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CONTENTS

1. Introduction	5
2. Area and Methods	11
3. General Characteristics of the Populations Studied	19
3.1. Bank Vole Population of Broad-Leaved Oak-Lime Forests	19
3.2. Bank Vole Population of Lime-Fir-Spruce Subtaiga Forests	25
3.3. Bank Vole Population of Spruce-Lime Subtaiga Forests	33
3.4. Bank Vole Population of True-Moss Spruce Midtaiga Forests	46
3.5. Northern and Grey Red-backed Vole Population of Siberian Mountain Taiga Coniferous Forests	58
4. Contribution of Endo- and Exogenic Factors into Population Control	74
4.1. Distribution of the Effects of Endo- and Exogenic Factors in the Optimum of the Area	74
4.1.1. The zone of broad-leaved forests	74
4.1.2. Taiga zone, the Udmurt stationary study plot	84
4.1.3. Optimal and pessimal habitats in the taiga zone	95
4.2. Distribution of Contributions of Intrapopulation and External Factors in the Pessimum of the Area	103
4.3. The Ratio and Total Integrated Effect of Intraspecific and Interspecific Interrelations between Forest Voles	112
5. Zonal and Biotopic Peculiarities of the Forest Vole Populations	120
5.1. Numbers and their Variability Level	120
5.2. Duration of the Reproduction Season	127
5.3. Age Composition	128
5.4. Sex Ratio	133
5.5. Ranking of the Effects Produced by Endo- and Exogenic Factors	135
Conclusion	147
Streszczenie	149
References	150

POLISH ECOLOGICAL STUDIES (Pol. ecol. Stud.)	18	1-2	3 – 158	1992
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FACTORIAL ANALYSIS OF POPULATION DYNAMICS IN RODENTS

This paper is aimed at multifactorial analysis of processes affecting abundance and population structure of 3 vole species inhabiting forests. Long-term studies in 5 sites located in different parts of the geographical range of the species involved have provided the empirical data. It is shown that during the breeding season demographic processes in the vole populations basically depend on intrinsic factors. The latter, however, are influenced by circumstances related to the location of the population within the species geographical range, as well as to the habitat quality. Extrinsic factors, like weather and food conditions, are the most effective in so-called transitory seasons, that is autumn-winter and winter-spring. The analysis of multi-annual population dynamics of 2 sympatric vole species shows that reproduction is influenced by the abundance and population structure of both of them. The presented concepts of intrinsic and extrinsic factors make a complementary system allowing for a rather full and precise evaluation of regularities in population dynamics of forest voles.

KEY WORDS: rodents, populations dynamics, external and internal factors.

1. INTRODUCTION

Population processes are intimately connected with the habitat conditions (climate, soil, vegetation, etc.) and biological peculiarities of the population properties (nutriment, sex and age composition, breeding rate, population size dynamics, etc.), its requirements and potentialities. The interaction of external and internal factors moulds a specific type of the population size dynamics. Most probably, different types of interaction between animals and the environment took shape historically during evolution both of animals and of the medium which the animals inhabit and, in the final analysis, the interaction types reflect the ways by which the entire complex of the external conditions can be used most optimally, with the potentialities of the population being realized to the same extent.

The problems of the regulation of murine rodent number have tackled for a long time and yielded rich literature (Pitelka 1964, Chitty 1967a, Koshkina 1967, Christian 1971, Ivanter 1975, Bashenina 1977, Shvarts 1980, Mazurkiewicz 1981, Chernyavski, Tkachev 1982, Abaturov 1984, Bujalska 1985, Krebs 1985, Stenseth 1985 and others). However, so far there is no clear understanding of the way these mechanisms are realized in nature.

The existing hypothesis on the mechanisms of the numbers regulation in populations of small mammals can be divided into two groups. The first group includes hypothesis according to which the birth and death processes that form the population numbers dynamics are determined by the factors external to the populations: meteorological conditions, food resources, and abundance of predators. Hypothesis of the second group rest on the concepts of the territorial relations between the animals entering a population; dynamics of the population demographic parameters is determined by the population density. The advocates of this theory showed an increase in the stress with density, this leading in turn to a drop in the living capacity and reproductive potential of the population. Transformations of the demographic structure and numbers of the population in response to the habitat variations proceed through a transformation of the population composition (different ratio of the genetic, social and physiological intrapopulation groups).

Over the last 60 years of investigations dedicated to the analysis of the population dynamics and factors determining its behaviour, extensive and diverse data have been accumulated on the character of changes occurring in the numbers of some species of small mammals that have different sociodemographic systems and that dwell under different geographical, climatic and biocenotic conditions. A detailed analysis of the materials on the influence of various factors upon the population dynamics can be found in numerous monographs and therefore is beyond the scope of the present study.

Cyclic changes of climatic conditions are reflected in fluctuations of the biocenosis productivity. However, the existence of a strict cyclicity of natural processes has been increasingly questioned. Spectral analysis of multi annual observations of the number of some rodent species shows that populations, in which numerous variations were earlier considered to be cyclic, actually suffer random oscillations (Garsed and Howard 1981). Therefore, when discussing fluctuations in the numbers of many rodent species, one should speak only about stability or instability of the population and not about regular cycles (Southern 1979), although natural cyclicity cannot most probably be rejected.

The genetic relations between the external rhythm drivers and vole numbers do not probably represent a mechanism that is common for all species and that determines the vole population numbers, because the effects with fluctuation of external condition show up most frequently indirectly through food chains (Okulova and Myskin 1973, Myrberget 1986). Besides, no short cycles of 3 to 4 years were found for climatic variations in many regions.

However, the role played by climatic and weather variations in the rodent population dynamics is undoubtedly large. Changes in weather can be either favourable or unfavourable for the growth of the vole population. Meteorological

factors affect the population density and reproduction activity of voles principally during the seasonal transitions autumn-winter and spring-summer (Smirin 1970, Okulova et al. 1978, Volkov, Erdakov 1978, Safronov 1980, Myllymäki, Hansson and Christiansen 1985,).

In addition to direct effects, weather influences indirectly populations of small mammals through variation in food resources and protection condition. The ratio of direct and indirect effects of weather is determined largely by biological features of the species (stenophagous-euryphagous, resistance of the animals to unfavourable conditions, etc.) habitat conditions (optimal, pessimal), geographical latitude of the species occurrence. Many researchers hold the opinion that meteorological conditions can exert a marked direct influence only on populations found in the phase of the numbers decrease, accelerating the population reduction rate. At the same time, growth of vegetation and bearing of vegetable food by favourable weather can facilitate the population growth. Thus, climatic and weather conditions serve as factors that limit the population dynamics (Ivanter 1975, Myllymäki 1975, Hansson and Zejda 1977).

Economic activities of man can be also referred to the factors that can change not only the numbers and structure of specific population but also faunistic and floristic complexes of biocoenosis by influencing it through partial or complete destruction of habitats typical of the species.

The increase of the agricultural burden on the ecosystems leads inevitably to substantial alternation in the population of small mammals and to pronounced changes in the dynamics of some species (Gladkina 1976, Maksimov 1984).

Studies of the relations between the phytocoenosis dynamics and the vole numbers variation show that the concept of food serving as the factor governing the population dynamics rests on adequate facts but cannot be used equally to explain the causes responsible for changes in the density of different species of small mammals (Tast and Kalela 1971, Laine and Henttonen 1983, Eurola, Kyllinen and Laine 1984, Tast 1984, Batzli 1985, Myrberget 1986). The study of the role of food in the rodent population dynamics is focused on the following principal directions: the role of phytocoenosis productivity; the influence of the food quality; winter food and related winter breeding and survival; experimental studies with extra food as regards its volume and quality; plant associations as habitats of small mammals.

Data on the role of diet in the fluctuation of the forest vole numbers are conflicting in many respects. The reason for these contradictions can be understood if we consider that the quantity of vegetation rejected by voles depends on the animal species peculiarities and particular ecological conditions. Besides, let be emphasized that the hypothesis on the determining role of food in the rodent demography do not go beyond suppositions and are not supported by convincing facts from field observations. Shortage of food for forest voles is quite a real problem but in winter season only. Shortage of food occurring in this period can increase the mortality and high abundance of food can encourage premature breeding. However, the negative effect of food security on the forest vole reproduction during the breeding season has not been proved.

It may be inferred that feeding conditions determine to a large extent the population numbers but they cannot probably be referred to the regulating factors, since the conditions determine only the food capacity of a biotope and, hence, the maximum population numbers. Therefore food resources (quality and quantity) should be referred to limiting factors similarly to other external effects. Besides, fluctuations of the feeding conditions influence markedly only populations that are in the phase of decline, making it still worse.

Many papers are dedicated to the influence of predators on the dynamics of their preys, but so far there is no commonly accepted this point of view (Boonstra 1977, May 1977, Smirin 1980, Durward 1980, Krivosheev 1981, Chernyavski and Tkachev 1982, Erlinge et al. 1983, Hansson and Henttonen 1985, Korpimäki 1986). The very existence of such relations is not questioned and principal differences are due to the absence of quantitative estimates of these relations. Some ecologists suppose that the influence of predators is large, while others believe that the influence is small.

The role of predators consists not only in the reduction of the population but also in changing the structure of the vole population through selective catching of most active representative of the population. Predators remove mainly the "population reserve", doing so, and do not affect considerably the reproductive part of the population (Durward 1980, Chernyavski and Dorogoi 1981).

The interrelations in the "predators-voles" system confirm the universally accepted opinion on the influence of predators upon the numbers of their preys but their impact is insignificant since in the phase of the small mammal population growth predators consume approx. 6% of voles, and they do still less, in the depression phase (Chernyavski and Dorogoi 1981, Krivosheev 1981, Erlinge et al. 1983).

Another factor determining the animal population is the interrelations of close-species animals inhabiting the same territory. As is known, intensity of interspecific relations is associated with the biotope quality and is typicality for each species entering the community, the degree of the ecological similarity of sympatric species, synchronism of their activity, and some other effects. The spatial and time division of the environmental resources is controlled by mechanisms worked out during the community evolution. Each species has its own specific niche, a fact which in the final analysis lowers the competition level. The mechanisms of ecological isolation of sympatric species are so reliable that multiannual changes in their numbers occur synchronously (Greenwood 1978, Wojcik and Wołk 1985, Zhigalski, Naumov and Zharkova 1987). Modern literature dealing with analysis of this phenomenon presents no single opinion on the role of interspecific relations in the formation of structure and numbers of sympatric species (Koshkina 1971, Shtilmark 1976, Hansson and Zejda 1977, Hansson 1983, Hallett, O'Connell and Honeycutt 1983, Shenbrot 1986, Zhigalski, Naumov and Zharkova 1987).

The population density grows until the birth and death rates become equal. Intensity of these processes can be changed due to the population density itself (this mechanism is called density-dependent mechanism (Krebs 1978) or to external factors. As was noted above, external factors play the limiting role and are capable

of presetting the population functioning level, while the density-dependent factors serve as regulating factors.

Modern hypothesis of the density-dependent regulation of the population rest on the concept which represent a population as a self-regulating system that its reproductive activity and mortality as a function of density, thus bringing the numbers in agreement with environmental conditions. If the density is low, the animals breed unlimitedly and their mortality is low. As the density rises, physiological stress phenomena inhibiting the population growth rate appear in the population.

The stress concept describes rather well many population phenomena but it is based on the assumption that all individuals in the population are similar and equal. However, a great number of facts indicate that a population is a highly structuralized system whose fate depends largely on what individuals enter this system (Rajska-Jurgiel 1976, Bujalska 1985, Masakado 1985). A certain plasticity of the structure can, in particular, account for different reaction of the population to analogous levels of population numbers. Moreover, re-arrangement of the population structure is in some cases the cause of transition from strictly territorial to group mode of life accompanied by establishment of a new hierarchy which permits the population to raise its numbers with the same resources.

As opposed to the advocates of the stress theory, Chitty (1967a, 1967b) suggested that fluctuation of the vole numbers were due to different quality of the animals setting up a population. He thinks that the genetic composition of the population changes during the cycle.

An analysis of applicability of Chitty's hypothesis for the explanation of the population dynamics of many species of small mammals (Mihok and Fuller 1981, Krebs 1985, Boonstra and Boag 1987) shows that the majority of the variations of the basic vital functions of the animals (growth rate, body weight, puberty age, mortality) are not of the genetic origin. Heritability of the parameters of the life cycle of the most of the vole species in nature is lower than it is necessary for an efficient functioning of the natural selection.

Charnov and Finerty (1980) put an original hypothesis of genetic variation in the population during the numbers cycle, which does not require a high degree of aggressive heritability.

Distribution of animals over the territory can play an essential role in the system of small mammal numbers control. In the case of animals that live singly or in families, to which bank voles belong, the spatial structure of the population is realized as a system of home ranges (Vittala 1977, Mazurkiewicz 1981, Nikitina 1980, Bujalska 1985, Bondrup-Nielsen 1987). The home-range size depends on the season, population density, and ecological capacity of habitats. The number of free sites is often related to the population breeding intensity. As a rule, only those animals reproduce that have their own territories. Animals that have no home range constitute a "reserve" of the population and proceed to breeding only after they get a nesting site. In this interrelation, the number of free sites can serve as a factor in control of reproduction and, hence, of the population numbers (Saitoh 1981, Bujalska 1985). However, while dispersion of voles over the territory can affect the population numbers, migration flows

cannot have a pronounced influence on the population, except its genetic (informative) aspect, since emigration does not exceed the level that would influence considerably the population processes.

The majority of modern hypothesis explaining regularity of changes in the numbers of small mammals have no formal description. They do not state prerequisites and conditions necessary for emergence of cycles and, therefore, the investigators who give preference to this or that hypothesis are often subjective in their choice.

The adequacy of theoretical concepts of the population control to real natural processes can be tested using mathematical models of the body of statistical estimates of the effects produced by the factors acting upon a population. Modern concepts of the role of intrapopulation mechanisms of the numbers control was analyzed most comprehensively and on sufficiently convincing materials by Stenseth (1985) who used a mathematical model. He showed that Chitty's hypothesis that suggests a genetically determined behavioural polymorphism of a population cannot account for the presence of cycles. Charnov-Finerty (1980) concepts, which are based on a phenotypic polymorphism of the behaviour and migration of animals, as well as the hypothesis due to Bujalska (1985), which is based on right territoriality of females, can ensure, under certain conditions, both appearance of cycles and the population stability. Moreover, mathematical models that take into account delays in the population responses to some effects can generate different-duration cycles but so far we have no realistic model of this kind for rodents. Finally Stenseth (1985) comes to the conclusion that it is impossible to explain fluctuations in the numbers of even one species of mammals in terms of a single-factor concept of the population dynamics since this process is diverse and versatile.

Another direction in the study of the population dynamics is based on statistical analysis of the factors acting upon animals. The analysis rests on ecological monitoring of populations. Our study refers to this direction. We have examined multi annual changes in the population numbers and structure of forest voles and accompanying fluctuations in weather and food conditions in five functionally different zones of the area. Demographic processes were analyzed using the procedure of screening analysis of the factors responsible for the numbers dynamics and subsequent estimation of their contribution to the processes of reproduction and mortality.

So, population numbers are controlled by a great variety of factors whose influence varies according to species and geography. It is quite obvious that the entire diversity of the population reactions cannot be explained by single-factor theories. In recent years, the majority of ecologists have become inclined to a multi-factor system of the population regulation. Although the multi-factor theory will probably be unable to give complete and final description of the population dynamics, it has a number of advantages:

1. Polyfactorness is consistent with the existing hypothesis and, besides, it takes into account, along with direct influence of factors, interaction effects (Lidicker 1978, Hilborn and Stearns 1982).

2. Accuracy of the prediction made using the multi-factor theory is the significantly higher than that obtained with the use of one or two factors.

3. It is only in terms of the multi-factor theory that one can raise the problems on time and spatial distribution of the effects from the factors acting upon a population.

4. The multi-factor approach allows the use of the entire data available at present on murine rodents.

Lidicker (1973, 1978, 1987) was the first to propose a multi-factor description of the population dynamics, although a principal possibility of such an approach had been suggested earlier. In spite of the fact that the number of studies based on the multi-factor ideology has been growing, especially recently (Lidicker 1978, Alibhai and Gipps 1985, Flowerdew 1985, Mihok, Turner and Iverson 1985, Stenseth 1985, Hestbeck 1986, Hanski 1987, Zhigalski and Bernshtein 1986, 1989a, 1989b), it failed to find an extensive application, because the very essence of the ideology calls for long-term comprehensive observations and the use of the body of the open-system theory, this making the approach not always accessible. This is both a merit and a shortcoming of the polyfactor description. It is quite clear however that this approach has a higher resolving power compared to a monofactor description.

A substantial contribution to the development of the general theory of the population dynamics regulation can be made by data banks storing information about various species of small mammals taking into account their spatial and geographical distribution and recording simultaneously weather, food and other characteristics of the habitat. It should be remembered however that working out a convincing description of the processes that form the population dynamics it is impracticable and biologically senseless if one uses some parameters of the population of a species and lacking characteristics from other species or populations. The last circumstance represents a rather cause of inconsistency of mathematical models since in this case some hypothetical population is analyzed, whose properties represent a combination of properties of several species and populations.

Thus, only the multi-factor approach can bring us closer to a most comprehensive understanding of the reasons responsible for fluctuations of the small mammals population numbers and structure. External effects are attributed to the role of limiting (determining the numbers level) factors, while intrapopulation effects are given the role of homeostatic mechanisms that bring the population numbers to the level determined by extrinsic conditions.

2. AREA AND METHODS

Many facts have been accumulated on the numbers dynamics and demographic structure of small mammal populations. These facts were used as the basis for devising a great variety of hypothesis but so far there is no adequate theory that would account for the entire diversity of the situations occurring within a population. In our opinion, one of the reasons for that is that most biologists use mainly the population numbers and a rather limited number of factors affecting the popu-

lation. To demonstrate adequateness of a particular theory, it is necessary to perform a comprehensive investigation of the population dynamic (numbers and their alternation rate, reproduction, mortality, age structure, etc.) and a complex description of the population living conditions (climate and weather, impact of predators, influence of co-occurring species, food, etc.). These observations should be conducted continuously for many years at stationary sites, with subsequent statistical description of the population characteristics and quantitative estimate of the distribution of the contributions made by factors affecting the population processes. Besides, it is necessary to undertake parallel observations in several functionally different parts of the species range so that results of the work are not only interpreted as a specific case characteristics of a particular species dwelling under some geographical and biotopic conditions.

Materials which are used herein to analyze population dynamics of forest vole fulfill all these requirements. The population numbers and structure of the bank vole (*Clethrionomys glareolus*) were studied at five geographically isolated places and these of northern red-backed vole (*Clethrionomys rutilus*) and grey red-backed vole (*Clethrionomys rufocanus*) were investigated on the territory of the Western Sayan permanent study plot. Location of each study plot was chosen in accordance with the objectives of the study of geographical and biotopic peculiarities of the forest vole demography. A detailed description of physico-geographical conditions of each permanent study plot is given in subsequent sections. Here we emphasize only their functional features.

The Tula study plot is located in the zone of broad-leaved forests and lies within a region that is optimal for the bank vole. The Tula permanent study plot occupied two sites in lime and oak-lime forests. Principal species are oak, lime, birch, and aspen. Underwood of hazelnut and other bushes and grass cover are well developed.

The Udmurt, Mari, and Karelia study plots are located in taiga zone but in different subzones. Lime-fir-spruce subtaiga forests dominate in the Udmurt study plot which can be also referred to the optimal range. In the Mari study plot the population dynamics was studied at five sites with different vegetation compositions: radical mature spruce-lime subtaiga forests, secondary birch forests with broad-leaved species replacing subtaiga forests, and felled areas with different time of standing. Habitats found in this study plot differ in quality and ecological capacity. The Karelia study plot is located in the subzone of midtaiga forests and represents a periphery of the bank vole range. Bank vole is undoubtedly the dominating species in the above-mentioned study plots.

The Western Sayan permanent study plot is situated in the subzone of coniferous mountain taiga forests and represents an extremely convenient conditions for investigation of interspecific relations between two species of forest voles (*C. rutilus* and *C. rufocanus*). This plot has territories with a clearly dominating species and areas, where the numbers of both species are the same. The work is based on the observations and collections made by the author, as well as on the material of multi annual studies, which was kindly presented to our disposal by A.D. Bernshtein (Tula and Udmurt permanent study plots), V.A. Korneev (Mari permanent study plot), T.V. Ivanter (Karelia permanent study plot), and R.L. Nau-

mov (Western Sayan permanent study plot). On the Tula study plot numbers were censused from 1966 to 1980 (15 years). During that time 91 000 trap-days were served and 13 500 bank voles were caught and examined. On the Udmurt study plot investigations lasted for 13 years (1973–1985). The forest stand consists mainly of spruce and lime in different proportions with admixtures of fir, birch and aspen. The underwood comprises sprouts of lime, button and cat trees, and other shrubs; grass cover is also well developed. The presence of old stumps and windfallen trees in combination with a rich food basis enhances the biotope capacity with respect to small mammals (Rastitelnost Evropeiskoi chasti SSSR 1980).

On the Mari study plot observations were carried out from 1972 to 1987 (16 years). The Mari permanent study plot is situated in subtaiga forests. About 60% of its total area is occupied by mature spruce-lime forests, 20% falls on birch forests including broad-leaved species in place of subtaiga forests, and 20% is covered by felled areas (young birch forests with admixture of broad-leaved species in place of subtaiga forests) of different standing. Spruce-lime forest is in the center of the study plot and birch forests and regenerating clearings (1960, 1968 and 1976) are adjacent to the birch forests on different sites. The permanent study plot represents a part of forest covering dozens of kilometers. The main regeneration species are self-sown birch and aspen and plantations of spruce which are currently under the canopy of birch-aspen sprouts. The forest stand structure does not change with time. The clearings of 1960 is currently a young birch forest including aspen and spruce undergrowth. Underwood consists of lime, maple, rowan tree, cranberry tree, wartybark evonymus, and button tree. The grass cover is typical, similar to the underwood, of subtaiga forests and comprises mainly *Aegopodium podagraria*, scilla, lungwort, fern, startwort, and others. Secondary birch forests replacing subtaiga forests represent the next stage of regenerating clearings. Spruce undergrowth starts to predominate with years and after some time comes to the upper story.

The most long-term observations were performed on the Karelia study plot (1966–1987). The Karelia permanent study plot is situated in the subzone of mid-taiga forests. Observations of small mammals were performed on two sites. One site is located in full-grown open true-moss spruce forests with an admixture of deciduous species and well-developed grass-layer and dwarf shrubage. The other site is characterized by mature deciduous and mixed forests and includes all secondary forest appearing after fellings, burning, clearings and other damages. The forest stand consists of birch, aspen and alder (with highly continuous canopy) and well-developed underwood. Favourable microclimatic conditions of the ground layer, abundant food, high herb stand, thick loose forest litter, many windfallen trees and old stumps in true-moss spruce and mixed forests ensure adequate protection for the life of small mammals. Shrews and rodents feed on seeds, green of herbs and various invertebrates. Berries and fungi are scarce.

Spruce, true-moss and grass spruce forests serve for most species as habitats, where forest mammals live all the year round as groups of animals which are stable in composition but are not always numerous. Derivative biotopes, primarily

regenerating clearings and areas of low forest, represent temporary habitats, where they live most often in summer.

C. rutilus and *C. rufocanus* live on the territory of the Western Sayan study plot. Observations lasted there from 1965 to 1983 (19 years). The Western Sayan permanent study plot is situated in the zone of Siberian mountain taiga coniferous forests on the northern slope of the Djoï ridge within the belt of mountain taiga; in the subbelt of mountain bilberry forests and in the subbelt of mountain taiga forests. The study plot area is about 25 km², with the altitude differential 600 to 1 400 m above sea level. Mountain bilberry forests are built up of firs with an admixture of Siberian stone pines, pines and birches, fruit shrubs, and well-developed rough grasses (600–800 m above sea level). In the subbelt of mountain taiga coniferous forests at an altitude 800 to 1 000 m, fir and fir-stone pine forests grow with a moderately developed undergrowth and grass layer. With altitude, the grass layer is replaced by true moss and fire disappear. Thus, at an altitude of 1 000–1 200 m stone pine-fir forests with true moss, bilberry and motley grasses prevail, while at 1 200–1 400 m true-moss stone-pine forests and light stone-pine forests with rhododendron shrub and high grasses along temporary water streams are predominant.

With each 100 m of altitude, the amount of precipitation (per month) increase by 70–100 mm, the mean daily temperature drops by 0.6, the sum of effective temperature lowers by 100, and the vegetation period shortens by 5–8 days (Protopopov 1965, Naumov, Labzin and Gutova 1984). A specific feature of the working site in abundance of shelters for small mammals: stone debris with different degree of vegetation covering and hollows between stones, which make it possible for the animals to travel dozens of meters without approaching on the surface. Observations of the forest vole populations on all the permanent study plots lasted on the whole for 89 years, the scope of surveillance works was on the total 423 500 trap-days, and the total number of the animals which were trapped and examined, amounted to 29 400.

To evaluate populations of forest voles, the method of relative assessment of murine rodents on standard trap-lines (Kucheruk 1952) was exploited, which enjoys great popularity among ecologists. The animals were caught using snap traps. Baits were bits of bread soaked in vegetable oil. Voles were censused on stationary plots using snap-trap lines of 50 pieces each, with the traps spaced 5 m apart. Census lines were exposed for 2 to 4 days. The traps were checked once a day. Voles were trapped at regular intervals four times a year (April, June, August, October) and in some years monthly throughout the reproductive period.

Morphological analysis of caught animals was performed following a common scheme. The age of bank voles was determined by the formation of the neck of the second upper molar and by the share of the root in the entire tooth height. The determination accuracy was within two months, but the study includes only three age classes: 7–16, 3–6 and 1–2 months (Tupikova, Sidorova and Konovalova 1970). Apart from age, the state of generative organs was checked in each animal caught. Pregnancy was determined by the presence of the copulation plug, yellow body in ovaries, and embryos in the uterus, while the number of litters delivered by a female was determined by occurrence of placental

scars. Litter size was estimated from the number of embryos. The age of embryos was determined by the external appearance of the uterus and dimensions of embryos with the sheath removed (Tupikova 1964). Gonads and their appendages were measured in males and spermatogenesis was registered (with random inspection of smears under a microscope). Sexually mature or breeding animals were considered to be pregnant and parturient females and males with developed appendages (at least 8–9 mm long) and spermatogenesis.

The state of the populations was described using two groups of parameters: relative numbers, groups of the same and different sexual maturity (number of individuals referred to 100 trap-days) and population structure parameters (fraction of groups of different sexual maturity). Each trapped animal was classified to the groups depending on sex, age and reproduction.

The first subdivision of the trapped animals is according to the age: a group of overwintered males and females at the age of 7–16 months and two groups of current-year voles ages 3–6 and 1–2 months. In each class, females were classified into groups of parous, pregnant and sexually immature animals and males were grouped sexually immature and mature individuals. All the specified elementary groups of voles were described using the relative numbers parameters; besides, estimation was made of the numbers of males and females, total number of animals in each age class, and the total population.

Another group of population characteristics is presented by the structure parameters. Three age classes were considered and fractions of different structure groups were calculated for each of the groups. Fractions of pregnant, parous and sexually immature females were calculated as the ratio of the numbers of the animals entering into the functional group considered to the total number of each age class multiplied by 100. The fractions of sexually mature and immature males were calculated analogously. The fraction of females and males is the ratio of the numbers of females and males to the total number of voles from each age class. In addition to structural parameters, estimates were made of the fraction of voles of particular age in the total population and the total fraction of breeding and sexually immature males and females within an age class.

The list of factors determining dynamics of the forest vole populations includes endogenic (intrapopulation) and exogenic (external to a population) ones. Endogenic factors that influence, for example, the reproduction activity of young voles comprise numbers and fraction of older males and females in a population, as well as the fraction of different-age animals in the population. In each specific case the number and structure of endogenic interactions were determined by preliminary statistical analysis.

Exogenic factors include weather conditions (monthly average air temperature, monthly precipitation or thickness of snow cover in winter), food conditions (crop of seeds of the main forest constituting species), as well as numbers and structure of co-occurring species. A detailed list of external factors for each specific population characteristics is given in subsequent chapters.

Demographic structure of the population was estimated proceeding from multi-annual values of population characteristics and degree of their variation (standard deviation and variation coefficient). The truth of the discrepancies in the level of

average was verified by the dispersion analysis and Scheffe method of multiple comparison (Glass and Stanley 1976, Pollard 1982). Conclusions on the significance of the fractions in the population and comparison of fractions belonging to different general populations were drawn using the method of random fractions (Glass and Stanley 1976).

Estimation of the effects of various factors on demographic changes in populations of small mammals presents difficulties due to the fact that, given a rather large number of factors, we have, as a rule, a limited term of observations. Besides, application of the majority of statistical methods calls for strict fulfillment of some requirements (definite ratio between the length of the series analyzed and the number of variables, normality of multivariate distribution, etc.) whose realization is not always possible during population investigations. Owing to this, two principally different methods were used parallelly to check the results obtained and to enhance their reliability: the method of many-criterion estimation of factorial effects (Brusilovski 1987) and the screening analysis of the factors affecting the population dynamics and assessment of their contribution to demographic processes, which is based on modified method of multiple regression analysis (Fenster and Renz 1983). The essence of the former method in relations between the dependent and independent variables are given by nine different measures (mean square error, maximum error modulus, correlation factor, mean error, mean error modulus, Theil divergence coefficient, discrepancy coefficient 1, discrepancy coefficient 2, correlation). The obtained estimates of the relation measures are then arranged in the order of the quality impairment for each independent variable with respect to all criteria and are assigned the numbers: 0 for last, 1 for the penultimate, $m - 1$ for the first, where m is the number of variables. The point sum is then calculated over all criteria for each variable. The variable that scored a maximum sum contributes most to the variability of the dependent variable (Litvak 1982).

The latter method, which was used by us to estimate the role of different factors in demographic processes, represents a screening procedure that comprises some stages. The first stage included computation of correlation between the dependent variable and each independent (factoral) variable and between all independent variables. At the second stage, statistically valid correlations were selected from a rest of correlation between the dependent variable and independent variables and mutually correlated relations were chosen from the correlation between explanatory variables. If the coefficient of correlation between two independent variables exceeded 0.5, one of the variables was excluded from consideration, thus meeting the requirement of multicollinearity in the multiple regression analysis. The problem of what characteristic precisely should be excluded from consideration has no rigorous theoretical substantiation and therefore it was solved in each specific case proceeding from biological expediency.

Proceeding covered over 50 population characteristics and about 30 operative factors. The nature of their relations was not investigated earlier and therefore several parameters of the relations were calculated: Pearson pairwise correlation coefficient, Spearman rank correlation coefficient, correlation ratio, curvilinearity and validity index of the above relation coefficient. Pearson and Spearman correlation coefficients

allow estimation of the degree of or relation between the population parameters and the factors affecting the latter, while the curvilinearity index permits determination of the degree of linearity of these relations (Glass and Stanley 1976, Iberia 1980).

