Russian Journal of Ecology, Vol. 33, No. 5, 2002, pp. 321–330. Translated from Ekologiya, No. 5, 2002, pp. 341–350.

Alternative Types of Ontogeny in Cyclomorphic Rodents and Their Role in Population Dynamics: An Ecological Analysis

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Received February 14, 2001

Abstract—Two alternative ontogenetic pathways regularly effected in the populations of small mammals are analyzed as a manifestation of developmental multiversality. The types of ontogeny in rodents are characterized. These data are reflected in the concept of the functional approach. Multiversality of development in plants and animals is considered. Based on the results of long-term (26-year) observations on the natural populations of six rodent species, the dynamics of relationships between the types of ontogeny, abundance, and basic population parameters are analyzed using an example of a background species (*Clethrionomys glareolus*). A trigger mechanism of switching to a certain type of ontogeny, the role of environmental factors in actuating this mechanism, and the role of the genotype as a basis of multivalence are discussed. The existence of two developmental variants is regarded as a basis for functional rearrangements providing for a high flexibility of population responses and as a mechanism of population regulation determining the dynamics of rodent fauna. An adaptive population response to a board spectrum of influences, including anthropogenic damage, depends not only on the type and strength of the influence, but also on the functional structure of the population. The concepts described in the paper may explain the significance of critical periods in the life of populations.

Key words: rodent populations, types of ontogeny, two variants of development, functional approach, trigger mechanism, adaptation.

PRINCIPLES OF STRUCTURAL AND FUNCTIONAL ORGANIZATION OF POPULATIONS

The analysis of a population as a system is expedient to begin with identification of a set of constituent elements and their ordering. It is known that individuals of the same species living in the same community differ in many traits and may be divided into groups with respect to age, size, developmental rate, and other parameters responding to changes in the environment.

Within the framework of an ecodemographic approach, differentiation by age is of special significance, as studies on population structure and dynamics basically deal with this differentiation. Each individual at a certain moment may be characterized in two ways: (1) by the absolute age, or the period of time elapsed since birth, and (2) by the biological (physiological) age, which is much more difficult to determine. Moreover, each organism at each moment has a specific complex of morphological, physiological, and other characters related to its physiological age.

Individual development is a continuous process. However, using a series of indications, it is possible to divide it into several major periods, which can be further subdivided into age-related stages. In population studies, it is much more important to determine the biological age than the absolute age. The point is that individuals of the same biological age may differ in their absolute age, although they are at the same stage of ontogeny and perform the same functions in their population. Characterization of the age structure of a population is not limited to determining he ratio of different age groups. Specific features of this structure depend on the rate of population renewal, biological specificity of different age groups, and their specific responses to periodic and random changes in the environment. This is evidence for the leading role of age structure in population dynamics. In rodent populations, this structure is very complex and provides a basis for a broad spectrum of transformations at the population level. The purpose of this work was to analyze the significance of diversity in the types of ontogeny for structurally heterogeneous intrapopulation systems, which are characteristic of murine rodents.

MATERIAL AND METHODS

The work is based on the synthesis of data obtained in the course of long-term monitoring (1975–2000) and generalizations made in previous studies. The material was collected in the Il'men State Nature Reserve (the Southern Urals) in two permanent plots located in biotopes of two types and one 1.5-ha test plot for animal marking, located on a peninsula. Virtually all data

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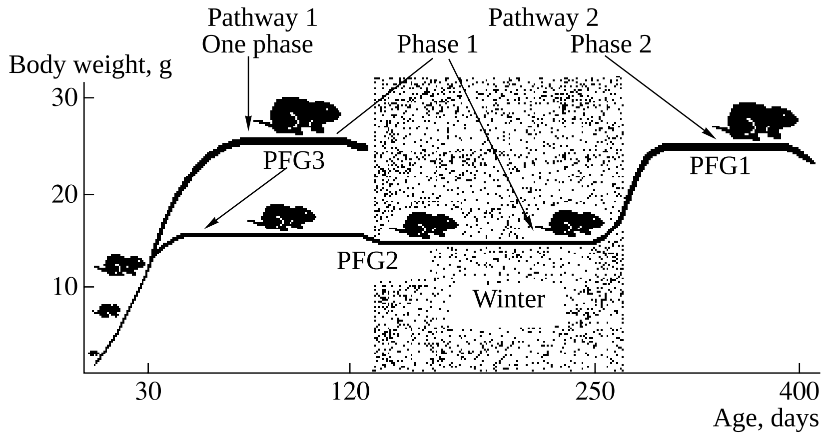

Fig. 1. Scheme of two ontogenetic pathways in murine rodents.

discussed below concern the bank vole *Clethrionomys glareolus* Schreber, 1780.

