Functional Patterns of Life Activities of Rodent Populations in the Winter Season

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Abstract—The results of 37-year continuous monitoring of basic rodent population parameters (the example of bank vole) are reviewed and generalized using the functional—ontogenetic approach. The role of the environment in synchronizing changes in certain biological indices is demonstrated. A detailed analysis is made of the pattern of change in population parameters during overwintering, including minimization of most biological parameters in this period and its adaptive significance. It is shown that successful winter survival largely depends on the functional status of animals (the type of ontogeny) and also on photoregulation. Consideration is given to the phenomenon of winter breeding and its types in murine rodents. A scheme is presented that describes the integrated (generalized), unspecific adaptive reaction of the population in response to irregular, extreme impacts of natural factors and some (short-term) anthropogenic impacts.

Keywords: functional—ontogenetic approach, types of ontogeny, bank vole, winter breeding, minimization of biological processes, cohorts, survival, sex ratio, generalized adaptive reaction

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Cyclomorphic mammals (small rodents) are a unique model for a broad spectrum of studies on the functioning of populations. Most murine rodent species are "ephemeral" animals characterized by cyclic changes in most biological parameters over a period of about 1 year, one-time serial reproduction, and generation overlap in the presence of two alternative developmental pathways (types of ontogeny). Seasonal cycles of environmental conditions play a major role in the life of these animals. Seasonal changes in life activities manifest themselves most clearly in species inhabiting the temperate zone of the Northern Hemisphere and its Arctic periphery, including the Ural region. The winter season in the life of rodents is the period when their populations survive through adverse conditions and preserve useful information necessary for their existence. Cyclic changes in life activities are governed by astronomical factors (photoperiod), with climatic conditions determining only the extent of these changes. The existence of two types of ontogeny characteristic of murine rodent populations is in fact a kind of adaptation facilitating winter survival.

There is still no comprehensive concept on the life activity pattern of rodent populations during the autumn—winter—spring period (for brevity, referred to below as winter season). This study is based on the results of author's own long-term studies, and its purpose is to systematize and interpret available data in order to create a comprehensive picture of rodent population functioning in the winter season.

MATERIAL AND METHODS

The study object was the bank vole, *Clethrionomys glareolus* Schreber, 1780. The material was collected in the Il'men State Nature Reserve (the Southern Urals) in the course of long-term monitoring (1975–2013) in two permanent plots located in biotopes of two types and one 1.5-ha test plot for animal marking, located on a peninsula. In addition, data on more than 9000 ind. were taken from a database.

Both conventional and original methods of field and laboratory studies were used, including the method of morphophysiological indicators (Shvarts et al., 1968), the capture—mark—recapture (CMR) method, the method of irreversible removal, a modified method for determining the absolute age of voles (Olenev, 2009). In previous studies (Olenev, 2002, 2004), two types of ontogeny in small rodents were revealed and analyzed in detail; thus, the phenomenon of multiversality of individual development in the class Mammalia was described for the first time. Methodologically, this study is based on the concept of functional—ontogenetic approach (Olenev, 2002). Its essence is that the main criterion for identifying structural units within a population is the functional unity of individuals in groups corresponding to the two types of ontogeny (Fig. 1). The following functional groups
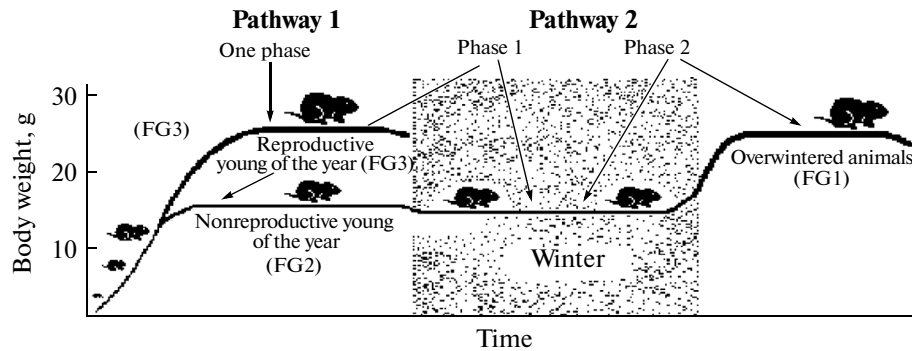
Fig. 1. Scheme of two alternative ontogenetic pathways in murine rodents (Olenev, 2002, 2004).

(FGs; previously, referred to as physiological functional groups, PFG) have been identified:

Reproductive young of the year (ontogeny type 1, one phase): rapidly growing and maturing animals (mainly from the first cohorts) whose function is to increase population size by entering reproduction in the year of birth.

Nonreproductive young of the year (ontogeny type 2, phase 1): animals that cease to grow at the age of about 1 month and fail to mature in the year of birth (most of them are from the last cohorts, but the group always includes representatives of the first cohorts); their function is to ensure population survival, with minimal losses, to the next spring, when they enter phase 2 (overwintered animals).

Overwintered animals (ontogeny type 2, phase 2) resume growing, rapidly mature, and start the cycle of population renewal. This group comprises animals from all cohorts born in the previous year.

