

Dynamics of Sex Ratio in Populations of Cyclomorphic Mammals (Rodentia, Cricetidae, Muridae)

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Abstract—Using the result of long-term monitoring (over 30 years) of the main population parameters of cyclomorphic mammals (genera *Clethrionomys*, *Microtus*, and *Sylvaemus*) in the Il'men Reserve (Chelyabinsk oblast, the Southern Urals), the phenomenology of the sex ratio and its dynamics in their natural populations are analyzed. The main factors potentially influencing the sex structure of rodents are considered, including isolation of settlements, relative abundance, population density, species-specific features, alternative types of ontogeny, exposure to extreme factors, sex-dependent asynchronous mortality, and age cross. It is shown that the analysis of sex structure in rodents should be performed taking into account the type of their ontogeny, with the CMR method (capture—marking—recapture) giving the most objective estimate of the sex ratio. An alternative approach is to analyze samples taken in autumn to winter, after the end of breeding and elimination of reproductive individuals from the population. It is concluded that the dynamics of the sex structure in murine rodents are conditioned ecologically and that no selective elimination of individuals depending on sex takes place upon overwintering. The sex ratio in cyclomorphic mammals is a variable parameter that fluctuates about the average value depending on both regular and random factors. Methodological recommendations are given for the assessment of sex structure in cyclomorphic mammals.

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INTRODUCTION

The sex ratio is an important demographic parameter pertaining to the maintenance of genetic heterogeneity of populations (Shvarts, 1969). The chromosomal mechanism of sex differentiation in mammals provides for the equal ratio of males and females at birth, while the dynamics of sex structure, being directly related to population reproduction and abundance, has an effect on the microevolutionary process (Bol'shakov and Kubantsev, 1984). Specialists distinguish the primary, secondary, and tertiary sex ratios in the population: among zygotes, newborns, and adult, reproductive individuals, respectively (Geodakyan and Geodakyan, 1985). Factors influencing the sex ratio include ambient temperature, diet, the age of parents, and behavioral features. It has been shown that the integrated action of external and internal factors produces an effect on the physical status and reproductive capacity of individuals (Evsikov et al., 1998), with metabolic resources of the mother during pregnancy having influence on the secondary sex ratio in the progeny (Nazarova and Evsikov, 2004). There are data on acceleration of sexual maturation in female house mice if they develop in utero near a male (Vandenberg, 1989) and, conversely, on reproductive suppression under condition of intrauterine localization near another female (Zielinski and Vandenberg, 1991).

The purpose of this study is to analyze the sex structure of natural populations in rodents of different species, taking into account the alternative types of growth and development; to consider probable factors influencing this structure; and to analyze the secondary sex ratio among animals from a laboratory colony. Another purpose is methodological: the examples given in this paper reflect the phenomenology of the sex ratio in natural rodent populations and illustrate the extent of possible contradictions and misunderstanding.

MATERIALS AND METHODS

The material was collected in the Il'men State Nature Reserve (Chelyabinsk oblast, the Southern Urals), in two types of biotopes in two permanent test areas and in marking plots on a peninsula (1.5 ha) and an island (2.2 ha). The bank vole *Clethrionomys glareolus* Schreber is the dominant rodent species in the study area (74.8%); then follow the pygmy wood mouse *Sylvaemus uralensis* Pallas (14.0%) and field vole *Microtus agrestis* Linnaeus (4.2%).

The main population parameters of these rodents, including the fine age structure, have been monitored for more than 30 years (since 1975). The fine age structure (an element of demographic structure) is understood as structure at the level of supraorganismal units within the population that allows a detailed anal-

ysis of intrapopulation events to be performed (Olenev, 2004). No analogs of such long-term continuous observations have been found in the literature. Field studies were performed by conventional methods such as removal trapping, the method of morphophysiological indicators, and capture—marking—recapture (CMR), which involved regular monthly trapping and description of every trapped animal (body weight, capture point, functional status with respect to maturity, involvement in breeding, etc.), with the fate of each individual being followed throughout life.

The analysis of sex ratio was performed using the original functional—ontogenetic approach (Olenev, 2002, 2004, 2009) based on the concept of multiversal-ity of individual development in small rodents. The essence of this approach is in identification of structural units within a population by the criterion of the unity of individuals in terms of their functional status (specific features of growth, development, and role in reproduction of the population) and the sequence of its changes in time. In particular, the following functional groups are distinguished (for details, see Olenev, 2002, 2004). Mature young of the year (ontogeny type I): actively growing animals (mainly of the first cohorts); their function is to increase population size by participating in breeding in the year of birth. Immature young of the year (ontogeny type II, phase 1): animals that fail to mature in the year of birth (mainly of the last cohorts, but representatives of the first cohorts are always among them); their function is to survive until the next spring and start the cycle of population renewal. Overwintered animals (ontogeny type II, phase 2): representatives of all last-year cohorts that remain immature until spring, when all of them reach sexual maturity and become involved in reproduction, irrespective of environmental conditions. Young of the year, unlike overwintered animals, can follow one of the two ontogenetic pathways, reaching maturity either in the year of birth or in the next year. This is why their analysis should be performed with regard to the type of ontogeny, and data on young of the year and overwintered animals are separately presented in the figures.

It should be noted that the functional—ontogenetic approach has made it possible to interpret a wide range of phenomena related to different aspects of animal—environment interactions under conditions of exposure to a variety of natural and anthropogenic factors. Evidence has been obtained for functional determination of many biological characteristics: demographic and spatial population structure; ontogenetic, morphological, morphophysiological, and unconventional interior parameters (Olenev, 2004); and resistance to acute (Grigorkina, 1998) and chronic radiation exposure (Grigorkina, Olenev, and Modorov, 2008). Both types of ontogeny manifest themselves most clearly in rodent populations of the temperate zone at its boundary with the arctic zone, where climate is sharply continental.