Both conventional and original methods of field and laboratory studies were used, including the capture–mark–recapture (CMR) method, the method of irreversible removal, a modified method for determining the absolute age of voles (Olenev, 1989), and the method of morphophysiological indicators (Shvarts *et al.*, 1968). The concept of the functional approach (Olenev, 1981a, 1981b, 1989) provided a methodological basis for analyzing age structure. To estimate the relation between the types of ontogeny, data obtained in June and July of each year were used. The reason is that May is the months when young of the year begin participating in breeding, and August–September is the period when reproduction gradually ceases and mated animals die. In midsummer, conversely, all intrapopulation groups are present, and the proportion of reproductive young of the year reaches a peak. The problems concerning animal growth rate are not considered in this work.

MULTIVERSALITY OF DEVELOPMENT IN PLANTS AND ANIMALS

Within the framework of the ecodemographic approach, the concept of multiversality of individual development was formulated as an integration of data on various manifestations of differentiation between individuals in plant populations (Sabinin, 1963). Subsequent studies showed that multiversality is widespread in the plant world (Matveev, 1975; Zaugol'nova *et al.*, 1988), and botanists revealed five variants of this phenomenon (Zhukova, 1986). The existence of intrapopulation groups differing in developmental rate was first described by specialists in forest science (Sukachev, 1941; Zavadskii, 1968). Attention was also given to retarded development and its cessation in plants that remain in the same age state (Zhukova, 1973; Rabotnov, 1978; Chistyakova, 1982).

It has been noted that ontogenetic multiversality in plants is an important mechanism of adaptation at the population level, which provides for dynamic heterogeneity of cenopopulations and contributes to their stability. This multiversality is based on the genetic polymorphism of plants and their nonheritable variation (modification) within the range allowed by the genotype. Ontogenetic multiversality in animals, being generally similar to that in plants, has major distinctive features. Unfortunately, published data on this problem are scarce, and most studies on animal ontogeny have only a distant relation to it. This work was intended to bridge this gap, at least partially.

SPECIFIC FEATURES OF ONTOGENY IN SMALL MAMMALS (AN EXAMPLE OF RODENTS)

The first studies related to the types of ontogeny in rodents are those advancing a hypothesis concerning the existence of physiological races (Stieve, 1923), or "seasonal generations" in rodents (Olenev, 1964; Shvarts *et al.*, 1964; Pokrovskii, 1967; Amstislavskaya, 1975). By definition, seasonal generations are the groups of animals born in different seasons, developing under different environmental conditions, and possessing certain biological properties. In most studies concerning the age structure of populations, S.S. Shvarts and his colleagues used the term "generation" in two senses. First, this term referred to the sum of offsprings born en masse in spring (*spring generation*) or autumn (*autumn generation*). Alternatively, each wave of mass births, beginning from the first one in spring, was regarded as a generation. This gave rise to some terminological confusion. It has been considered that virtually all animals, including young of the year, are involved in reproduction in spring. However, as follows from the results of long-term animal marking, the spring generation (by Shvarts) consists not only of reproductive young of the year, which determine the physiognomy of this seasonal generation. In fact, *it always includes a large proportion of young animals*

Two types of ontogeny as characterized by some morphophysiological and age indices in three physiological functional groups (PFG) of *Clethrionomys glareolus* voles sampled in July (most informative values are shown in boldface)

Index	Sex	Ontogeny type 1 (one phase)			Ontogeny type 2					
					phase 1			phase 2		
		PFG3 (reproductive young of the year)			PFG2 (nonreproductive young of the year)			PFG1 (overwintered animals)		
		$\bar{x}$	*n*	St D	$\bar{x}$	*n*	St D	$\bar{x}$	*n*	St D
Body weight, g	females	**25.0**	86	4.73	**16.6**	194	1.9	**26.8**	116	8.0
	males	**20.6**	70	3.25	**17.1**	308	1.9	**25.1**	164	4.06
Adrenal index, ‰	females	**0.42**	86	0.19	**0.24**	192	0.14	**0.42**	115	0.19
	males	0.23	68	0.09	0.22	302	0.08	0.27	160	0.25
Thymus index, ‰	females	**1.05**	84	1.17	**2.25**	194	1.65	**0.05**	116	0.22
	males	**1.46**	70	1.39	**2.44**	305	1.62	**0.01**	164	0.09
Testis weight, mg		**306.0**	64	92.2	**11.7**	247	10.8	**390.0**	158	123.0
Absolute age, days	females	**67.0**	86	23.7	**76.1**	194	33.3	**313.0**	116	50.1
	males	**56.0**	70	25.3	**73.9**	308	29.8	**377.0**	163	58.5
Physiological age, days	females	**~120**	86		**76.1**	194	33.3	**~380**	116	
	males	**~100**	70		**73.9**	308	29.8	**~470**	163	