It is noteworthy that the functional–ontogenetic approach has provided the possibility of interpreting a wide range of phenomena related to various aspects of animal–environment interactions under conditions of exposure to various natural and anthropogenic factors. In particular, evidence has been obtained for functional determination of most biological characteristics (Olenev, 2002, 2004) and also of resilience to acute (Olenev and Grigorkina, 1998) and chronic radiation exposure (Grigorkina and Olenev, 2011).

RESULTS AND DISCUSSION

The Environment Synchronizes Population Changes

The dynamics of a population is an integrated indicator of its status, an epitome of its interactions with the environment. The wintering part population consists exclusively of individuals with ontogeny type 2, which mature and enter reproduction only in the next spring. Importantly, this group is uniform with respect to the functional status of constituent individuals, which synchronously respond to environmental influences. This is of principal importance for subsequent analysis. An illustrative example is provided by data on changes in animal body weight during two years (Fig. 2). It can be seen that these changes take place synchronously in almost all animals (short-term trends), reflecting at the level of individuals the response of the population to changes in the environment that usually escape the attention of researchers (the population responds as a single entity). Before wintering, variation in body weight decreases considerably owing to elimination of marginal variants, i.e., the animals whose weight is beyond a certain range (in the bank vole, 14−19 g). Within this range, the body weight is restricted to still narrower limits that vary between years, e.g., from 14−17 g (Fig. 2a) to 17−19 g (Fig. 2b). I named these limits a ***gate*** (Olenev, 1979); in the 1990s, the existence of this phenomenon, referred to as a ***bottleneck***, was confirmed by foreign researchers (Garza and Williamson, 2001).

Another manifestation of population response to environmental change is a decrease in the relative weights of internal organs whose functions are in no or little demand during the period of winter depression (Fig. 3). We have previously described basic trends of changes in wintering populations, which can be epitomized as ***winter minimization of biological parameters*** (Olenev et al., 1980). The long observation period (37 years) allowed us to reveal statistically significant differences between the average values of these parameters in samples taken in September and December. In particular, this concerns a decrease in body weight ($p = 0.0005$, df $= 156$), kidney index ($p = 0.03$, df $= 151$), adrenal index ($p = 0.040$, df $= 145$), testis weight ($p = 0.001$, df $= 89$), and heart index ($p = 0.00006$, df $= 143$). Differences in the liver index lacked statistical significance ($p = 0.075$, df $= 125$). According to published data, the average brain weight and skull size in rodent populations also decrease in winter (Dehnel, 1949; Yaskin, 2013).

Attention in this context should be paid to the phenomenon o*f pseudominimization* observed in animals with ontogeny type 1, most of which die in autumn, after the end of the breeding season. Some of these animals show a slight decrease in body weight and rapid degradation of generative organs. In particular,
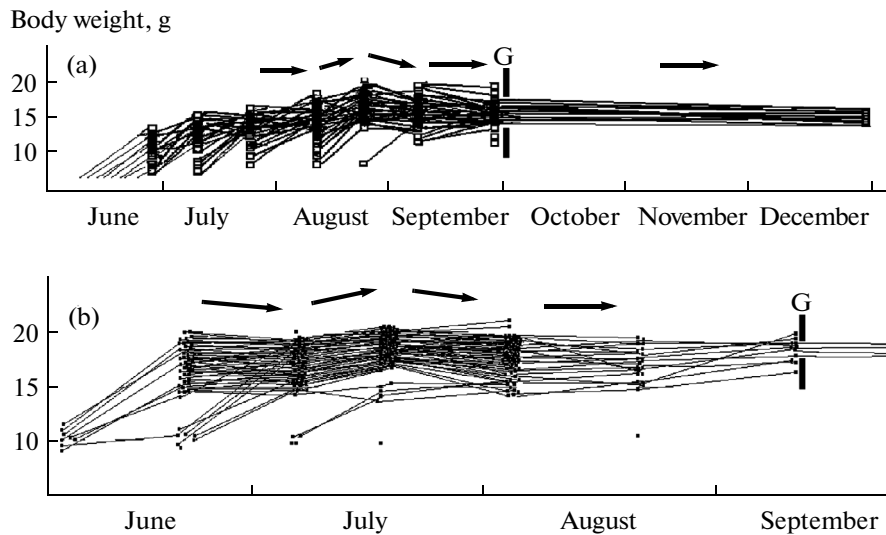
Fig. 2. Synchronous changes of body weight in individually marked bank voles with type 2 ontogeny in (a) an ordinary year and (b) a drought year (before depression). Arrows indicate trends, G is a gate (bottleneck).

their testes decrease in weight, acquire a dark color, lose turgor pressure ("collapsed testes"), and seminal vesicles degenerate (Bashenina, 1981); as a result, the animals are often erroneously classified as nonreproductive young of the year. We regard such changes as an attempt to "pass through the gate (bottleneck)," but postreproductive animals usually die in early winter even if this attempt is successful. Their death is inevitable in regions with severe winters; if winter conditions are relatively mild, such animals may successfully overwinter and even participate in reproduction in the next spring, but their role in this process is negligible. We have repeatedly observed such a situation in a vivarium, under mild wintering conditions. Two exceptions from the "winter minimization rule" should be specifically noted: (1) an increase in the relative weight of the epiphysis, with consequent reduction of gonads (Reiter, 1975), and (2) an increase in the heart index (see Fig. 3) conditioned by change in the rate of energy metabolism (Olenev, 1964; Shvarts et al., 1968), which is a means of metabolic acclimation to seasonal conditions (Sakai, 1976).