On the whole, about 3000 ind. were analyzed by the CMR method and 9000, by means of removal trapping with subsequent processing by the method of morphophysiological indicators. The figures show the most informative data on 1300 individually marked *C. glareolus* voles, 440 *S. uralensis* mice, and 400 *M. agrestis* voles (the CMR method) and on 900 *C. glareolus* voles removed from the population. The secondary sex ratio was analyzed among 150 pups from 33 litters produced in the laboratory colony of bank voles (22 pairs) whose founders were captured in the Il'men Reserve.

The data were processed statistically using the Excel 6.0 program package. Differences in the sex ratio between samples taken during different rounds of trapping were evaluated by the χ^2 , and pairwise comparisons between the samples were made using a two-tailed separate variance *t*-test (Bailey, 1964). The calculated values of these tests and their table values are presented for each group includes in analysis. Differences were considered significant at $p < 0.05$.

RESULTS AND DISCUSSION

Sex Ratio in Years with Different Levels of Animal Abundance

It is known that the rates of population growth and decline depend on birth rate, fecundity, and individual life span characteristic of a given species (Severtsov, 1941). For the pygmy wood mouse, the Il'men Reserve is not the optimal part of the range: the abundance of these rodents usually remained low and peaked very rarely.

In the low-abundance year 1979 (no more than 15 ind./ha even at the seasonal peak), the sex ratio among overwintered pygmy wood mice proved to change (Fig. 1a), but the difference between the numbers of males and females lacked statistical significance ($\chi^2 = 4.62$, table value = 11.07, $p > 0.05$).

In the high-abundance year 1980 (over 20 ind./ha), the density of pygmy wood mice exceeded that of bank voles. The sex ratio in the overwintered group was shifted toward males in April to July, but only females were trapped in August and September (Fig. 1b) (differences nonsignificant: $\chi^2 = 5.27$, table value = 11.07, $p > 0.05$). Among young of the year, the proportion of males was 53% ($\chi^2 = 6.65$, table value = 11.07, $p > 0.05$). In general, this year was characterized by a slight (1.2-fold) prevalence of males over females.

Overwintered bank voles in the low-abundance year 1998 (7 ind./ha) showed no changes in the sex ratio (Fig. 1c) ($\chi^2 = 5.65$, table value = 11.07, $p > 0.05$), whereas in the high-abundance year 1977 (52 ind./ha in the marking plot) the proportion of males was significantly (1.7-fold) higher than that of females (Fig. 1d) ($\chi^2 = 5.44$, table value = 3.8, $p \leq 0.05$). A significant prevalence of males was also observed among young of the year ($\chi^2 = 23.24$, table value = 3.8, $p \leq 0.05$).

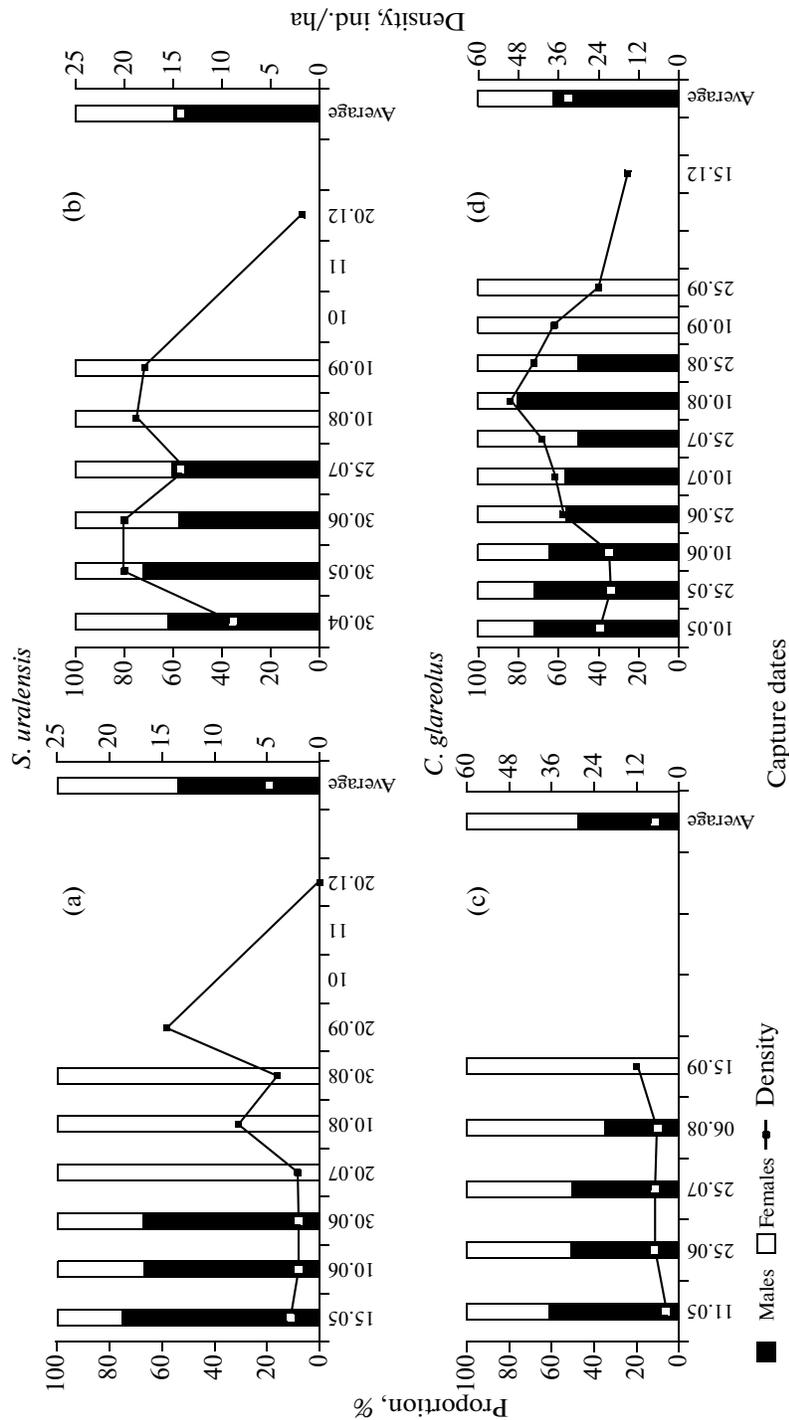


Fig. 1. Seasonal dynamics of sex ratio in the group of overwintered animals (peninsula) under conditions of (a, c) low abundance and (b, d) high abundance (here and in Figs. 3–5, dates are shown in DD/MM format).