Having considered the correlations and having reduced the criteria space, we are in a position to turn to the procedure of estimating the influence of the factors affecting the population. To this end, the mathematical body of the multiple regression is used. The analysis of the correlation linearity made it possible to restrict ourselves to the consideration of the linear dependence between the dependent variable (y) and explanatory (independent) variables (x_1, x_2, \dots, x_n). Thus, b_1 shows the mean variation value of y when x_1 changes by unity provided all the other variables remain unchanged, i.e. gives the corresponding averaged specific effects of variables, assuming that the remaining explanatory variables are preserved at a constant level: b serves as the equalization function.

Multiple regression describes simultaneous effects of all explanatory variables but naturally disregards the influence of discarded factors. Thus, given empirical numerical material for several factors, it is more and theoretically substantiated to construct regression rather than regression on one factor for the dependent variable.

The procedure of constructing a multiple regression is elaborated but it has been adequately founded mathematically and described in special literature (Dreiper and Smith 1973, Afifi and Eisen 1973, Pollard 1982, Ferster and Renz 1983) and therefore is no sense in emphasizing on it.

Total variance (S) of the dependent variable is resolved in regression analysis into two components: variance due to the operative factors included in the regression (S_r) and residual variance (S_e) that includes the variance associated with the influence of the explanatory variables not involved in the analysis and the variance caused by the random observation errors:

$$S = S_r + S_e \quad (1)$$

$$\sum_{i=1}^n (y_i - \bar{y})^2 = \sum_{i=1}^n (\hat{y}_i - \bar{y})^2 + \sum_{i=1}^n (y_i - \hat{y}_i)^2 \quad (2)$$

The quotient of S_r by S is called the determination coefficient and is named R .

$$R^2 = S_r / S = \left\{ \sum_{i=1}^n (\hat{y}_i - \bar{y})^2 / \sum_{i=1}^n (y_i - \bar{y})^2 \right\} \quad (3)$$

It performs two functions: first, reflects the fraction of variability caused by regression in the total variance of the dependent variable and, second, serves as the criterion of the regression quality. If R is statistically significant, the regression equation derived reflects the actual relation between the characteristic being analyzed and the set of explanatory variables. A special transformation (Iberia 1980) was used to determine significance of R . When the calculated R is higher

than R , the null hypothesis is realized: multiple determination coefficient statistically significantly differs from zero.

Note one more feature of the multiple determination coefficient: it equals the sum of the products of the normal regression coefficients (b) and the correlation coefficient (r) (Ferster and Renz 1983):

$$R^2 = b_1' r_{y1} + b_2' r_{y2} + \dots + b_m' r_{ym} \quad (4)$$

The summands entering the sum represent quantitative estimates of the contributions made by each factor into the formation of the dependent variable. If some summand is of great magnitude, the respective variable makes a large contribution to the regression determination and is responsible for a considerable part of the variance incurred in demographic characteristics being analyzed.

The factors affecting the population, as obtained by the methods of multiple regression and many-criterion estimates, do not differ in qualitative parameters and show only some quantitative distributions. For example, Table 1 summarizes the results obtained for the bank vole population in Udmurtia.

Table 1

Ranking of the effects produced by endogenic and exogenic factors, as determined by the methods of multi-criterion estimation (numerator) and multiple regression analysis (denominator)

Characteristic	Endogenic factors at moment of time		Exogenic factors	
	preceding	current	climatic	food
Total number of voles in April	2.8/3.0	0	69.4/57.8	27.8/39.2
Number of overwintered voles in April	37.0/52.4	0	63.0/47.6	0
Fraction of 1-2-month old pregnant females (July)	21.3/24.9	78.8/75.1	0	0
Fraction of 1-2-month old immature females (July)	8.3/9.0	91.7/91.0	0	0

These data permit one to draw a conclusion on the adequacy of both methods. Therefore ranking and estimation of the influence of the factors acting upon a population can be performed using either of the methods. However, the computation procedure of the multiple regression equations with subsequent estimation of the contributions made by the factors is much simpler and, in addition, it allows the use of the statistical deduction theory which is well developed for this method. Below are given results of the multiple regression analysis.

We computed indices of density variations, the coefficient of variation, standard deviation of the density data transformed by logarithm of basee (Hansson and Henttonen 1985).

To compute parameters of the multiple regression equation, subprograms of the package of applied programs "PAST" were used as the basis for development of a program in "Fortran-IV" language for the CM-3 computer. All statistical par-

ameters were estimated also on the CM-3 computer using both unique and standard programs.

3. GENERAL CHARACTERISTICS OF THE POPULATIONS STUDIED

3.1. BANK VOLE POPULATION OF BROAD-LEAVED OAK-LIME FORESTS

Over 16 years of observations on the Tula study plot (from 1966 to 1980) about 91 000 trap-days were served and over 13 500 bank voles were trapped. Apart from bank voles, the study plot was inhabited by grey red-backed voles, mice, insectivorous and other species. Judging by the mean numbers and its variation in summer months (Table 2), grey red-backed vole is the most abundant species. Its fraction in the population fluctuates from 59 to 90% in different years and accounts on the average for 84% over the breeding season in oak-lime forests.

Table 2

Population numbers and structure of small mammals (Tula permanent study plot, 1966-1980)

Month	Species	Characteristic			
		Mean (vole per 100 trap-days)	Standard deviation	Variation coefficient (%)	Species fraction (%)
April	bank vole	11.1	10.1	90.9	81.6
	mice	1.0	0.6	59.6	7.4
	shrews	0.7	0.9	130.6	5.2
	other rodents	0.8	1.5	192.8	5.9
	total numbers	13.6	8.8	64.4	—
June	bank vole	15.0	9.9	66.5	87.2
	mice	1.4	1.1	78.3	8.2
	shrews	0.5	0.6	132.1	2.9
	other rodents	0.3	0.6	176.0	1.7
	total numbers	17.2	10.1	58.9	—
August	bank vole	24.3	12.4	50.9	84.7
	mice	1.7	1.3	72.8	5.9
	shrews	1.8	1.8	101.8	6.3
	other rodents	0.9	2.0	235.5	3.1
	total numbers	28.7	13.2	46.1	—
October	bank vole	20.3	10.4	51.0	81.2
	mice	2.3	1.8	78.6	9.2
	shrews	1.9	1.8	92.9	7.6
	other rodents	0.5	1.1	104.8	2.0
	total numbers	25.0	12.8	51.5	—
Totally per reproduction season	bank vole	17.6	11.9	67.6	83.8
	mice	1.6	1.3	82.7	7.6
	shrews	1.2	1.5	122.4	5.7
	other rodents	0.6	1.3	219.1	2.9
	total numbers	21.0	13.1	62.5	—

The fraction of other species does not as a rule exceed 10%. Bank voles are most abundant and, in addition, their numbers change less than that of the co-occurring species.

Abundance of small mammals on the Tula permanent study plot has a seasonal component. For the bank vole the seasonal component is at a maximum at the beginning of the breeding season (91%) and then lowers gradually. The numbers variation coefficient equal 76% in June and 51% in August–September. Numbers of other species fluctuate to a much higher extent (60–235%). Although the numbers of separate species fluctuate over rather broad limits, changes in the average abundance of the guild dwelling on the study plot are lower and attain 46 to 65% in different months (Table 2).

To estimate the interactions between different species of mammals inhabiting the study plot, correlation coefficients were calculated. No statistically valid negative or positive correlations were detected for multi-annual numbers variations. This suggests that an increase in numbers of a species does not invoke a decrease in the population of another species and, hence, is indicative of the absence of the competition relations throughout the reproductive period. The absence of the correlations indicates to a sufficient independence of the variations in the animal numbers.

As was shown above, bank vole represents the most abundant species on the study plot and its population dynamics is independent of the changes in the population numbers and structure of other species.

Dynamics of the bank vole population has two clear-cut components : seasonal and interannual (Fig. 1). The abundance cyclicity index of the animals, which equals 0.33 at the beginning of the breeding season, and at the mid of the season it amounts up to of 0.37, characterize the population as noncyclic. Statistical estimates of the numbers and structure of the bank vole population on the Tula permanent study plot are given in tables.

At the beginning of the breeding season (April), the relative numbers are equal to 11.1 (mean multi annual value) and vary between 0.6 and 30 from year to year. During summer the relative numbers increase gradually and attain a maximum value of 24.3 (minimum 9.7, maximum 43.6) in late July–early August. By mid-October the numbers again lower to 20.3 and change from 0.5 to 38.6 (Fig. 2) in different years. Two periods are clearly traced in seasonal dynamics: increase (April–August) and decrease (August–October–April of the next year), which is typical in general of small mammals inhabiting temperate zone forests (Fig. 2).

In different years the bank vole population on the Tula study plot increased by 1.1 to 5.2 times (2.2 times on the average) from spring to the seasonal peak in October, and dropped again by 1.8 times from October to April of the next year. The population numbers increase on the average by 2.2 times over a reproduction cycle.

The interannual variation of the total population of the bank vole exhibits a seasonal behaviour: the variation coefficient is at a maximum in spring, accounting for about 90%, drops to 66% by June, and then remains at a level of 50% till the end of the breeding season (Fig. 2). Coefficients of weather factor variation change much in the same manner. Thus, variability of the air temperature attains

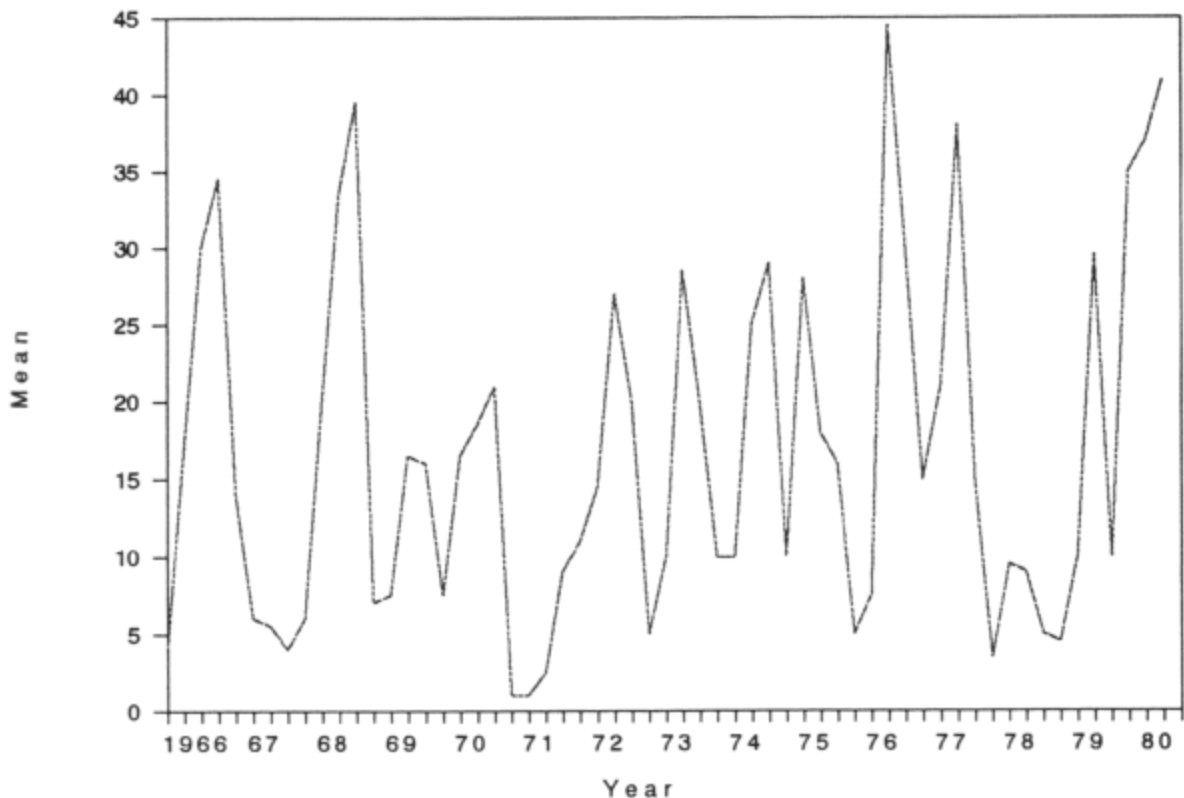


Fig. 1. Multiannual dynamics of relative abundance (numbers caught per 100 trap-days) of the bank vole at Tula permanent study plot.

a maximum in March (105%), decreases gradually to 10-15% in June–August, rises to 76% by October, and drops again to 30% in December–February. The amount of precipitation varies in different years over rather broad limits but it is sufficiently stable during the reproduction period (variation coefficient changes from 50 to 70%). High variability of climatic conditions is accompanied by high variability of population characteristics. This makes it possible to suggest that the processes of reproduction and mortality and, consequently, the total population size are susceptible in spring to considerable fluctuations owing to instability of external conditions and different response of the population to these changes. It is at the beginning of the breeding season that the population characteristics influence very weakly the reproduction intensity and the rate of sexual maturity of the voles. In autumn, they play, along with enhancing variability of weather conditions, an increasing role in the formation of the population numbers.

Duration of the reproduction season changes from year to year. The reproductive process proceeds most intensively usually from April to August but in some years reproduction is observed in other months, including winter and early spring (November–December, January–March). In 15 years under analysis, animals born from November to March were noted in seven cases.

The age structure of bank vole population on the Tula study plot is subject, similar to other characteristics, to considerable changes both within a single reproductive period and in different years. Multi-annual mean values and their variability indices (Fig. 2) were used to characterize the age structure. In April, the population consists mainly of overwintered animals and, naturally, the principal

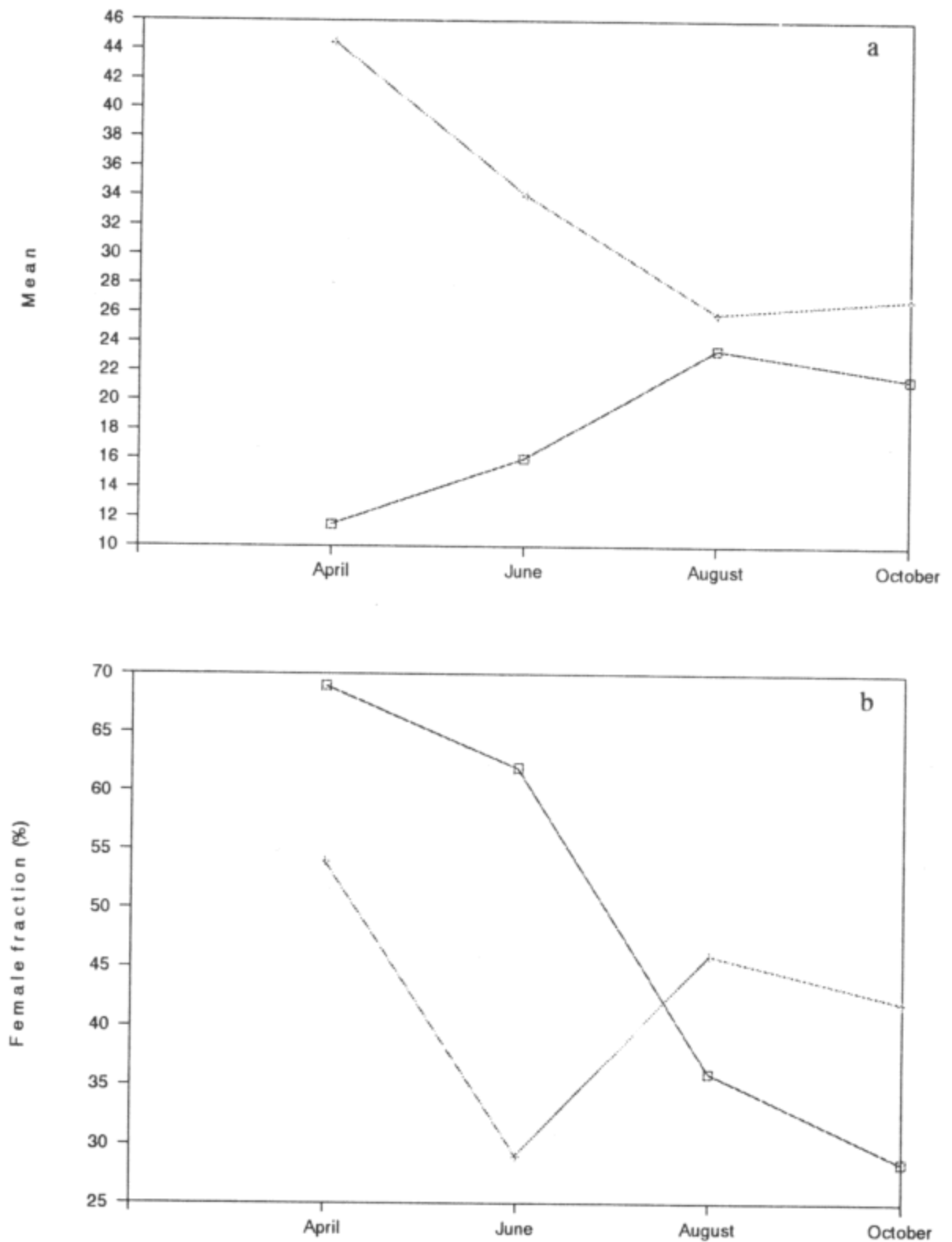
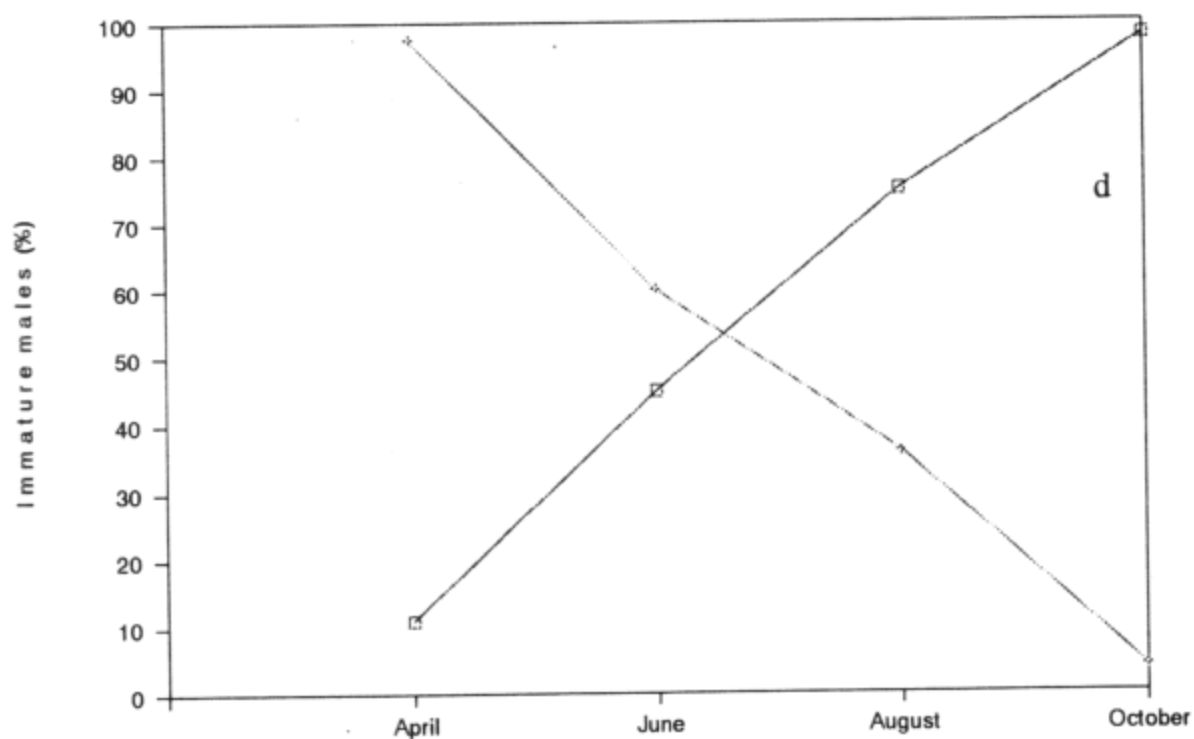
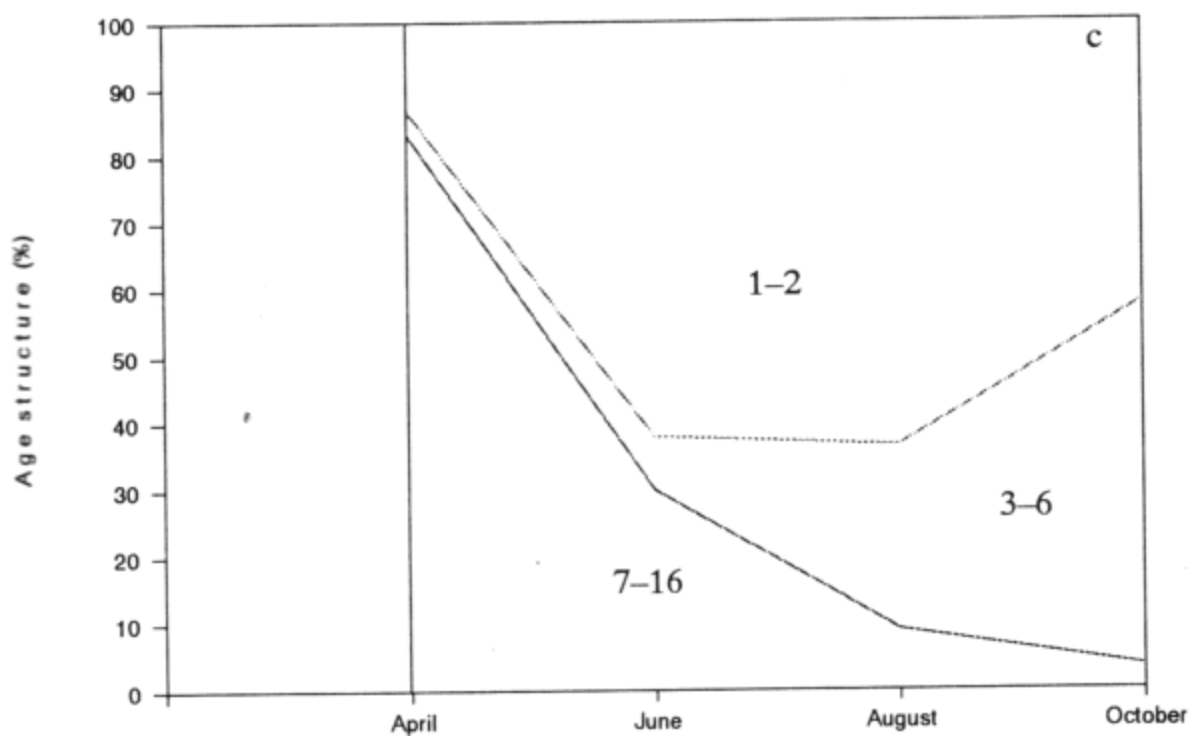


Fig. 2. Mean values of demographic variables in the bank vole population at Tula permanent study plot
 Rectangles and continuous line – a variable, crosses and continuous line – coefficient of variation (%)
a – numbers caught per 100 trap-days, *b* – fraction of breeding females, *c* – age structure (in months),
d – fraction of immature males



contribution to the population growth is made by this group of voles (87%). In June, young voles 1–2 months of age start to dominate: their fraction in the total population rises to 62% but only 49% of females reach puberty. Their contribution to the potential increase in the population (47%) is therefore insignificantly larger than that of overwintered voles (39%) which are less abundant compared to the current-year animals but practically all of them participate in reproduction. In August, overwintered animals account for only 6% of the population and the fraction of the youngest cohort attain maximum values. However, at the late summer less than 10% of the 1–2 month-old animals are pregnant, whereas among young females of earlier litters as much as twothirds can reproduce. As a result, 3–6 month-old females give 63% of the total offspring of the population, while overwintered and young animals of 1–2 months old bring 20 and 15% respectively.

In October, 55% of the population are voles at the age of 3–6 months and 42% are younger animals. Only in separate years overwintered animals are present in the population. Of all age groups, only overwintered females fully participate in reproduction. However, in autumn their number, if they are even present in the population, is extremely small and therefore their contribution to the population accounts only for 15%; about 7% of the offspring is due to 1–2 month-old cohort, while the main contribution is made by voles 3–6 month of age.

The population age structure alters markedly during the breeding season (April–October). Besides, the fact that different-age animals participate in reproduction to a different degree brings about a change in the specific importance of cohorts in the formation of the total population numbers (Gliwicz 1975, 1983, Bujalska 1983). At the onset of the breeding season the leading role in the processes of the population growth belongs to overwintered animals. Starting from June the potential increase in the population is determined principally by the reproduction intensity of the current-year voles: first of the 1–2 month age class, and then of the 3–6 month age class. The fraction of sexually mature males in the population reduces from 96% in April to 4% in October, with the maximum reduction rate of the reproductive activity observed in August–October.

Table 3 specifies the fraction of females entering into three groups: overwintered at the age of 7–16 months, current-year animals at the age of 3–6 and 1–2 months, as found for different months of the breeding season. Considerable changes in the sex structure of overwintered animals are observed from spring to autumn: at the beginning of the breeding season males dominate (61%) over females but the fraction of the former drops gradually to 20% by October. During the breeding season (April–October) mortality of overwintered males on the average over the reproduction period amounts to 71% and that of females is 49%, and therefore 13% of females and only 2% of males are left in population by October. In the autumn–winter period a reverse picture is observed: mortality of females (63%) is higher than that of males (43%). Predominance of males in spring can be explained by higher mortality of females in winter and partially by selective trappability of males due to their high mobility. In autumn, on the contrary, females predominated because males, which are more mobile, exhibit higher mortality rate than that of females in spring, and summer (Bolshevikov and Kubantsev 1984).

Table 3

Sex ratio (fraction of females) in the bank vole population (Tula permanent study plot)

Month	Age in months			Totally per month
	7-16	3-6	1-2	
April	0.39*	0.67	0.61	0.49
June	0.53	0.58*	0.52	0.47
August	0.50	0.54*	0.47	0.45*
October	0.80	0.49	0.51	0.50
Totally per reproduction season	0.43*	0.52	0.49	

* Values significant at $p = 0.05$.

The sex structure of the current-year animals also changes throughout the breeding season. Males dominate somewhat in the group of 1–2 month-old voles but despite the fact that these changes are trustworthy in some cases, these are so insignificant that are unlikely to influence considerably maturation and reproduction of females. In the cohort of 3–6 month-old voles the sex ratio is shifted in favour of females within the breeding season, especially during its first half, this allowing the population to accelerate still further the numbers growth rate. By autumn the sex ratio for young voles of both sex does not differ statistically from 1:1. They are sexually immature in their majority and are subject to a rather stringent selection as regards a number of physiological indices (animals in the population become "sexless"), circumstances which probably level off the numerical difference in the sex ratio.

3.2. BANK VOLE POPULATION OF LIME-FIR-SPRUCE SUBTAIGA FORESTS

Numbers and demographic structure of the bank vole population were censused in Udmurtia on a permanent study plot in the subzone of lime-fir-spruce subtaiga forests. Over thirteen study years about 20 000 trap-days were served and more than 2500 bank voles were trapped.

The Udmurt permanent study plot is inhabited by bank and northern red-backed voles, wood mouse (*Apodemus sylvaticus*) and striped field mouse (*Apodemus agrarius*), grey red-backed voles and shrews. Proceeding from the mean numbers of the species inhabiting the study plot and from the numbers variability (Tables 4 and 5), the bank vole dominates on the territory studied over small mammals in all summer months. As follows from multi-annual observations, the fraction of this species in the entire population fluctuates in different months from 46 to 60% and accounts for 56.5% on the average over the reproduction period, whereas the fraction of the species that is second in number (northern red-backed vole) attains only 20% in all summer months. The fraction of other species is still

Table 4

Estimates of the population numbers and structure of small mammals on the Udmurt permanent study plot

Month	Species	Characteristic			
		Mean (vole per 100 trap-days)	Standard deviation	Variation coefficient (%)	Species fraction (%)
April	bank vole	6.3	4.6	70.8	54.8
	<i>C. rutilus</i>	2.4	3.1	132.9	20.9
	shrews	2.6	1.5	58.8	22.6
	other rodents	0.2	0.2	118.4	1.7
	total numbers	11.5	6.5	55.8	—
June	bank vole	12.8	11.9	93.5	60.3
	<i>C. rutilus</i>	4.5	4.9	108.9	21.3
	shrews	3.7	2.2	59.4	17.5
	other rodents	0.2	0.2	137.3	0.9
	total numbers	21.2	16.1	75.8	—
August	bank vole	20.9	11.4	54.6	59.5
	<i>C. rutilus</i>	6.9	5.7	81.4	19.7
	shrews	6.0	3.0	50.0	17.1
	other rodents	1.3	1.8	140.3	0.4
	total numbers	35.1	14.5	41.3	—
October	bank vole	13.7	10.4	75.9	45.8
	<i>C. rutilus</i>	5.4	5.6	103.1	18.1
	shrews	9.3	7.7	82.9	31.1
	other rodents	1.5	1.8	114.9	5.0
	total numbers	29.9	21.6	72.2	—

less. Along with the fact that the bank vole predominates in the population, the amplitude of its numbers variation is small (Table 4). In summer months the number variation coefficients fluctuate between 54 and 93%, and are equal to 81.1% on the average over the breeding season. For example, variability of the numbers of the northern red-backed vole is within 81–132% and is on the average 20% higher than that of the bank vole. The bank vole population is most stable in August (54.5%) during the seasonal peak period, and is most unstable in July (93.5%) in the phase of maximum increase.

As is seen from Table 5, no negative correlations were found between the variations in the numbers of small mammals on the study plot. However, positive correlations were detected, testifying to synchronous dynamics of all the species inhabiting the study plot. In early summer the number of significant correlations (Table 5) is small, this testifying to a considerable independence of the numbers variations caused by different terms at which different species start breeding. As the breeding season approaches its end, the number of significant correlations and their numerical value increase, a fact which is probably related to the general de-

Table 5

Contingency estimates of multi-annual changes in the numbers of small mammals
(Udmurt permanent study plot)

Month	1	2	3	4	5
April	1	—	—	—	0.85
	2	—	—	—	0.72
	3	—	—	0.49	—
	4	—	—	—	—
June	1	—	0.76	0.66	0.93
	2	—	—	—	0.61
	3	—	—	—	0.76
	4	—	—	—	0.54
August	1	0.45	—	—	0.91
	2	—	—	—	0.69
	3	—	—	—	—
	4	—	—	—	—
October	1	0.55	0.51	—	0.94
	2	—	0.63	—	0.76
	3	—	—	—	0.91
	4	—	—	—	—
Totally over reproduction season	1	0.59	0.47	0.30	0.92
	2	—	0.46	0.29	0.79
	3	—	—	0.46	0.70
	4	—	—	—	0.46

1 — bank vole, 2 — northern red-backed vole, 3 — other species, 4 — shrews, 5 — total number of all species. Only statistically valid Spearman correlation coefficients are given. Values significant at $p = 0.05$.

crease in reproductive activity of all species, general cessation of the numbers growth, and its stabilization.

Bank vole dominates on the study plot, its population dynamics is synchronous with other species, and therefore are no groups to consider interspecific relations as competitive.