The winter decrease in the body and internal organ weights is apparently explained mainly by seasonal changes in environmental conditions, namely, a drop in ambient temperature and deterioration of food resources, with the timing of this decrease being determined by photoperiod (see below). Against the background of *seasonal change in food spectrum* (Bashenina, 1981), a *decrease in the amount of food consumption* is observed in winter (Andrzejewski and Mazurkewicz, 1976). In the absence of winter breeding and increased demand for food, animal activity becomes lower to reduce energy expenditures. Thus, according to the results of radioactive tagging, the average distance covered by a bank vole over 24 h decreases from 1288 m in summer to 910 m in winter, with consequent decrease in the size of individual home ranges (e.g., from 0.192 ha in November to 0.075 ha in February) (Bashenina, 1981).

Animal activity on the snow surface is decreased or even ceases. Since the animals are immature, *their social and sexual relationships are also altered*: they do not perceive each other as sexual partners, and their social behavior is suppressed. As a consequence, they are not engaged in aggressive, antagonistic, or other energy-expensive interactions, which, in turn, allows cohabitation of several animals in the same shelter and provides for reduction of unnecessary energy losses (Andrzejewski and Mazurkewicz, 1976; Olenev et al., 1980).

Seasonal variations of immunity have been noted in small mammals (Lokhmiller and Moshkin, 1999). Animals with splenomegaly (oversized spleens) almost never occur in winter (Olenev and Pasichnik, 2003), which is indirect evidence for the absence of susceptibility to transmissible infections, while the picture observed in the spring period of animal maturation is radically different. All the above facts suggest that animals with type 2 ontogeny are more resilient to adverse effects of natural factors (winter, drought, high population density, etc.). Due to a relatively low metabolic level, they also are more resistant to acute radiation exposure (Olenev and Grigorkina, 1998).

Special attention should be paid to *age-dependent dental changes* (ADCs) in voles as an indicator of the rates of metabolic processes and senescence (Olenev, 2002). The rate of ADCs in overwintering animals is at its annual minimum, being significantly lower than in mature young of the year (Olenev, 2009), but increases upon their maturation in spring, along with intensification of metabolic processes. This is evidence that the rate of senescence in winter also decreases to a mini-
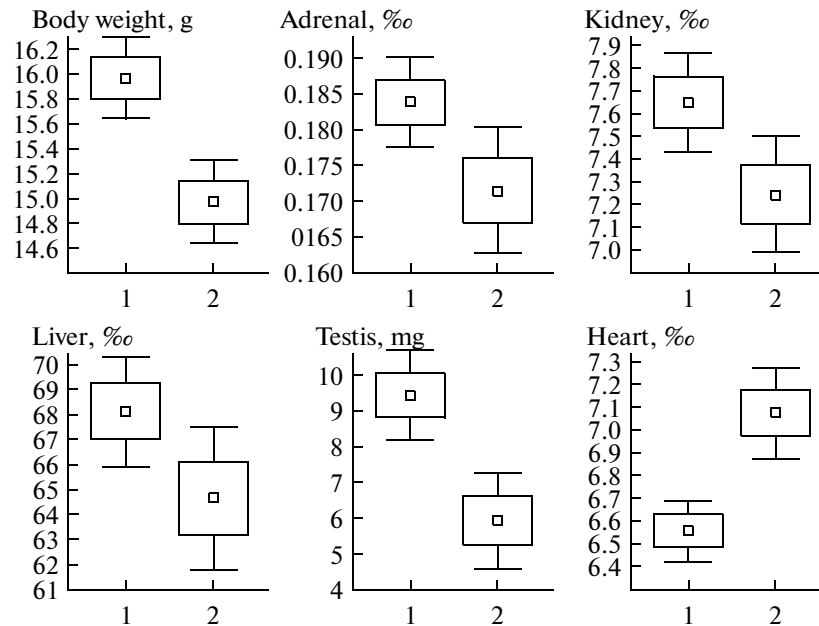
Fig. 3. Minimization of morphophysiological parameters in bank voles with type 2 ontogeny during the winter season: (*1*) September, (*2*) December.

mum, allowing the population to retain a younger biological age by the spring maturation period. In the hypothetical absence of minimization, the biological age of overwintered individuals would have been almost 5 months older, with their chronological age remaining the same.

Thus, *winter minimization* is an adaptive phenomenon providing for reduction of energy losses. Attenuation of almost all life functions is explained by the fact that it is not energy efficient to have well-developed generative organs when no breeding takes place or large-sized kidneys, adrenals, and liver when the animal does not need to maintain a high metabolic rate. Living under snow, individuals with ontogeny type 2 escape the impact of external factors, which facilitates their main function: *to overwinter with minimal losses.* This way to survive adverse conditions is a good alternative to extreme survival strategies such as winter hibernation or activation of foraging behavior.