Comparisons between species should be made taking into account their mode of life, abundance, and type of ontogeny. Specific ecological features of species usually determine the size of individual home ranges. For example, the home range size reaches 2–3 ha in microtine voles *M. oeconomus* and *M. agrestis*

(Karaseva and Il'enko, 1957) and 5–8 ha in forest voles *C. glareolus*, *C. rutilus*, and *C. rufocanus* (Okulova, Aristova, and Koshkina, 1971) but is no less than 15 ha in mice *A. agrarius* and *S. uralensis* (Nikitina, 1961). It has been shown that the home range size in bank voles with different types of ontogeny directly

depends on their functional status: home ranges of reproductive individuals are always significantly larger than in immature young of the year (Maklakov, Olenev, and Kryazhinskii, 2004). In the Il'men population of pygmy wood mice, we revealed different variants of the sex ratio, with differences between them often being random. A no less interesting fact is that samples taken during the same round of trapping from different (dry and moist) biotopes also proved to differ in the proportions of males and females. These results confirm the conclusion that the sex composition of pygmy wood mice is extremely unstable, which is characteristic of all age groups of this species (Kubantsev, 1972).

Our long-term observations confirm that the numbers of males in rodent populations are sufficient. In some years, almost all female bank voles in the marking plot (peninsula) were mated by single overwintered males. Mice are still more mobile: during one tour of trapping, the same marked overwintered male was trapped at several points located very far from each other. A number of authors (Brown, 1956; Ambrose, 1969; Gromov, 2008) consider that the size of an individual home range is adequately characterized by the distance between the remotest points of capture (record) of the same individual, or range length (RL).

Sex Ratio and Interannual Population Dynamics

We have analyzed the interannual sex ratio and population dynamics of pygmy wood mice over five years with different levels of animal abundance (1979–1983) using individual marking. The pooled data on overwintered animals and young of the year (Fig. 2a) show that the sex ratio varied between years, but, in general, males slightly prevailed in the population. A pairwise comparison of values recorded in years with high and low animal abundance (1980 and 1983) provides evidence for the absence of significant changes in the sex ratio ($t = 0.78$, table value = 1.96, $p > 0.05$). A detailed analysis by the types of ontogeny showed that the proportions of males and females were equal (1 : 1) in the overwintered group (Fig. 2b) and that males slightly prevailed over females among young of the year (Fig. 2c) ($t = 1.0$, table value = 1.96, $p > 0.05$).

A similar analysis was performed in bank voles collected by the method of removal trapping between 1993 and 1999 (Fig. 2d). As in the previous case, no correlation between the sex ratio and animal abundance was revealed: the proportions of males and females in the years of population decline (1993, 1994), depression (1996), and growth (1998, 1999) were almost equal. However, the proportion of males proved to increase in the years of population peak (1995) and growth (1997), reaching 64 and 67%, respectively. A comparison of sex ratios recorded in 1995 (peak) and 1996 (depression) confirmed the absence of significant differences in the sex structure

of population between phases of the population cycle ($t = 1.13$, table value = 1.96, $p > 0.05$).

None of the species showed any trend in the sex ratio depending on population dynamics, with the proportion of males being slightly higher in both cases.

Sex Ratio in Plots with Different Degrees of Isolation (Peninsula and Island) and under Extreme Weather Conditions

Years with extreme weather conditions are of particular interest for population studies, since adaptive changes at different organization levels manifest themselves especially clearly (Glotov, 1983). An extreme situation for typical murine rodent species of the forest zone developed during the drought of 1975, which occurred for the first time over the past 80 years of meteorological observations in the Ural region. The bank vole population in summer was undergoing processes characteristic of the autumn–winter–spring period, i.e., aimed at the maximum possible reduction of energy expenditures by means of suspended growth and maturation of young animals. All young of the year were characterized by type II ontogeny (failed to mature), with type I animals being completely absent (Olenev, 1981). Thus, normal population processes, including reproduction, were disturbed, which resulted in the formation of an atypical age structure (the whole generation was missing). Young animals remained immature instead of contribution to population growth. The sex ratios in groups of overwintered animals (Fig. 3a) and young of the year (Fig. 3b) did not differ statistically ($\chi^2 = 0.88$, table value = 11.07, $p > 0.05$; and $\chi^2 = 8.52$, table value = 14.07, $p > 0.05$, respectively). The average numbers of males and females were also similar ($t = 0.36$, table value = 1.96, $p > 0.05$). Hence, it follows that (1) the sex ratio in the bank vole population remained approximately equal even in the year with extreme conditions and in a partially isolated plot (peninsula), and (2) no selective sex-biased elimination of animals took place under such conditions.

Unlike in the bank vole, the field vole population in the same year contained type I individuals, although their proportion was significantly smaller than usual. In May to October, the sex ratio varied among overwintered animals and young of the year marked on the peninsula, with the proportion of males in both groups being significantly greater than that of females ($\chi^2 = 8.64$, table value = 3.84, $p \leq 0.05$ and $\chi^2 = 4.65$, table value = 3.84, $p \leq 0.05$, respectively). It is noteworthy that the latest trapping of overwintered females was recorded in early July, while that of overwintered males, in early August (Table 1). All animals in catches were young of the year, with males prevailing (60%), while overwintered individuals were absent.