The absence of deep depressions and large number of years with high numbers (14 on the average) at the end of the breeding season indicate that the living conditions are favourable for the bank vole (Fig. 3). The cyclicity index equal to 0.42 characterizes this population as noncyclic, but at the same time the annual amplitude of the numbers fluctuations is higher than that of the bank vole population in Karelia and Tula. Seasonal dynamics is typical of small mammals in the forests of temperate zone (Tupikova and Konovalova 1971, Ivanter 1975) (Fig. 4). At the beginning of the breeding season (April), the relative numbers are equal to 6.3 (mean multi annual value) and vary between 0.1 and 15 in different years. During summer the population numbers increase gradually and attain their maximum value of 20.9 by the late July-early August (minimum 1.0 and maximum 45.5). By mid-October the vole population decreases again and reaches 13.7 (varies from 2.0 to 35 in different years).

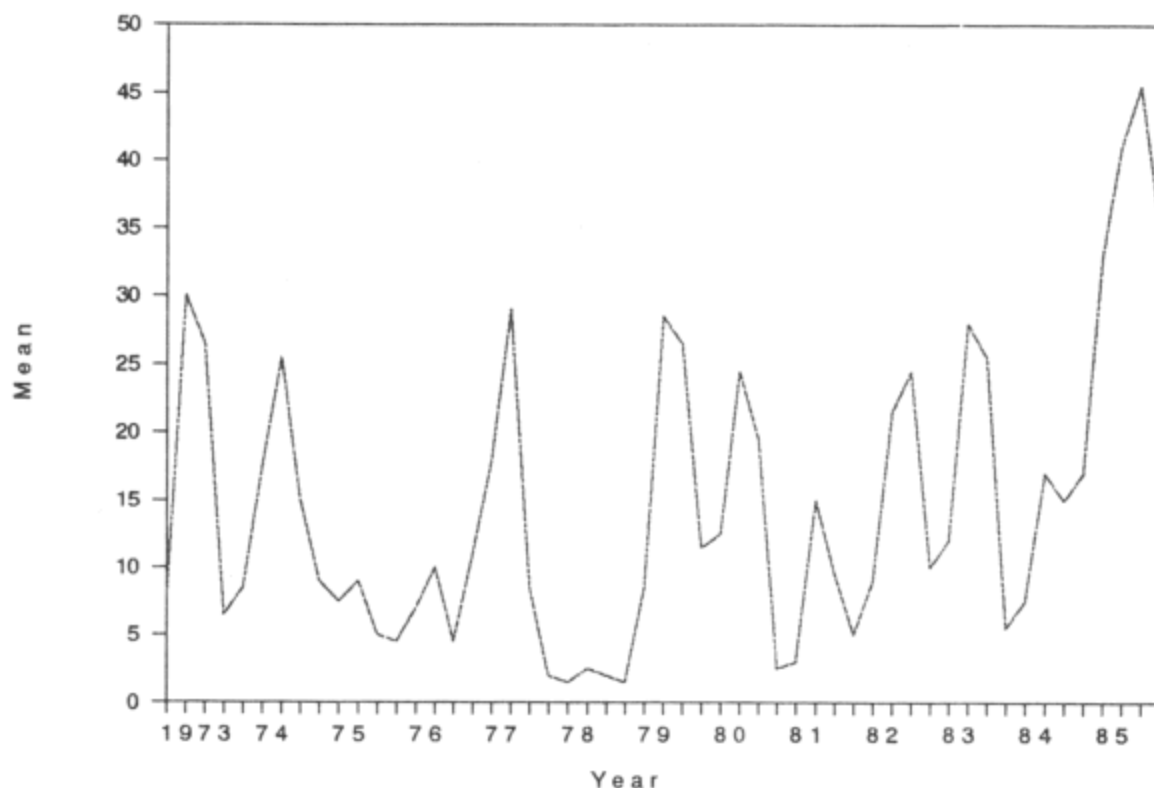


Fig. 3. Multiannual dynamics of relative abundance (numbers caught per 100 trap-days) of the bank vole at Udmurt permanent study plot

From spring to the moment of the seasonal peak attainment the population numbers increase in different years by 1.3–6.3 times (3.3 times on the average). From the seasonal peak to October the numbers decrease by 1.5 times and, in addition, by 2.2 times from October to April of the following year.

Variability of the population numbers, as well as the population mean numbers, exhibits a clearly pronounced seasonal dynamics: the variation coefficient is at a maximum in June in the period of the maximum population growth rate (93.5%), decreases to 54.6% by August, and increases again to 76% by October.

Duration of the bank vole breeding season in Udmurtia fluctuates over considerable limits. In most cases reproduction-active females are found for 4–6 months but the terms of the breeding start and end vary greatly (variation coefficient approx. 70%). Pregnant females appear in April with the terms of their appearance being extended for about two weeks. In some years under-snow and late-autumn (November–December) breeding is observed, sometimes early-spring (February–March) reproduction is noted, and in 1985 reproduction persisted throughout the autumn–winter period. Mass reproduction of the bank vole on our study plot ends, as a rule, in late August-early September; however, in some years reproduction terminates in July, and in others reproductive females are still present in the population in October. Under most favourable conditions the reproduction period can

last continuously for 15 months: from late April of one year to August–September of the following year.

In April the population consists mainly of overwintered animals (multi-annual mean is 85.5%) and, naturally, this group of voles makes a principal contribution (70.4%) to the population growth. Variability of the numbers and fraction of this age class in the population in different years is low compared to other age groups. Young voles 1–2 months of age predominate in June: their fraction in the total population attains 72.7% but only 33% of them reach puberty and therefore their contribution to the potential increase of the population accounts for 44.8%. At this period overwintered animals are already less in numbers than the current-year voles but the offspring of the former accounts only for 42.5% of the potential population offspring. In June the numbers variability of overwintered animals remains at a level close to that of April and the variability of the fraction of these animals rises from 16% in April to 46% in June. This is accompanied by stabilization of the numbers and percentage of the current-year voles, which is especially pronounced for youngest animals. By August, overwintered animals account only for 4.8%; the number of 1–2 month-old voles reaches maximum values but their reproduction intensity drops still further. Among young voles at the age of 1–2 months only 6.3% of females participate in breeding, while in the 3–6 month age group this figure amounts to 84.6%. As a result, 49.5% of the potential offspring of the population is due to current-year females 3–6 month of age, and overwintered and young animals bring 25.3% and 25.2% respectively, i.e. approximately one-half of the offspring. In August the population numbers are close to the seasonal maximum, and their variability are at a minimum. The population of current-year animals is most stable during this period. The coefficient of their numbers variation is 59% for 1–2 month-old animals, 55% for 3–6 month-old animals, and 96% for overwintered animals. Variation coefficient of the structure indices (fraction of different ages and the total population) also lowered in the group of current-year animals and account for 11.4% for 1–2 month-old voles, 71% for 3–6 month-old voles, and 80.1% for overwintered animals. In October 64.2% of the population consists the voles at the age of 1–2 months but the females of this age class do not participate in reproduction at all. Out of the other two age groups only overwintered females fully participate in reproduction but their fraction in the population is only 2.2% and therefore their contribution to the population growth accounts only for 7.9% whereas the contribution of 3–6 month-old females is the maximum (92.1%).

In autumn, a rise in the variability of the total population is accompanied by an increase in the variability of the numbers and fractions of different cohorts in the population.

The fraction of sexually immature males in the population also has a seasonal component: the fraction lowers from spring (95%) to autumn (1.4%) and is largely determined by the age-class composition of the population. Variability of maturation of males is higher than of females but general trends of their changes are similar. In spring, the variation coefficient of the fraction of sexually immature males is at a maximum and attain 150%. In August it is at a minimum (65%) and remains approximately at this level till the end of the breeding season.

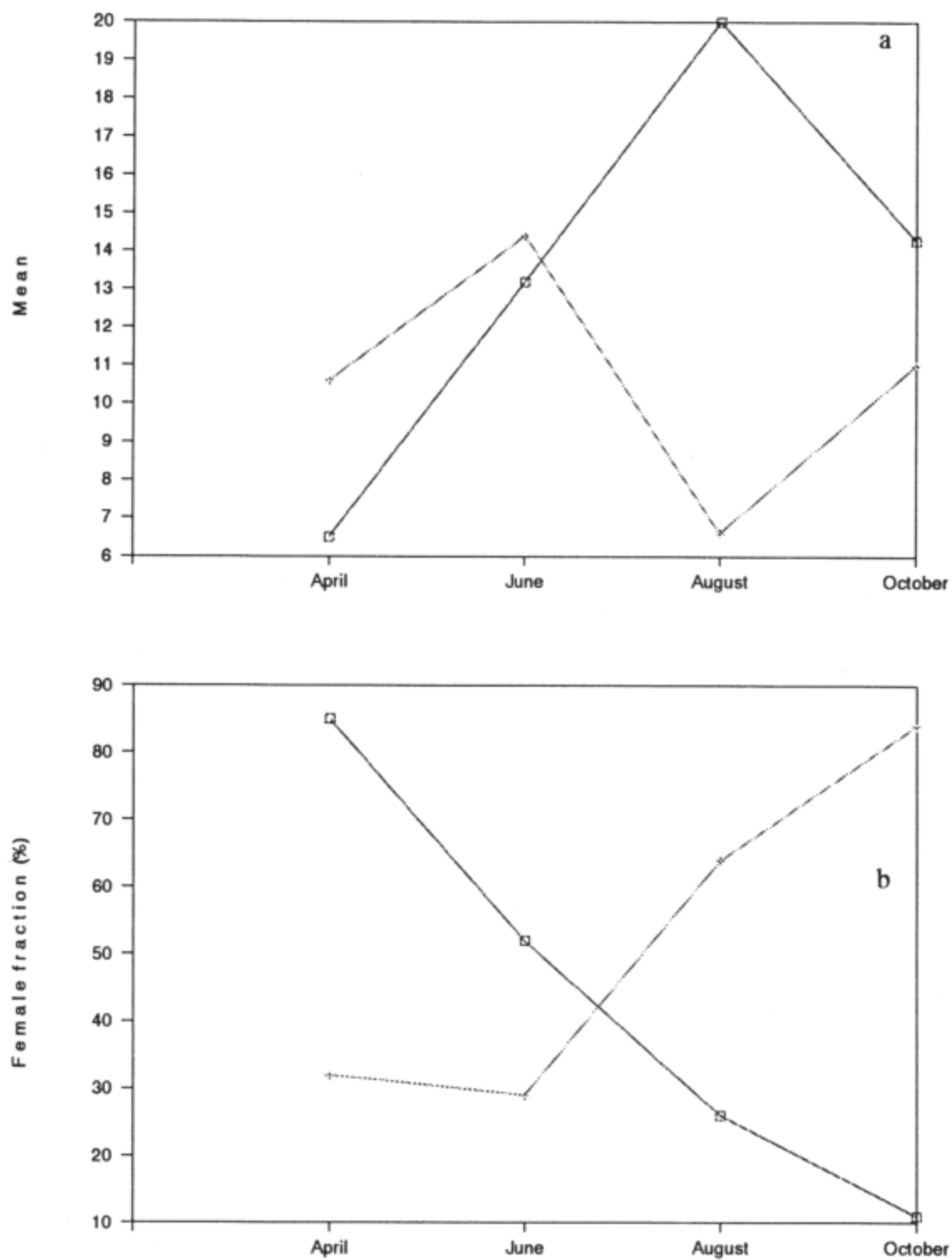
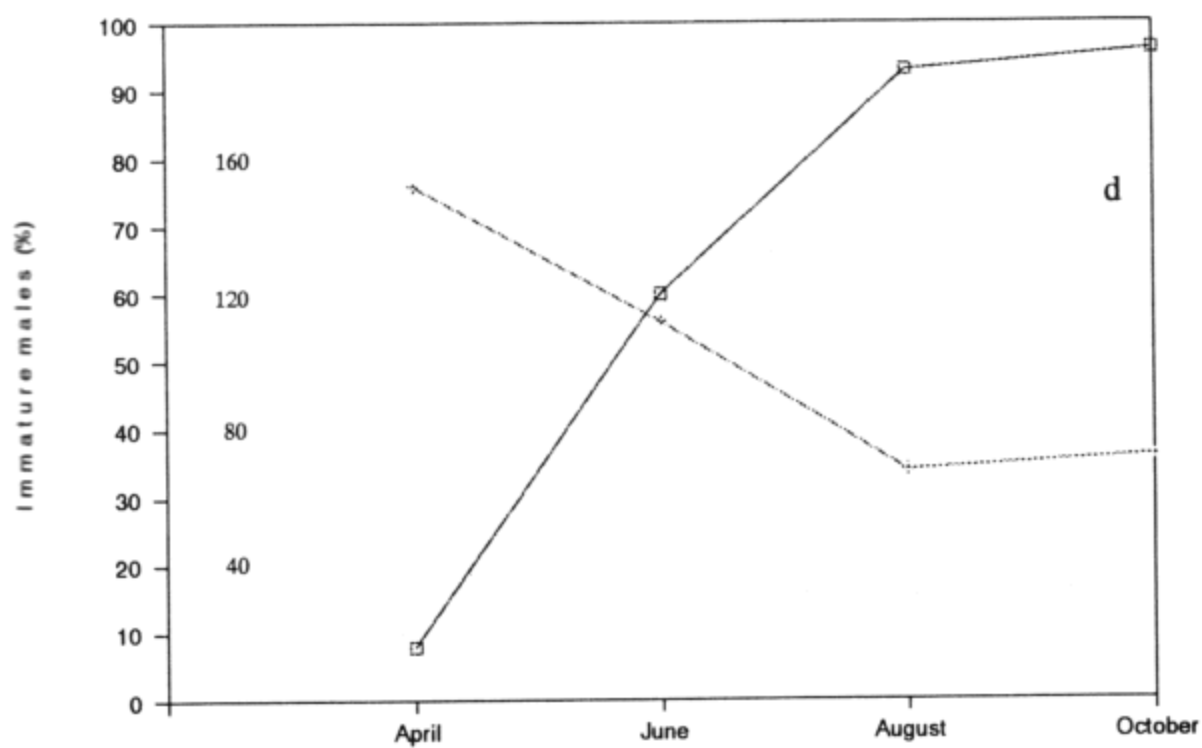
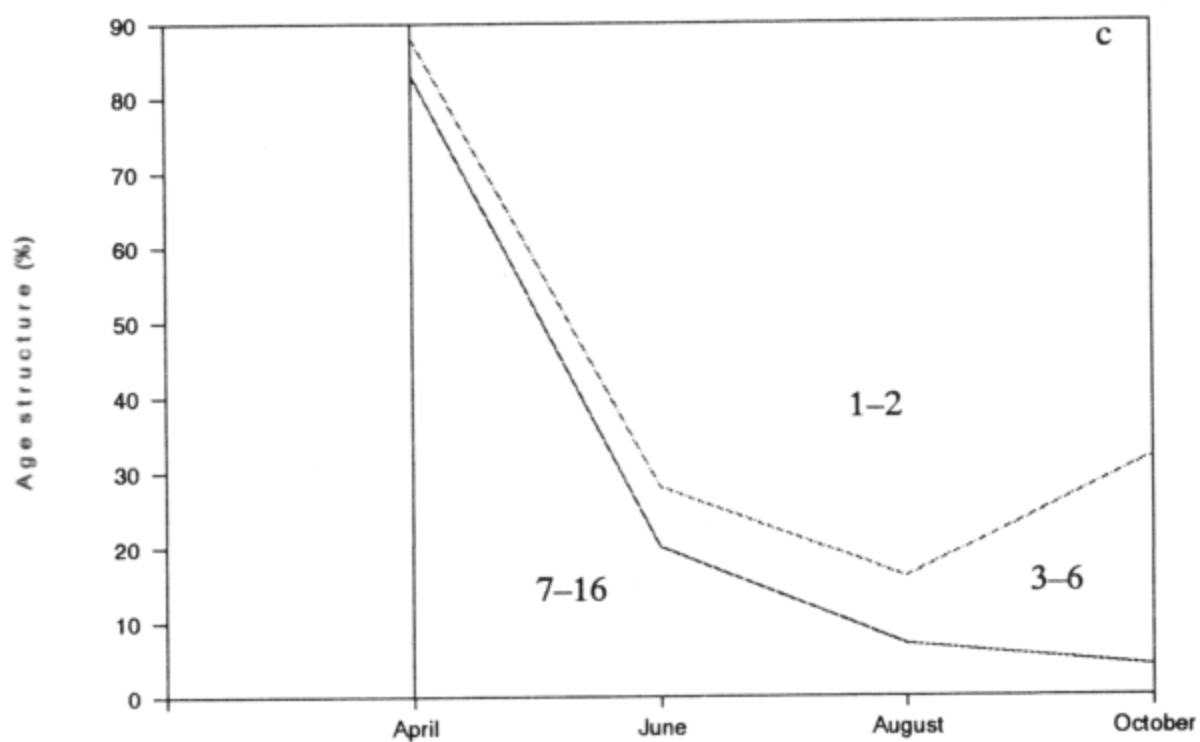


Fig. 4. Mean values of demographic variables in the bank vole population at Udmurt permanent study plot. For explanation see Fig. 2



It is customary to analyze the sex structure by the primary (at conception), secondary (at birth), tertiary (at waning), and quaternary (in adults) ratios of the numbers of males and females. Taking into account the conditions under which our works were performed, we considered only tertiary and quaternary sex ratios although these cannot be strictly distinguished at all times.

In spring (April), males predominate largely over females in the population among overwintered voles but already from June and till the end of the breeding season females are predominant. The predominance of males in the spring population cannot be explained solely by the change in mobility of males and females. It is determined to a great extent by the fact that already in autumn of the preceding year males predominated among young voles (Table 6) and, besides, in the autumn-winter period mortality of females is somewhat higher than that of males. However, during the reproduction period overwintered females predominate over males, which is connected most likely with higher mortality of males. Females dominate in the group of current-year voles at the age of 3–6 months and it is only by the late summer that the sex ratio is equalized and the fraction of females becomes close to 50% (Table 6). The fraction of 1–2 month-old females approaches the size of the male fraction only in early summer, while later on animals

Table 6

Estimates of the sex ratio in the bank vole population on the Udmurt permanent study plot (numerator shows the fraction of females, denominator indicates the fraction variation coefficient (%))

Month	Age in month			Totally per month
April	$\frac{0.38^*}{35.7}$	—	—	0.43*
June	$\frac{0.58^*}{42.6}$	$\frac{0.63}{118.3}$	$\frac{0.51^*}{28.2}$	0.53
August	$\frac{0.57^*}{91.6}$	$\frac{0.67^*}{37.1}$	$\frac{0.44^*}{24.3}$	0.47*
October	$\frac{0.55}{162.8}$	$\frac{0.49}{46.4}$	$\frac{0.43^*}{57.6}$	0.46
Totally over reproduction season	0.46*	0.57*	0.46*	

* Values significant at $p = 0.5$.

of this group are dominated by males. This male dominated sex ratio is maintained in the population till spring of the following year (Table 6).

In spring, the fraction of overwintered females is relatively stable in different years but by autumn the fraction variability increase almost five-fold. One of the causes of this phenomenon may be small numbers of overwintered animals in October and, as a consequence, high randomness of trappability of each animal. Another cause is that with different seasonal dynamics, mortality is higher alterna-

tively for males and females, this resulting in considerable fluctuations of the sex ratio in autumn. The sex ratio variability in the group of 1–2 month-old animals is low in all summer months. In the age group of 3–6 months, the sex ratio is shifted quite clearly in favour of females, probably as a result of higher mortality of males, although the effect of different mobility of males and females cannot be excluded altogether. Large variation coefficients of the fraction of 3–6 month-old females occurring in June are due to low numbers of voles of this age.

3.3. BANK VOLE POPULATION OF SPRUCE-LIME SUBTAIGA FORESTS

About 25 000 trap-days were served and approximately three thousand bank voles were caught on the Mari permanent study plot over 16 years of observation (1972 to 1987). The territory of the study plot is inhabited by bank and northern red-backed voles, common field and striped field mice, voles of the genus *Microtus*, and shrews. Judging by the mean numbers and their variability, the bank vole dominates in summer in all of the biotops studied (Tables 7, 8, 9). According to multi annual observations, its fraction in the entire population fluctuations in different months from 60 to 85%, and over the reproduction period accounts on the average for 76% in spruce-lime forests, for 68% in secondary birch forests, and for 60.5% in clearings. The fraction of other species is much lower. The lower degree of dominance of the bank vole in secondary birch forests and especially in clearings is probably due (Tables 7, 8, 9) to the fact that living conditions improve for mice in damaged areas in birch forests and for *Microtus* voles in clearings. Apart from the fact that the bank vole dominates in the population in all biotopes, its numbers variability is lower than that of other co-occurring species. The bank vole population is most stable in spruce-lime forests: the numbers variation coefficient equals 86% in summer. In birch forests and clearings the numbers variation coefficients increase (155 and 118%), this testifying probably to an impairment of the living conditions for the bank vole in these areas.

In June (in the phase of the maximum population growth) variability of the numbers of both the bank vole and other species entering into the population of the study plot is at a maximum in all the biotopes.

The seasonal abundance peak is observed in August in spruce-lime forests and birch forests and in August–October in clearings, and at this time stabilization of the animal numbers is noted. Lowering of the numbers variability level during the seasonal peak period is most likely due to the fact that the abundance of voles reaches its upper limit characteristic of each biotope and further growth is impossible.

The numbers of some species of small mammals change in different years over extremely broad limits (variation coefficients oscillate between 80 and 235%), whereas variability of the total number of animals inhabiting the study plot is considerably lower in all cases, in spite of different conditions of each year.

The living space can be divided between the bank vole and other species inhabiting the study plot either as a result of competitive relations or due to different requirements imposed by each species upon the habitat. In our case, no statisti-

Table 7

Estimates of the population numbers and structure of small mammals on the Mari permanent study plot (spruce-line forests)

Month	Species	Mean (vole per 100 trap-days)	Standard deviation	Variation coefficient (%)	Species fraction (%)
April	bank vole	11.2	9.8	87.8	84.2
	nothern red-backed	0.3	0.7	254.8	2.3
	shrews	0.2	0.5	250.0	1.5
	other rodents	1.6	2.0	121.5	12.0
	total numbers	13.3	12.1	90.8	—
June	bank vole	16.9	18.6	110.3	77.2
	nothern red-backed	0.6	1.5	246.4	2.7
	shrews	0.1	0.4	254.2	0.5
	other rodents	4.3	4.9	114.3	19.6
	total numbers	21.9	17.5	80.1	—
August	bank vole	34.9	19.2	55.1	80.2
	nothern red-backed	2.3	3.2	142.2	5.3
	shrews	1.5	2.2	144.9	3.5
	other rodents	4.8	6.0	125.3	11.0
	total numbers	43.5	21.5	49.5	—
October	bank vole	20.9	13.3	63.7	66.3
	nothern red-backed	1.4	2.3	162.5	4.5
	shrews	2.8	2.5	91.3	8.8
	other rodents	6.4	4.4	68.7	20.4
	total numbers	31.5	14.6	46.3	—
Totally over reproduction season	bank vole	10.9	18.0	85.9	76.0
	nothern red-backed	1.1	2.3	197.7	4.0
	shrews	1.2	1.9	171.3	4.4
	other rodents	4.3	4.8	111.8	15.6
	total numbers	27.5	20.3	73.8	—

cally valid negative or positive correlations were detected in the course of multi-annual changes in numbers of different species of small mammals. The absence of positive correlations is indicative of a sufficient independence of the changes in the animal numbers and, probably, is determined by biological features of each species (onset and intensity of breeding, reasons determining mortality and migration flows, etc.).

Table 8

Estimates of the population numbers and structure of small mammals on the Mari permanent study plot (birch forests)

Month	Species	Mean (vole per 100 trap- days)	Standard deviation	Variation coefficient (%)	Species fraction (%)
April	bank vole	3.4	4.1	120.7	64.2
	nothern red-backed vole	0.1	0.3	400.0	1.9
	shrews	0.5	0.8	174.6	9.4
	other rodents	1.3	1.6	124.6	24.5
	total numbers	5.3	4.9	92.5	—
June	bank vole	9.8	11.4	116.0	68.5
	nothern red-backed vole	0.4	0.7	187.9	2.8
	shrews	0.3	0.4	163.8	2.1
	other rodents	3.8	5.6	147.9	26.6
	total numbers	14.2	14.3	100.4	—
August	bank vole	21.6	14.4	66.6	69.6
	nothern red-backed vole	0.8	1.0	136.7	2.6
	shrews	2.0	2.0	99.8	6.5
	other rodents	6.6	6.9	106.2	21.3
	total numbers	31.0	16.8	54.1	—
October	bank vole	11.0	12.7	115.5	65.2
	nothern red-backed vole	0.4	1.0	236.6	2.3
	shrews	3.2	3.5	107.9	18.9
	other rodents	2.3	2.0	88.0	13.6
	total numbers	16.9	10.9	64.3	—
Totally over reproduction season	bank vole	11.5	13.2	115.3	68.0
	nothern red-backed vole	0.4	0.9	205.5	2.4
	shrews	1.5	2.4	158.4	8.9
	other rodents	3.5	5.0	142.7	20.7
	total numbers	16.9	15.4	91.2	—

The above-given data suggest that the bank vole dominates on the territory of the permanent study plot. The bank vole population dynamics is independent of changes in the population numbers and structure of other species living on the study plot. As it is seen from Figure 5 and Table 10, despite considerable differences in the numbers levels, the annual fluctuations of numbers occur synchronously

Table 9

Estimates of the population numbers and structure of small mammals on the Mari permanent study plot (clearings of different standing)

Month	Species	Mean (vole per 100 trap- days)	Standard deviation	Variation coefficient (%)	Species fraction (%)
April	bank vole	3.1	3.5	113.8	52.6
	nothern red-backed vole	0.1	0.3	238.2	1.7
	shrews	0.2	0.4	219.3	3.3
	other rodents	2.5	2.2	89.2	42.4
	total numbers	5.9	4.7	80.4	—
June	bank vole	7.0	8.3	119.5	55.6
	nothern red-backed vole	0.3	0.6	216.4	2.4
	shrews	0.3	0.6	176.8	2.4
	other rodents	5.0	4.2	82.6	39.6
	total numbers	12.6	10.1	79.7	—
August	bank vole	18.0	13.9	77.3	64.3
	nothern red-backed vole	0.4	0.7	194.6	1.4
	shrews	2.6	2.5	93.5	9.3
	other rodents	7.0	5.7	81.4	25.0
	total numbers	28.0	13.8	49.3	—
October	bank vole	15.3	12.0	78.3	63.2
	nothern red-backed vole	0.8	1.5	200.6	3.3
	shrews	3.1	3.1	97.4	12.8
	other rodents	5.0	3.2	63.5	20.7
	total numbers	24.2	12.1	49.9	—
Totally over reproduction season	bank vole	10.9	12.9	118.5	60.5
	nothern red-backed vole	0.6	1.5	135.4	3.4
	shrews	1.6	2.6	165.9	8.8
	other rodents	4.9	4.4	91.0	27.3
	total numbers	18.0	15.7	87.2	—

in all the biotopes. Besides, owing to small area of the study plot (about 4 km²) a free exchange of animals is possible between all its areas.

Therefore it may be assumed that a single population of bank voles inhabits the study plot territory. The differences observed in the numbers are due mainly to changes in the intensity of the population processes which are synchronized by the factors that are the same for the entire territory. Out of the biotopes considered, the spruce-lime forest represents an optimum habitat because it is precisely in this territory that the bank vole numbers are high during the breeding season, while the numbers variability is lower than in other biotopes.

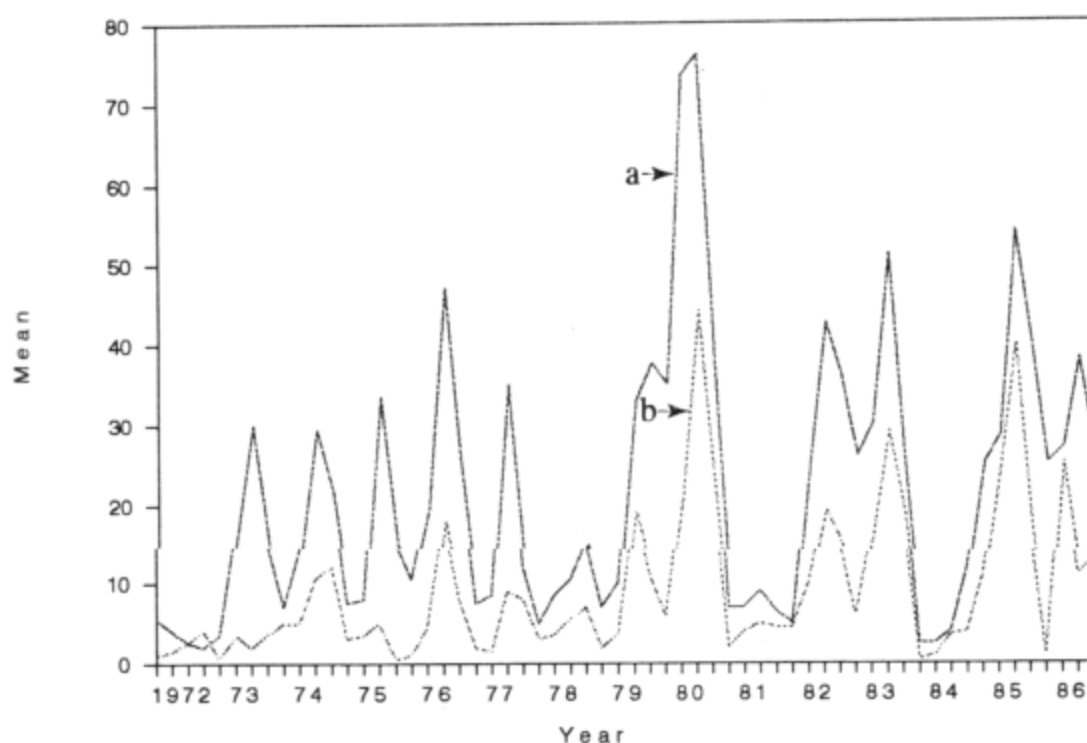


Fig. 5. Multiannual dynamics of relative abundance (numbers caught per 100 trap-days) of the bank vole at Mari permanent study plot. Four estimates per year made in April, June, August and October. Continuous line – spruce-lime forest, dashed line – 1968 cutover

Table 10

Estimates of the synchronism in multi-annual changes in the bank vole population on the Mari permanent study plot (Spearman correlation coefficients)

Biотopes*	April			June			August			October		
	2	3	4	2	3	4	2	3	4	2	3	4
Numbers												
1	0.77	0.63	0.64	0.91	0.92	0.74	0.88	0.70	0.88	0.90	0.89	0.77
2	–	–	0.48	–	0.92	0.64	–	0.63	0.88	–	0.86	0.91
3	–	–	0.65	–	–	0.54	–	–	0.59	–	–	0.77
Fraction of overwintered voles (7–16 months old)												
1	–	–	–	–	0.82	–	–	–	–	–	–	–
2	–	–	–	–	0.59	0.43	–	–	–	–	–	–
3	–	–	–	–	–	–	–	–	–	–	–	–
Fraction of current-year voles (1–2 months old)												
1	–	–	–	–	0.65	–	0.56	0.48	–	–	–	–
2	–	0.82	0.95	–	0.53	0.54	–	–	–	–	–	–
3	–	–	0.80	–	–	–	–	–	–	–	–	0.63

* 1 – spruce-lime forests, 2 – secondary birch forests, 3 – 1957 clearing, 4 – 1968 clearing.