Integrated Adaptive Reaction

Natural changes leading to deterioration of environmental quality, such as drought or high population density, evoke an integrated population reaction manifested in the retarded growth of the young and block to their sexual maturation (the reduction in numbers or absence of individuals with ontogeny type 1) (Olenev, 1981, 2002). In any case, there is a complete analogy with the reaction to the onset of winter season, which involves minimization of almost all biological processes. Factors triggering type 2 ontogenetic pathway (or, more correctly, blocking type 1 pathway) may

be different, not only natural but also anthropogenic. Figure 4 shows a scheme of *integrated, unspecific adaptive reaction of the population in response to irregular, extreme influences of adverse natural and some anthropogenic factors.*[1] This reaction basically does not differ from adaptations developed in the course of evolution in response to regular (habitual) exposure to adverse factors (in our case, winter conditions). In other words, it involves *untimely activation of the survival mechanism that is historically inherent to the species (population) as a reaction to regular environmental influences.* This mechanism corresponds to type 2 ontogeny. The reaction of the population to a broad spectrum of extreme influences is based on fundamental, evolutionarily established mechanisms providing for the resilience of living systems and the possibility of their adaptation to changing environmental conditions. We were the first to reveal these regularities and assume that it is possible to predict population responses to adverse anthropogenic influences (Olenev, 1981). This assumption was subsequently evaluated by Bezel' (2006) and confirmed in studies on population adaptations (Maslov, 1988), including those to anthropogenic factors (Grigorkina and Olenev, 2011). In general, the essence of this ecological regularity (unspecific reaction) is that it allows an individual (population) to avoid or escape damage from harmful exposure, in the same way as the penis is

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[1] In this context, an analogy can be drawn between the integrated adaptive reaction of the population and the general adaptation syndrome described by Hans Selye at *the organismal level.* In our case, such a unified, unspecific reaction to specific adverse factors of different nature is observed at *the population level.*

vulnerable to damage when erect but is withdrawn from damage when limp.

Role of Photoregulation in Population Overwintering Success

The photoperiod serves as a kind of navigator for a population, allowing the animals to adjust their biological functions adequately to changes in environmental conditions (Reiter, 1975), minimizing their activity in winter (in the Northern Hemisphere, the deepest depression is observed in February) and intensifying it to a maximum in spring. Moreover, the animals are guided not by the photoperiod itself but rather by its regular change with time, since their reliance on the photoperiod alone, as well as on any other factor (food resources, temperature, etc.), would have inevitably disturbed the adequacy of population response to regular changes in the environment. Thus, the daylight period on September 23 and March 23 is the same, but the population on the first date is in prospect for overwintering (therefore, animal maturation can have grave consequences), whereas on the second date it is already undergoing rearrangements preliminary to breeding. This is confirmed by our observations that even major warm spells in December (up to +5°C and 10 days long) fail to trigger animal maturation. On the other hand, synanthropic rodents have lost reaction to changes in the photoperiod and, hence, can breed year round.

Trends of Change in Population Parameters during Overwintering

The age structure of the population in a given year is optimal to the existing ecological conditions, allowing full realization of its reproductive potential (Olenev, 2004). The basis for the age structure of the wintering group (nonreproductive young of the year → overwintered animals) is laid during the breeding season (Fig. 1). Changes in the majority of population parameters in winter show certain trends. The functional–ontogenetic approach allows detailed analysis of these trends, with a high level of detail and objectivity being provided for by consistent use of the CMR method over a long period of time.

Heterogeneity of overwintered group. This group has been shown to be markedly heterogeneous. It consists mainly of animals from the third and fourth cohort; the fifth cohort, the smallest in numbers is not represented in some years. Another important fact is that each cohort is also highly heterogeneous by origin, because its members are the progeny of individuals from several cohorts belonging as a rule to different generations. Since this group comprises animals from all generations born in the previous year, there is the possibility of genetic information transmission not only in a series of generation but also directly from the first generation of a given year to the first generation of

the next year, i.e., of *transgenerational transmission* (Olenev, 2002, 2004). In addition, heterogeneity may increase due to the so-called age crossing (Olenev and Grigorkina, 2011). The high heterogeneity of the overwintered group is of special importance in extreme situations, when the maturation of young of the year is partially or completely blocked under the effect of adverse factors (severe drought, high population density, etc.) (Olenev, 1981; Kolcheva and Olenev, 1991). On the other hand, all animals of overwintering cohorts are physiologically and functionally equal. The net result is that the age structure of the overwintered group reflects ecological conditions of the previous breeding season.

Proportions of cohorts during the winter season. The proportions of cohorts formed in the population by the onset of wintering do not change significantly by spring, despite inevitable death of some animals (Fig. 5). For example, the proportion of the first versus last cohorts (1 + 2 vs. 3 + 4) decreased from 65.98% in October 1975 to 48.31% in May 1976; the respective values for 1976–1977 were 20.88 and 20.11%, and for 1977–1978, 30.7 and 20.98%; i.e., this proportion remained almost unchanged. The hypothesis that overwintering success is independent of belonging to a certain cohort was verified with data on three seasons using Fisher's exact two-tailed test. As a result, no significant differences between cohorts were revealed either for each overwintering alone ($p = 1.0$) or for the pooled sample ($p = 0.83$). Therefore, although part of the population is inevitably lost during winter, no selective elimination of animals from certain cohorts takes place.