Of special interest are data on rodents living on the island, i.e., under conditions of isolation. An analysis

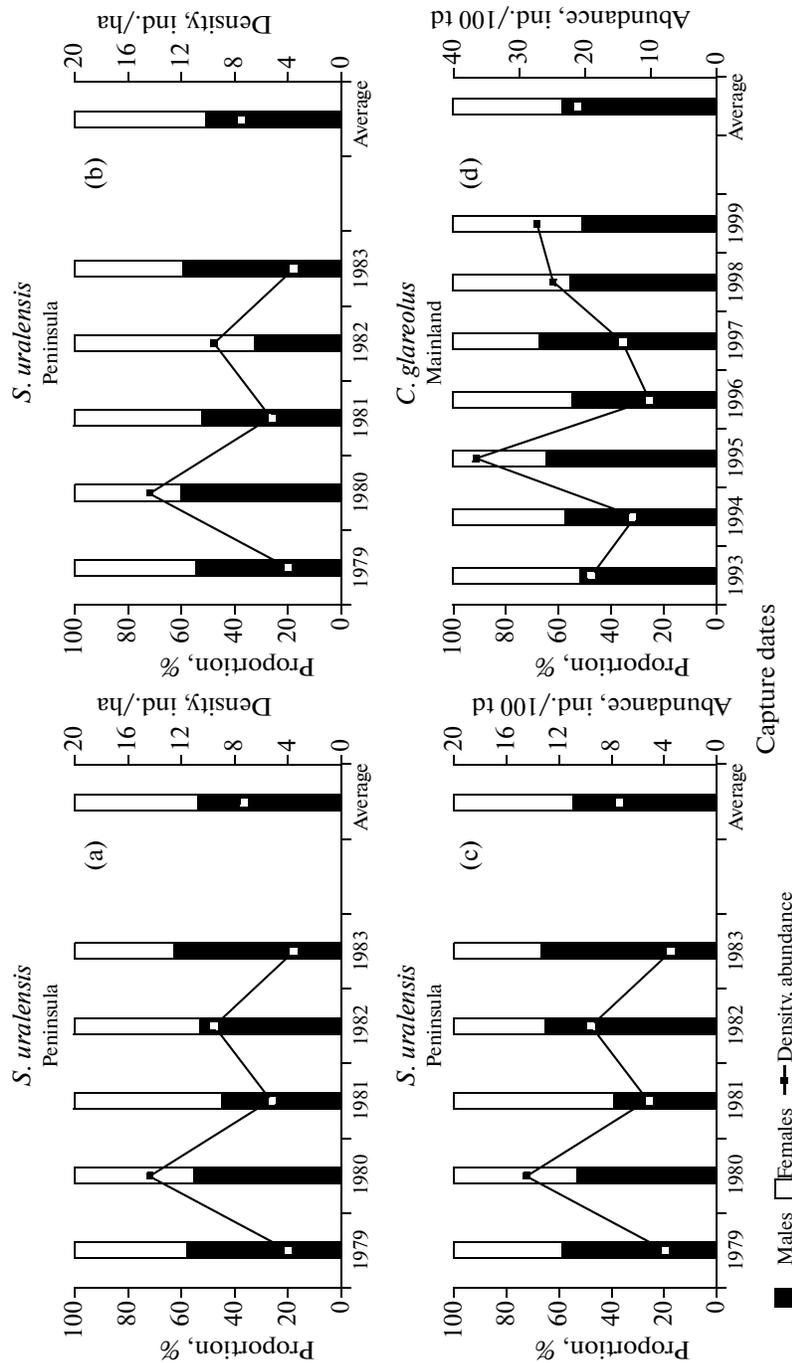


Fig. 2. Interannual dynamics of sex ratio: (a, d) both overwintered animals and young of the year, (b) overwintered animals, (c) young of the year.

of sex structure in the island population of field voles showed that the proportions of males and females varied between the rounds of trapping both among overwintered animals (Fig. 3c) and among young of the year (Fig. 3d) ($\chi^2 = 2.01$, table value = 12.59, $p > 0.05$ and $\chi^2 = 3.22$, table value = 14.07, $p > 0.05$, respectively). The proportion of females was greater (57%) in the group of overwintered animals ($\chi^2 = 1.52$, table

value = 3.84, $p > 0.05$), while males prevailed significantly (62%) among young of the year ($\chi^2 = 19.59$, table value = 3.84, $p \leq 0.05$). It should be noted that on the island, unlike on the peninsula, males were eliminated from the population two months earlier than were females (Table 1). As a result, significant differences in the sex ratio between overwintered field voles and young of the year were revealed on the island ($t =$