Great number of years with high numbers levels occurring both at the beginning and end of the breeding season suggests that the living conditions are favourable for the bank vole (Fig. 5). The cyclicity index for different biotopes (0.44 for spruce-lime forests, 0.42 for secondary birch forests, 0.54 for the 1976 clearings, 0.49 for the 1968 clearings, 0.43 for the 1957 clearings) characterizes the population as a whole and the population of individual biotopes as noncyclic.

Seasonal dynamics has the form typical of small mammals in temperate-zone forests (Tupikova and Konovalova 1971, Ivanter 1975, Zhigalski and Bernshtein 1986). At the onset of the breeding season (April) the relative numbers of the Mari population are 11.2% (mean multi annual value) and vary from 1 to 32 (in the optimum biotope) in different years. During summer the population numbers increase gradually and attain a maximum value of 34.9 (minimum 2.0 maximum 76) by early August. By mid-October the population numbers drop again and reach 20.9 (vary from 1.3 to 50 in different years) (Figs. 6, 7).

Biotopic differences in the seasonal dynamics of the bank vole numbers in birch forests and clearings of different standing compared to spruce-lime forests consist in different numbers levels and in a later termination of reproduction in clearings. From spring to the seasonal peak the population numbers increase on the average by 3.1 times for spruce-lime forests, 6.4 times for secondary birch forests, 0.4 times for the 1957 clearings, and 6.8 times for the 1968 clearings. From the seasonal peak to October the numbers decrease by 1.7 times in spruce-lime forest, 2 times in the secondary birch forest, 1.3 times in the 1957 clearings, 1.2 times in the 1968 clearings, while in the latest clearings even an increase in the numbers is observed. A high rate of the population increase in the first half of summer and a slow decrease in the population in the second half in the birch forest and in clearings as compared to spruce forest cannot be explained by changes in reproduction activity, because the fraction of breeding females in the first half of summer is approximately the same as in spruce forests and in other areas, and in the second half even a slight lowering is observed. The differences detected in the population growth and drop are probably determined by the dispersal of young animals from the spruce-lime forest to birch forests and clearings, where the population density is much lower.

From October to spring of the following year the vole population drops by 1.9 times in spruce-lime forest, 3.2 times in birch forest, and 3.2-5.7 times in clearings of different standing. In the latest clearings of 1976 overwintered animals are not trapped at all in spring. A considerable decrease in the spring population of voles in birch forests and clearings can be explained by a higher mortality of the animals in the autumn-winter period or by a higher migration activity of the animals from those areas to spruce-lime forests which afford more favourable conditions of living.

The population variability, as well as population numbers, exhibits a clear-cut seasonal dynamics: maximum variation coefficients are observed during the period of the maximum population growth in all the biotopes. In August, at the time of the seasonal peak, the population variability is at a minimum. It rises again in all the areas in October.

Duration of the bank vole breeding season varies on the Mari study plot over rather wide limits. In the majority of cases reproduction-active females are found during 4–6 months; however, the terms of the beginning and end of reproduction fluctuate heavily. Mass appearance of the young falls on the 2–3 decade of May. Winter reproduction is noted in some years and first young animals appear early in January. In April most of the overwintered females are pregnant for the third time. Simultaneously, current-year females start reproducing. On the Mari plot mass reproduction of the bank vole stops as a rule in late September. However, in high-density years reproduction terminates in June–July and in some years reproduction-active females are present in the population even in October.

The population age structure depends directly on the terms of the breeding onset and termination, and also on the reproduction intensity during the season. In April, the spruce–forest population comprises 87% overwintered animals and only 13% current-year early-spring and winter litters (Fig. 6). However, in birch forests and in clearings (going from early to latest clearings) the fraction of overwintered voles is reduced and in the 1968 clearings overwintered animals account only for 30% and current-year 1–2 months-old voles for 70% of the population (Fig. 7). In the latest 1975 clearings there is no permanent population in April and it is only in some years that single individuals are caught. Predominance of young voles in clearings is probably due to migration of young voles from the spruce–lime area of the study plot, where their numbers are rather high already in spring.

In June, one more age group appears in the population – current-year voles 3–6 months of age, but most numerous are 1–2 months-old animals. In the spruce–lime forest the fraction of the latter age group in the population accounts for 55% while in birch forests and clearings it reaches 65%. In August, the fractions of the youngest voles in the population of all areas become equal and approach 60%. The fractions of current-year 3–6 months-old voles are equal and account for 33–35% in all the biotopes.

In October, the population is represented basically by voles at the age of 3–6 months. The fraction of these animals varies from 70 to 80% for different areas of the study plot. Only in the 1976 clearings their fraction is about 45%. The increase in the numbers of 1–2 months-old voles in those clearings is undoubtedly connected with persistent reproduction of voles in that area, which is probably due to a low population density level. Attenuation of breeding is observed in all the other biotopes.

In spring (April), the potential increase of the population depends only on overwintered animals in all the habitats' areas. But already in June the population growth is determined in 50% by current-year 1–2 months-old animals practically in all the biotopes (Table 11).

In August, the reproduction intensity lowers (the fraction of breeding females is reduced to 25%) and the main contribution to the population growth processes is made by voles of 3–6 months of age, despite the fact that during this period the voles are dominated by 1–2 months-old females; however, practically all of the latter are sexually immature and therefore their contribution to the population growth does not exceed 10%. In October, about 18% of the females of all ages

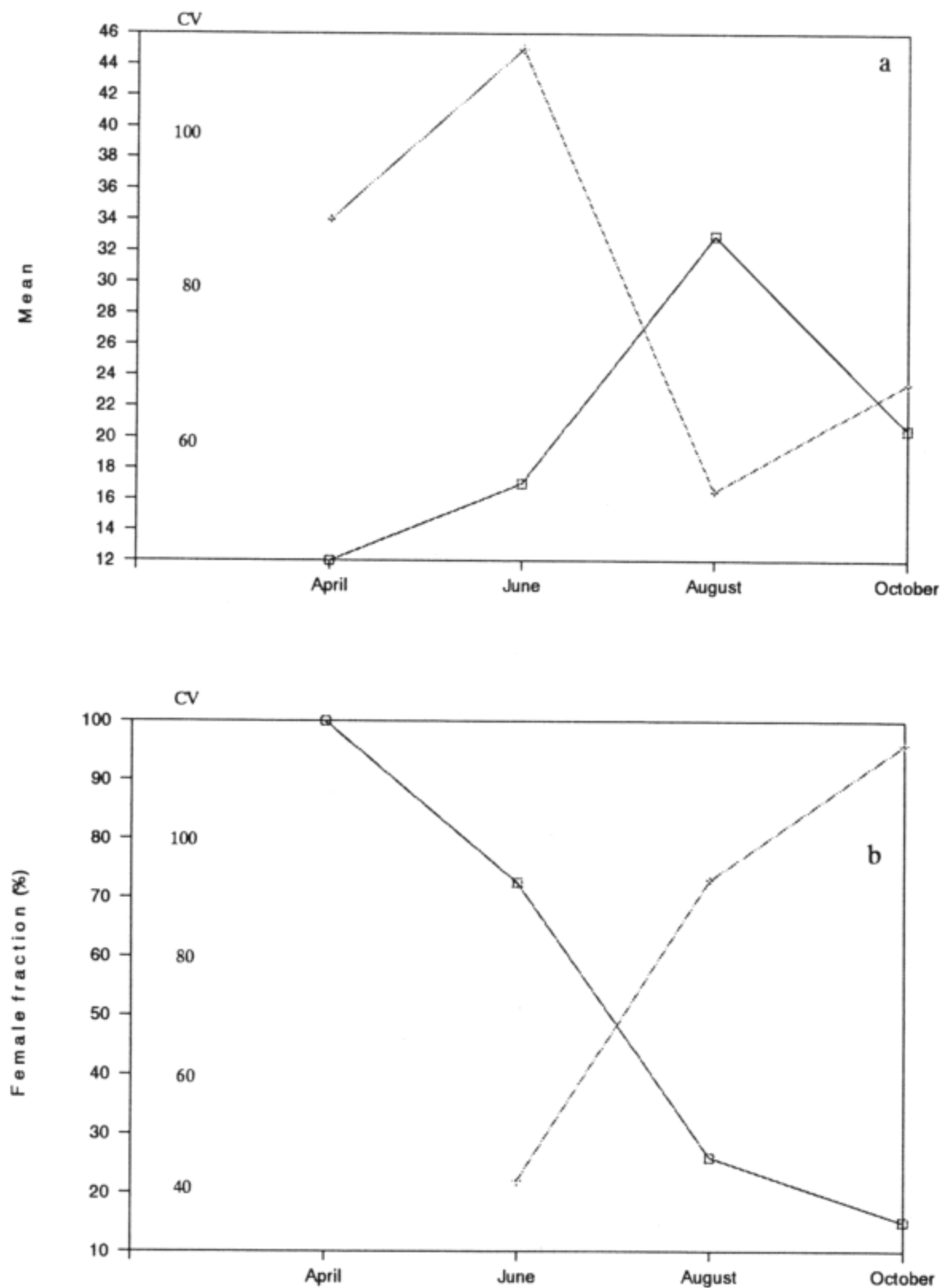
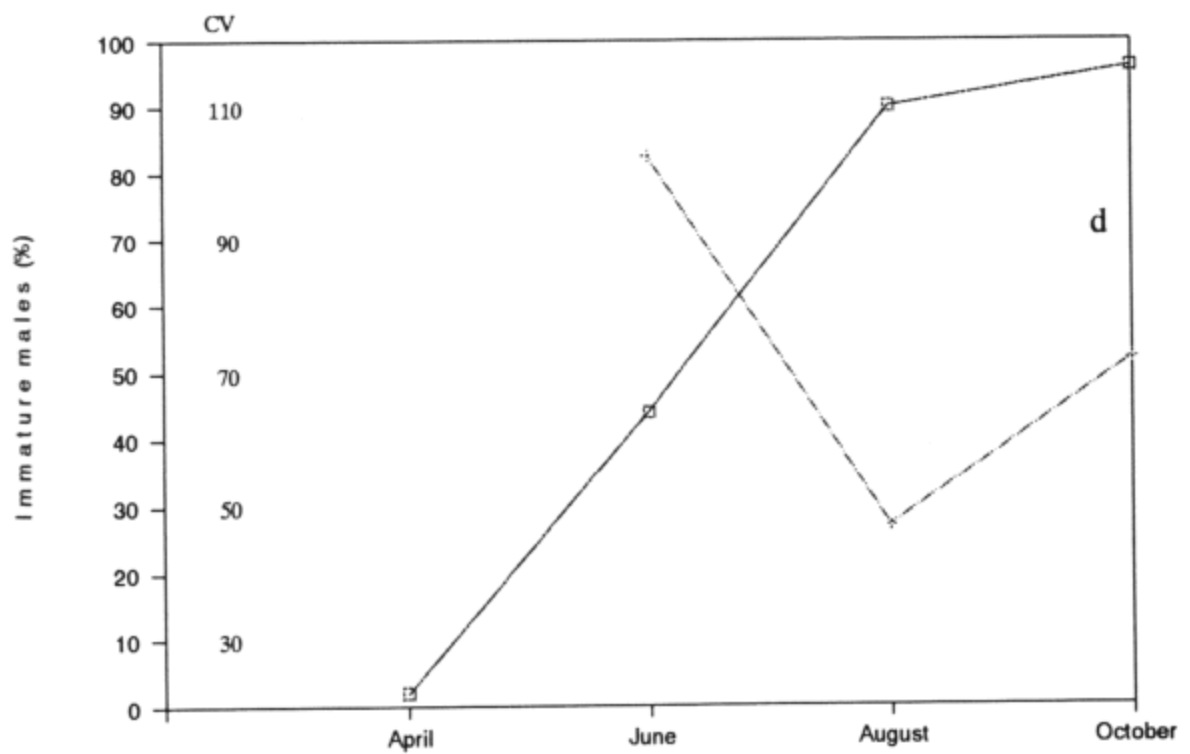
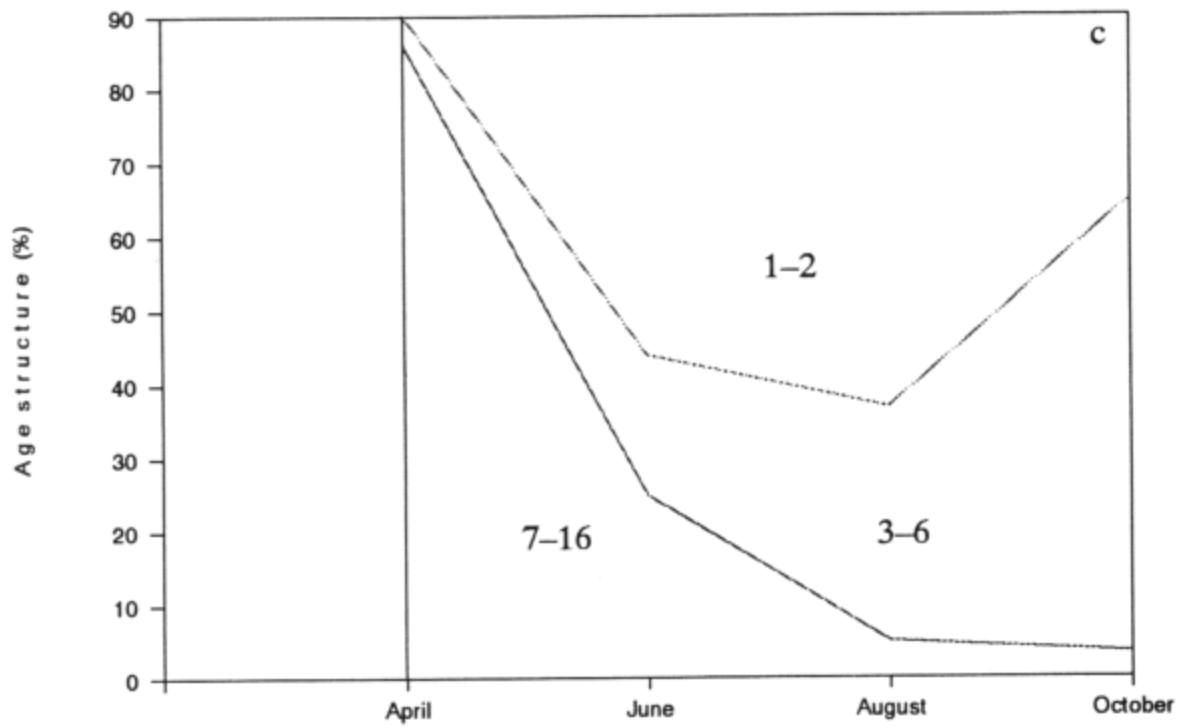


Fig. 6. Mean values of demographic variables in the bank vole population at Mari permanent study plot (spruce-lime forest). For explanation see Fig. 2



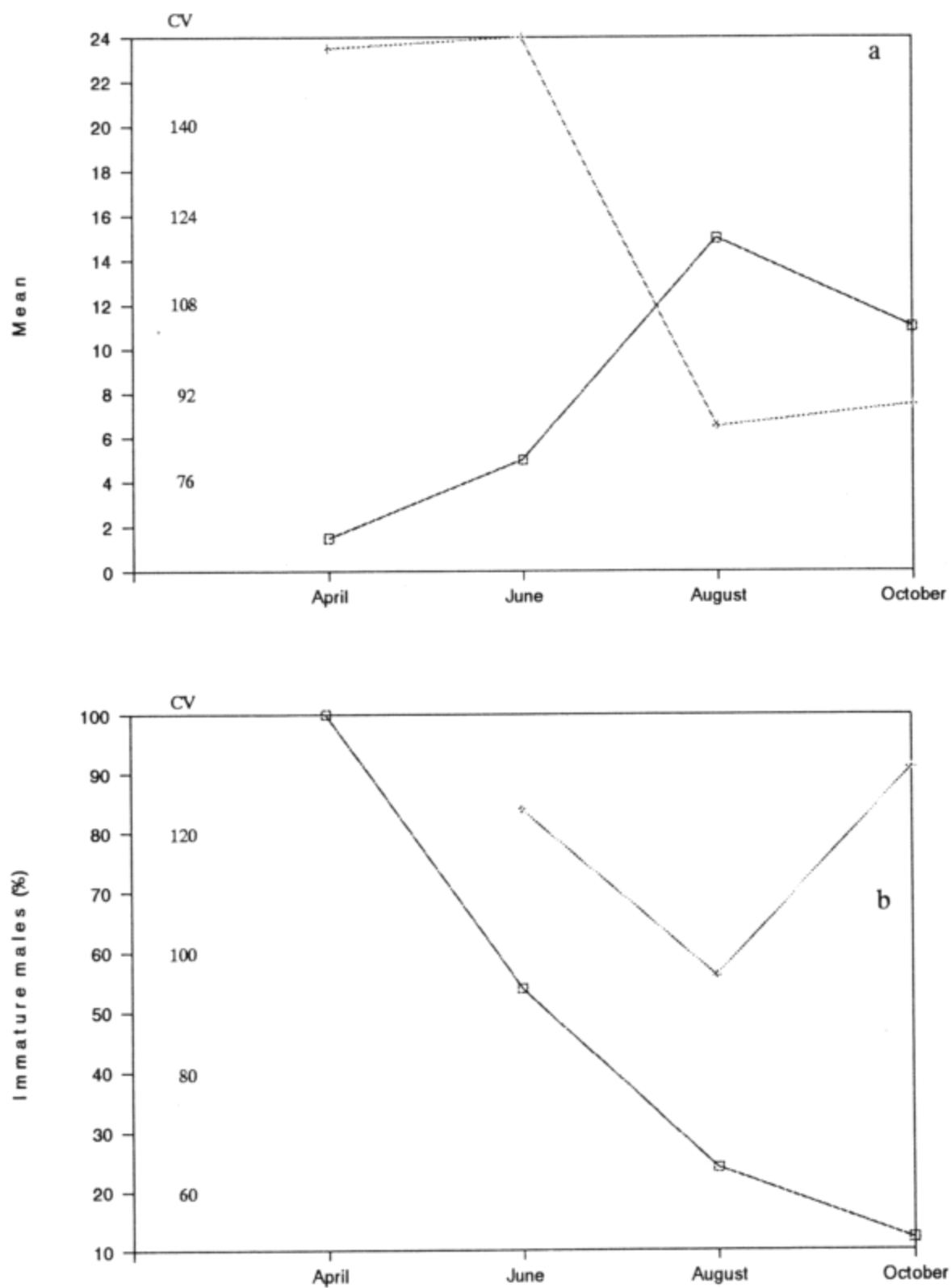


Fig. 7. Mean values of demographic variables in the bank vole population at Mari permanent study plot (1968 cutover). For explanation see Fig. 2

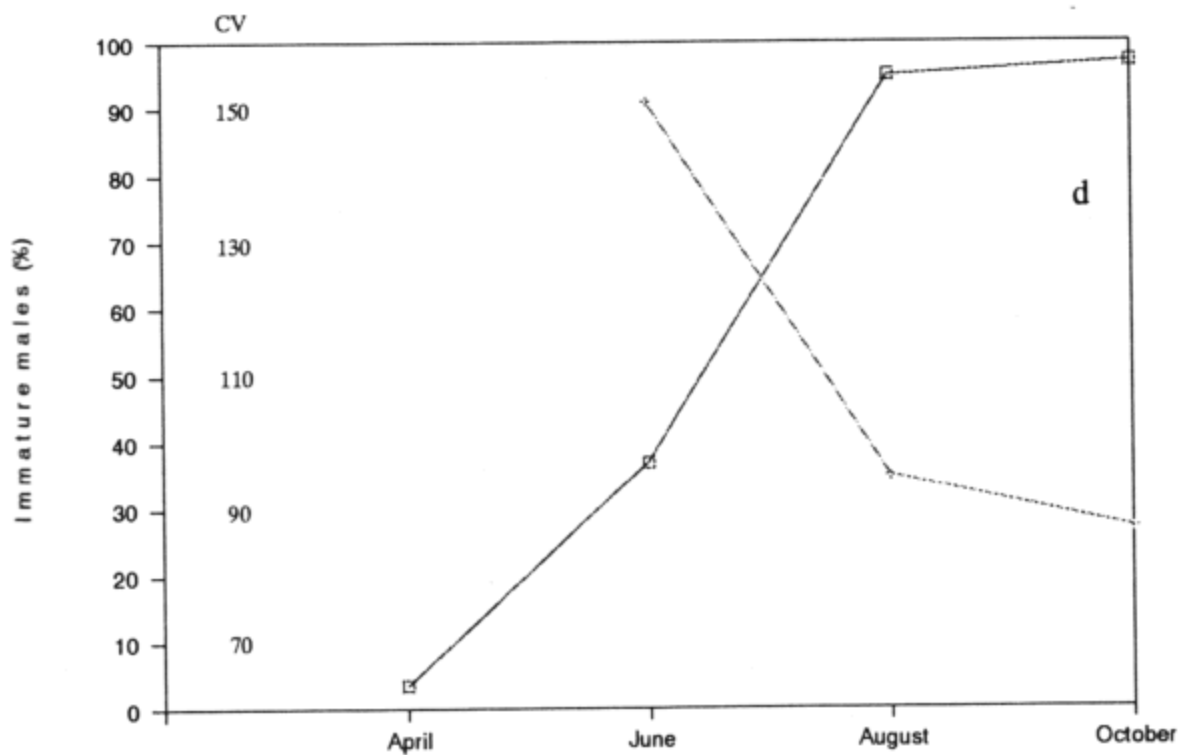
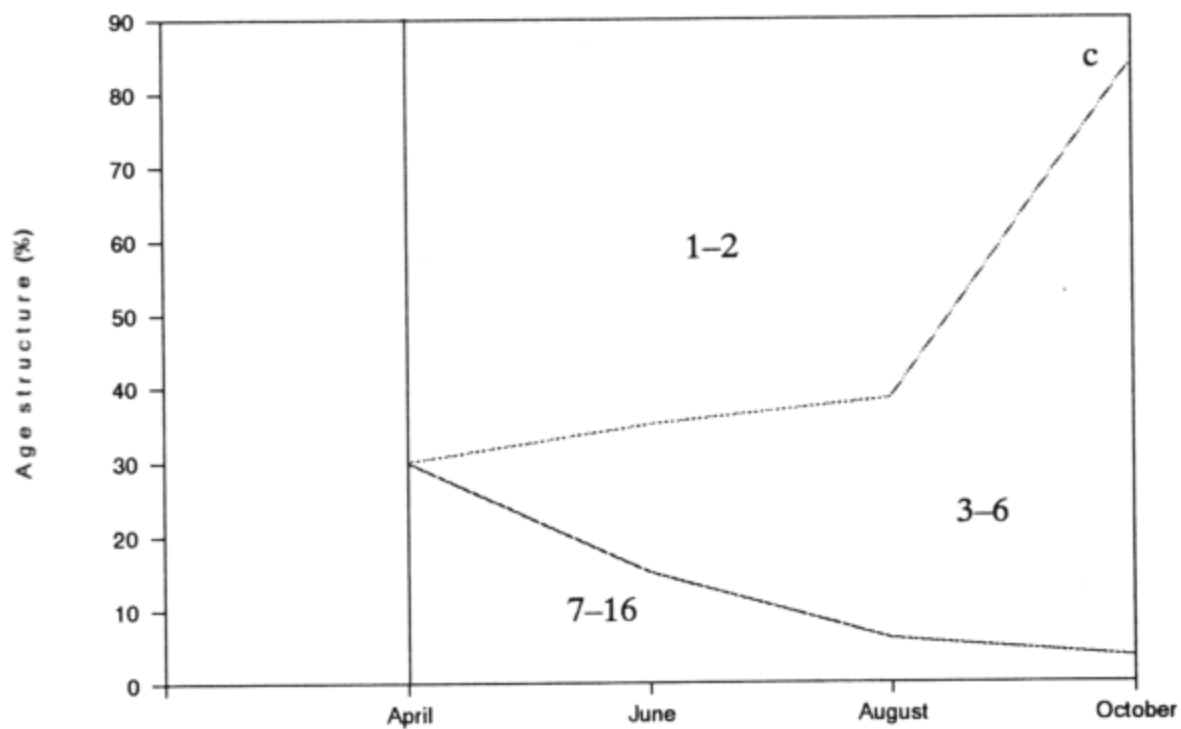


Table 11

Contribution made by different-age voles into the potential increase of the population
(mean multi annual value)

Month	Age (months)	Biotope			
		spruce-lime forests	secondary birch forest	clearing	
June	7-16	24.7	18.4	24.4	21.1
	3-6	27.5	18.4	22.2	26.3
	1-2	47.8	63.2	53.4	52.6
August	7-16	25.0	19.2	40.6	18.2
	3-6	70.0	73.1	56.3	81.8
	1-2	5.0	7.7	3.1	0
October	7-16	23.1	0	0	12.5
	3-6	69.1	75.0	95.0	87.5
	1-2	7.7	25.0	5.0	0

participate in reproduction, whereas in August the basic contribution to the population growth is made by 3-6 month-old voles.

During the breeding season (April-October) substantial changes occur in the population age structure and the degree to which animals of different age take part in reproduction. This leads to considerable alternations in the specific weight of the age groups in the formation of the total population numbers. At the beginning of the breeding season the population numbers raise is the most rapid and the most essential part in the realization of this process is played by overwintered animals and starting from June by the animals belonging to 1-2 months age group. In the second half of summer the population numbers start lowering, reproduction processes cease, migration and emigration of animals increase. Nevertheless, part of females continue breeding and the determining role belongs here to animals 3-6 months of age. Overwintered animals are already small in number and therefore they cannot play a significant role and 1-2 months-old voles are sexually immature in their majority.

Maturation rate of both females and males has a seasonal component. In spring, the population includes predominantly overwintered males, almost all of them being mature at this period. During the period of the maximum population growth the number of current-year animals rises and the fraction of sexually immature males increases parallelly (Figs. 6, 7). In August, at the time of the seasonal peak, the population contains only about 10% of reproduction-active males. In October, their fraction drops to 2-3 %, whereas the fraction of breeding females remains at a level of 20%.

The sex ratio was studied for voles belonging to three age groups and therefore only the tertiary and quaternary sex ratios were analyzed. The first half of summer, in spruce-lime forest the number of males is much higher than that of females among overwintered animals but beginning from August the population is determined by females. Throughout the breeding season males predominate among overwintered animals in birch forest, while in clearings the spring sex ratio is close to unity. In June, it changes in favour of males and in August the overwintered group is dominated again by females (Table 12). A considerable shift of Table 12 – the sex ratio in favour of males in spruce-lime forest cannot be ex-

Table 12

Sex ratio (fraction of females) in the bank vole population on the Mari permanent study plot

Month	Age in months			Totally per month
	7-16	3-6	1-2	
Spruce-lime forest				
April	0.32*	—	—	0.32*
June	0.40*	0.70*	0.56	0.55*
August	0.59*	0.49	0.42*	0.45
October	0.75*	0.41*	0.35*	0.39*
Totally over reproduction season	0.44*	0.47*	0.44*	—
Secondary birch forest				
April	0.41*	—	—	0.41*
June	0.29*	0.70*	0.63*	0.55*
August	0.39*	0.54*	0.31*	0.39*
October	—	0.45	0.57*	0.47
Totally over reproduction season	0.36*	0.51	0.43*	—
1957 clearing				
April	0.50	—	—	0.50
June	0.37*	0.56	0.56	0.52
August	0.72*	0.58*	0.41*	0.50
October	—	0.47	0.37*	0.45
Totally over reproduction season	0.50	0.52	0.45	—
1968 clearing				
April	0.56*	—	—	0.56
June	—	—	0.59*	0.59*
August	—	0.59*	0.39*	0.46
October	—	0.41*	0.57*	0.44*
Totally over reproduction season	0.56*	0.47	0.46	—

* Values significant at $p = 0.05$

plained only by changes in the mobility of males and females. The shift is determined largely by the fact that already in autumn of the preceding year young voles were dominated by males, with the mortality of males and females being practically the same. On damaged territories the sex ratio occurring in autumn of the preceding year in the group of young voles is shifted somewhat in favour of females and this situation is preserved in spring. The only exception are the early 1957 clearings.

In spruce-lime forest the group of current-year voles, especially at the age of 3–6 months, is dominated (Table 12) in June by females but nearer to autumn their fraction decreases gradually and the majority of the population is constituted of males. A qualitatively different picture is observed in other biotopes. The principal difference is that in secondary forests among young voles 1–2 months of age females predominate almost throughout the entire breeding season (Table 12). One may suppose that the dominance of females in secondary forests is caused by the response of the population to low densities in these biotopes. An increase in the fraction of females in the population will not influence the population dynamics of the given year since a major part of young females do not mature in the year of birth but can add considerably to the population growth rate in spring of the following year, because in spring, too, females predominate on these areas.

As follows from our long-term observations made on the Mari permanent study plot, the fraction of overwintered females in the population is most stable in April (variation coefficients for different biotopes are about 60%) and increases gradually by autumn, reaching 170%. In the group of current-year animals the sex ratio variability fluctuates insignificantly over the entire reproduction period and lies within 50–80% (Table 12).

3.4. BANK VOLE POPULATION OF TRUE-MOSS SPRUCE MID-TAIGA FORESTS

Over 22 years of observations on the Karelia permanent study plot (1966 to 1987) 71 500 trap-days were completed and 1 200 bank voles were trapped. In addition to the bank vole, the study plot is inhabited by five species of *Sorex*, yellow-necked mouse, striped field mouse, wood lemming (*Myopus schisticolor*), northern red-backed vole, field vole (*M. agrestis*), and root vole (*M. oeconomus*).

Out of the forest voles living in Karelia, the bank vole is most numerous but it is not a pronounced dominant species. In different years its fraction among all small mammals fluctuates from 42 to 68% (Table 13), whereas on other permanent study plots the fraction of the bank vole is at least 54%. The decrease in the degree of dominance of the bank vole in secondary biotopes, especially in fresh clearings, is probably due to the improvement of the living conditions for shrews in damaged areas.

The next most numerous group is represented by shrews, out of which common shrew (*Sorex araneus*) is most abundant. The fraction of these animals in the entire population of the permanent study plot changes from 34 to 57%. Shrews and bank voles differ greatly as regards the mode of life, food, and many other biological features, and therefore it is hardly possible that competitive relations exist between these

Table 13

Population numbers (a) and structure (b-species fraction in%) of small mammals on the Karelia permanent study plot

	Biotope	Bank vole	Nothern red-backed vole	Shrews	Other species	Total numbers
<i>a</i>	True-moss spruce forests	2.8	0.3	2.3	0.3	5.7
<i>b</i>		49.1	5.3	10.3	5.3	—
<i>a</i>	Mature deciduous and mixed forests	2.4	0.04	2.7	0.3	5.4
<i>b</i>		44.1	0.7	49.7	5.5	—

species. Besides, it was shown (Ivanter E. V. and Ivanter T. V. 1983) that all correlations between changes in the numbers of different species of small mammals in the Pre-Ladoga region are positive a fact which also testifies to the absence of antagonistic relations. The bank vole dynamics is independent of the changes in the population numbers and structure of other species inhabiting the permanent study plot.