not involved in reproduction, which varies from 10–30% in the years with usual conditions to 100% under extreme conditions, such as drought (Olenev, 1981a) or very high animal density (Shilov *et al.*, 1977; Kolcheva and Olenev, 1991).

Our studies showed that a seasonal generation consists of two animal groups, so that the majority of its parameters are determined by the functional state of these groups. Thus, the samples analyzed in the aforementioned studies were intrinsically heterogeneous, and this was the source of significant errors. The functional approach (see below) makes it possible to avoid such errors by analyzing "pure" intrapopulation groups. Nevertheless, studies on the specific features of seasonal generations (Shvarts, 1969) were prerequisite to the development of knowledge about the functional structuring of rodent populations. This work continues and further develops these studies.

CHARACTERIZATION OF TWO TYPES OF ONTOGENY IN CYCLOMORPHIC RODENTS

Cyclomorphic mammals, including most species of small rodents, are characterized by rhythmical changes in most biological parameters over a period of approximately one year, one-time serial reproduction, and generation overlap in the presence of two alternative ontogenetic pathways. Both types of ontogeny fully manifest themselves in rodent populations inhabiting the temperate zone of the Northern Hemisphere and its Arctic periphery, where the climate is sharply continental.

The First Ontogenetic Pathway (Figs. 1, 5; table)

Monophasic growth. Young animals reproducing in the year of birth (PFG3). In this physiological functional group (PFG), most animals (usually 70–90%) belong to the first cohorts. They rapidly grow, mature, and enter reproduction upon reaching the definitive body size and weight characteristic of overwintered animals (25 g); thereafter, their body weight remains approximately the same.[1] These animals have a high metabolic rate, rapidly grow old, and die in the year of birth. The initial stage of tooth root formation is observed at the age of 65–75 days (relative tooth root length is 0.1–0.3). Life span ranges from three to five months. Behavior is characterized by some manifestations of aggressiveness. The function of this group is to increase population size by entering reproduction in the year of birth.

The Second Ontogenetic Pathway (Figs. 1, 5; table)

The growth is biphasic (PFG2 ⟶ PFG1). Most animals are of the last cohorts, but there is always a considerable proportion of first-cohort animals remaining nonreproductive in the year of birth. Life span is 13–14 months; correspondingly, relative tooth root length is 0.6–0.7. The main function is to preserve this

[1] As young of the year and overwintered animals have similar body sizes and weights, they fall into the same *weight groups* that usually serve as a basis for identifying the juvenis, subadultus, adultus, and senex groups (Figs. 1, 5). Thus, errors in age may exceed one year (table), and this imposes serious limitations on the use of such approach in most studies.

part of the population with minimal losses until next spring and to begin the cycle of its renewal.

The first phase. Young animals remaining nonreproductive in the year of birth (PFG2). The phase covers the period from birth to the spring peak of growth and maturation in the next year. At the age of approximately one month, irrespective of the date of birth, body weight ceases to grow upon reaching 14–20 g.[2] The animals have a low metabolic rate. The rate of aging and physiological age are almost half those in PFG3. The initial stage of tooth root formation takes place at the age of 120–130 days. The animals belonging to different cohorts remain in this phase for 200–300 days. The animals of PFG2 are a kind of population reserve, especially in critical periods, as they are most resistant to a broad spectrum of adverse influences. Their behavior is not aggressive. The main function of this group is to ensure population survival, with minimal losses, under possible adverse influences before and during wintering.

The second phase. Overwintered animals (PFG1). This phase begins in next spring, when the animals resume growing after the "conservation" period and mature within two to three weeks. Their body weight stabilizes again upon increasing to 24–27 g (the definitive value for the species). The rates of metabolism and senescence are similar to those in PFG3, although the absolute age of overwintered animals is much greater. The duration of this phase is 120–200 days. The behavior of animals has some elements of aggressiveness. The main function of this group is to begin the cycle of population renewal, notwithstanding any adverse influences.