It also follows from Fig. 5 that ***the life span of cohorts*** born in the same year is almost the same, regardless of different dates of their birth, whereas the corresponding interannual differences are considerable. Thus, animals born at different times die upon reaching approximately the same absolute age (i.e., *the cohorts die off successively, depending on the time of birth*), but their life span markedly varies from year to year. Likewise, ***the survival (mortality) rates*** of cohorts born in the same year are similar, but they differ significantly between years. For example, differences in survival were recorded during the winter seasons of 1975–1976 and 1976–1977: the survival rate by the spring of 1976 was 3% in the first and second cohorts and 7% in the third and fourth cohorts, whereas the respective values by the spring of 1977 were 23 and 44% (Fig. 5).

All these data allow the conclusion about *specificity of population (individuals) born in each particular year.* The transfer of all population information through the winter is accomplished by animals with the same type of ontogeny (type 2), which ensures minimal losses. The retention and transmission of genetic information are accounted for not only by the age population structure formed in the previous year but also by specific features of constituent individuals, which bear an imprint of their birth year. Moreover, no selective
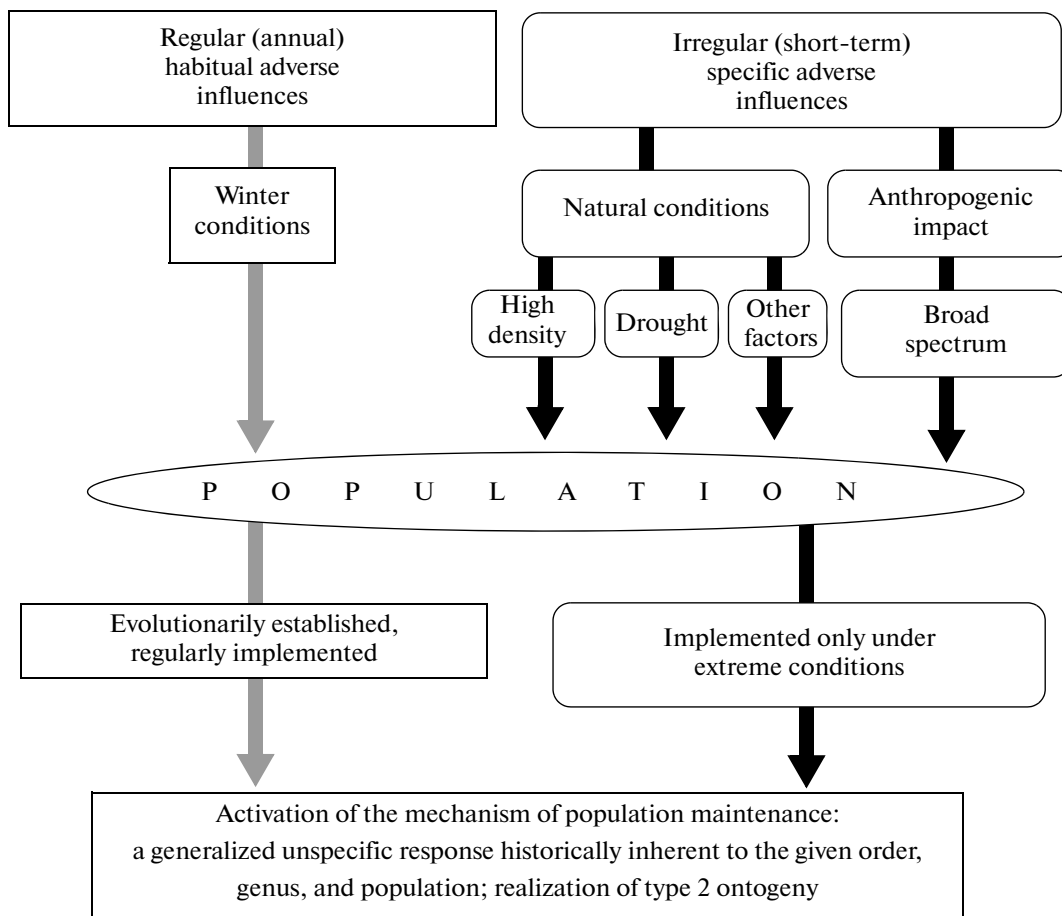
Fig. 4. Scheme of generalized, unspecific adaptive population reaction to short-term specific influences of adverse environmental factors (Olenev, 2004).

elimination of animals (e.g., from certain cohorts) takes place. *The time of birth, pedigree, and even absolute age hold no major significance for the fate of an individual during the severe overwintering period. The survival of animals entering the winter season depends primarily on their functional status (the type of ontogeny)* (Olenev, 2002, 2004).

Sex ratio. As noted above, postreproductive rodents (whose function is completed) rapidly senesce and die, and the population entering the winter season consists of young of the year with type 2 ontogeny, which similarly respond to changes in environmental conditions. Prior to spring maturation, males and females do not differ in most parameters, including mobility and capture rate. We analyzed changes in the sex ratio among young of the year with type 2 ontogeny during the period from entering the winter season to spring maturation, when these animals, by definition, form the overwintered group. This allowed us to evaluate the winter mortality of males and females over a series of years (e.g., 1993–1999) and make an attempt to confirm or deny whether this mortality has a differential pattern (Fig. 6) (Olenev and Grigorkina, 2011).