The total number of small mammals in all the biotopes of the Karelia study plot is lower than on the other permanent study plots and does not exceed 6%. The number of the bank vole is still lower and varies from hundredth of a per cent to 17% depending on the conditions of each year. Multiannual variations in the number of bank vole in both biotopes (Fig. 8) occurs synchronously, with the correlation coefficient equal to 0.62. Besides, spruce forests alternate with mixed forests and therefore a free exchange of animals between them is quite possible, this in turn indicating that a single population of the bank vole inhabits the study plot. The differences observed in the numbers are mainly due to changes in the intensity of the population processes, which are however synchronized by the same factors for the entire territory.

It is extremely difficult to determine an optimal habitat for the bank vole in the Pre-Ladoga region proceeding from the numbers indices: in early summer the animals are somewhat more abundant in spruce forests than in secondary forests and a reverse situation is observed in August. Another index that characterized the population state is annual numbers variability. If the optimal biotope is chosen using this parameter, an unambiguous conclusion is possible: the numbers variability level in all summer is lower in spruce forests (variation coefficient do not exceed 100%) than in other forests types, where two numbers variation coefficients do not drop below 110%. In addition, the variation dynamics changes in different biotopes. Thus, from June to July the variability level remains unchanged in spruce forests and drops from 135 to 110% in deciduous forests. From July to August variability of the total abundance of voles in spruce forests drops to 75%, while in secondary forests it rises again to 135% (Figs 9, 10).

A rather high variability in the abundance of voles in deciduous forests is caused primarily by the fact that these areas have no permanent population in the autumn–winter period. Overwintered animals occur there in early summer either

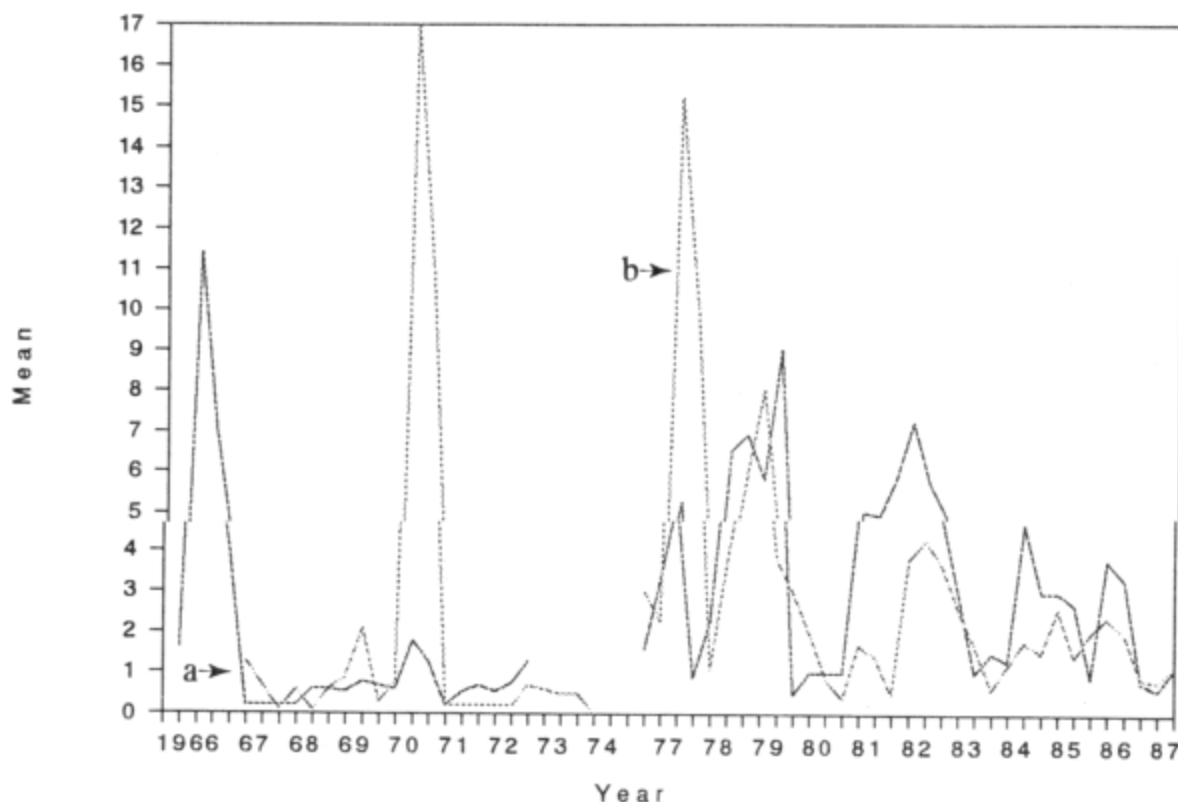


Fig. 8. Multiannual dynamics of relative abundance (numbers caught per 100 trap-days) of the bank vole at Karelia permanent study plot. Three estimates per year made in June, July and August. Continuous line *a* – true-moss spruce forest, dashed line *b* – secondary deciduous forest

after winters or when they migrate there for some reasons from native biotopes (their numbers variation coefficients attain 100% in secondary forests and are twice as a low (49%) in spruce forests). Variabilities in the numbers of young voles in June censuses are close in both biotopes and are determined by the reproduction activity of overwintered animals. In July, variability of the total abundance of voles in deciduous and coniferous forests is also close in values (Figs 9, 10) and is at a level of 70–80%. This is probably due to the absence of the factors limiting the population growth. However, in spruce forests variability of the numbers of overwintered animals rises from 49% in June to 105% in July, while in mixed forests it drops from 100 to 78%. Variability in the numbers of 1–2 months-old voles lowers in both cases but it is still higher in mixed forests than in spruce forests.

It is the decrease in the level of variability in the abundance of overwintered and young voles in July that led to the general reduction of the total numbers variation coefficients in secondary biotopes, while in spruce forests a higher variability of overwintered animals and lower variability of current-year animals resulted in a situation, where the general numbers variability in those biotopes was kept at the same level.

In deciduous and mixed forests productivity of grass communities fluctuates over much broader limits than in spruce forests. As a result, variability of the vole population increases in secondary forests and lowers in spruce forests. In addition to the estimation of the variability level, variation coefficients were used to calculate cyclicity indices for various biotopes. The cyclicity index equal 0.8 for true-moss spruce forests and 0.84 for mixed and deciduous forests. Such high cyclicity indices characterize the bank vole population of the Karelia mid-taiga forests as cyclic.

Out of all the biotopes considered, true-moss spruce forests can be classified among optimal habitats of the bank vole in the Pre-Ladoga region (despite little differences in the population levels in different types of forest). In true-moss spruce forest annual fluctuations of the vole numbers are less than in deciduous and mixed forests and, only in spruce forests the voles live throughout the year.

At the beginning of the breeding season (May) the relative numbers of the Karelia population of the bank vole account only for 0.2 per 100 trap-days (mean multiannual value). During summer the population numbers rise gradually (Figs. 9, 10) and by September (by the time of the seasonal peak) they reach 9.2 in true-moss spruce forests and 7.7 in deciduous forests. Starting from the second half of September the bank vole population lowers. Numbers were censused in October only in some years and therefore one may speak about trends rather than precise numerical estimates.

Seasonal growth of the population from June (onset of the intensive reproduction period) to the seasonal peak fluctuates over rather wide limits in different years and on the average the increase is 4.7 – fold for true-moss spruce forests and 6.1 – fold in secondary forests. These high rates of the population increase during summer are due to high reproduction activity of both overwintered and current-year voles. On the area of the Karelia permanent study plot the fraction of breeding in spruce forests is maintained at a level of 60% throughout summer and drops to 20% by September only, while in deciduous forests it is kept at a level of 50% in September, too. On the other permanent study plots the reproduction intensity lowers steadily starting from the onset of the reproduction period and in a majority of cases drops to 20% already in August. Increased percentage of breeding females and large increases of the Karelia population of the bank vole are most likely connected with an insignificant impact of the factors inhibiting these effects.

Duration of the breeding season of the bank vole in the Pre-Ladoga region varies rather largely. In a majority of cases reproduction-active females are found during 4–6 months but the terms of the reproduction start and stop are extended greatly. First overwintered pregnant females were sometimes trapped in the third decade of April, and sometimes in the third decade of May (the span is one month), and on the average in the first decade of May. First current-year animals were caught in the first decade of May (the earliest term) and up to mid-June (the latest term). The multi-annual mean for different biotopes is late May-early June but a mass appearance of the young falls on the second half of June. The terms of the reproduction end fluctuate much more than the terms of the reproduction onset and, as reasonably noted by some investigators (Tupikova and Konvalova 1971, Ivanter 1975), apart from phenologically induced reduction in

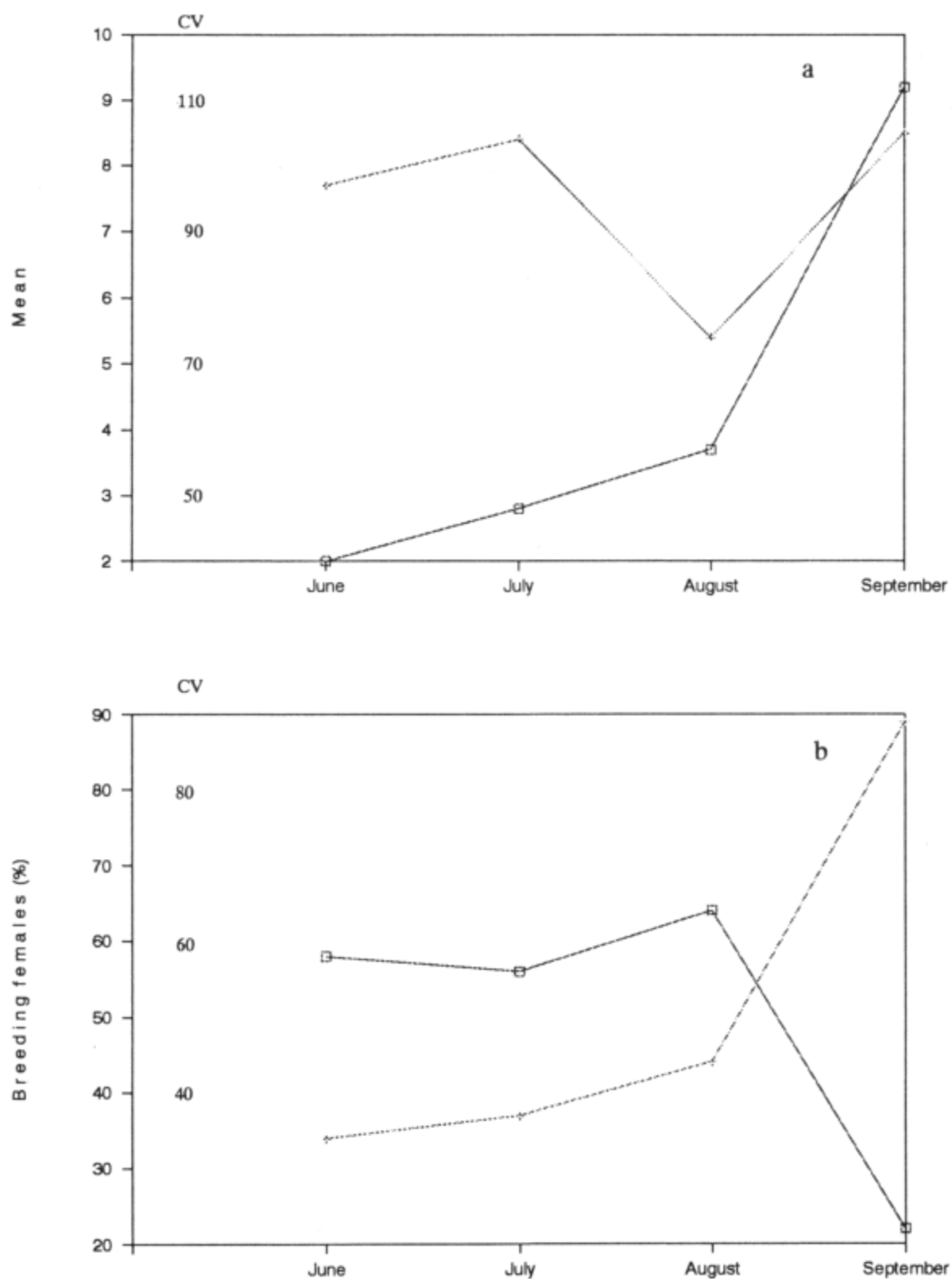
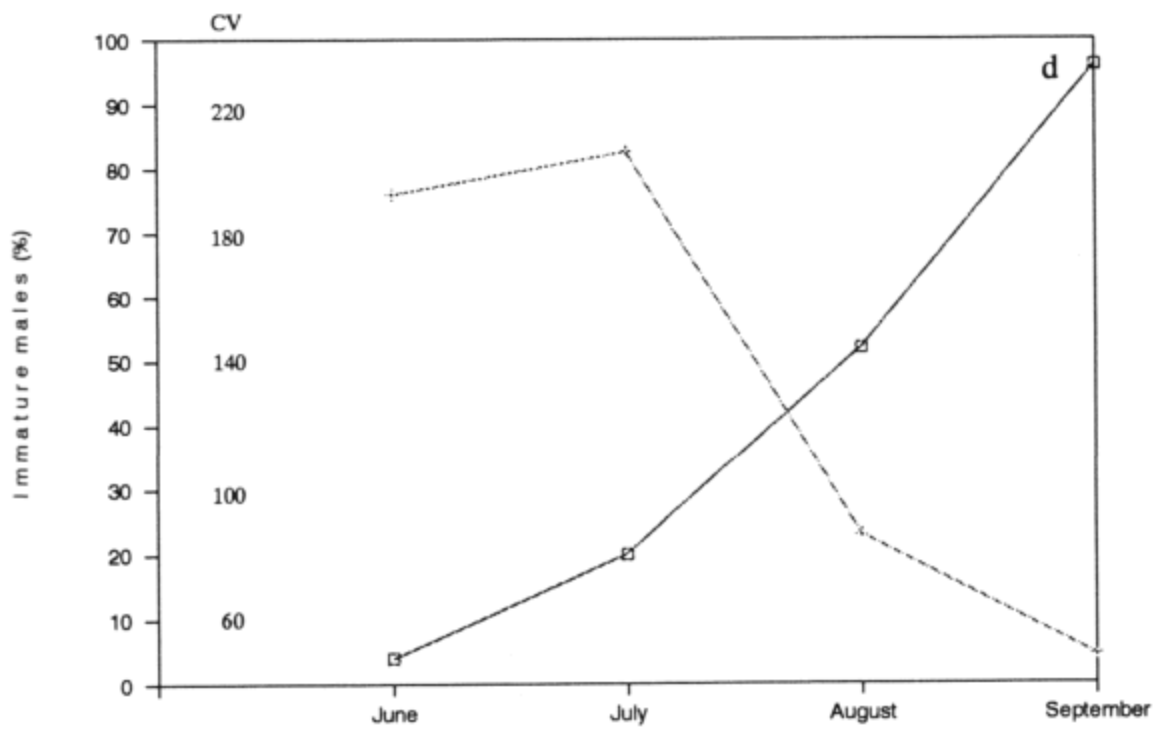
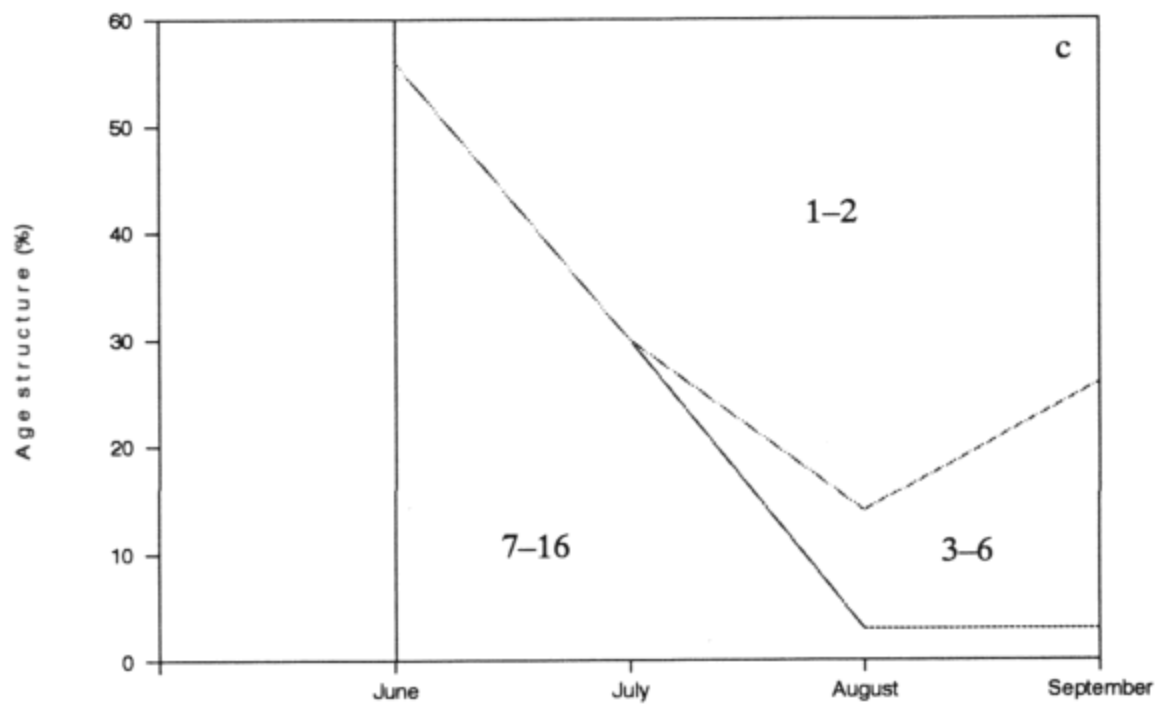


Fig. 9. Mean values of demographic variables in the bank vole population at Karelia permanent study plot (true-moss spruce forest). For explanation see Fig. 2



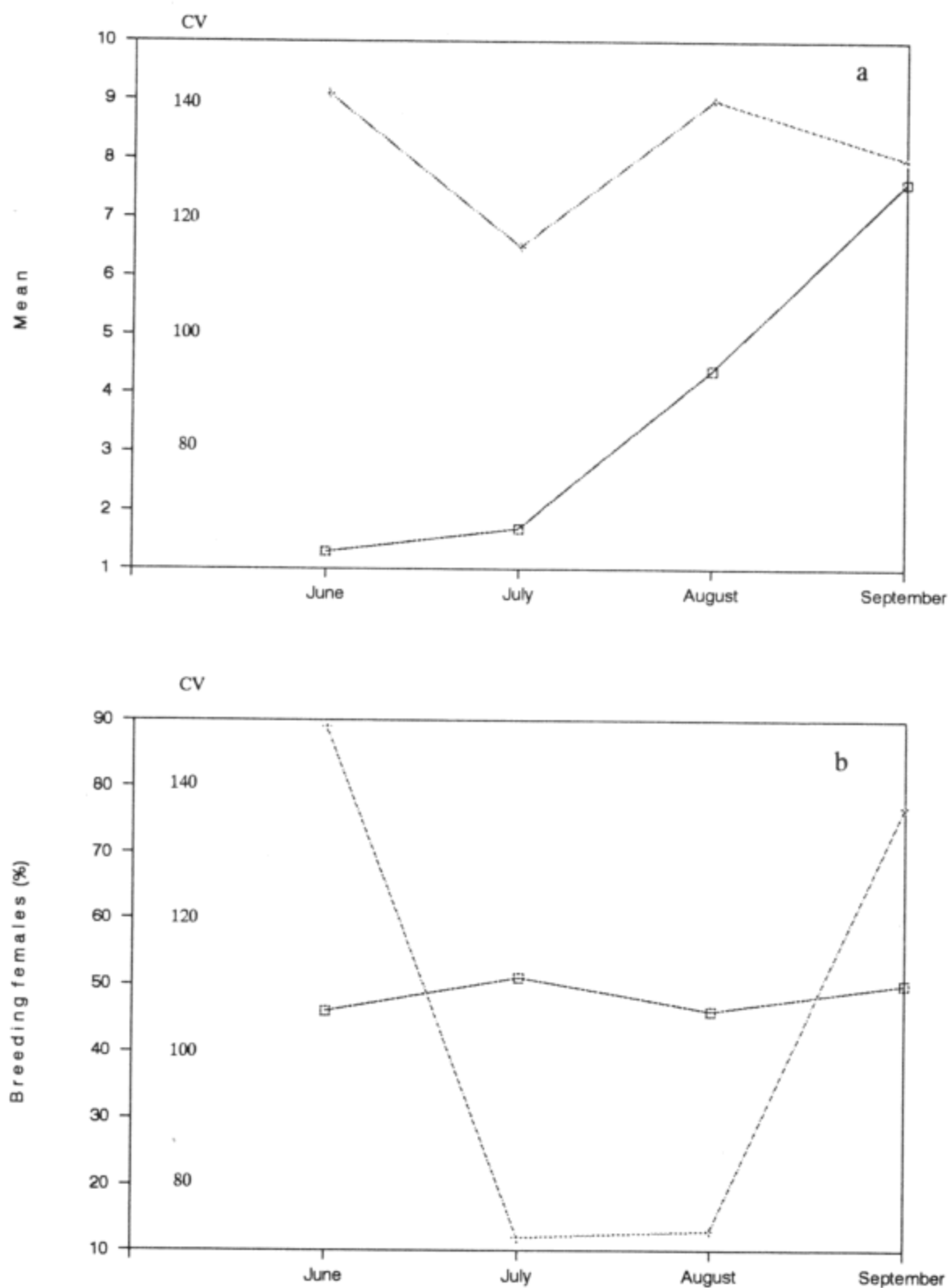
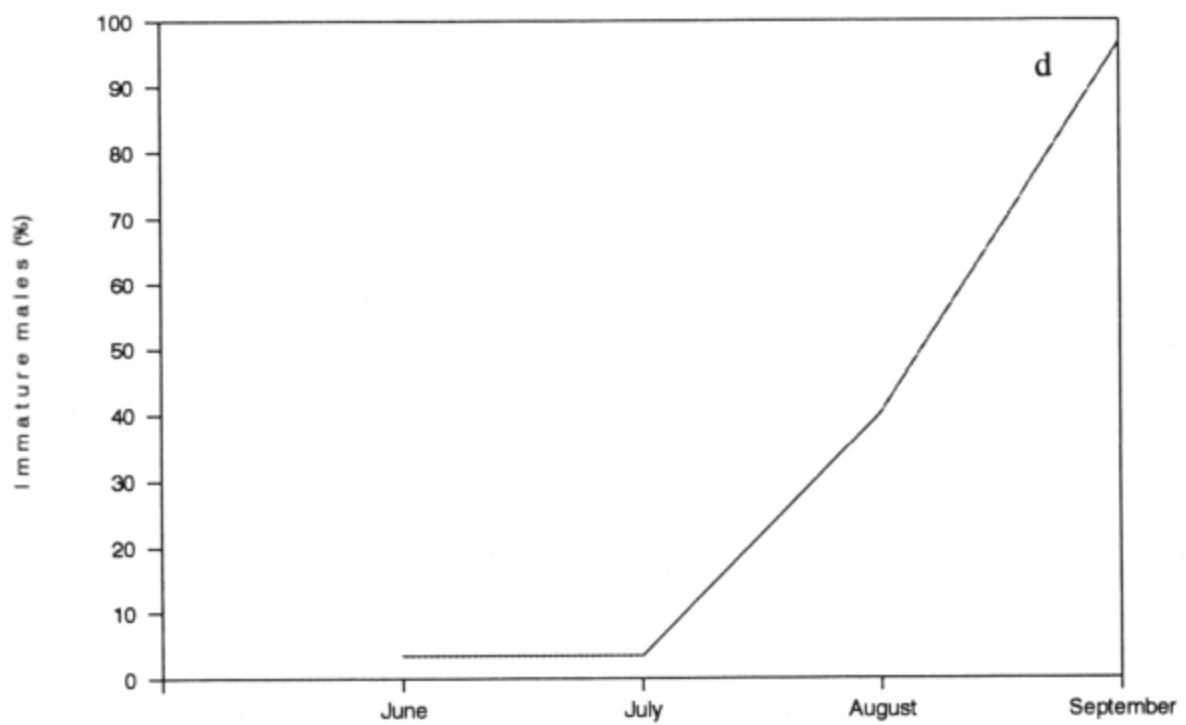
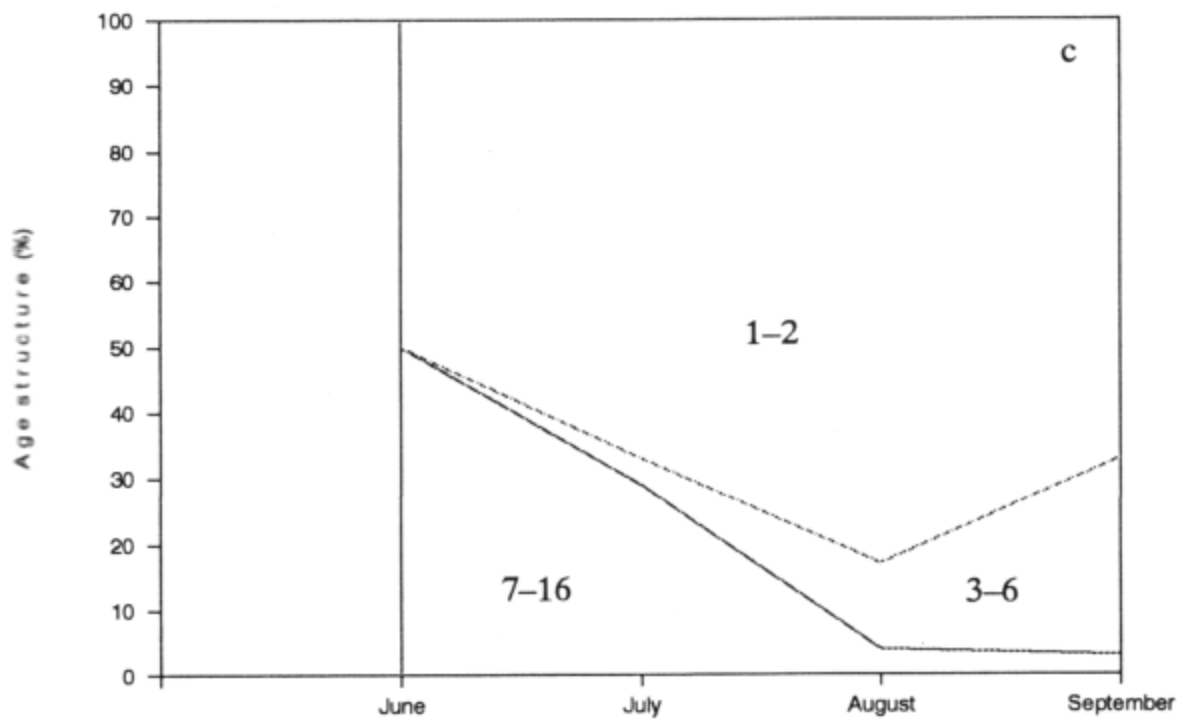


Fig. 10. Mean values of demographic variables in the bank vole population at Karelia permanent study plot (secondary deciduous forest). For explanation see Fig. 2



the intensity of reproduction and its complete termination in the second half of summer, reproduction depends also on the population numbers. If the population level is high in summer, reproduction stops already in August, while in the years of low numbers reproductive females are found even in late September.

This phenomenon is vividly traced if one compares the reproduction levels in spruce and mixed forests (Figs 9, 10). The stock of animals is higher in primary biotopes than in secondary ones. Although the differences are insignificant, they are probably quite sufficient for "engagement" of intrapopulation mechanisms hindering reproduction, this leading to rather considerable differences in the fractions of breeding females (21 and 50%). 21% of breeding females in spruce forests consists of mainly young voles of early-summer litters which reproduce in summer but do not participate in reproduction in September, while in mixed forests these are joined by 30% of females of late-summer litters, which are pregnant in September, too.

The age structure depends directly on the terms of the reproduction start and stop, on the mean population numbers, and on the breeding intensity during the reproduction season. There is no doubt that the age structure (dominance in the population of animals from particular age groups) is no less important for the population phenomena. In Karelia the bank vole starts breeding in May and it is therefore quite natural that in April and May the population consists only of overwintered animals. However, in June one more age group appears in the population: 1–2 months-old animals account for little more than one-half of the population both in spruce and deciduous forests. In July, animals which are 3–6 months-old at that time appear in the population; however, their fraction in the population is very small and they are present in the population only in the case of early reproduction onset. The fraction of overwintered animals drops from 50% in June to 30% while that of 1–2 months-old animals rises. In August, the difference in the population quality becomes still greater mainly due to the animals born in May but their fraction in the population does not exceed 20%, although a much greater number of the animals of this age could be expected in August if one considers unlimited reproduction activity of overwintered females. These phenomena can be explained only by changes in mortality of voles. Emigration of the animals is another probable cause of the low numbers. Then the abundance of the animals of this age group should increase in other biotopes, which is not the case (Figs 9, 10).

The numbers of overwintered animals decrease in August still further and account only for 2% in both habitats. Young 1–2 months-old animals represent the most numerous group in August (82 to 85% of the total number of animals in the population). Only single individuals of overwintered voles are censused in September. The specific weight of the 3–6 months-old age group increases still further and beginning from August the animals of early-summer litters replace overwintered voles and function as "adults". Despite the fact that from August to September the fraction of breeding females drops sharply (to 20%) in spruce forests, and is maintained at a level of 50% in secondary forests, the fractions of young 1–2 months-old voles are almost equal in both biotopes. Most probably, in spruce forests progeny numbers increase due to high numbers of reproducing animals (overwintered and 3–6 months-old females), while in deciduous and mixed forests

Table 14

Potential contribution (%) of different-age animals into the increase of the bank vole population
(Karelia permanent study plot)

Biotope	Month	Age in months		
		7-16	3-6	1-2
True-moss spruce forests	May	100.0	0	0
	June	62.5	0	37.5
	July	43.4	8.0	48.6
	August	3.0	17.4	79.6
	September	0.1	84.5	15.4
Mixed and deciduous forests	May	100.0	0	0
	June	82.6	0	17.4
	July	15.5	4.2	80.3
	August	5.8	32.7	61.5
	September	5.4	58.6	36.0

with low numbers of reproducing animals the progeny number increase because both the fraction of breeding voles and recruitment of young rapidly attaining maturity 1-2 months-old voles and higher.