THE CONCEPT OF FUNCTIONAL APPROACH

To analyze the dynamics of basic population parameters, I proposed and tested a functional approach (Olenev, 1981b, 1989). This gave rise to studies dealing with the analysis of fine age structure in cyclomorphic mammals (Olenev, 1982) and, as a continuation, investigation of populations from various aspects on the basis of their functional structuring (Bezel' and Olenev, 1989; Testov, 1993; Vasil'ev, 1996; Luk'yanov, 1997; Ignatova, 1998; Olenev and Grigorkina, 1998).

The essence of the functional approach 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. In other words, these groups are identified on the basis of the functional status of individuals (with respect to specific features of growth, development, and reproductive conditions) and the synchronism of its changes in time. To simplify the situation, I proposed to distinguish three *physiological functional groups* (PFGs), each consisting of individuals united by their functional role in reproduction of the population (for details, see Olenev, 1989).

The cornerstone of the functional approach and the main difference between PFGs and seasonal generations is that the criteria for identifying these groups are the functions performed by individuals belonging to any cohort emerging during a year and the temporal sequence of these functions (phases of ontogeny). The time of birth (emergence of cohorts) and the absolute age of animals are not principally important.[3]

POSSIBILITIES OFFERED BY THE FUNCTIONAL APPROACH. ADDITIONAL CHARACTERIZATION OF TWO TYPES OF ONTOGENY

A major advantage of the functional approach is that it offers the possibility of analyzing "pure" intrapopulation groups, which makes this analysis more correct and logical. Moreover, differences revealed in a number of parameters are often so great that no tests for their statistical significance are required. This approach, in various aspects, has been successfully used in a broad spectrum of studies and proved to be simple and convenient. Some results of these studies are of practical importance. In groups with the two alternative types of ontogeny, we revealed strict functional determination of ontogenetic changes in age markers (Olenev, 1989); significant differences in metabolic rate, the rate of senescence, and life span (Olenev, 1981, 1991a); differences at the tissue (Olenev *et al.*, 1983) and biochemical levels (Gulyaeva and Olenev, 1979); differences in the accumulation or heavy metals and sensitivity to them (Bezel' and Olenev, 1989); differences in natural radioresistance (Olenev and Grigorkina, 1998), the dynamics of unconventional interior indices (an example of spleen hypertrophy) (Olenev and Pasichnik, 1999), and cytogenetic instability (Rakitin, 2000); and differences in the response of extreme influences, both natural (Olenev, 1981; Olenev and Kolcheva, 1987) and anthropogenic (Bezel' *et al.*, 1994; Luk'yanova, 1990). Due to the existence of two alternative types of ontogeny, the influence of adverse environmental factors is "refracted" by this specific population structure and

[2] At the first phase of this ontogenetic pathway (Fig. 1), before wintering, variation in body weight and other parameters of rodents decreases considerably owing to elimination of marginal variants, i.e., the animals whose parameters are below or above certain limits. For example, body weight in the bank vole must be within the range of 15–19 g and remain so throughout winter (Fig. 5). 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. It is noteworthy that postreproductive animals (PFG3 and PFG1) in autumn often manifest a decrease in the weight and size of gonads ("collapsed" testes) and in some other parameters, thus making an attempt to "enter the gate." However, all of them die in early winter.

[3] It has been shown that there is no selective elimination of animals belonging to certain cohorts during the autumn–winter–spring period. Neither the origin nor the absolute age of an individual are limiting factors under unfavorable environmental conditions: the main role belongs to the functional status of animals entering the winter period (Olenev, 1982, 1991a).