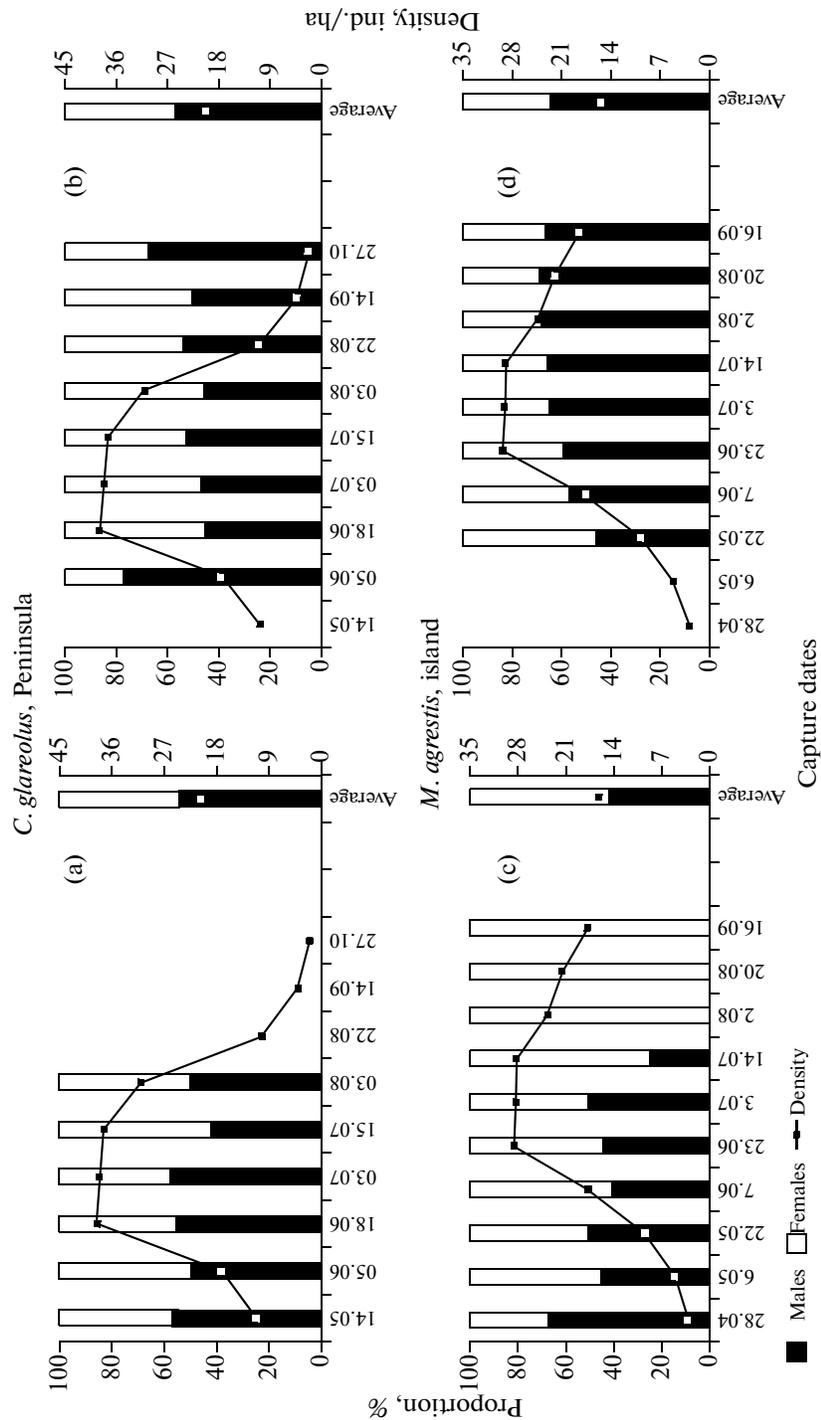


Fig. 3. Seasonal dynamics of sex ratio in the year with extreme conditions (drought) among (a, c) overwintered animals and (b, d) young of the year.

2.96, table value = 1.96, $p \leq 0.05$). Thus, populations of *Microtus* voles inhabiting areas isolated to different degrees were characterized by a significant prevalence of males over females in the year with extreme conditions. This is evidence that microtine and forest voles differ in population response to drought. The observed

adverse effect is due not so much to unfavorable abiotic conditions as to related biotic factors mediating their influence, such as the reduction of food supply and impairment of foraging conditions (Olenev, 2002; Severtsov, 2004). In the situation described above, the simplified age structure of the bank vole population

was optimal for preserving its young component. In the field vole population, conversely, young of the year participated in breeding, but almost all animals of this age group died by the next (1976) spring, so that the relative abundance of field voles dropped by an order of magnitude, from 14 to 1 ind./100 trap–days (td). Today, this parameter remains at a level of 0.1–2 ind./100 td. It appears that extreme environmental changes such as the 1975 drought stimulated the transition of the field vole population to a different level of fluctuations in animal abundance (Olenev and Kolcheva, 2007).

Sex Ratio and the Time Course of Elimination of Males and Females

The latest dates of animal capture in the marking plot in years with extreme conditions (Table 1) were used to trace in detail the sequence in which overwintered males and females were eliminated from the population, since differences in the time of their death could be significant for sex ratio assessment. In the drought year 1975 (the block of growth and maturation in young of the year), dates of death for males and females in the bank vole population were similar, falling on early August (Fig. 4a). In the next year, when weather conditions (including precipitation) were close to the norm, the overwintered group had a simplified age structure (Olenev, 1982), because the animals born in the drought year failed to participate in breeding, and the whole generation was missing (see above). However, population growth in 1976 did take place due to an unusually long breeding period in overwintered females: 5.5 months, compared to 3.5 months in the norm (Table 1). This was a phenomenon of aftereffect (Polyakov, 1954; Olenev, 1979). During this period, the females produced five to six litters each and lived for 16 months, compared to three or four litters and 12–13 months in the norm. Overwintered females mated overwintered males only until midsummer, when the latter died and were replaced by male young of the year from the first cohorts (female young of the year participated in breeding only slightly); i.e., an age cross took place (Olenev, 1982). Thus, the life span and reproductive period of overwintered females were prolonged, compared to those of males. This phenomenon (a specific physiological state accounted for by conditions of growth and development in the previous season) can be interpreted as an adaptive response of animals aimed at the maximum possible realization of the potential for population growth while preserving the young population component. Note that the above phenomena could only be revealed by analyzing population events on the basis of the functional–ontogenetic approach.

We remind that the essence of age cross is in pair formation from individuals of different ages, generations, and functional groups. According to Shvarts (1969), the main cause of this phenomenon is that males and females mature at different rates. In our

Table 1. Time course of elimination (death) of overwintered voles in different habitats (dates are shown in DD/MM/YYYY format)

Species	Capture site	Latest capture dates	
		Males	Females
<i>S. uralensis</i>	Peninsula	30.06.1979	30.08.1979
	"	25.07.1980	10.09.1980
	"	10.08.1981	15.09.1981
	"	10.06.1982	15.09.1982
<i>M. agrestis</i>	Peninsula	15.06.1983	25.08.1983
	"	03.08.1975	03.07.1975
<i>C. glareolus</i>	Island	01.07.1975	16.09.1975
	Peninsula	03.08.1975	03.08.1975
	"	22.07.1976	18.10.1976
	"	25.08.1977	25.09.1977
	"	01.08.1998	01.09.1998
<i>C. glareolus</i>	"	01.09.1999	01.08.1999
	Mainland	15.07.1994	15.06.1994
	"	15.07.1995	15.06.1995
	"	15.07.1996	15.10.1996
"	15.10.1997	15.07.1997	

Note: The later date in each pair is boldfaced.

opinion, the behavioral dominance of adult males combined with the nonsimultaneous death of overwintered males and females can also result in age cross. In rodents, females mature earlier than males and usually mate overwintered males even in the presence of mature young of the year, which lose competition for mate to more aggressive older males. In our opinion, high abundance of mature overwintered males can result in retarded sexual maturation of male young of the year.