Since in spring the population comprises only overwintered animals, the potential increase of the population depends on their reproduction activity. In June, with appearance of 1-2 months-old animals, the contribution of overwintered voles lowers and that of current-year voles rises, this being especially pronounced in true-moss forests (Table 14). In July, differences in the distribution of potential contribution of different-age animals living in primary and secondary forests enhance still further. In spruce forests overwintered and current-year voles 1-2 months-old make approximately the same contribution to the processes of the population growth. In mixed and deciduous forests more than two-third of animals are offspring of 1-2 months-old voles and only 16% was born by overwintered voles. A larger role of young voles in the increase of the population abundance in July is due principally to an unlimited reproduction of current-year animals, which is likely connected with the fact that both young and overwintered animals are immigrants in secondary forests and therefore the competition occurring between them for the space is pronounced much weaker than in spruce forests, where overwintered animals present the greater part of settled population. Since the numbers of 1-2 months-old voles are high in secondary forests at that time, the fraction of breeding animals from this cohort is large, too, and, consequently, the contribution of young voles to the numbers variation is great.

A similar picture is observed in August also in true-moss spruce forests with the only exception: while in July in secondary forests about 16% of the population

increase is due to overwintered voles, here 17% of the increase is due to 3–6 months-old animals which replace the group of overwintered animals by that time. In deciduous forests in August a little more than 60% of the population increase is associated with 1–2 months-old animals and 33% is due to animals 3–6 months old. The contribution of overwintered voles to the population growth does not exceed 6% on all sites. Variable effect exerted by 1–2 months-old and 3–6 months-old animals, can be explained mainly by a stronger competition between these groups for the territory. As a result, the fraction of 1–2 months-old females participating in reproduction lowers in secondary forests (Table 14). In spruce forests the youngest among the current-year animals are not affected by older voles and contribute much more to the population growth.

In September, in radial forests the reproduction intensity drops to 20% mainly at the expense of excluding 1–2 months-old animals from reproduction. As a result, the potential contribution of the animals from late-summer litters to the population growth processes decrease to 15% and the decisive role in changing the population numbers (85% of the population increase) belongs to the animals from early-summer litters. In deciduous forests the vole numbers is not so close to the maximum permissible level and the level of competitive relations is lower than in spruce forests. As a consequence, some part of 1–2 months-old females continue breeding, making their contribution to the potential increase of the population so high.

The distribution of the contribution made by voles of different age to the population growth changes in the course of the reproduction period. The distribution is connected, on one hand, with fluctuations of the population age structure and changes of the functional significance of overwintered animals of early- and late-summer generations in different months of the snowless period, and is determined, on the other hand, by competitive (for the living space) interrelations between voles, which are also subject to seasonal changes and are specific to each habitat.

Sexual maturation of males and, hence, the fraction of sexually mature individuals among them (the same applies to females) is connected with their age and the phase of the reproduction cycle (Figs 9, 10). In May, the population contains only overwintered males, almost all of them participating in reproduction (active spermatogenesis). At the beginning of the phase of interactive reproduction all overwintered males participate, as before, in reproduction. At that time young animals mature at a maximum rate, although a part of them remains sexually immature. Their fraction is extremely low and accounts for about 1% in deciduous forests and 4.5% in spruce forests. In June, most of males take an active part in breeding as before and it is in true-moss spruce forests that up to 20% of males is sexually immature. The numbers are somewhat higher on the last site than on the others, a circumstance which probably led to a delay in sexual maturation of males. Maturation of females is more dependent on changes in the population numbers and structure than that of males since the latter responded little, if at all, to insignificant differences in the total numbers.

In the second half of summer the fraction of sexually immature males grows persistently and in September only individual animals (5% maximum) participate in reproduction, while the fraction of sexually mature females is much higher

Table 15

Fraction of bank vole females (Karelia permanent study plot in 1966-1987)

Month	Age in months			Totally per month
	7-16	3-6	1-2	
True-moss spruce forests				
June	0.24*	—	0.44*	0.33*
July	0.59*	—	0.44*	0.48
August	0.80*	0.43*	0.39*	0.40
September	—	0.82*	0.44*	0.49*
Totally over reproduction season	0.40*	0.65*	0.42*	—
Deciduous and mixed forests				
June	0.21*	—	0.48	0.35*
July	0.35*	—	0.44*	0.41*
August	0.79*	0.70*	0.45	0.48
September	—	0.79*	0.43*	0.47
Totally over reproduction season	0.36*	0.75*	0.44*	—

*Values significant at $p = 0.05$.

(about 20 and 50% for spruce and mixed forests, respectively). In autumn, males stop reproducing earlier than females do (decay of spermatogenesis and degeneration of gonads). It is quite probable that along with seasonal factors, the decrease in sexual activity of males is caused by their higher sensitivity to changes in demographic situations and especially to the rise in numbers.

An analysis of the sex structure of the bank vole population of the Karelia permanent study plot shows that the fraction of females in the population varies as a function of age and the reproduction cycle phase (Table 15). In the beginning of reproductive season males predominate among adults. In the group of overwintered animals the fraction rises from 24% in June to 80% in August–September. At the moment of its appearance the age class of 3–6 months-old voles is dominated by males (although their dominance is not so great as for overwintered animals) but in autumn, when these animals functionally replace the group of overwintered animals, which have already almost disappeared, the sex ratio shifts in favour of females and by that time their fraction attains 80%. The dominance of females in spring is determined, on one hand, by high mortality of females in the autumn–winter period (it is probably the decisive factor) and, on the other hand by the selective trappability of males. Somewhat higher numbers of males among 3–6 months-old voles is probably due to an uneven number of males and females born and to a higher mobility of males, which determine trappability (Ivanter 1975). As overwintered animals and voles from early-summer litters continue to

exist; females accumulate in these age groups owing to a slightly higher mortality of males (Bolshakov and Kubantsev 1984).

In June, young 1–2 month-old voles are dominated by males, which can be attributed, on the one hand, to a higher sex ratio at birth, although by autumn the number of males become equal to those of females owing to a somewhat higher mortality of males. On the other hand, in autumn the animals are in their majority sexually immature and represent a rather uniform rigorously selected group as regards their physiological and behavioural features, exhibiting the same activity and survival, factors which can, in the final analysis, neutralize the numerical difference between males and females.

No principal differences were detected in the sex structure of different-age animals inhabiting true-moss spruce and deciduous forests, while the existing distributions are not of decisive character.

3.5. NORTHERN AND GREY RED-BACKED VOLE POPULATION OF SIBERIAN MOUNTAIN TAIGA CONIFEROUS FORESTS

On the Sayan permanent study plot observations lasted from 1965 to 1983. The territory is inhabited by northern red-backed voles, grey red-backed voles, bank voles, and shrews. The fraction of forest voles in the population accounts for about 90%, while the total fraction of the other species does not exceed 10%. Besides, the population level and variability give grounds to consider northern red-backed voles and *C. rufocanus* as the dominant species. Over nineteen study years about

Table 16

Changes in numbers of grey red-backed vole during the breeding season (June–August, 1965–1983, Western Sayan)

Altitude, a. s. l. m	Population increase		Decrease in the number of over-wintered animals
	total	current-year	
600-790	<u>1.3</u>	<u>2.3</u>	<u>1.7</u>
	7.3	18.9	13.9
800-990	<u>1.4</u>	<u>2.5</u>	<u>1.6</u>
	8.8	19.7	12.7
1 000-1 190	<u>2.1</u>	<u>4.8</u>	<u>1.2</u>
	17.4	26.3	5.9
1 200-1 400	<u>2.2</u>	<u>3.7</u>	<u>1.1</u>
	18.4	24.4	2.5

*The numerator shows the multiple of the numbers changes during the breeding season; the denominator indicates numbers changes per month, %.

20 000 trap-days were served and approximately 4 500 northern red-backed and 3 800 grey red-backed were caught.

In Western Sayan, the numbers of grey red-backed voles vary from 1.26 to 4.30 at different altitudes in May, increase gradually during the reproduction season, and attain a maximum value (5.21–7.35) in August. From June to August the total numbers rise 1.8-fold (on the average over all study years and over all the habitats) and are made up of the variations in numbers of current-year and overwintered animals. The numbers of current-year voles increase 3.7-fold, while that of overwintered voles lowers 1.4-fold (Table 16).

Apart from changes in the demographic structure of *C. rufocanus* population during the reproductive season, the structure fluctuates with altitude. No statistically significant differences in numbers of overwintered animals were found in May over all the study years; however, in June an altitude differentiation of the vole population is shown up. At that time differences in the numbers (with altitude) attained high values and, as a consequence, the entire altitude range is divided with statistical validity into two regions: 600–900 m and over 1 000 m. In August, differences are statistically insignificant.

The numbers of current-year voles are at maximum (the mean over the reproduction period equals 5.7) at altitude 600–790 m decrease gradually with altitude to 3.1 in true-moss stone-pine forests (at altitude over 1 200 m). However in June and August these differences proved to be statistically invalid and only in July at altitude up to 990 m the numbers of voles were statistically valid: 2.1 times as high as at altitude over 1 000 m.

The numbers variability, as well as the fluctuations of the numbers themselves, has two components, namely, variability determined by the reproduction cycle phase, and the one determined by the altitude gradient. The total numbers variation coefficient is (average over all altitude) 75% at the onset of reproduction, rises to 102% at the time of intensive breeding, and drops again to 79% at the end of the breeding season. Variability of the numbers of current-year animals has a maximum amplitude: 112% in June, then lowers a little, and becomes equal to 76% by August. High variability of the numbers of current voles at the onset of the reproduction season can be explained by the fact that in different years differences in breeding conditions are more pronounced at the beginning than in the middle or at the end of the reproduction season. Variability of the numbers of overwintered animals is also at a maximum in spring (May, June – 85%), then lowers to 65%, and remains at this level till the end of the reproduction season.

The vole numbers variation coefficients change also according to the second component of variability (dwelling, altitude): these are minimum (78% on the average over all the months) at altitudes 600–790 m, then increase, and at altitude 1 200–1 400 m attain 102%. Variability of the numbers of the young with altitude exhibits a slightly different behaviour. It has low values (of the order of 89%) at altitude 600–790 m, rises to 101% at 800–990 m, and lowers again to 92% at latitudes over 1 000 m.

Thus, the region of high numbers (600–990 m) coincide with the region of the minimum numbers variability, which is true only for the period of intensive re-

production. At the beginning and end of the reproduction season grey red-backed voles inhabit uniformly all altitudes.

In Western Sayan, reproductive season of grey red-backed starts almost simultaneously at all altitudes in late April–early May. In some years, few females (sometimes up to 17%) which gave birth to one litter are already found in the population in May but the variation coefficient of the fraction of breeding females is about 300% and, hence, females which produced even one litter represent a rare event in May. The mean multi annual numbers of breeding males and females of the preceding year of birth are highest in spring and lower by autumn. The numbers are at a maximum at altitudes 600–990 m and are much lower over 1 000 m; in August, however, the difference in the numbers with altitudes is neutralized. Variations in the numbers of overwintered breeding voles are proportional, both during summer and with the altitude gradient, to the changes occurring in total numbers. However, application of relative indices of the production intensity (evaluated by the fraction of males or females taking part in reproduction) shows that the degree of participation of overwintered voles in reproduction remains statistically invariable throughout the season and at all altitudes. Of overwintered females, the fraction of non-breeding animals in May is 3.5–7.8% on the average over all the study years and is kept at this level till the end of the reproduction season. The fraction of non-breeding overwintered males is higher (up to 14%) than that of females and is practically constant throughout the reproduction season. Variability of the fraction of breeding overwintered males and females is greatest in May and June, and is due to the fact that in different years the onset and intensity of reproduction are highly unstable.

The numbers of young voles participating in reproduction vary as the total numbers of current-year voles.

The degree to which females participate in reproduction has seasonal behaviour, it is at a minimum in June (57%), reaches a maximum value (67%) in July, and drops again to 62% in August. Along with seasonal behaviour, changes in the reproduction intensity of young voles with altitude were detected. An analysis of the findings made it possible to distinguish two regions, where the fractions of breeding females are approximately the same: 600–990 m and 1 000 m, where the fraction of breeding young females is somewhat larger than at other altitudes. No differences were found in the reproduction intensity of young males living at different altitudes. It is worth noting that the fraction of breeding current-year females is always larger than that of males, which is probably due to different rate of sexual maturation of males and females.

The sex ratio in the population of grey red-backed voles was studied separately for current-year and overwintered animals. At the beginning and end of the reproduction season overwintered females dominate over males in the entire altitude range, and during the period of intensive reproduction (June–July) trapped animals are dominated by males. The shift in the sex ratio first towards females, then in favour of males, and again towards females cannot evidently be caused by a real bias in sexes but is probably due to different mobility of voles during intensive reproduction periods.

Table 17

Sex ratio (fraction of females) in the grey red-backed vole population
(Western Sayan permanent study plot)

Month	Age group	Altitude a. s.l., m			
		600-790	800-990	1 000-1 190	1 200-1 400
May	overwintered	0.57*	0.60*	0.63*	0.64*
June	overwintered	0.43*	0.52*	0.48*	0.56*
	current-year	0.58*	0.49	0.57*	0.62*
July	overwintered	0.38*	0.37*	0.45	0.45
	current-year	0.53	0.46*	0.54	0.48
August	overwintered	0.61*	0.51	0.48	0.60*
	current-year	0.55*	0.56*	0.56*	0.57*

*Values significant at $p = 0.05$.

Females dominate current-year voles in different months of the reproduction season and in different habitats. It is only in June and July over the altitude range 800–1 000 m that a little predominance of males was detected (Table 17). Our data (Table 17) does not permit an unambiguous determination of the reason for significant changes in the sex ratio of grey red-backed voles. Two explanations are possible: either the changes are such that the primary and secondary sex ratios are already shifted in favour of females as is the case, for example, with *Myopus schisticolor*. Young and adult voles have mean litters of 5–6 young per females and the mean litter size is statistically independent both of month and habitat.

Thus, animals of older cohorts include at all times about 5% dry females whose fraction does not depend on the habitat or time. Out of the young, 45–69% animals participate in reproduction. Their fraction changes both with time (within the reproduction season) and according to the altitude gradient. A small difference in the reproduction intensity of young animals, actually complete participation of the adults in reproduction, and the same size of litters make it possible to suggest that considerable differences in the vole numbers with altitude and months are probably due not to the changes in the reproductive potential (fractions of breeding animals differ ultimately by 10%) but to variations in mortality and migration activity of animals from older cohorts and those going to winter.

The differences detected (with altitude) in the numbers and reproduction parameters of grey red-backed voles may be due to two reasons. First, reproduction and population growth processes can be subjected to conditions specific to each altitude range. Second, the processes responsible for the numbers formation can be synchronized at all altitudes by the same external factors and the differences

detected are only due to changes in the intensity of the population processes. A correlation analysis was used to check these propositions. The calculated correlation coefficient reflect the degree of synchronism with which changes in the numbers of structure groups occur in time and space. The Spearman correlation coefficient, the correlation ratio, the curvilinearity index, and the validity index of the calculated coefficients were calculated for each pair analyzed. The use of several correlation indices is dictated by the necessity of choosing the most adequate index of the in-step changes of demographic parameters. Significance level is 0.05.

In June changes in the numbers of overwintered animals occur synchronously at all altitudes, while in July and August synchronous changes in the numbers take place only at altitudes over 800 m (Table 18). Parallel changes in the numbers at different altitudes in June are probably due to a single factor that affects cycle of reproduction. Subsequently, distribution of adult voles over the territory proceeds independently from each other and is determined by local conditions at altitude below and above 800 m.

Fluctuations in the numbers of young animals occur synchronously at all altitudes throughout the reproduction cycle (Table 18), with maximum correlation coefficients usually noted for neighbouring pairs of altitudes, which decrease as the altitude gradient grows. While for overwintered animals the determining factors are those triggering another cycle of reproduction, a high correlation between

Table 18

Estimates of synchronism of changes in the number of grey red-backed vole with altitude (Spearman correlation coefficient) (Western Sayan)

Altitude a. s.l., m	June			July			August			Totally per season		
	2	3	4	2	3	4	2	3	4	2	3	4
Number of overwintered voles												
1	0.46	0.53	0.64	—	—	—	—	—	—	0.45	—	—
2		0.81	0.67		0.99	0.76		0.48	0.50		0.68	0.50
3			0.76			0.76			—			0.67
Number of current-year voles												
1	0.87	0.78	0.50	0.64	0.64	0.67	0.69	0.64	0.79	0.71	0.73	0.72
2		0.98	0.70		0.68	0.62		0.72	0.54		0.71	0.54
3			0.76			0.76			0.74			0.73
Total numbers												
1	0.78	0.58	0.59	0.62	0.74	0.64	0.78	0.59	0.58	0.70	0.55	0.51
2		0.68	0.54		0.68	0.63		0.68	0.54		0.71	0.63
3			—			0.83			—			0.74

1 – 600–790 m, 2 – 800–990 m, 3 – 1 000–1 190 m, 4 – 1 200–1 400, values significant at $p = 0.05$.

changes in the numbers of current-year animals can be explained only by a high degree of synchronism in the reproduction processes of both young and adult animals over the entire territory. The correlation coefficients calculated using the data total over all months for adults made it possible to divide the entire altitude range into two regions (up to and over 800 m), each exhibiting synchronous numbers changes. Changes in the numbers of the young occurring synchronously over the entire territory.

As one would expect from the analysis of multi annual dynamics of current-year and overwintered voles, within the mountain taiga belt the total numbers change synchronously over all altitudes, too (Table 18). As regards the total numbers, number of sex-age classes and the degree of their variability, the entire territory inhabited by grey red-backed is functionally divided into two regions: a region of optimal habitats and a region of pessimal habitats. However, since changes in numbers occur synchronously in these regions, there are all grounds to assume that the entire territory studied (about 25 km²) is inhabited by a single population of *C. rufocanus*.

Northern red-backed voles inhabiting Western Sayan have a species-specific population dynamics: the numbers level is at a minimum in May, rises by mid-

Table 19

Estimates of changes in the number of northern red-backed vole during the breeding season (Western Sayan)

Altitude a.s.l., m	Increase of total numbers	Increase in the number of current-year voles	Decrease in the number of overwintered voles
600–790	2.2/18.5	3.6/24.0	1.1/2.1
800–990	1.7/12.0	6.4/27.8	2.0/16.6
1 000–1 190	1.4/9.9	7.9/29.1	1.9/16.2
1 200–1 400	1.9/15.8	5.6/27.4	1.5/11.5
Mean values	1.8/14.1	5.9/27.1	1.6/11.6

Numerator shows the multiple of the numbers changes in July–August, the denominator indicates numbers changes per month, %.

summer, and reaches maximum values in August. From June to August the increase of the total numbers vary from 1.4 to 2.2 for different altitudes, and the increase ratio of current-year animals is 3.6 to 7.9. By late summer the numbers of overwintered animals lower 1.8– fold and depend weakly on altitude (Table 19). If we assume that during the reproduction season the total numbers change linearly, then a monthly increase of the numbers is 9.9–18.5% depending on altitude. The number of current-year animals increases by 24–29.1% a month, i.e. approximately twice as high as that of the total numbers. A monthly loss of overwintered animals is within 10.5–12.7% and approximately equals the difference in

the rates of increase in the numbers of current-year animals and the total numbers of voles.

The total numbers variation coefficients are at a maximum in May (80–110%), lower to 50–80% in June, and rise again by August. No statistically significant changes in the variance of numbers of overwintered animals were found; however, the variance is somewhat higher at the beginning of the breeding season, decrease in June, and subsequently remains practically constant. Variability of the numbers of current-year animals changes analogously: it is at a maximum in June (90–110%) and drops to 55–70% in July and August. High variability of the numbers at the onset of the breeding season is probably due to the fact that living conditions for northern red-backed voles vary to a much greater extent during that period than in the middle or at the end of the season.

Apart from variations in the demographic structure of *C. rutilus* population occurring during the reproduction season, fluctuations of the demographic structure with altitude were detected. For both age classes, the numbers are at a maximum at altitude 800–1 190 m and are approximately twice as low as at altitude 600–790 m and over 1 200 m. However, no statistically valid differences in the distribution of northern red-backed vole with altitude were found in May over all the study years. But already differentiation of the population with altitude starts to show up. During this period differences in the numbers (with altitude) attain maximum values and, as a result, we have a statistically valid division of the entire altitude range into two regions: 800–1 190 m and the territory above and below this altitude. In July and August bilberry forests (up to 800 m) are different from mountain taiga forests (over 800 m) as regards the total number of animals. Within the subbelt of mountain taiga forests differences in the population are statistically invalid.

Population of overwintered animals is at a minimum at altitudes 600–790 m, increases at altitudes 800–1 190 m, and decreases again over 1 200 m. However, this picture is typical only of the beginning of the reproduction season. By the end of the breeding season differentiation of overwintered animals with altitude becomes less pronounced. In July, bilberry forests (up to 800 m) and mountain taiga forests (800–1 400 m) are distinguished for the number of overwintered animals. In August, differences between the subbelts with respect to this parameter are neutralized. This situation is possible if the rate of loss of overwintered animals at altitudes 800–1 190 m is higher than that at other altitudes. The calculated loss rates turned out to be about 13 and 10% per month. This small difference in the rates is quite sufficient to level off (by the end of summer) the differences in the numbers of overwintered animals that occur in early summer.

Changes in the number of current-year animals at different altitudes are similar in character to the changes in the number of older animals: the numbers are low at altitudes 600–790 m and over 1 200 m, and are at a maximum at altitudes 800–1 190 m. However, checking of the statistical significance of differences in the distribution of current-year animals shows that in June the entire territory is inhabited uniformly by young animals. But already in July and August reliable differences are noted in the numbers of current-year voles in the subbelt of bilberry forests (up to 800 m), on the one hand, and at all altitudes in the subbelt of mountain taiga (over 800 m), on the other. An increase in the numbers of young animals is due to a higher re-

production intensity and lower mortality of current-year voles at altitudes over 800 m. The number of current-year animals rises approximately by 24% per month in bilberry forests (up to 800 m) and approximately by 30% per month in mountain taiga (over 800 m).

In all the above-considered cases, the analysis of the total numbers and the numbers of current-year and overwintered voles gives grounds to divide the study territory into three parts: the region of high numbers at altitudes 800–1 190 m and two regions of low numbers at altitudes up to 800 m and over 1 200 m. During the breeding season, differences in the population of animals on these territories are due to different causes: at the beginning of the reproduction season the differences are connected with spatial differentiation of overwintered animals, and at the end of the season – with re-distribution of young over the territory.

Population fluctuation with altitude are accompanied by changes in the population variability. The total numbers variation coefficients are at a maximum altitudes 600–790 m (their values vary between 75 and 110% during the breeding season), lower to 50–65% at altitudes 800–1 190 m, and increase again to 75–95% at altitudes over 1 200 m. The number variabilities of overwintered and current-year voles change similarly. Minimum variation coefficients of these parameters are also found at altitudes 800–1 190 m.

As is seen, the region of high numbers (800–1 190 m) coincides with the region of minimum numbers variability, a fact which suggests that living conditions of northern red-backed vole at these altitudes are close to optimal ones (here the numbers are always higher and the numbers variability is lower). At altitudes up to 800 m and over 1 200 m living conditions of northern red-backed become worse; here the numbers are always lower, while the numbers variability is higher.

Breeding season of northern red-backed voles starts in Western Sayan in late May – early June practically simultaneously at all altitudes. However, in different years spread in terms and intensity of breeding is considerable. Thus, in some years it is already in May that we encounter overwintered females which gave birth to one litter each, and in some cases their fraction attains 25%. Variation coefficient of parous females varies at about 200–250%, this suggesting that in May females, which produced even one litter, occur rather rarely. The mean multi-annual number of breeding males and females of the preceding year of birth is greatest in spring and lowers by autumn. If we consider the numbers variation with altitude, the numbers are at a minimum in the subbelt of bilberry forests (up to 800 m) and are almost 2.5 times in the subbelt of mountain taiga forests. By autumn the difference in the number of breeding animals with altitude becomes insignificant. Changes in the number of breeding voles both in the course of summer and with altitude gradient are proportional to the variation in the number of overwintered voles with respect to these two parameters. The use of the relative indices of reproduction intensity (estimated according to the fraction of males and females participating in reproduction) made it possible however to conclude that the degree to which current-year males and females breed remains statistically constant throughout the season and at all altitudes. The fraction of non breeding females among overwintered animals accounts in May on the average over all study years for 42–48% at altitudes 600–790 m and over 1 200 m and for 67%

at altitudes from 800 to 1 190 m. In June, the fraction of immature females drops to 4.5% and does not depend on altitude, and in July and August no immature females are encountered among overwintered animals.

Overwintered males become sexually active earlier than females do. In May trappings, about 6% of sexually immature males occur only at altitudes up to 900 m. No sexually immature males were found in June in all trapping years; however, in August overwintered immature males are sometimes encountered (their fraction can be as high as 5%).

The number of breeding young voles changes proportionally to the variations in the total number of current-year animals. In June and July, an altitude region of 800–1 190 m, where numbers are maximum, becomes rather clearly pronounced; in August, differences in the numbers of breeding animals is much lower. The foregoing applies equally to individuals of both sexes.

The degree to which current-year females participate in breeding does not show clear-cut variations from month to month: it is low in June, rises slightly by mid-summer, and lowers again by late summer. However, in different subbelts the degree to which young voles participate in reproduction varies considerably. The analysis of the data obtained made it possible to single out two regions, where the fraction of breeding animals are approximately equal: 28–40% of females and up to 20% of males in bilberry taiga (up to 800 m), and 55–60% of females and 30–50% of males in mountain taiga forests (over 800 m). It is worthwhile noting that the fraction of breeding young females exceeds that of breeding young males. Most probably, this is due to different rate of sexual maturation of young males and females.

The numerical sex ratio of northern red-backed vole was studied separately for overwintered and current-year animals. Throughout the reproduction period *C. rutilus* population is dominated by males. In different months, over the altitude range 600 to 800 m they account for 65 to 80%, whereas in the population of grey red-

Table 20

Sex ratio (fraction of females) in the northern red-backed vole population
(Western Sayan permanent study plot)

Month	Age group	Altitude a. s.l., m			
		600-790	800-990	1 000-1 190	1 200-1 400
May	overwintered	0.30*	0.33*	0.41*	0.69*
June	overwintered	0.35*	0.39*	0.44*	0.64*
	current-year	0.59*	0.59	0.40*	0.33*
July	overwintered	0.20*	0.35*	0.38*	0.35*
	current-year	0.37*	0.48	0.44*	0.53
August	overwintered	0.32*	0.38*	0.33*	0.39*
	current-year	0.47	0.51	0.46	0.39*

* Values significant at $p = 0.05$.

backed voles the fraction of males is within 40–60%. Besides, as the altitude and population level increase, so does the fraction of northern red-backed females. It is only in May at altitudes over 1 200 m that overwintered females dominate over males (Table 20).

Dynamics of the sex composition of the young exhibits, as distinct from overwintered animals, a clearly pronounced seasonal behaviour. In June, almost 60% of current-year voles are females; however, by late August the sex proportions become equal. Such phenomena are observed in the belt of mountain bilberry forests and partially in the subbelt of mountain taiga forests at altitudes up to 1 000 m. In the zone of Siberian stone pine-fir forests and open forests of Siberian stone pine at altitudes over 1 000 m predominate (Table 20). It is interesting to note that at altitudes 600 to 1 000 m during the autumn-winter period mortality and migration activity of females are higher than those of males. As a result, with the proportions of males and females being approximately the same in autumn, males predominate in spring. A reverse picture is observed at altitudes over 1 200 m: here, males exhibit higher mortality or spatial activity in the autumn-winter period, and while males predominate in autumn, domination of females is observed in spring. It is practically impossible to estimate separately the role of mortality and spatial movements but, evidently, the contribution of the migration activity into the sex ratio variations is low, especially during the autumn–winter period.

Young and adult voles bring an averaged litter of 5–6 newborn per female: the litter size is statistically independent either on a particular month or on the altitude of habitats.

An analysis of the reproduction activity of northern red-backed vole allows one to conclude that practically all animals of older age groups participate in breeding, whereas the degree to which young animals take part in reproduction changes over wide limits and is determined by both the time (within the breeding season) and the habitat. The population numbers are regulated at the expense of changing the fraction of young animals participating in reproduction, whereas large increases of the population occurring at altitudes 800–1 190 m are due to the largest fraction of breeding current-year animals (with the other reproduction characteristics unchanged) rather than to a rise in mortality of voles at other altitudes.

Correlation analysis was used to check whether space and time changes in the numbers of structural groups occur synchronously. Only statistically significant correlation coefficient are given in the text and in Table 21.

It is seen from Table 21 that in June changes in the numbers of overwintered voles occur synchronously at all altitudes, while in July and August the numbers change independently.

The numbers of young animals at various altitudes fluctuate differently. In June and July, the numbers change synchronously only at altitudes over 1 000 m, and it is only in August that the numbers of current-year animals change parallelly at all altitudes. Maximum coefficients are characteristic of pairs of closely spaced altitude zones and decrease with gradient.

Correlation coefficient calculated using the data sum over all months for adults and young voles show that the numbers of these groups change synchronously at

Table 21

Estimates of synchronism of changes in the number of northern red-backed vole with altitude
(Spearman correlation coefficient) (Western Sayan)

Altitude a. s. l., m	June			July			August			Totally per season		
	2	3	4	2	3	4	2	3	4	2	3	4
Number of current-year voles												
1	—	—	—	—	—	—	0.61	0.64	0.45	0.62	0.55	0.49
2		—	0.69		—	—		0.81	0.69		0.78	0.68
3			0.81			0.69			0.85			0.83
Number of overwintered voles												
1	0.58	0.63	0.51	0.65	—	—	—	—	—	0.43	0.59	0.40
2		0.87	0.65		—	—		—	—		0.81	0.52
3			0.82			—			0.77			0.65
Total numbers												
1	0.74	0.62	0.54	—	—	—	0.45	0.46	0.58	0.54	0.45	0.55
2		0.73	0.69		—	0.43		0.81	0.77		0.70	0.68
3			0.71			0.76			0.89			0.81

1 – 600–790 m, 2 – 800–990 m, 3 – 1 000–1 190 m, 4 – 1 200–1 400, values significant at $p = 0.05$.

all altitudes (Table 21). But, as we could see, the synchronism is due to different reasons at particular phases of the reproduction cycle.

As would be expected from the analysis of multi-annual dynamics of current-year and overwintered voles, their total numbers in the belt of mountain taiga change synchronously over the entire territory. Correlation coefficients of total numbers changes for different conditions fall within 0.54–0.81 with maximum coefficients being typical of closely spaced altitudes. Synchronous numbers fluctuations infer that the entire territory at altitudes 600 to 1 400 m is inhabited by a single population of northern red-backed voles. Differences in numbers are mainly due to change in the intensity of population processes which are synchronized by the factors that are the same for all the altitudes.

Changes in the levels of the main population characteristics of *C. rutilus* and *C. rufocanus* are determined by two processes. The first of them is reproductive cycle phase which is in turn subdivided into three functional periods: beginning and end of the breeding season, and the period of maximum reproduction intensity. The onset of the reproductive cycle is characterized by small numbers of the animals, small fraction of breeding animals, and high variability of the majority of the population characteristics.