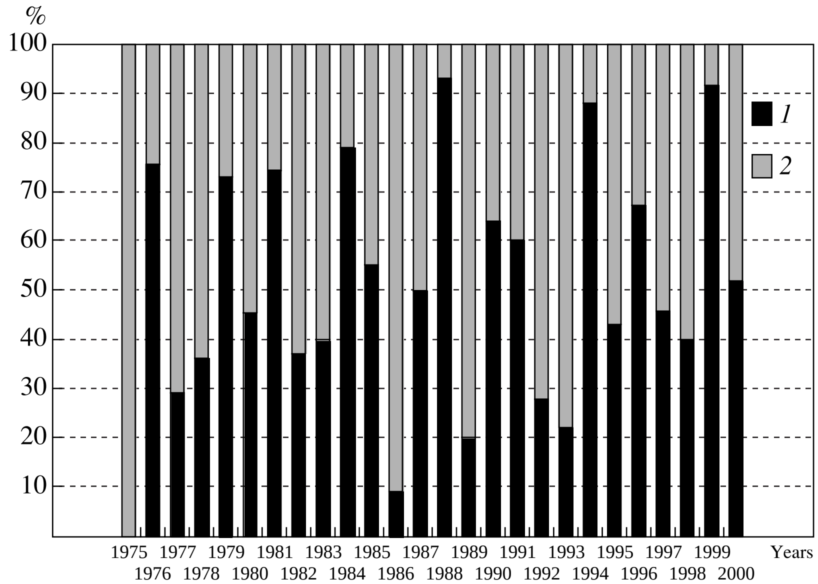

Fig. 2. Dynamics of the ratio between the types of ontogeny in murine rodents (an example of bank vole): (*1*) ontogeny type 1, (*2*) ontogeny type 2.

may result in damage to certain functional groups, depending on the type of influence.

DYNAMICS OF THE RATIO BETWEEN THE TYPES OF ONTOGENY (INTERPRETATION OF FACTUAL DATA)

Owing to continuous observations on the same rodent populations over 26 years, we can analyze the long-term dynamics of the ratio between the two types of ontogeny and discuss their features. Figure 2 shows that this ratio varied within a broad range covering virtually all possible values, from 0 to 93%. In some years (as a rule, with extreme conditions), the factor responsible for the prevalence of a certain type of ontogeny was apparent. For example, the absence of animals with the first type of ontogeny in 1975 (all young of the year failed to mature) was explained by severe drought (Olenev, 1981a). In 1986, the proportion of such animals was less than 10% because of early arrest of sexual maturation, which could be explained by abnormally high (for the forest zone) population density in July and August (Kolcheva and Olenev, 1991). In both these years, only overwintered animals were involved in reproduction and provided for population growth. It is noteworthy that the pattern of seasonal population dynamics in such cases may have no significant differences from its long-term variants, but the qualitative composition of the population changes drastically: the entire generation is lost. The role of overwintered animals deserves special attention because of the following inverse relationship: *if young of the year are actively involved in reproduction, overwintered animals cease to reproduce early in this year, and vice versa* (Olenev, 1981b). Moreover, PFG1 includes the animals of all generations born in the previous year, and this provides the possibility of transmitting genetic information not only through the sequence of generations during the current reproductive season (horizontal transmission), but also directly from the first generation born in one year to the first generation born in the next year (vertical transmission). In addition, heterogeneity may increase due to the pairing of individuals belonging to different generations born in the current or previous year (the so-called age crossing; Olenev, 1982).

Special attention should be paid to the distinct inverse relationship between the proportion of animals with the first type of ontogeny and population size: Spearman rank correlation coefficient $R = -0.76$, $\rho = 0.000013$ (Fig. 3). A similar relationship, although less distinct ($R = -0.66$, $\rho = 0.076$), was revealed by analyzing the samples taken from an *Apodemus (Sylvaemus) uralensis* population over eight years. Phenomenologically, the situation is as follows: population size increases in the years in which the proportion of animals with the first type of ontogeny becomes smaller than in the previous year, and vice versa. As follows from Fig. 3, this trend is observed irrespective of population size. However, the idea that the prevalence of animals with a certain type of ontogeny is the factor directly determining population size should be regarded with caution. It is more correct to consider no more than the relationship between the ratio of the types of ontogeny and population size, although the aforementioned phenomenon is certainly of interest. Analyzing the factors accounting for such a strong correlation, it is possible to draw an analogy to the hypotheses of self-regulatory processes, in which attention is focused on the internal factors of cyclicity (Christian, 1950; Krebs, 1970; Stenseth, 1983). Within the frame-