The analysis was complicated by the fact that overwintered females mature and become territorial by the time of spring censuses, while males (the most mobile component of the population) have overlapping home ranges and often form aggregations, so-called clans (Bujalska and Saitoh, 2000), which have a hierarchical social structure (Shilov, 1972). The main task for a male in spring is to find and mate a female; therefore, the proportion of males in spring catches is usually higher, which may give a false impression of change in the sex ratio (Olenev and Grigorkina, 2011). Although the situation with overwintering is highly variable, the sex ratios in samples taken in autumn and next spring are usually similar ($\chi^2 = 21.55$, $p > 0.05$) (Fig. 6). The years 1993–1994 are the only exception in this series: the proportion of females was significantly greater among animals entering the winter season, whereas samples taken in next May were dominated by males ($t = 2.6$, $p \leq 0.05$). Hence it follows that "the sex ratio in *spring does not differ from that in the previous autumn, because no selective elimination of males or females takes place during the winter season.*
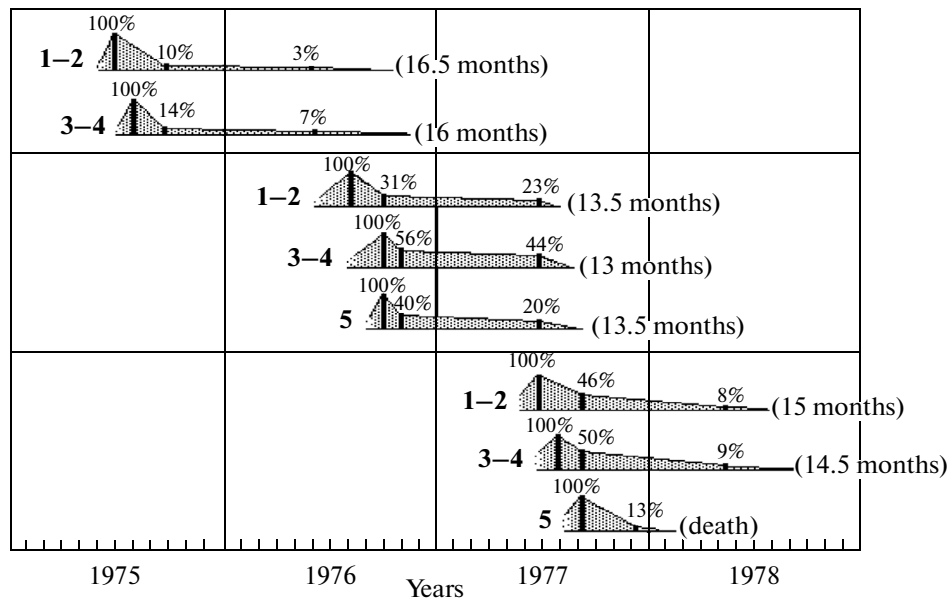
Fig. 5. Dynamics of the age structure, life span (months), and survival rate (%) of individual cohorts (1−5) in a natural bank vole population during 4 years.

Winter Maturation and Breeding

Cases of rodent maturation and breeding in winter (under snow) deserve special consideration. There are several types of winter breeding, and difficulties arise both in its diagnosis as well as in its interpretation. Breeding under snow has been described in different rodent species, including the steppe lemming (*Lagurus lagurus*), field vole (*M. agrestis*), northern redbacked vole (*Clethrionomys rutilus*), mice of the genera *Apodemus* and *Mus*, root vole (*Microtus oeconomus*), common vole (*M. arvalis*), and narrow-headed vole (*M. gregalis*) (Nikiforov, 1956). However, a more detailed analysis shows that most such cases have been conditioned by anthropogenic factors, primarily additional food sources such as winter crops, postharvest residues, haystacks, grain stores, garbage dumps, etc. We classify this type as ***artificially stimulated winter breeding***.

Prolonged breeding in late autumn or ***its untimely onset in early spring*** are often retrospectively interpreted as winter breeding. According to our observations in the Zhitomir region of Ukraine, such types are common in regions with mild winters, where the "untimely" progeny have a chance to survive. Of special interest are cases of ***year-round breeding*** in central Europe (Zejda, 1971).

Finally, ***winter breeding in true sense*** refers to "untimely" maturation and breeding of rodents in natural biotopes, under typical winter conditions, in the absence of additional food sources provided by humans. This phenomenon periodically occurs in lemming populations in the Subarctic. Breeding of this type starts early, before the snow melts, and usually at the phase of population growth (Krebs, 1988;

Chernyavskii and Lazutkin, 2004). Under such conditions, the additional third generation may appear in the population, and the total number of cohorts may be greater than five.