The number of young voles rises during the period of intensive reproduction. The fraction of breeding current-year reaches 60% in the case of northern red-backed and 67% for grey red-backed voles. Practically all overwintered animals

of both species participate in reproduction. A decrease in the variability of majority of population characteristics is observed during this period. At the end of the breeding season the total numbers of northern red-backed and grey red-backed voles are at maximum, the degree to which current-year voles participate in reproduction lowers, while all overwintered animals, take part in breeding. During this period overwintered animals account for about 30% of the population and therefore their contribution to the numbers variation is extremely small.

A decrease in the variability of the number of different structural groups and other indices reflecting the state of a population, which occurs in the second half of the season, is due, on the one hand, to a lower variability of weather conditions (Drozdov and Grigorieva 1971) which do not fluctuate beyond an optimal zone ensuring survival of voles and, on the other hand, to the fact that the spread in the terms of the reproduction onset and intensity (associated with differences in the numbers of different population groups) are neutralized largely in the second half of summer. At the beginning of the reproduction season weather conditions vary the most. Besides, it is during this period that changes in the external conditions can be of disastrous character for the animals (ice crust, re-appearance of snow cover, repeated subzero air temperature, etc.), leading to higher mortality (especially of the young) and changes of the reproduction level and, consequently, to considerable variability of all population characteristics (Koshkina and Korotkov 1975, Okulova 1975, Naumov, Labzin and Gutova 1984).

Another factor that determines variability of the population characteristics is the distribution of the animals over the territory and, in particular, their distribution with altitude. Maximum total numbers and maximum number of all population groups of *C. rufocanus* were registered in the subbelt of mountain bilberry forests (600–790 m) and lower part of the subbelt of mountain taiga forests (800–990 m). The altitudes 600–790 m show also a minimum variability of the numbers. The coincidence of the regions of the maximum numbers and a minimum variability is noted only during the period of intensive reproduction: at the beginning and end of the reproduction season grey red-backed voles inhabit rather uniformly all the altitudes. The fact that the numbers of *C. rufocanus* become equal at all altitudes in late summer is due to primarily low increase of numbers of current-year animals at altitudes over 1 000 m. In spring of the following year the numbers of grey red-backed vole are higher at 600–990 m than at other altitudes. The cause of this difference is winter mortality of the animals.

At altitudes 800–990 m the numbers of grey red-backed vole lower but are sufficiently high (Fig. 11), while the numbers variability, especially for current-year animals, is much larger than that in the subbelt of mountain bilberry forests. This is probably due to the fact that at these altitudes maximum abundance and reproduction intensity of northern red-backed vole occur. Apart from the fact that maximum numbers of northern red-backed fall on the altitudes 800–1 190 m, it is precisely on this territory that the northern red-backed numbers variability is at a minimum and the reproduction intensity is the highest. Therefore habitat at altitudes 600–790 m are close to optimal ones for grey red-backed and those at altitudes 800–1 190 m – for northern red-backed vole, this being in full agreement with the concepts of optimal biotopes (Ivanter 1975).

However, regions of pessimal conditions exist for both species. In the case of northern red-backed vole this region encircles the optimal region at altitudes up to 800 m and over 1 200 m, and in the case of grey red-backed vole – the territories lying at altitudes over 800 m. Lower numbers of voles and high level of numbers variability are always observed in the pessimal regions.

Apart from the seasonal and spatial components, the numbers and distribution of grey red-backed voles on the permanent study plot are determined by the mutual influence of the species. This is the more interesting, because within an area there are sites, where one or the other species predominates, as well as sites, where the numbers of both species are equally low or equally high (Fig. 11).

Interrelations between northern red-backed and grey red-backed voles were estimated proceeding from a set of characteristics: population level and growth rate, distribution over territory, degree of participation in reproduction, mortality of animals, food species, and synchronism of the numbers variations.

In spite of the general similarity of the seasonal population dynamics of both vole species, pronounced time shifts are observed in attainment of seasonal peaks. Maximum numbers of grey red-backed vole are noted in the first half of August, and those of northern red-backed vole – in late August–early September. A similar picture of the shift in the seasonal peak is observed for these species in the Far East (D y m i n 1981) and Salair Ridge (K o s h k i n a 1967). Most probably, this reflects specific features of the species and not of the habitat.

Maximum increases of the grey red-backed vole population (about 35%) are registered at the beginning of the reproduction season and lower by August (to 17%). An opposite situation is observed for northern red-backed vole: the numbers rise only by 10% from May to June and by 30% in July–August (Fig. 11). The fact that maximum increase in the population of both species occurs at different terms of the reproduction season agrees well with different terms of the reproduction onset: reproduction of grey red-backed vole starts almost a month earlier than that of northern red-backed vole. In late June, when overwintered northern red-backed voles bring newborn of the first litter, overwintered grey red-backed voles have already a second litter and current-year grey red-backed voles bring their first litter. In the case of northern red-backed vole such a coincidence in the terms of appearance of the second litter of the overwintered animals and of the first litter of the current-year voles occur only in late July–early August. A minimum population increase falls on this period, too. Such a phenomenon was noted in Western Sayan in 1961–1962 by F. R. S h t i l m a r k (1976). The differences regularly observed in the population growth rates of two sympatric species allow to draw a conclusion about time discrepancy in the intensity of the mechanisms which are responsible for the numbers formation and which are determined most likely by specific features of the species rather than by competitive relations between northern red-backed vole and grey red-backed. Although it is possible that competition could serve as an evolutionary impetus to such a discrepancy.

The entire area inhabited by voles at altitudes 600 to 1 400 m and located within mountain taiga can be divided into regions where dominance of this or that species is clearly pronounced, and the region, where the numbers of both species are high. As is seen from Figure 11, grey red-backed vole dominates clearly in

Table 22

Overlapping northern red-backed and grey red-backed vole niches (Western Sayan, 1965-1983)

Species	Niche width (<i>B</i>)			
	space	time	food (general)	food (green)
Northern red-backed	0.91	0.94	0.54	0.57
Grey red-backed	0.94	0.91	0.36	0.80
Niche overlapping (<i>Q</i>)	0.90	0.99	0.98	0.79

mountain bilberry forests at 600 to 800 m a.s.l., where its numbers is 2.3 times as high as these of northern red-backed vole. In the subbelt of mountain taiga forests at altitudes 800 to 1 000 m, differences in the numbers of both species are insignificant. In Siberian stone pine-fir true-moss forests (1 000 to 1 200 m) and in true-moss Siberian stone pine forests and Siberian stone pine open forests (1 200 to 1 400 m) the numbers of northern red-backed is 1.7 times higher than those of grey red-backed vole.

The width of the spatial niche is somewhat larger for northern red-backed vole, though its values for both are sufficiently high (Table 22) and overlap by 90%. As was shown above, the optimum region of northern red-backed vole is located in the subbelt of mountain taiga at altitudes 800–1 200 m that of grey red-backed vole – is mountain bilberry forests at altitudes 600–800 m. In the subbelt of open Siberian stone pine forests at altitudes 1 200 to 1 400 m the numbers of both species lower, while the numbers variability rises. In the lower part of mountain taiga forests at altitudes 800 to 1 000 m the numbers of both species are high but the numbers fluctuation of northern red-backed are 20% lower than those of grey red-backed. The former is always in abundance and its living conditions in these regions are close to optimum.

The presence of optimum regions and their different location lead to the conclusion that the entire inhabited space is divided between northern red-backed and grey red-backed voles, with the division being probably due to different requirements imposed by the species on the habitat rather than competitive relations between the species.

The numbers and percentage of young northern red-backed voles participating in reproduction (Fig. 11) change parallelly. In the case of grey red-backed, the numbers lower at altitudes over 800 m, while the fraction of breeding young females rises. This is possible only when mortality of the animals varies in different habitats (intensive migration of voles over the territory is hardly probable, since in none of the points high increases of population were noted, which would not be proportional to the reproduction level). Otherwise, an increase in the fraction of breeding young females of grey red-backed vole would lead to an increase in the population of this species, i.e. starting from 600 m the population should grow and it is only altitude over 1 200 m that some decrease in the population could

be expected. Differences therefore in the population of grey red-backed vole in various habitats are due to changes in mortality of the animals. Parallelism of these processes in the case of northern red-backed vole is the cause that mortality of the animals of the species is constant on the entire territory and changes in numbers are connected with changes in the reproduction activity of young females (almost all overwintered females of both species participate in breeding).

Mortality can vary due to several reasons. One of them is higher mortality in species of relatively low density when the numbers of the dominating species are high, as a result of competition for the living space (Koshkina 1967). In this case, at altitudes over 800 m northern red-backed vole may reduce the numbers of grey red-backed one (due to higher mortality of the latter), and at altitudes 600 and 800 m the numbers of northern red-backed vole and mortality of the species should rise (in this region the numbers of grey red-backed are much higher). In fact, an increase in the population of northern red-backed vole is accompanied by rise in mortality of grey red-backed, and not vice versa. Therefore it is quite possible that northern red-backed vole is the dominating species over grey red-backed vole.

Another reason of changing mortality is represented by biological features of a particular species. Grey red-backed vole can be referred to species that regulate their numbers according to the *r*-type, since high reproduction activity is accompanied by higher mortality. In the case of northern red-backed, a rise in the numbers of breeding females takes place at constant mortality values.

One more reason of changes in mortality is different requirements of each species to the habitat conditions. A species responds to one and the same change in surrounding conditions (weather or climatic) in accord with its biology depending on the habitat (optimal or not). Our data do not allow assessment of each of the above-mentioned components of mortality but the influence of competition on mortality seems to be probable.

One of the probable reasons of different habitat preference between northern red-backed and grey red-backed vole may be differences in the food spectrum and occurrence of the plants preferred by the voles under conditions of each altitude range. Plants entering into the food ration of northern red-backed and grey red-backed are specified in the works due to L. R. Michurina (1974), F. R. Shtilmark (1976) (Western Sayan), V. S. Surkov (1976) (Sakhalin island), and G. E. Korolenko (Korolenko T. I. and Korolenko G. E. 1979) (north-east of Western Sayan). Materials of these papers were used to calculate the width of the niche and the degree to which the food niches of both species overlap. Forest voles feed on (as determined by microscope analysis of the stomach content) green parts of plants, pine nuts, seeds of various plants, berries and fungi. Since both species inhabit a common territory, it could be expected that their food spectra are rather close. However, contents in the stomachs of northern red-backed and grey red-backed voles differ by 40%, 19%, 25% and 44% as regards occurrence of green parts of plants, seeds, berries, and pine nuts, respectively (Specific weight of nuts in the total volume of food is small – about 10% – and since nuts are found mainly in the autumn–winter period, they can hardly contribute much to the energetics of the animals during the reproduction season). Despite the

fact that the lists of plants consumed by either species overlap to a great extent, which is also confirmed by the values of Q (Table 22), each species has its own most preferable food. Northern red-backed tends to euryphagous animals since it does not keep to some specific food, while grey red-backed voles approaches stenophagous animals because its food niche is much narrower.

Principal quantitative differences in the content of vole stomachs are for green parts of plants. Out of 75 species of green food offered (Michurina 1974), grey red-backed voles used 80% and northern red-backed – 57% but at the same time the spectra of green parts of plants used for food overlap by 79%. From this it follows that in Western Sayan mountain both species adapted themselves rather well to a broad floristic diversity (regarding the number of plant species used for food) and, probably, feed mostly on the plants that predominate in this or that season in their habitat.

The presence of a wide range of food plants, their rather high productivity, and almost complete overlapping of food niches suggest that space and time division of northern red-backed and grey red-backed voles cannot be a consequence of the competition for food between these animals.

As was already noted in the foregoing, territorial and time division of the living space between northern red-backed and grey red-backed voles can be due to competitive relations between these space or to different requirements imposed by each species upon the habitat. If the first proposition is true, then at the moments when the numbers of one species are high, those of the other should be low, and changes in external in local conditions should lead to still greater contrasts in the numbers. If the second proposition is true, the numbers of both species should change independently from each other, while weather and climatic conditions may serve as factors synchronizing these changes. A correlation analysis was used to check territorial and time division of the living space between species: correlation coefficient reflect the degree of synchronism with which changes in the vole numbers take place. Table 23 gives only statistically valid correlation coefficients (statistical significance level 0.05).

An examination of Table 23 shows that no negative correlation between in the vole numbers was found, which means that an increase in the numbers of one

Table 23

Synchronism of changes in the numbers of northern red-backed and grey backed voles
(Spearman correlation coefficients) (Western Sayan 1965–1983)

Altitude a. s.l., m	May	June	July	August	Total per summer
600–790	–	0.60	–	0.55	0.39
800–990	–	–	0.64	0.84	0.51
1 000–1 190	–	0.66	0.50	–	0.33
1 200–1 390	–	–	–	–	0.28

Values significant at $p = 0.05$.

species does not lead to a decrease in the numbers of the other species in none of the given cases. However, positive correlations were detected, indicating to a synchronism in the vole population dynamics. It could be expected that competitive relations would arise (showing up in opposite changes of the numbers) in mountain taiga forests (800–1 000 m), where the numbers of the animals of both species are rather high and close in value. But it is at these altitudes that the numbers of both species vary most synchronously. This makes one think that co-occurrence of both species leads not to aggravation of competitive relations but to division of the living space between northern red-backed and grey red-backed voles in accord with biological features of each species.

4. CONTRIBUTION OF ENDO- AND EXOGENIC FACTORS INTO POPULATION CONTROL

The first stage of studying the influence of endogenic and exogenic factors on the population characteristics involved calculation of correlations between dependent (studied) and independent (factor) variables and establishment of correlations between independent variables. At the second stage, statistically significant correlations were selected among the former, and non-correlating relations were chosen among the latter. Subsequently, a multiple regression analysis was performed so as to estimate the contribution of each variable into the population characteristic variability. We do not present here correlation matrices (these are very cumbersome) and, besides, this is useless since the correlation coefficient values cannot serve as a criterion of the contribution made by an independent variable into a dependent one, and therefore only the correlation sign is informative. If the sign is positive, the dependent and independent variables change in the same direction, and the sign is negative, growth of one variable is accompanied by a drop in the level of functioning of other, and vice versa. In what follows only statistically valid relations are described.

A study of literature shows that indices of the spring and autumn population, estimation of the population at the seasonal peak, numbers variation rate, terms of the reproduction onset and termination, and some other parameters are used to describe the state of natural populations. All these characteristics combine the long-timed effects of population and habitat-forming factors and therefore their analysis with respect to the influence upon a certain parameter presents interest in terms of applied and theoretical biology.

3.1. DISTRIBUTION OF THE EFFECTS OF ENDO- AND EXOGENIC FACTORS IN THE OPTIMUM OF THE AREA

4.1.1. The zone of broad-leaved forests

The state of the bank vole population inhabiting broad-leaved forests (Tula permanent study plot) is described in detail in Chapter 3. The vole numbers in spring and the numbers in autumn of the preceding year exhibit a positive correlation (high autumn numbers are followed, as a rule, by spring numbers). Proportionality of changes occurring in these characteristics is connected only with fluctuations

in mortality of the animals during the autumn-winter period; mortality taken on the average over all the study years is 54.7% and accounts for 3 to 93% from year to year depending on particular conditions. However, if we take into account that winter is survived mainly by animals which not take part in reproduction in the preceding season, the winter mortality of sexually immature voles is still lower and accounts for 46.8%. In years with late-autumn or early-spring reproduction, proportionality in the changes of the numbers existing in autumn of the preceding year and spring is disturbed and the population is transformed from "passive" into active. Such being the case, the spring population is determined not only by mortality of voles but also by their reproduction processes. Besides, the numbers of voles in April exhibit a positive correlation with the fractions of different structural groups in the population in autumn of the preceding year; however, these are connected with the numbers of the structural groups (Table 24).

Another factor determining the numbers of voles at the beginning of the reproduction season is climatic and meteorological conditions of overwintered and, in particular, amount of precipitation, air temperature, and snow thickness. A positive correlation was detected between the spring population and the total amount of precipitation falling out from October to April of the preceding year.

This correlation means that the more precipitation (mainly in the form of snow) falls out during this period, the higher population can be expected at the beginning of the following reproduction cycle. The next step was to study the relations existing between the spring population and meteorological conditions of each month throughout the autumn-winter-spring period. The spring population exhibits a positive correlation with the amount of precipitation in November and a negative correlation with air temperature in the same month.

At this period, the snow cover is formed in the Tula region and it is quite natural that the thicker the snow cover, the higher its heat-insulating effect and, consequently, the less dependent is the life of the animals on low winter temperatures.

The relation between the spring population and the thickness of the snow cover in November turned out to be positive, too. The snow cover thickness varies over sufficiently broad limits: from 0 to 22 mm snow cover thickness in November that determines survival of the animals. Therefore, neither the air temperature, nor the amount of precipitation, nor the snow cover thickness in December, January or February influence the mortality and, hence, the abundance of bank voles in spring. By that time the earth is covered with a minimum necessary snow cover possessing sufficient heat-insulating properties and ensuring survival of the animals and their independence of cold impacts.

The spring population of the animals correlates negatively with the air temperature in March; at this period the temperature rises above zero and causes thawing of snow which cannot already as an efficient thermal screen, and any cold lowers the rate of thawing (Table 24). The spring population is similarly affected by precipitation in March, a fact which is probably due to impairment in the heat-insulating properties of the snow cover. Besides, in March precipitation frequently occurs in the form of rain, this leading to formation of ice crusts and, hence, to higher mortality of bank voles. The amount of precipitation in April has a positive correlation with the population numbers at the onset of the reproduction season.

Table 24

Relationship between demographic and weather factors and the bank vole population state indices
(Tula permanent study plot)

Indices	Demographic factors		Weather factors	
Spring numbers	N _a	0.71	A _p (II)'	0.64
	F ₁ (8)'	0.51	T _a (II)'	-0.49
	F ₂ (10)''	0.56	T _{sc} (II)'	0.73
	F _{si2} (8)'	0.82	T _a (3)	-0.73
			A _p (3)	-0.48
			A _p (4)	0.50
Winter survival	N _a '	-0.77	A _p (II)'	0.42
	F ₃ (10)'	0.47	T _{sc} (II)'	0.56
			T _a	-0.73
			A _p (3)	0.44
Breeding onset	N _a '	0.74	-	-
	S _w	-0.70		
	F ₁ (6)'	0.69		
	F ₂ (6)'	-0.74		
	F _p (6)'	-0.58		
	F _p (10)'	0.45		
Seasonal peak numbers (NP)	N (4)	0.53	-	-
	N (6)	0.60		
	F ₂ (6)	0.62		
	F _p (6)	0.48		
	F _p (8)	-0.55		
Autumn numbers (N _a)	N (4)	0.43	-	-
	N (6)	0.56		
	N (8)	0.65		
	F ₂ (6)	0.60		
	F ₃ (8)	0.47		
Termination of breeding (T _b)	N (4)	-0.44	T _a (9)	0.54
	N _m	-0.45		
	N (10)	-0.49		
	F ₂ (6)	-0.52		

Values significant at $p = 0.05$. Here r stands for the Spearman correlation coefficient; N denotes the numbers; F₁, F₂, F₃ the fraction of animals at the age of 7–16, 3–6 and 1–2 months; F_{si} and F_p are the fractions of sexually immature and pregnant females; T_a is the air temperature; A_p is the amount of precipitation; T_{sc} is the snow cover thickness. Numerals in the brackets denote the month number. Variables marked with a prime refer to the preceeding year.

Precipitation falling out in March when the mean air temperature below zero is probably responsible for the death of voles, while in April precipitation adds to survival of the animals at the expense of improving food resources.

A multiple regression analysis made it possible to estimate comparative contribution of all effects to the spring population numbers. The fraction of the total

numbers variance, which due to the influence of the above-considered factors, is very high and accounts for 95%. The main contribution is made by weather and food factors, while endogenic factors have a much lesser effect (Table 25).

Factorial loads determining abundance of overwintered voles in spring exhibit a different distribution. In this case weather conditions in the autumn-winter period prevail over other effects (the former account for 56% of the controlled variance). The influence of the abundance and structure of the population at the end of the preceding reproduction cycle and the amount of seeds of the principal forest-forming species does not exceed 42%. The dependence of the spring population upon food resources is primarily connected with the fact that given adequate food resources in the autumn-winter period, winter breeding is observed, which is not typical of the bank vole inhabiting the middle zone.

The proportional changes detected in the population of the voles in spring and the numbers of the animals in autumn of the preceding year are due mainly to fluctuations in survival of the animals in winter; the survival is determined by the population level and the age structure in autumn of the preceding year, as well as by weather conditions in autumn and spring (Table 25). However, this correlation is realized indirectly via the population structure and is determined by what animals formed the group of animals going to winter (time of birth, birth and development conditions).

Survival of the voles from October to April, as well as the state of the population in spring are undoubtedly influenced by wintering conditions (Table 24). Valid correlations were found only for weather in November and March, i.e. during transient periods, where temperature and precipitation conditions are most unstable.

The effects of weather and intrapopulation factors that determine survival of the voles in winter fall almost in equal proportions on the population numbers and structure at the end of the preceding reproduction cycle, weather factors, and food resources (Table 25). The contribution of the population abundance and structure at a given moment of time is very small since no considerable influence of these parameters on winter survival was revealed. Then survival of the voles from October to April is more determined by exogenic factors which accounts for 63% in the total variability; the fraction of endogenic factors is 37%.

The terms at which breeding of the bank vole starts in the Tula region (disregarding winter breeding) fluctuate from 15 to 20 days in different years and correlate positively with the total numbers of voles in autumn of the preceding year and with different structural groups characterizing the age composition and breeding intensity of the preceding reproduction cycle (Table 24). No direct correlations with weather and food conditions were found in the autumn-winter and spring periods. The winter breeding is as a rule observed in the years, where the numbers are low in the preceding autumn and the population consists mostly of young animals 1–2 months of age. Besides, winter breeding is accompanied by high yield of lime, oak and birch seeds.

In all summer months the vole numbers exhibit a positive correlation with the population of the animals in the preceding month. The presence of positive correlations between the numbers for two successive time intervals is quite under-

Table 25

Influence of the factors acting upon the bank vole population (Tula region)

Month	Population characteristic	Endogenic factors at moment of time		Exogenic factors		Fraction of explainable variance
		preceding	current	climatic	food	
	1	2	3	4	5	6
April	Total numbers	26.8	0	40.2	28.4	95.4*
	Number of overwintered voles	41.2	0	56.4	1.0	98.6*
	Fraction of overwintered pregnant females	39.0	0	29.4	5.1	73.5
	Winter survival	36.6	0	23.4	39.8	99.8*
June	Fraction of 1-2 months-old pregnant females	8.6	70.3	5.3	0	84.2
	Fraction of 1-2 months-old parous females	4.8	57.4	17.0	0	79.2
	Fraction of 1-2 months-old sexually immature females	0.9	70.3	14.3	0	85.5
	Fraction of 1-2 months-old sexually immature males	16.8	49.6	28.1	0	94.5*
	Fraction of 3-6 months-old parous females	19.5	40.5	11.7	0	71.7
	Total fraction of breeding females	4.6	73.2	11.3	0	89.1*
	Total fraction of sexually immature males	24.9	39.7	32.5	0	97.1*
	Number of pregnant females	28.7	38.0	9.5	0	76.2
August	Fraction of 1-2 months-old breeding females	25.1	50.2	9.8	0	85.1
	Fraction of 1-2 months-old sexually immature females	3.7	84.6	4.7	0	93.0
	Fraction of 1-2 months-old sexually immature males	53.5	22.2	5.4	0	81.1
	Fraction of 3-6 months-old breeding females	40.0	44.5	15.2	0	99.7*
	Fraction of 3-6 months-old sexually immatures females	24.8	62.1	2.0	0	88.9*
	Fraction of 3-6 months-old sexually immatures males	48.2	23.6	20.0	0	91.8*
	Total fraction of breeding females	66.0	6.0	13.8	0	85.8
	Total fraction of sexually immature males	54.2	33.9	8.5	0	96.6*
	Number of 1-2 months-old pregnant females	46.7	10.0	22.2	0	78.9
	Number of 3-6 months-old pregnant female	12.3	38.3	18.5	0	69.1
October	Fraction of 3-6 months-old breeding females	76.3	7.1	6.7	0	90.0
	Fraction of 3-6 months-old sexually immatures females	67.0	4.6	19.3	0	91.0*
	Fraction of 3-6 months-old sexually immatures males	53.9	20.0	15.5	0	89.4
	Total fraction of breeding females	35.9	4.4	56.0	0	96.3*

Figures in columns 2–5 denote the share of the explainable variance due to the contribution made by each group of factors into the changes of the population characteristics. Explainable variances marked with an asterisks are values significant at $p = 0.05$.

standable and is due to proportional changes in the numbers realized during reproduction. Animals that are more numerous have a more numerous offspring and, consequently, affect mostly the total numbers at the following moment of time. However, this situation is noted only in the case of small numbers. In the years of high densities, a strict proportionality of these relations is upset under the action of density-dependent inverse relations which lower the population numbers at the expense of sharp drop in the reproduction intensity of the young (Z h i g a l s k i and B e r n s h t e i n 1986). Of interest is the fact that under optimal conditions variations of the bank vole numbers in August (the usual time of the seasonal peak attainment) turned out to be much less (50%) although fluctuations of the spring numbers were substantial (90%). Most probably, intrapopulation self-control mechanisms maintain the numbers during this period at some level close to a maximum permissible for the given conditions (they let the numbers grow rapidly at low densities and limit the growth at high densities).

The seasonal peak of the numbers falls as a rule in August and the time of its attainment has no statistically valid relations with either of the factors considered. By contrast, the time of reproduction termination fluctuates in different years from August to October and exhibits a negative correlation with the level of the vole population in spring and at the end of the reproduction season, and also with the age structure of the population in summer. Besides, the reproduction period is extended if the air temperature rises in September (Table 24). In the years of high densities breeding stops already in August, with the population factors being the only limiting, whereas at low densities the time of reproduction attenuation is influenced to some extent by weather conditions in September, too.

The increase of the population from spring to the seasonal peak exhibits negative correlations with the vole numbers in April and June (Spearman correlation coefficients are: -0.42 and -0.48). The presence of these correlation is primarily due to the action of density-dependent factors that inhibit the population numbers growth through lowering of the reproduction intensity. Weather conditions from May to August influence little the population growth since these have no valid relations with either of the above-considered population indices.

The reproductive potential of the bank vole is controlled by changing either the fraction of non-pregnant sexually mature females or the terms of sexual maturation of the young. The intensity of each of these ways is in turn connected with state of the population at preceding moments of time, with the processes that take place in the population at the moment of study, with the biological features of the seasonal vole generations, and also with external factors including meteorological conditions. In the course of summer the efficiency of each group of the factors changes. Table 26 presents only statistically significant relations between the fractions of pregnant and sexually immature females and the above-given factors.

In April, the reproduction intensity is determined primarily by the vole demography in autumn of the preceding year (numbers, age structure, and breeding intensity) and also by the air temperature in October and November, i.e. in period, where a group of animals going to winter and constituting the basis of another reproduction cycle is formed in the population. So far the mechanism that realizes these relations is unclear. One of the possible explanations is a reconstruction of

sexual, age and genetic structures of the population under the influence of high densities and unfavourable weather conditions, with the reconstruction aimed at selection (during the autumn-winter period) of the animals that have some advantages in reproduction and survival. Let it be emphasized that a low reproductive activity of the voles in spring is preceded by high autumn numbers, considerable number of 3–6 months-old voles, and a large fraction of unbreeding animals. This combination of population characteristics is observed for high numbers. The effect of densities shows up, on the one hand, in lowering of the reproduction activity and raising of mortality of adults and, on the other hand, in subsequent lowering of viability and breeding intensity of the voles which were (in the period of high numbers) at the stage of embryonic development or early stages of postembryonic development (J a s z c z a k 1974, 1975, M e d v e d e v et al. 1983). The distribution of the factor components determining the fraction of pregnant females among overwintered females in April (Table 25) shows that changes in the fraction factors, and 26% by uncontrolled and random effects. The population numbers and structure in autumn of the preceding year and overwintered weather conditions determine mainly the breeding intensity of the bank vole in spring (Table 25). The abundance of voles in April and the yield of lime, oak and birch seeds influence very little the reproduction activity.

In June, reproduction of overwintered females is not limited by anything and the degree to which current-year voles born in winter-early spring (3–6 months old) participate in breeding is controlled mainly by the numbers existing at the time of study and is not connected with the population prehistory. At the same time, sexual maturation of the young (1–2 months-old) is practically equally determined by the population density in spring and at the time of study. Weather conditions in May and June influence little if at all the reproduction characteristics (Table 25).

June is the time of a maximum reproduction activity: 62% of the population are young animals 1–2 months of age. The fraction of pregnant females among these animals depends on all the factors considered, of which the main one is the demographic situation existing at the given time (70%). Weather conditions and the population prehistory have little effect. The fraction of breeding young females (1-2 and 3-6 months old) depends mainly on the demographic situation in the population in June and the effect of weather conditions accounts for not more than 17%. Since the group of breeding females includes pregnant and nursing females and also those that are not pregnant at the given time, the increase of the role played by the population prehistory and weather factors, especially in the senior-age group, is quite understandable. The abundance and population structure in June have a lesser effect on the fraction of breeding females and the proportion of pregnant females among them since this group includes also the voles which reproduced at earlier moments of time and therefore it is natural that the population situations existing in April and May determine this function (Table 25).

Sexual maturation of 1–2 months-old males is connected with all groups of factors, out of which the most essential is the demographic situation in June; however, the role of weather conditions and of the processes occurring in the population in preceding months is also sufficiently high (Table 25). So, the reproduc-

tive potential of the bank vole is determined in June mainly by endogenic factors, with the contribution made by the total numbers in June and the numbers of different population groups decisive.

In August, the major portion of the population is constituted by current-year animals (Fig. 2). Their reproduction activity always lowers by the end of summer owing to the natural cyclicity of this process in nature; however, in different years the reproduction activity is subject to considerable fluctuations, with the reproduction parameters in each age class depending on a series of conditions. Reproduction of few overwintered females is limited neither by numbers variation nor by the population structure at the given time, but it shows valid significant correlations with weather factors (Table 26).

The fraction of pregnant and sexually immature females among current-year voles of both age groups in August is connected with the population density and reproduction intensity at preceding periods, as well as with the population level at the given time. Judging by the partial correlation coefficients (Table 26), these factors influence most the young (1–2 months old). Attention is attached to a close relation between the fraction of sexually immature females born in spring and early summer (3–6 months old) and the population level in April, and between the reproduction activity of the females of the younger age group (1–2 months old) and the numbers in June. It may be supposed that similar to the situation in spring the population density influences the young through the parent generations. Besides, the fraction of sexually immature voles among current-year animals lowers and that of pregnant females rises as the air temperature increases and the quality of precipitation drops in August. Most probably, the part of energy, which is used for reproduction or sexual maturation at optimal temperatures, should be consumed for additional thermoregulation as temperature decreases.

In August, the vole population rises and it is probably for this reason that the influence of endogenic factors increases from 69% in June to 80% in August (Table 25). Note that while in June the influence of the demography at the given time prevailed in this group, the effects due to changes in the population characteristics at preceding periods of time grow considerably in importance in August. Thus, the variability of the fraction of 1–2 months-old females in August is determined 25% by the population prehistory, while in June 5% only. However, the fraction of sexually immature young females is determined mainly, as in preceding months, by the population numbers and structure in August (Table 25).