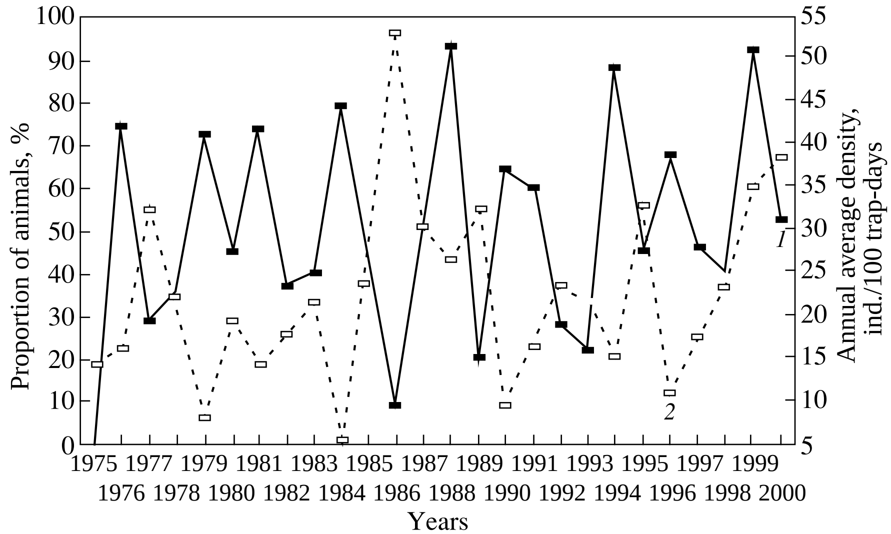

Fig. 3. Changes in the proportion of animals with the first type of ontogeny (*1*) and population dynamics (*2*) in bank vole.

works of these hypotheses, population are completed with the suppression of animal reproductive capacity at high population densities. Thus, the dynamics of the ratio between the types of ontogeny is apparently a more sensitive indicator of intrapopulation processes, as it is effective in the entire range of population densities (rather than at peak densities only).

The general pattern of population size in six rodent species (Fig. 4) shows that population changes in different species occur asynchronously, and exceptions to this rule are rare. It is logical to assume that the same concerns the dynamics of the ratio between the types of ontogeny in different species. Indeed, this assumption has been confirmed using an example of bank vole and pigmy wood mouse populations. Apparently, specific influences of the same environmental factors are differently perceived by cohabitant species and, hence, evoke different adaptive responses that involve changes in the ratio between the types of ontogeny and, hence, in population dynamics.

NONSPECIFIC TRIGGER MECHANISM OF THE TWO TYPES OF ONTOGENY IN RODENTS

Analyzing the problem of mechanisms and factors determining the divergence between animal groups following the alternative ontogenetic pathways, I proposed the existence of some unspecific trigger mechanism switching animal growth and development to a certain pathway, which comes into action under specific influences of abiotic and biotic factors playing the role of an actuator (Olenev, 1987). We performed phenogenetic analysis of intrapopulation groups corresponding to the two types of ontogeny with respect to a complex of nonmetric threshold characters (Barry and Searl, 1963) and obtained evidence that qualitative genetic differences between these groups are insignificant. The results of multifactor morphometric analysis with the use of the genetic mandibular test (Festing, 1972) are in good agreement with the results of phenetic analysis (Olenev, 1991b). A similar conclusion can be drawn from the work of Kryazhimskii (1989).

Thus, changes in relative growth rate are unspecific and nonheritable. On this basis, I proposed that *each animal is polyvalent, i.e., it inherits two alternative ontogenetic programs determined by the genotype,* but environmental conditions allow only one program to be realized (Olenev, 1995) (Fig. 6). The environment appears to direct animal development along one of the two ontogenetic pathways, although the type of ontogeny in a concrete animal is unlikely to be strictly determined. The genotype determines individual characteristics of animals; within the framework of the proposed idea, this means that specific influences of the same environmental factors are perceived by animals in different ways, triggering one of the two alternative types of ontogeny.

Indirect evidence for this conclusion is provided by rare cases in which only one type of ontogeny was observed in all members of a natural population, as it occurred in the years with extreme conditions (e.g., 1975), as genetic determination of the same type of ontogeny in all animals born in the same year is unlikely. An opposite situation—an increase in the proportion of rodents with the first type of ontogeny—is possible to simulate in laboratory colonies by modifying the conditions of animal keeping, including ration (Bashenina, 1977).

The ability to develop several phenotypes on the basis of one genotype is acquired in the course of long-term selection (Mednikov, 1987). It is logical to assume that the initial ontogenetic variant was of the second