True winter breeding is very rare in regions with distinct winters, such as the Urals. Thus, we observed it in only single cases over the 37-year study period, in 1985 and 1986 (Olenev, 2009), with very few individuals reaching maturity and participating in breeding. In 1986, we managed to reveal probable factors that accounted for this phenomenon in one of biotopes studied (the floodplain of a forest river with abundant shelters for small mammals). They included a deep snow cover that began to form in autumn and an unusually high yield of bird cherries, which were found in large numbers in the stomachs of voles sampled in winter. After the snow melted, we have found numerous "feeding tables" with bird cherry seeds gnawed by the animals. Subsequent observations provided a basis for the conclusion that the probability of survival for the winter-born progeny in the Urals is very low, and the survivals rarely live to maturity. It is not excluded, however, that this population reserve can be realized in certain cases.

Prior to determining the type of winter breeding, it is necessary to make certain that it has indeed taken place. In spring, this is confirmed by the presence of juveniles in samples taken before the onset of mass breeding and by the functional status of internal (reproductive) organs in adults; in summer samples, by unusually high values of age markers (e.g., ADCs) in some young of the year, compared to others, which fall out of the general pattern in a plot (Olenev, 2009). After being recorded for the first time, such "outliers"
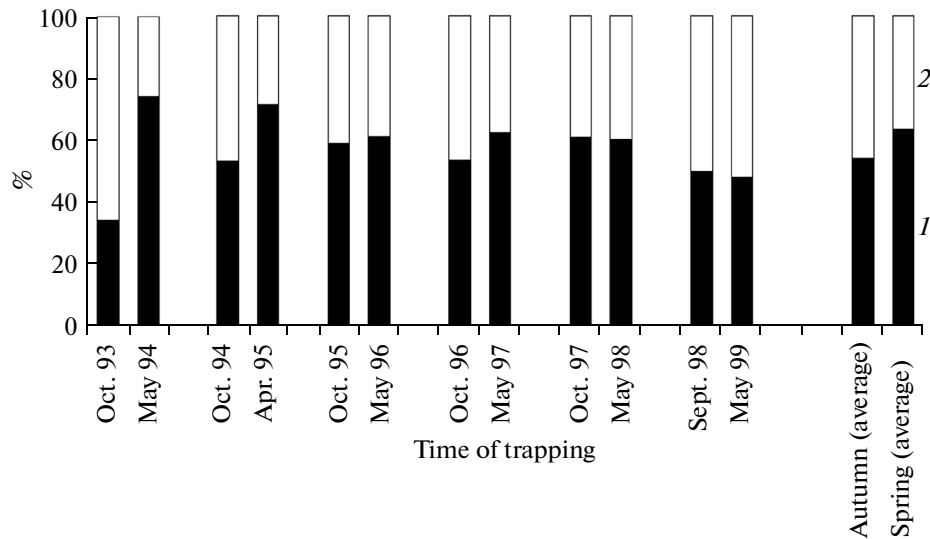
Fig. 6. Changes in sex ratio (*1*, males; *2*, females) during overwintering.

may as well be detected in subsequent samples, with the magnitude of their difference from the general pattern remaining unchanged until these animals die. It should be noted that the calculated dates of their birth fall into the previous winter season.

Prerequisites for true winter breeding. Available data show that winter breeding in voles is possible only on condition that the daylight period tends to increase (in the Northern hemisphere, after December 22); i.e., the animals are guided not by the photoperiod itself but rather by ***the tendency in its change*** with time. The second necessary condition is, as a rule, the availability of sufficient food resources, which stimulate maturation to a certain extent and satisfy increased energy requirements in the breeding period. No less important are snow depth and, to a smaller extent, external temperature conditions. The biological significance of winter breeding is in the potential possibility for the additional winter progeny to survive and mature, thereby increasing the population size by the onset of a new breeding cycle. This conclusion is confirmed by analogy with lemmings (Chernyavskii and Lazutkin, 2004).

Features of winter maturation and breeding in laboratory colonies. Some natural trends manifest themselves when voles are kept in a vivarium, i.e., under stable conditions including unlimited access to food. Reproductive young of the year trapped in autumn and kept in pairs continue mating during the winter season (prolonged breeding), whereas nonreproductive young of the year brought to the vivarium on the same dates and kept under the same conditions fail to mature by spring (Pokrovskii, 1967). A diet supplemented with green food can stimulate maturation and breeding as early as February, but this effect is absent if the daylight period is decreasing (Pokrovskii and Bol'shakov,

1979); i.e., the animals should undergo "vernalization," by analogy with plants. The life span of voles in laboratory colonies increases to more than 2 years.

Why Predictions Fail

Predictions concerning the abundance of rodents in the next year are usually made in autumn, after breeding ends, based on the assessment of population status (by a set of relevant parameters) and the personal experience of the researcher. It is a priori assumed that their winter mortality is at long-term average, but actually it is subject to significant deviations. Our results (Fig. 7.) show that the situation before and after overwintering may differ significantly. In most cases, the relative abundance of voles entering the winter season usually was consistently higher than that recorded in spring; in other cases, their relative abundance in autumn and spring catches was almost equal or, rarely, was higher in spring than in autumn (in 1984–1985, 1994–1995, 2004–2006). Such variants are usually a consequence of inevitable sampling errors due to seasonal differences in animal mobility, local migrations, etc. It follows from Fig. 7 that the actual winter mortality of voles deviated to different extents from long-term average (50%), with cases of mass mortality being of special interest. Their causes remain largely obscure, but high mortality (over 90%) was sometimes recorded in winters characterized by alternation of powerful warm and cold waves. Conversely, low mortality (less than 20%) was more often observed in snowy winters with consistently low temperatures, without thaws.

