969), intergenerational crossing is due mainly to the difference in the rate of maturation between males and females. In the spring of 2010, overwintered males mated overwintered females, and the latter produced two or sometimes even three litters by the middle of summer. The relative abundance of overwintered females in summer was low because of their early mortality, which was probably explained by adverse drought conditions, but there was a large proportion of mature female young of the year, which were also mated by overwintered males. Morphophysiological parameters of male young of the year indicated that they were not involved in breeding. Apparently, it is the numerical dominance of overwintered males and the difference in the timing of death between overwintered males and females (Olenev and Grigorkina, 2011) that prevented sexual maturation of male young of the year and thereby stimulated intergenerational crossing.

Intergenerational crossing in rodents of the genera *Clethrionomys* in the Ilmen reserve (1976) and *Sylvaeomys* in the EURT zone (2010) is an adaptive strategy aimed at the maximum utilization of possibilities for population growth along with preservation of the young and improvement of genetic heterogeneity. Such a strategy may be a consequence of early elimination of either males or females.

In essence, intergenerational crossing is a transgenerational pathway of hereditary information transmission. Its significance increases not only in years with extreme conditions (drought, excessive population

density, etc.) but also in a human-modified (radioactively contaminated) environment, as shown in our previous study (Grigorkina and Olenev, 2012). This pathway is an ecological mechanism for maintaining population heterogeneity as well as a channel for transgenerational transmission of genetic and epigenetic effects induced by technogenic (radioactive) pollutants when animals from the zone of local radioactive contamination (EURT) migrate to neighboring areas (Grigorkina and Olenev, 2013).

Thus, the status of species under conditions of changing environment and exposure to extreme factors mainly depends on its ecological plasticity, which is achieved due primarily to the flexibility of extremely complex intrapopulation structure and changes in the ratio of functional groups (types of ontogeny) characteristic of murine rodents. Observations on changes in the demographic structure and abundance of rodents from different taxa provided evidence for the existence of **different forms of population response** to drought (adaptive strategies).

One form of response (in *Clethrionomys* voles) is that **population abundance increases due only to breeding among overwintered animals, with sexual maturation of the young being blocked** (minimization of metabolic processes). This adaptive strategy proved to be optimal (most expedient) under drought conditions. The pattern of *Cl. glareolus* population dynamics has been stable since 1977, with the species being dominant in abundance throughout this period.

Another form of response (in *Microtus* voles) is that **both overwintered animals and young of the year contribute to population growth in the drought year, despite extremely unfavorable conditions**. This resulted in a sharp decrease in animal abundance and population transition to a lower functional level.

In addition to the early block of sexual maturation in young of the year and minimization of metabolic processes, adaptive strategies of rodents under extreme environmental conditions include intrapopulation mechanisms such as **intergenerational crossing and prolongation of breeding period in overwintered females**, which provide for effective utilization of possibilities for population growth along with preservation of the young and improvement of genetic heterogeneity. In all the cases considered above, a very **important role** is played by the **group of overwintered animals** (formed in the previous year): they provide for the growth of population and serve as an ecological reserve for maintaining its heterogeneity, which is especially important in years when reproductive contribution from young of the year is low.

Different species of cyclomorphic rodents exposed to the impact of the same extreme factor (drought) **utilize different adaptive strategies**, which hold different promises on an evolutionary scale.

Thus, the consequences of exposure to drought in murine rodents are not limited to the population

response to this factor itself but can markedly extend in time, being fixed in a series of generations. Real-time observations described above show the possibility of extremely rapid population rearrangements on an evolutionary scale that occur in the absence of long-term influence from an extreme environmental factor. There are grounds to expect that the impact of other adverse factors, including those resulting from human activities, can have similar consequences for biotic communities.

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