In 1977, foraging conditions for rodents were favorable, and the abundance of bank voles was high. The overwintered group was fairly heterogeneous with respect to origin. The last overwintered males were trapped in late August, about a month earlier than were the last overwintered females (Fig. 4b). The life span of individual cohorts in the overwintered group proved to be reduced to a minimum. The population was maintained due mainly to active reproduction of young of the year and, by spring, comprised representatives of seven cohorts (Olenev, 1982). Throughout the season, males significantly prevailed over females in relative abundance (Fig. 1d).

Nonsimultaneous elimination of overwintered males and females was also observed in the population

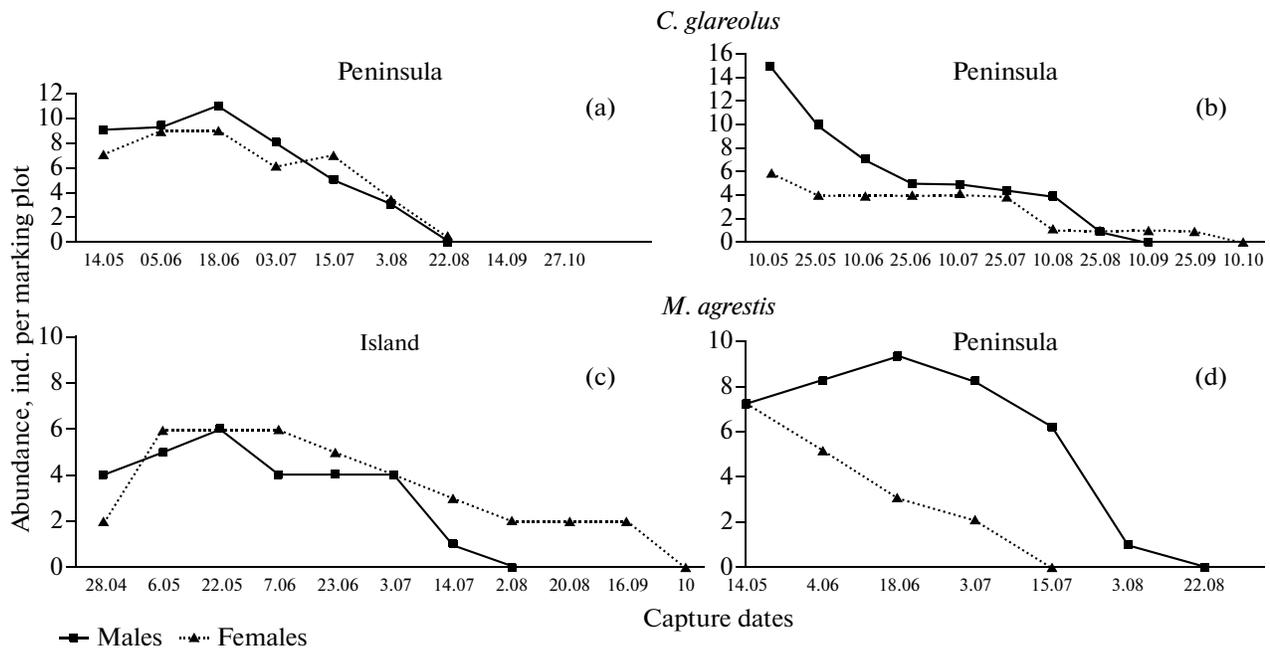


Fig. 4. Seasonal dynamics of abundance and time of death of overwintered males and females in the marking plot (a, c, d) in the extreme (drought) year and (b) in the year of high animal abundance.

of marked field voles (1975). Males, compared to females, disappeared from catches 2 months earlier on the island (Fig. 4c), but two months later on the peninsula (Fig. 4d). Therefore, differences in the date of death between overwintered males and females were observed in both bank and field voles living in areas with different degrees of isolation. It should be emphasized that, in both marking plots, males numerically prevailed over females throughout the season (Figs. 3c, 3d). A comprehensive analysis of these and other long-term data shows that deviation from the normal sex ratio observed in natural small mammal populations may be far from the real situation.

Sex Ratio upon Overwintering

As noted previously (Olenev, 2002, 2004), rodents that have fulfilled their reproductive function, either overwintered or mature young of the year, are eliminated (with symptoms of deep senescence), and the population in autumn and winter consists of immature young of the year. It was interesting to analyze probable changes in the sex ratio upon overwintering. For this purpose, we studied groups of immature young of the year in the period from the onset of wintering to the next spring, when such animals by definition become overwintered. This allowed us to estimate mortality among males and females during the autumn–winter season over six years (1994–1999). The results showed that the situation before entry to and upon exit from wintering could vary (Fig. 5a). In some cases, the number of animals before the onset of wintering was greater than in the next spring (1996–