It is known that weather cataclysms may be much more harmful to rodent populations in spring than in autumn. This is explained by the fact that changes
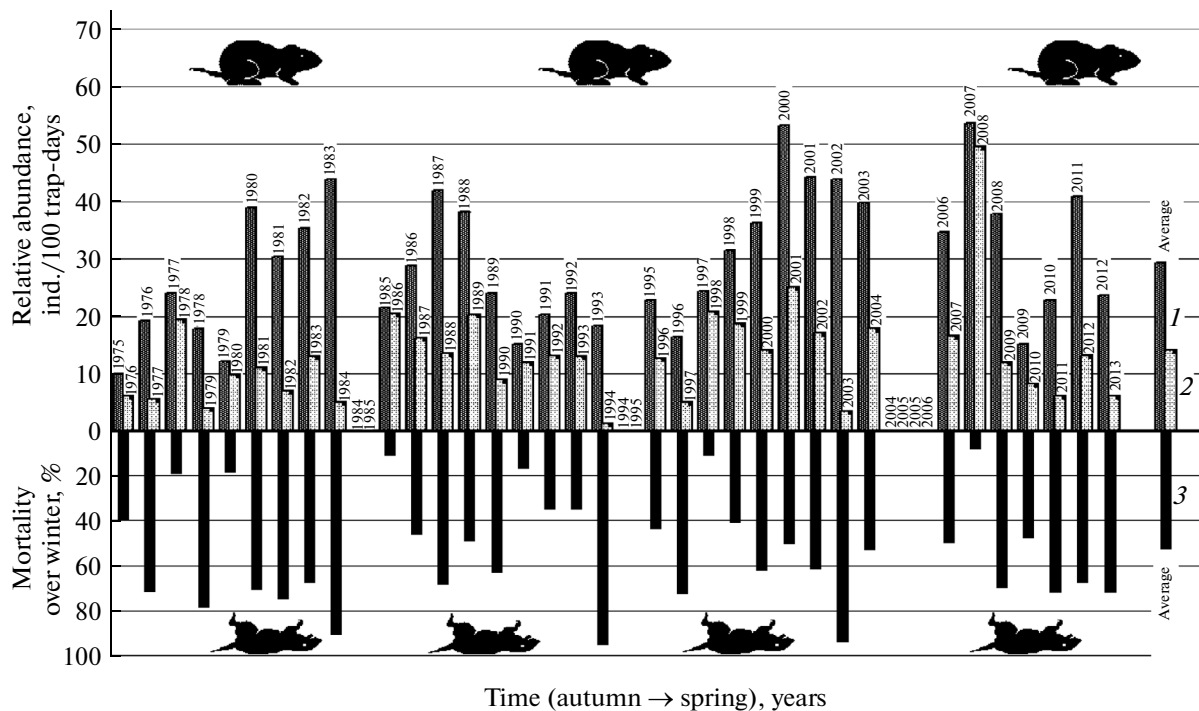
Fig. 7. Dynamics of interannual differences in the survival and mortality of bank voles with type 2 ontogeny during the winter season: (*1*) September, (*2*) May, (*3*) mortality over winter.

occurring in the population in autumn (primarily minimization of biological parameters) prepare it to further deterioration of environmental conditions, whereas spring cataclysms affect the population when it is undergoing changes oriented toward the expected improvement of these conditions. This primarily concerns intensification of metabolic processes associated with animal growth, maturation, and breeding.

As for success in predictions, the following conclusion suggests itself: regardless of the methods and algorithms we use, the correctness and representativeness of previous collections, and the richness of our invaluable experience, an unexpected cold spell with snow in spring or a winter thaw followed by sudden freezing will instantly destroy all our efforts, leaving little optimism for a correct prediction of animal abundance.

CONCLUSIONS

In our studies on small rodents, multiversality of individual development (two types of ontogeny) in the class Mammalia was demonstrated for the first time and analyzed in detail (Olenev, 2004), providing a basis for this study on life activities of rodent populations in the winter season. All adjustments in the population prior to entering the winter season have adaptive significance and allow it not only to overwinter successfully but also to withstand a wide range of adverse influences in any season. The winter is an unfavorable period in the life of rodents that is repeated every year, and populations of cyclomorphic

mammals have successfully adapted to winter survival. As a result, they have made a major advancement by developing two alternative ontogenetic pathways in response to regular exposure to winter conditions.

Of basic significance for the overwintering population is minimization of biological processes aimed at surviving the severe period with minimal losses. It is also important to preserve the qualitative composition of the population that has been formed in the previous year.

We have shown that the absolute age of animals is of no major significance for their winter survival: the decisive factor is the functional status (the type of ontogeny) of individuals entering the winter season (Olenev, 2002, 2009). The population information is "conserved" during overwintering (in the absence of breeding) to be realized in the next generative period. Although predictability of population events is limited (which is inevitable in the changing environment), the concepts presented above will hopefully help to take a fresh look on the role of the winter season in the life of rodent populations.

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