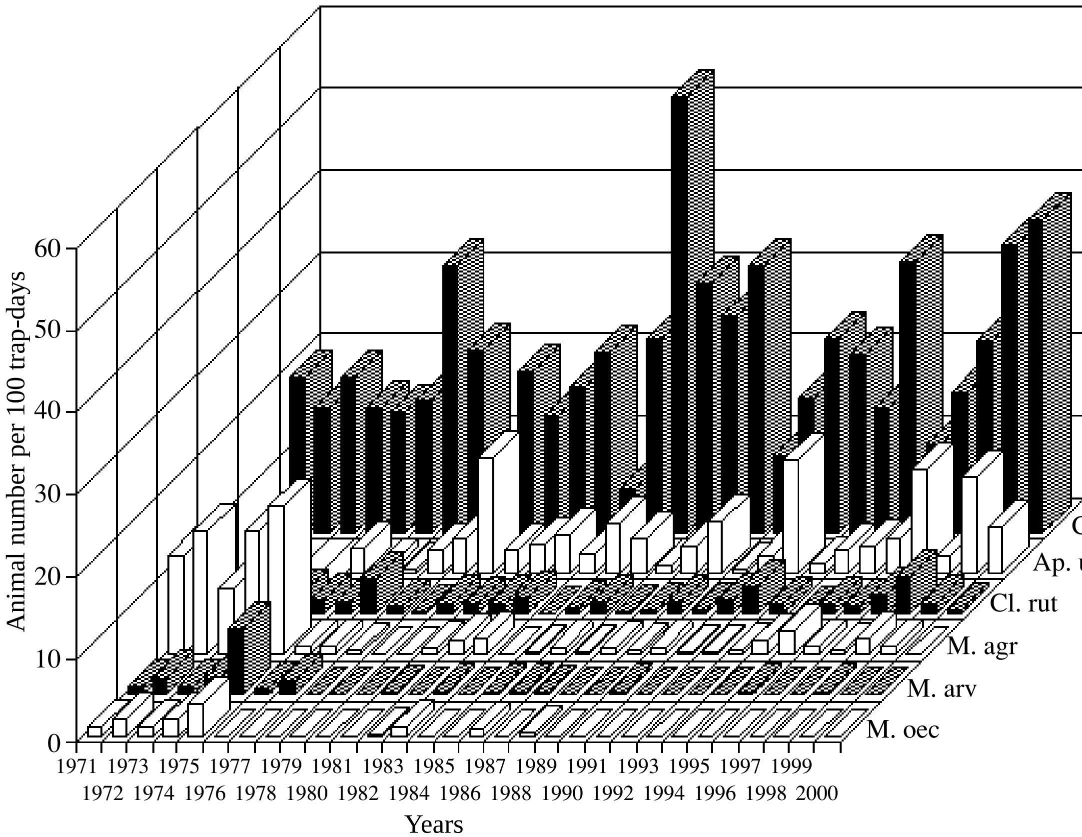

Fig. 4. Population dynamics in six rodent species (annual average values): Cl. gl, *Clethrionomys glareolus*; Ap. ur, *Apodemus uralensis*; Cl. rut, *Clethrionomys rutilus*; M. agr, *Microtus agrestis*; M. arv, *Microtus arvalis*; M. oec, *Microtus oeconomus.*

type (maturation in the second year after birth), as is now characteristic of most small representatives of the order Insectivora, a more ancient group of mammals.

Manifestations of bivariant development are typical of virtually all species of murine rodents. Their hereditary ability to follow one of the two ontogenetic pathways depending on existing environmental conditions is obviously of adaptive significance, being most apparent in extreme situations. The mechanism of switching to a certain type of ontogeny is mainly triggered by environmental factors, including cold spells in spring, drought, and overmoistening (e.g., in 1988 and 1999). In addition, an important role belongs to stimulating and signal factors: day length, products of life activities of other animals, acoustic and visual signals, composition and quality of food, etc. These external factors usually act as a complex, with their effects modifying each other. Naturally, animals respond to these factors differently, depending on their individual features.

I regard bivariant development as a nonspecific regulatory mechanism and a basis for structural and functional rearrangements in the population, which provide the possibility of "adaptive maneuver" in response to changes in environmental conditions. The ratio of animals belonging to different PFGs determines specific features of the population, its physiognomy at a specific moment of time. The absolute age of animals in a PFG is of little importance.

The adaptive population response to a broad spectrum of influences, including anthropogenic damage, depends not only on the type and strength of the influence, but also on the functional structure of the population (in this case, specific features of rodents with two alternative types of ontogeny). The functional approach makes it possible to significantly reduce errors in assessing the consequences of harmful influences and, hence, can provide a reliable methodological basis for such assessment.

The concept of bivariant development may explain the significance of critical periods in the life of populations. Therefore, studies on the mechanisms of alternative types of ontogeny are directly related to the analysis of factors determining rodent population dynamics. In this work, attention was focused on advantages offered by the functional approach. Any sample from a natural population consists of individuals that qualitatively differ from each other with respect to the type of ontogeny and have the corresponding combinations of traits, and analysis should be performed with due regard to this fact. The functional approach has a sound theoretical basis and provides conditions for competently analyzing a variety of biological parameters.