1997); in other cases, their numbers in autumn and spring catches were almost equal (1995–1996, 1997–1998, 1998–1999) or spring catches were greater (1994–1995). This variation is due to the effects of different factors (weather conditions, local migrations, etc.) on the efficiency of trapping. However, the sex ratio recorded in autumn remained unchanged in the next spring ($\chi^2 = 21.55$, table value = 25.0, $p > 0.05$) (Fig. 5a). The only exception was recorded in 1993–1994, when the proportion of females was significantly greater before wintering but proved to be smaller than that of males in next May ($t = 2.6$, table value = 2.04, $p \leq 0.05$). It should be noted that the autumn population consists of animals with low metabolic parameters, which do not perceive each other as sexual partners until the onset of maturation in spring. This period is characterized by the absence of sex-related differences in the absolute majority of test parameters, including mobility and therefore, the frequency of falling in traps. In spring, overwintered females occupy individual territories, while males as the most mobile population component have overlapping home ranges and can form so called clans (Vitala, 1977; Bujalska and Saitoh, 2000) with a hierarchical social structure (Kock and Rohn, 1971; Shilov, 1972; Osipova, 1993; etc.). They actively travel over the area in search of mate, and this is why the proportion of males in spring catches is usually greater. Generalizing the above data, conclusions can be drawn concerning putative (in some cases) changes in the sex ratio, the absence of selective sex-biased elimination of individuals, and the maintenance of the sex ratio upon over-

wintering. All this is obviously related to the basic function of animals with type II ontogeny: to preserve the population in the unfavorable winter season and to begin the spring cycle of its renewal.

Sex Ratio in Laboratory Colony

We analyzed the sex ratio in 33 litters produced by bank voles from the laboratory colony in June to November. The litter size varied from 2 to 7 (on average, 4.5) pups, decreasing by autumn. Figure 5b shows different variants of sex ratio revealed in small and large litters, from equal to strongly biased or even to same-sex litters. On the whole, the proportions of males and females among 150 pups differed insignificantly: 53 vs. 47%, respectively ($\chi^2 = 0.67$, table value = 3.84, $p > 0.05$). The secondary sex ratio among 669 newborns from the laboratory colony of large-toothed red-backed voles (*C. rufocanus*) was equal, although the offspring of some females contained significantly greater proportions of males or females, as in our case (Shlyapnikova and Gileva, 1990). These authors revealed no relationship between the body weight of females and the sex ratio in their offspring and confirmed the absence of differential mortality of males or females in utero and during early postnatal development. Analysis of samples pooled by sex and complete or incomplete litters showed that the secondary sex ratio does not depend on the offspring affiliation to a certain vivarium generation or birth during a certain season, unlike in some other mammals (Clutton-Brok and Iason, 1986). The fact that the sex ratio among newborns is equal was confirmed on the study on 3126 pups from 1079 litters of three species of spiny mice (Muridae, *Acomys*) from Egypt, Turkey, and Israel (Novakova et al., 2006). Similar results were obtained in Norway rats: the proportion of males among 2000 embryos was 52.8%, increasing to 54.3% at a high population density (Kozlov, 1980). The secondary sex ratio also proved to be equal in ground squirrels (*Spermophilus*), but among adult animals it tended to shift toward females (Hoffmann et al., 2003; Gur and Barlas, 2006). Reproductively active females were found to prevail in a colony of northern mole voles *Ellobius talpinus* Pallas 1770 (Novikov, Petrovskii, and Moshkin, 2007) which the authors interpreted as an adaptation counterbalancing increased mortality among animals living at the periphery of the species range. Thus, our own and published data provide evidence for the balanced sex ratio at birth in many species of dioecious mammals.

Sex Ratio among Bank Voles with Different Types of Ontogeny

We have considered factors that potentially can affect the sex ratio in a population. It should be noted once again that the functional—ontogenetic approach is instrumental for assessing the formation of the

actual sex structure of populations. This is confirmed by calculations of energy expenditures in small mammals differentiated by body size. It has been shown that the coexistence of animals with two alternative types of growth and development in the same population provides for an increased efficiency of energy fluxes and can be interpreted as a group adaptation allowing the general level of energy expenditures to be reduced (Kryazhimskii and Bol'shakov, 2008). As follows from Table 2, the proportion of females is slightly higher than that of males in the group of mature young of the year but is lower in all other groups. A probable explanation to this situation is as follows. As a rule, female young of the year mate overwintered males, which are larger and more aggressive than male young of the year. The male hierarchy of dominance in the breeding period is usually conditioned by competition for females. Dominant males gain access to receptive females and mate them more frequently than do low-rank males (Gromov, 2008). Note that dominant status does not confer absolute superiority over other males but provides more freedom in courting females, which ensures greater reproductive success. Moreover, the presence of mature overwintered males retards maturation of some male young of the year; as a result, the proportion of males with type I ontogeny decreases, while that of immature male young of the year with type II ontogeny increases (Table 2). The numerical prevalence of males over females ($t = 0.74$, table value = 1.96, $p > 0.05$) is also observed after wintering, which is evidence for the absence of sex-biased animal mortality. Naturally, the sex ratio may differ from year to year depending on environmental conditions (see above).

CONCLUSIONS

Murine rodents—ephemeral animals with a short life cycle—are also cyclomorphic animals; i.e., their reproduction has a seasonal rhythm, and the population is almost completely reviewed within a year. They are characterized by a high ecological dynamism based on extremely complex intrapopulation structuring in time and space, which makes the population capable of timely adaptive response to change in environmental conditions.

The actual sex ratio can be correctly estimated only by means of individual marking and recapture (the CMR method). This approach allows a detailed analysis of intrapopulation events. A kind of alternative to the CMR method is analysis of samples taken in autumn and winter, after the end of breeding and almost complete elimination of reproductive individuals (unfortunately, this approach does not cover the whole pattern of seasonal life activities). Small mammal populations in this period consist of immature young of the year with low parameters of metabolism, stress reactivity, and senescence processes, which are highly tolerant to the impact of adverse natural and

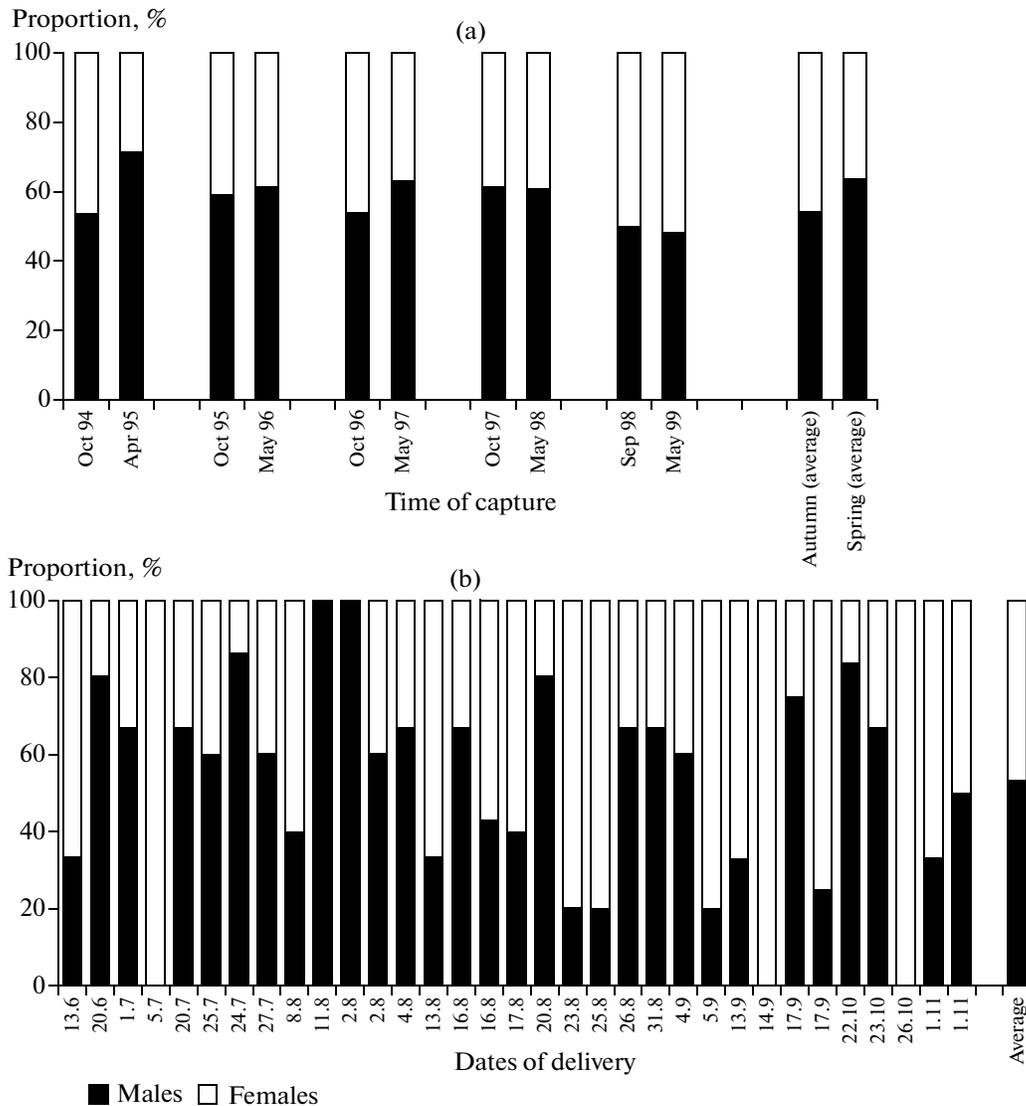


Fig. 5. Sex ratio among bank voles (a) upon overwintering and (b) in laboratory colony.

anthropogenic factors. It is especially important that, until the next spring, these animals do not perceive each other as sexual partners and do not differ in the absolute majority of parameters, including mobility and therefore, the frequency of falling in traps.

The sex ratio remains unchanged by spring, because no selective elimination of males or females takes place in background or anthropogenically disturbed areas. In particular, this follows from our observations on the sex population structure in rodents (*S. uralensis*, *A. agrarius*) inhabiting the zone of local radioactive contamination (Olenev and Grigorkina, 2009). In spring these animals rapidly grow and mature and become highly stress-responsive. This period is characterized by the highest rates of metabolism and senescence. As a rule, males prevail in spring and summer catches, since their migration activity throughout the breeding season is markedly higher

than in females. For this reason, samples taken by some specialists in summer and especially in spring, at the peak of breeding, can provide information that does not adequately reflect the actual sex ratio and can hardly be interpreted correctly. Such a possibility is definitely confirmed by the results of long-term studies by the CMR method, which show that males may prevail in catches during one round of trapping, but no such prevalence is observed during the next round. However, we do not exclude the possibility that changes in the sex ratio do indeed occur.

Attention should be paid to methodological details that may be important not only for a correct assessment of the sex structure of small mammals in natural populations. Requirements set for studies by the method of removal trapping are as follows: (1) a sufficiently long period of sampling (long-term monitoring); (2) correct choice of permanent plots in the main

Table 2. Sex ratio among marked *C. glareolus* voles with different types of ontogeny between 1988 and 1997

Ontogeny	Males	Females
Type I, mature young of the year	76 (46.9)	86 (53.1)
Type II phase I, immature young of the year	261 (55.6)	208 (44.4)
Phase II, overwintered animals	163 (58.4)	116 (41.6)
Total	500 (54.9)	410 (45.1)

Note: Figures show the number of animals and, in parentheses, their proportion (%) of the total number of animals with a given type of ontogeny.

types of biotopes, with regard to the mosaic pattern of the environment; (3) replacement of rap lines within a biotope during the season; (4) standardization of census methods; (5) sufficiently large sample size ensuring representation of all age groups occurring in the population at a given time; (6) classification of trapped animals by the type of ontogeny; (7) synchronous application of different trapping methods; (8) critical analysis of original results and published data; and (9) creative approach to the study.

The sex ratio in cyclomorphic mammals is a variable parameter that fluctuates about the average value depending on both regular and random factors. There appears to be a tendency toward its shift toward males, but in most cases it lacks statistical significance.

Although there are limitations on predictability of population events (which is inevitable under continuously changing environmental conditions), the data and concepts presented above may be of theoretical and practical use for the analysis of sex population structure in cyclomorphic mammals.

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