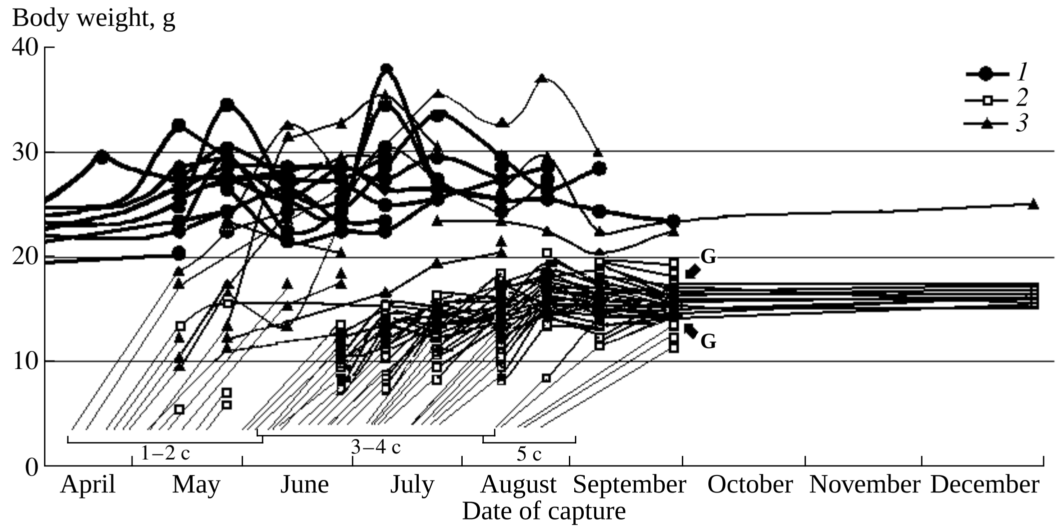

Fig. 5. Dynamics of abundance and body weight in the bank vole in 1977 (results of individual marking in a 1.5-ha plot): (*1*) PFG1, (*2*) PFG2; (*3*) PFG3; (G) gate (bottleneck); (c1)–(c5) cohorts, dates of emergence.

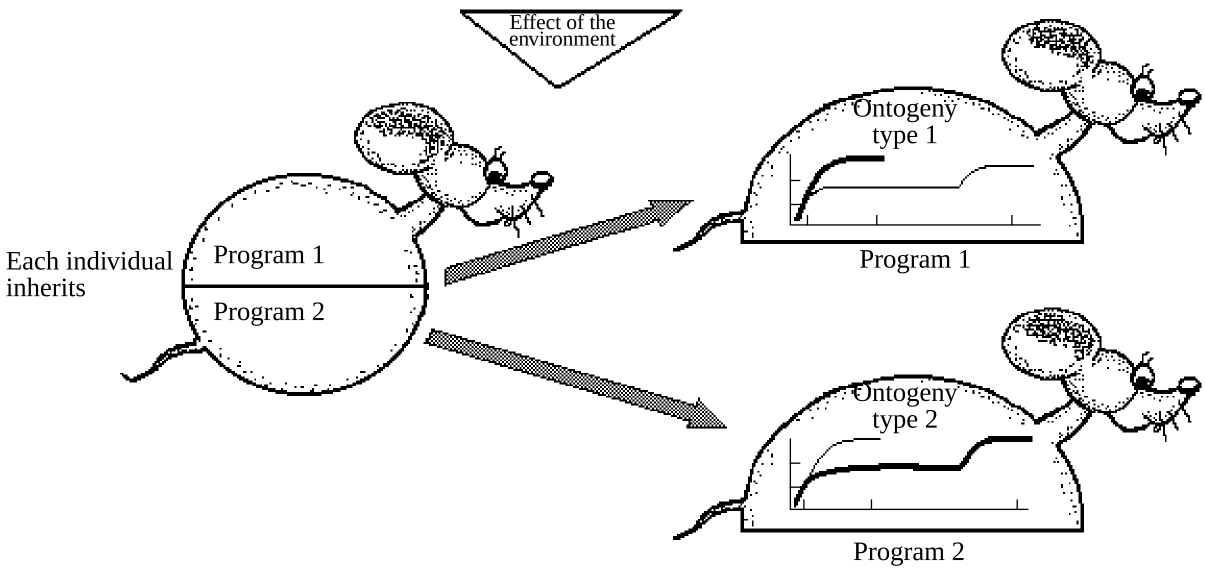

Fig. 6. Scheme of the development of two alternative ontogenetic pathways in rodents (the genetic aspect).

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research, project no. 02-04-49451.

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