High dependence of the sexual maturation rate of current-year voles on changes in the activity of the population processes in August is principally due to the fact that it is at that time that young voles can proceed to breeding. However, if in preceding months the population level reached the values close to limiting ones, sexual maturation of young animals could be subject in August, as for example in October, to considerable influence of the population prehistory. The intensity of sexual maturation of 1–2 and 3–6 months-old males is connected mainly with changes of intrapopulation mechanisms, out of which the most essential are processes occurring in the population in June and July. The fraction of pregnant and nursing current-year females (3–6 months-old) and the part of sexually immature

Table 26

Relationship between population and weather factors and the reproduction activity of the bank vole population (Tula permanent study plot)

Month	Fraction	All ages							
		factors		factors		factors		factors	
April	I	F _p I(4)	0.95	F _p (4)	0.95	–	–	–	–
		F _{si} 2(10)'	-0.48	F _{si} (10)	-0.46				
		T _a (10)'	0.50	T _a (10)'	0.49				
	II	N(10)'	0.46	N(10)'	0.43	–	–	–	–
		F ₃ (10)'	-0.52	F ₃ (10)'	0.42				
		F _{si} 3(10)'	0.56	F ₁ (10)'	-0.43				
		T _a (10)'	-0.42	F _{si} (10)'	0.55				
June	I	N(6)	-0.43	–	–	–	–	N(6)	-0.53
		F _{si} (6)	-0.79	–	–			F _p (6)	0.56
	II	N(4)	0.64	No. sexually immature		–	–	N(4)	0.62
		N(6)	0.69					N(6)	0.67
August	I	N(6)	-0.63	P _p (6)	0.48	N(4)	-0.43	N(6)	-0.74
		N(8)	-0.72	F _{si} (6)	-0.38	N(8)	-0.40	N(8)	-0.62
		T _a (8)	0.49	A _p (6)	-0.45	F _p (6)	0.46	F _p (6)	0.49
				T _a (8)	0.70	F _{si} (6)	-0.44	F _{si} (6)	-0.61
	II					T _a (8)	0.43	T _a (8)	0.54
		N(6)	0.54			N(4)	0.82	N(6)	0.75
		N(8)	0.64			N(6)	0.56	N(8)	0.62
		F _p (6)	-0.46			N(8)	0.52	F _p (6)	-0.40
		F _{si} (6)	0.45	–	–	F _p (6)	-0.54	F _{si} (6)	0.52
		A _p (6)	0.46			F _{si} (6)	0.54	T _a (8)	-0.49
		T _a (8)	-0.58			A _p (6)	0.58		
		A _p (8)	0.38			T _a (8)	-0.43		
October	I					A _p (8)	0.46		
		N(6)	0.45			N(6)	0.63		
		N(8)	0.48			N(8)	0.71		
		F _p (6)	-0.64			N(10)	0.48		
		F _p (8)	-0.42			F _p (6)	-0.46		
		F _{si} (6)	0.57			F _p (8)	-0.69		
		F _{si} (8)	0.53			F _{si} (6)	0.49		
		A _p (8)	0.40			F _{si} (8)	0.70		
		T _a (10)	-0.58			A _p (9)	0.41		
						T _a (10)	-0.43		

Values significant at $p = 0.05$, I – pregnant; II – sexually immature; variables marked with a prime refer to the preceding year. For abbreviations see Table 24.

voles among them are controlled predominantly by the processes taking place in the population in June and July (Table 25).

In October, when the population becomes still younger, reproduction continues only in the years of low numbers. Almost all animals 1–2 months old and most

females born in July (3 months old) remain sexually immature owing to biological features of these generations (P o k r o v s k i 1967). At the same time, the fraction of sexually immature voles among current-year females of the senior age class is connected with a number of factors: numbers level in the summer-autumn period; population reproduction intensity in preceding months; and weather in September-October. The rate of sexual maturation of females in autumn and the entire set of factors with which the rate correlates determine the state of the population by the following spring rather than their reproduction activity at the given time (Table 26).

Contributions made by exo- and endogenic effects to the characteristics of the bank voles reproduction are presented in Table 25. The distribution of factorial loads changes markedly in October but, as in the preceding summer months, the leading role in the regulation of the reproductive function of the voles belongs to intrapopulation factors, with a clear-cut predominance of preceding situations. Weather conditions have approximately the same effect as in August. An exception in the fraction of breeding females which is influenced most (56%) by fluctuations of meteorological conditions. The abundance and population structure of voles in October influence very little (10%, maximum) the reproduction. During this period all the effects analyzed here account for 82 to 96% of the total variability in the reproduction parameters.

Thus, the efficiency of density and weather factors affecting the population dynamics exhibits a pronounced seasonal behavior. With a relatively mild climate and a high numbers level, weather conditions affect numbers and reproduction activity mainly during transition periods (November, March, September-October), while the population factors exert their influence to different extent throughout the year. In cold season, survival of the voles is determined, in addition to the population density, mainly by the terms of the snow cover setting-in, its thickness and duration. The snow cover is usually formed by December and possessed adequate heat-insulation properties. This ensures independence of animals of low temperatures throughout winter. In warm season (May-August), as opposed to what was observed by N. M. O k u l o v a (1986) in Western Siberia, weather conditions influence insignificantly the population. The absence of correlations between the numbers and the population growth rate and weather in summer months suggests that in northern forest steppe variations of the air temperature and the amount of precipitation do not as a rule exceed the values that are critical for the bank vole (Table 24).

Participation in breeding and sexual maturation of the bank vole are determined at the Tula permanent study plot at least by four groups of factors: state of the population at preceding moments of time; state of the population at the time of study; set of weather conditions; and biological features of animals born in different reproduction periods. As is seen, during the reproduction season each group of factors acts with different efficiency (Table 25). The abundance of voles in April, their survival during the autumn-winter period, and reproduction activity are controlled mainly by the population state in autumn of the preceding year (numbers, age composition, and reproduction intensity) and also by air temperature variations in September and October, i.e. in the period when a group of animals going to winter and constituting the basis of another reproduction cycle is formed

in the population. Besides, a rich crop of lime, oak and birch seeds has an effect only on survival of the bank vole during the winter period and its winter breeding and, consequently, on the numbers and population structure in spring. It is worthwhile noting that low reproduction activity of voles in spring is preceded by high autumn numbers, considerable number of 3–6 months-old voles, and a large portion of animals which did not reproduce in autumn of the preceding year. This combination of population characteristics is observed in the years of high numbers. Under the influence of the numbers and low air temperatures a group of animals with a low level of mortality and reproductive potential is formed in the population. It is impossible to trace genetic relations of these phenomena using our material but we can with good reason assume that the population structure existing in autumn of the preceding year determines the level of the population functioning in spring.

Thus, in the course of the reproduction cycle of the bank vole (except spring) the deciding are intrapopulation processes; at the beginning of summer the processes taking place in the population at a given moment are dominant, and in the second half of summer the processes occurring at preceding moments prevail. Besides, reproduction is inhibited in late summer still further owing to adverse effects of weather conditions and season-dependent elongation of the terms during which voles from late-summer litters attain puberty.

4.1.2. Taiga zone, the Udmurt stationary study plot

For general characteristics of the bank vole population inhabiting this study plot see subsection 3.2 and Table 2.

In spring (April), the total population of the bank vole is influenced by the population structure and numbers existing in autumn (October) of the preceding year, as well as by meteorological conditions and food supply in wintering. However, contributions of these factors to the numbers variation, as determined by the multiple regression analysis, are different (Table 27). The maximum contribution is made by meteorological factors (56.9%) out of which 50% is due to the amount of precipitation and thickness of snow cover in November–December. Food supply accounts for 38.9%, with the greater part constituted by the yield of lime seeds in the preceding year. With abundant food supply, winter breeding is observed. As a result, the total abundance of voles in April may rise up to 20% relative the mean multi annual level, and this, in turn, leads to considerable transformation of the typical age structure and provokes a sharp growth of the summer population.

The number of overwintered voles in April is determined almost equally by the numbers and sex-and-age structure of the population in September–October of the preceding year, as well as by meteorological conditions in winter, and is almost independent of the yield of spruce and lime (Table 27).

Out of the meteorological factors, the most essential are the amount of precipitation and thickness of snow cover in October–December of the preceding year (41.3%). Spring weather conditions also influence overwintered animals but their contribution is much less and accounts for only 0.8% in the total variability of the number of overwintered animals. Out of endogenic factors, the contribution of the

indices of the population numbers in autumn (which is mainly the total numbers in September–October) of the preceding year is 14.2%. The structure indices (sex-and-age composition, degree of participation in reproduction) determine the number of overwintered animals by 32%; breeding intensity in August–October of

Table 27

The effect of factors acting upon the population (contribution of each group of factors into the total variance caused by the operation of the factors included in the analysis)

Month	Population characteristics	Endogenic factors at moments of time				Exogenic factors			Share of explainable variance
		Preceding		Current		Climatic		Food	
		Numbers structure		Numbers structure		Air temperature	Amount of precipitation and Tsc (7)		
April	N (4)	2.9	0	0	0	3.4	53.5	38.9	98.7*
	N ₇ (4)	14.2	32.0	0	0	0	42.1	0.2	88.5
	S _w	10.2	21.2	9.5	6.8	4.8	40.5	99.5*	—
	F _{p7} (4)	0	47.5	2.3	21.0	5.3	0	7.4	83.5
	F _{si7} (4)	0	33.3	3.9	25.4	26.4	0	3.4	97.8
	T _b	1.3	30.3	16.4	0	0.9	44.7	5.3	99.7*
June	N (6)	13.5	1.5	74.7	10.3	0	0	0	99.9*
	F _{p7} (6)	23.5	13.6	1.5	0	2.5	0	0	41.1
	F _{p3} (6)	0.02	0	91.7	1.8	0.1	0	0	93.6*
	F _{p1} (6)	15.6	0	18.0	28.8	0	0	0	62.5
	F _{si1} (6)	7.7	0	34.3	44.0	0	0	0	85.1
	F _{s1} (6)	2.0	0	0.8	95.8	0	0	0	98.6*
	F _p (6)	0	0	59.0	13.0	0.1	0	0	72.1
	N _{par7} (6)	9.9	26.2	33.8	25.9	0	0	0	95.8*
	N _{par1} (6)	0	46.0	35.8	0	0	0	0	71.8
	N _{s-1} (6)	10.8	35.3	32.6	20.6	0	0	0	99.4*
August	N (8)	1.5	0	98.2	0	0	0	0	99.7*
	F _{par3} (8)	17.9	10.4	33.1	1.7	0.2	0	0	63.3
	F _{si3} (8)	24.1	25.9	33.1	7.8	2.5	0	0	93.4
	F _{s+3} (8)	21.9	17.8	36.0	20.5	2.5	0	0	98.8*
	F _{par1} (8)	1.0	17.8	7.1	68.8	2.6	0	0	97.2
	F _{si1} (8)	5.8	23.7	0	58.4	0.4	0	1.3	89.5
	F _{s+1} (8)	0.9	19.7	18.5	52.9	0	0	0	92.1
	N _{par3} (8)	0.2	0	0	70.0	0	0	0	70.1
	N _{si3} (8)	23.5	14.4	9.2	25.0	3.5	0	0	75.6
	N _{s+3} (8)	18.9	0	21.0	46.9	0	9.7	0	96.6*
	N _{par1} (8)	4.6	2.6	27.9	53.2	0	0	0	88.5
	N _{si1} (8)	40.9	47.6	3.2	4.2	0	4.2	0	99.6*
	N _{s+1} (8)	4.7	0	55.8	26.6	0	11.2	0	98.3*

Table 27 cont.

October	N (10)	3.5	5.2	91.1	0.2	0	0	0	99.7*
	F _{si3} (10)	16.9	38.9	26.4	16.8	0	0	0	98.9*
	F _{s+3} (10)	32.5	1.7	64.1	0	0.1	0	0	98.6*
	F _{si1} (10)	19.8	6.7	17.7	24.5	8.1	20.1	0	95.9
	F _{s-1} (10)	12.8	3.0	21.8	54.7	0	0	0	92.3
	N _{si3} (10)	10.7	13.9	51.8	23.5	0	0	0	99.9*
	N _{si1} (10)	36.5	3.8	26.8	25.4	0	0.4	0	97.9
	N _{s-1} (10)	8.2	2.5	69.6	16.5	0	1.2	0	98.1*

S_w stands for the winter survival; N the numbers; F denotes the fraction of the individuals being considered in the population or age group (p, par, si stand for pregnant, parous and sexually immature respectively); s- denotes sexually immature males; s+ stands for sexually mature males; numerals denote age groups; 1 - 1-2 months old; 3 - 3-6 months old, and 7 - 7-16 months old; numerals in the brackets denote the month number; T_b the time of the breeding beginning; T_{sc} the snow cover thickness. Explainable variances marked with an asterisk are values significant at p=0.05.

preceding year (20%) and the fraction of the youngest animals in the population (11.8%) have the most considerable effect. If winter breeding is absent, the population numbers during the autumn-winter period can change only at the expense of the death of the animals, with the mortality being equally determined by endo- and exogenic factors. Note that one of the major roles among population factors is played by the demographic situation that is formed in the population at the end of the last reproduction cycle (Table 27). Most probably, winter mortality of the animals is not connected directly with the autumn numbers and sex-and-age structure but is determined by the population group to which parents of the animals going to winter belonged and by the conditions under which those animals lived during the phase of rapid growth (till the time of sexual maturity). At the same time, air temperature fluctuations, amount of precipitation and thickness of snow cover can influence directly mortality of the voles.

In April, the fraction of overwintered pregnant and parous females is about 70% and that of immature females is 30%. The involvement of overwintered females into breeding in spring is determined to a greater extent by density-dependent factors (Table 27). However, while the fraction of pregnant females depends mainly on the population prehistory, maturation is determined almost equally by the state of the population in autumn of the preceding year, its state in spring, and weather conditions in spring (air temperature in April is 22.5%). No sexually immature animals were noted among overwintered males in April over the entire study period, a fact which means that sexual maturation is attained earlier in males than in females and depends on fewer factors.

The term of mass breeding of the bank vole is also determined by the operation of all the four groups of factors, out of which the most contribution is made by climatic conditions (amount of precipitation and thickness of snow cover in Fe-

bruary–March) (45.6%) and the condition of the autumn population (31%); a rather high contribution is due to the spring population (the higher the size of population, the later starts breeding).

Having estimated the contributions of various factors into formation of the population characteristics, let us give relations of these characteristics to particular variables.

The numbers of bank voles in spring (April) exhibit a positive correlation with the population numbers in autumn (October) of the preceding year, thickness of snow cover in November, air temperatures in April, amount of precipitation in February, and yield of seeds in the preceding year. An increase in the values of all these variables is accompanied by a rise in the spring population. Negative relations have been detected only with the amount of precipitation in December.

The numbers of overwintered voles in spring exhibit a positive correlation with the population numbers and fraction of immature females in October of the preceding year and the amount of precipitation in November, and have a negative correlation with the fraction of young 1–2 months-old voles in August and the fraction of pregnant females among the young animals, as well as with the amount of precipitation in September–October of the preceding year and that in March. Survival of voles in the autumn-winter period (October to April) exhibit a positive correlation with the fraction of pregnant females in the age groups of 7–16 and 3–6 months and with the air temperature in March; it correlates negatively with the numbers in October of the preceding year, the fraction of 7–16 months-old females in the population in August, the fraction of immature females at the age of 3–6 months in October, and the amount precipitation in April.

The fraction of pregnant overwintered females in April correlates positively with the fraction of 3–6 months-old pregnant females in August of the preceding year, numbers of voles and air temperature in April, and the stock of lime seeds from the preceding-year yield; it has a negative correlation with the fraction of overwintered voles in April and air temperature in December.

The fraction of immature females in April exhibits a positive correlation with the onset of breeding and the fraction of overwintered voles in spring; it shows a negative correlation with the fraction of 3–6 months-old pregnant females in August, the total numbers in spring, air temperature in December of the preceding year and in April of the current year, and yield of lime seeds in the preceding year.

The onset of mass reproduction of voles in spring exhibits only one positive correlation with the fraction of 3–6 months-old immature females in October and shows a series of negative relations with the fraction of 3–6 months-old animals in the population in August and the fraction of pregnant females among them, the total population numbers in April, amount of precipitation in October of the preceding year, amount of precipitation and thickness of snow cover in February, yield of spruce seeds in the preceding and current years.

The total numbers of the bank vole in July, August and October are almost independent of weather and food (excluding catastrophic weather phenomena) but is determined mainly by the population demography in each of these months (Table 27) and, chiefly, by the numbers of the age group that is most numerous at a given time, although it may be assumed that the number of animals at a cur-

rent moment of time should be determined by the state of the population at preceding moments.

Breeding intensity of overwintered females in June is only in 41% determined by the factors considered, while 59% of the reproduction activity is due to uncontrolled processes of endogenic and exogenic character. Out of 41%, 37% of the variability is due to the effect of preceding population events.

The fraction of pregnant 3–6 months-old females in June accounts for 23% of the total number of females of this age (Fig. 4). It is determined (92%) by changes in the population numbers and structure in June and depends mainly on the number of overwintered voles. The contribution made by changes in the number of males and females into variability of the fraction of pregnant females are approximately the same.

The intensity with which the youngest voles participate in reproduction in June is connected only for 62% with the operation of the factors included in the consideration and depends in 38% on the action of neglected factors, such as food, genetic and physiological composition, and other factors. Similar to the case of 3–6 months-old females, the fraction of 1–2 months-old pregnant females is determined chiefly by the population numbers (18%) and structure (29%) at a current moment of time. Sexual maturation of 1–2 months-old females is connected for 85% with the factor considered, out of which 78% is determined by the demographic situation in the population in June. The role of females in sexual maturation of young voles is almost twice as high as that of males (45.8 and 26.8%).

The fraction of sexually immature males (1–2 months-old) is connected for 98% with the indices of the population state in June and depends almost equally on the numbers and structure of the overwintered part of the population and 1–2 months-old animals. The role of males in these age groups is much larger than that of females 87 and 10%.

The total fraction of pregnant females of all ages in June is connected mainly with the structure and numbers of bank voles exactly at that month, with overwintered voles determining greatly the involvement of current-year females in reproduction. The former are responsible for about 52% of the regression-induced variability of this process. The contribution of young animals is of the order of 20%. Numbers and age structure of females influence for 59% the intensity at which current-year females are involved in reproduction. The role of males in limiting the reproduction of females is small and does not exceed 13%.

The number of breeding overwintered females depends mainly on the state of the population at the current moment of time, whereas the fraction of pregnant voles among them is determined essentially by the population prehistory (Table 27). Considerable restrictions on the reproduction activity of overwintered females are imposed precisely by the overwintered part of the population.

The total number of breeding young voles is limited primarily by the population demography at preceding moment of time, most probably, indirectly via changes in growth and development. The number of sexually immature males 1–2 months of age depends mainly, on the contrary, on the situation existing in the population at the current moment of time.

Correlations of various population indices with the factors operating in July were calculated in the same way as for the population in April. The total number of voles in June correlates positively with that in April, the number of overwintered animals in April, the number of overwintered females in June, the number of 1–2 months-old young voles in June and their fractions in the population in the same month. Negative correlations were found only with the overwintered part of the population in April and June. The fraction of overwintered pregnant females depends weakly on the factors considered. However, it exhibits a positive correlation with the fraction of 1–2 months-old voles in October of the preceding year and air temperature in June and shows a negative correlation with the fraction of 3–6 months-old voles also in October of the preceding year.

The fraction of 3–5 months-old pregnant females correlates positively with the number of males and females of the same age in June and with the fractions of current-year voles of both ages in the population in June. Negative correlations were found with the number of overwintered animals in April, the fraction of overwintered animals in June, and air temperature in April and June.

The fraction of 1–2 months-old pregnant females shows a positive correlation with the fraction of overwintered males in June and has negative correlations with the number of overwintered females in April, the number of overwintered males in June, the number of overwintered breeding females of 1–2 months-old males and females in June, and the fraction of males of the same age group in the population.

The fraction of 1–2 months-old immature females in June exhibits a positive correlation with the fraction of overwintered females in April, the number of overwintered breeding females in June, the number of overwintered males in June, the number of 1–2 months-old females and males in June. Negative correlations were found with the fraction of overwintered males in June and the fraction of overwintered voles in June.

The number of overwintered breeding females in June correlates positively with the number of overwintered females and males in April, the number of overwintered males in June, the number of 1–2 months-old females and males in June, and the fraction of overwintered females in June. Negative correlation were established with the fraction of 3–6 months-old voles in October of the preceding year and the fraction of overwintered males in June.

The number of 1–2 months-old breeding females correlates positively with the number of 1–2 months-old females and males in June and negatively with the fraction of overwintered females and males in April. The number of sexually immature males 1–2 months-old correlates positively with the number of 1–2 months-old females and males in June and fraction of males of the same age in June.

The fraction of 3–6 months-old breeding females in August is determined 63% by all the effects taken into consideration, out of which the main role belongs to endogenic factors (divided almost equally between preceding and current demographic situations in the population). The fraction of breeding females of different age in August is influenced mainly by current-year animals as follows; 35% is due to 3–6 months-old animals, 8.4% is due to 1–2 months-old animals, while the in-

fluence of overwintered voles is estimated at 19.3% only. The contributions made by males and females are approximately the same. The fraction of sexually immature females at the age of 3–6 months in population accounts for 21% and the rate of their sexual maturation is determined chiefly by the operation of endogenic factors (the population structure and numbers in June and July are responsible for 50% and about 41% of the variance is due to the population density and composition in August). The numbers and the degree to which the voles from the age class of 3–6 months participate in breeding have the greatest controlling effect. The number and age structure of females determine for 47% the rate of sexual maturation of young females, whereas males can change this process only by 12%.

The fraction of 3–6 months-old males in the bank vole population is determined, as is the degree to which females of the same age group participate in breeding, for 96% by intrapopulation control mechanisms, with the major role played by processes occurring in population at a current moment of time. The age group of 3–6 months hinders most sexual maturation of males. No sex-dependent differences in the influence on this process were found.

The intensity of participation in breeding and the rate of sexual maturation of current-year females and males 1–2 months-old in August are determined to a great extent by intrapopulation processes, mainly by the population numbers and structure in August and to a lesser extent by the state of the population at preceding moments of time (Table 27). Breeding activity of the females of this age group is limited almost equally by 1–2 and 3–6 months-old current-year animals, while the degree to which males of this age group participate in reproduction is limited by overwintered animals.

The number of breeding current-year females and males is determined, as the breeding structure indicates, essentially by the population demography in August; however, the contribution of population situations which took place in preceding months is substantial, too. The number of immature females entering the age group of 3–6 months depends equally on preceding population situations and the state of the population at a current moment of time. Voles at the age of 3–6 and 1–2 months control chiefly the number of the breeding part of the population, despite the fact that at that time the population is dominated for 83% by 1–2 months-old animals.

The following relations have been established between the population characteristics in August and the perturbations acting upon them.

The total numbers of the population in August exhibit only positive correlations with the number of overwintered and 1–2 months-old males and females in June, the number of 3–6 months-old voles in June, and the number of current-year voles of both ages in August.

The fraction of 3–6 months-old breeding females in August has a positive correlation with the fraction of 1–2 months-old mature males in June and the fraction of overwintered males in August; it shows a negative correlation with the number of overwintered voles in June, the fraction of 3–6 months-old females in June, the number of 1–2 months-old males and females in August, the fraction of the youngest males in August, and air temperature in May and June.

The fraction of 3–6 months-old immature females in August correlate positively with the number of 3–6 months-old voles in June, the fraction of females of the same age in June, the number of 1–2 months-old males in August, and the fraction of 1–2 months-old voles in August; it correlates negatively with the fraction of 3–6 months-old voles in August and air temperature in June.

The fraction of 3–6 months-old mature males in the population in August has positive correlations with the fraction of 1–2 months-old mature males in August and air temperature in August. Negative correlations are found with the number of overwintered females in June, the number of 1–2 months-old females and males in June and August.

The fraction of 1–2 months-old breeding females in August correlated positively with the fraction of females of this age in June and the fraction of 3–6 months-old females in the population in August. Negative correlations were established with: the number of overwintered females in June, the number of 1–2 months-old males in April, the fraction of overwintered females in the same month, the number of overwintered females in August, the number and fraction of 1–2 months-old females in August, the fraction of current-year voles in the population, and air temperature in August.

The fraction of 1–2 months-old immature females in August shows a positive correlation with the number of overwintered females in June, the fraction of males of the same age in June, the fractions of overwintered and 1–2 months-old voles in August, and air temperature in August; it correlates negatively with the fraction of overwintered males and 1–2 months-old females in June, the fraction of females and total fraction of 3–6 months-old animals in the population in August.

The fraction of 1–2 months-old mature males in August exhibits a positive correlation with the fraction of overwintered males in June, the number of overwintered males in August, the fraction of 3–6 months-old mature males in August, and the fraction of overwintered males in the same month. Negative correlations were established with the number of overwintered females and the fraction of 1–2 months-old males in June, the number of overwintered breeding females and the fraction of 1–2 months-old males in June, the number of immature females of this age in August, the number of overwintered females in August, the fraction of 1–2 months-old pregnant females and fraction of overwintered breeding females in August.

The number of 3–6 months-old breeding females in August correlates positively with the number of animals of the same age and the fraction of females among them in June and August, the fraction of overwintered voles and the fraction of females among them in August, the fraction of 3–5 months-old voles and the fraction of males among them in August. It correlates negatively with the fraction of 1–2 months-old voles in the population, the fraction of females of this age in August, and the fraction of overwintered animals in the population.

The number of 1–2 months-old breeding females in August shows a positive correlation with the fraction of females of this age in June, the number of pregnant females and the number of 3–6 months-old males in August. It has a negative correlation with the number of overwintered females and males in June, the num

ber of 1–2 months-old mature males and the total fraction of the animals of this age group in August.

The number of 3–6 months-old mature males in August correlates positively with the number of 1–2 months-old mature males in June, the number of 3–6 months-old voles and the fraction of the animals of this age group in August, the number of 1–2 months-old pregnant females in August, and the amount of precipitation in August. It correlates negatively with the number of overwintered voles in June, the fraction of 1–2 months-old immature males and the total fraction of this age group in the population in August.

The number of 1–2 months-old mature males in August exhibits positive correlations only with the population and external factors in August, including the number of breeding males and females at the age of 3–6 months, the number of 1–2 months-old breeding females, the fraction of 3–6 months-old males in the population, and the amount of precipitation in August. Negative correlations were established with the number of 3–6 months-old animals in June, the number of 1–2 month-old females in June, the number of 1–2 month-old males in August, the fraction of 1–2 month-old pregnant females and the fraction of 3–6 month-old immature males in August.

In October, the bank vole population comprises 66% of young animals 1–2 months old, 32% of animals from early-summer litters when reached the age of 3–6 months, and only 2.5% of overwintered animals (Fig. 4). The sex ratios in each age group are given in Table 6. Reproduction processes attenuate in the population during this period and females in all age groups are dominated by immature ones (88.4%) and their fraction varies insignificantly from year to year (variation factor 11.4%). The fraction of sexually immature males is still higher (98%), with the variation factor being 70%.

In addition to a regular attenuation of reproduction in autumn, the rate of vole maturation is limited also by intrapopulation control mechanisms and weather changes; however, these factors act differently. As in summer, the fraction of sexually immature males and females which could probably become sexually mature is determined by intrapopulation processes, with the number and structure of the bank vole population in October being most essential. The influence of weather conditions (air temperature and amount of precipitation) on the population activities rises also but it is rather low compared to endogenic factors and is equal on the average for various characteristics to 2.9% in August and 3.7% in October. This means that the seasonal attenuation is decisive for the vole reproduction in October. In the years, when conditions in autumn are favourable for the bank vole reproduction, these processes are controlled in the main by intrapopulation density-dependent mechanisms (Table 27). Age peculiarities of sexual maturation of males and females are qualitatively similar. In the older group of current-year voles the effect of preceding population situations are somewhat higher than for animals 1–2 months old. The state of the population in October determines to a greater extent their sexual maturation (Table 27). As one would expect, demographic peculiarities of current-year animals determine chiefly sexual maturation of males and females. In October, as taken over all population characteristics, the contribution of current-year voles into the reproduction variation accounts for

91.4%, which is distributed with ages as follows: 56% is due to 1–2 months-old voles and 35.4% to 3–6 months-old animals.

The correlations between the population characteristics and the factors acting upon them in October are the following.

The numbers of the bank vole in October correlate positively with the number of overwintered animals in August, the number 1–2 months-old males and females in August, the fraction of voles of this age in the population in August, the number of 3–6 months-old females and males in October, the fraction of 1–2 months-old immature males and females in October, the fraction of 3–6 month-old immature males in October. Negative correlations were established only with the fraction of females and the total fraction of 3–6 months-old voles in the population in August.

The fraction of 3–6 months-old immature females in October exhibits a positive correlation with the number of 1–2 months-old mature males in August, the fraction of 1–2 months-old females in August, the number of 3–6 months-old males and females in October, and the number of males of this age in October. It shows negative correlations with the number and fraction of 1–2 months-old pregnant females in August, the fractions of females and males, and also the fractions of sexually mature voles among them in the age group of 3–6 months in August.

The fraction of 3–6 months-old immature males in October has a positive correlation with the number of overwintered males, the number of 1–2 months-old males and females in August, and also the numbers of 3–6 months-old males and females and 1–2 months-old immature males and females in October. Negative correlations are with the fraction of 3–6 months-old females in August and air temperature in July.

The fraction of 1–2 months-old immature females in October correlates positively with the number of overwintered females and 3–6 months-old breeding females in August, the number of 3–6 months-old breeding females in October, the number of immature voles and the total fraction of 1–2 months-old females in October, air temperature in July and August. Negative correlations were established with the fraction of 3–6 months-old males in October, and amount of precipitation in October.

The fraction of 1–2 months-old immature males in October shows positive correlations with the number of overwintered 1–2 months-old females in August and 3–6 months-old breeding females in October, the number of 1–2 months-old immature males and females and also their fractions in the population in October, the fraction of males from early-summer generations in October. Only one negative correlation was established with the fraction of 1–2 months-old pregnant females in August.

The number of 3–6 months-old immature females in October correlates positively with the number of 1–2 months-old males and females and also the fraction of the animals of this age in the population in August, the number of 3–6 months-old animals and their fraction in the population in October. It correlates negatively with the fraction of 1–2 months-old mature males, the fraction of 3–6 months-old mature males, and the total fraction of these animals in August.

The number of 1–2 months-old immature females in October exhibits a positive correlation with the number of overwintered animals in August, the number 1–2 months-old males and females in August, the number of 3–6 months-old females in October, the number of 1–2 months-old immature males, the total fraction of these animals and the fraction of females of this age in the population in October. It has negative correlations with the number of 3–6 months-old females and the total fraction of the animals of this age in August, the fraction of 3–6 months-old males in October, and the amount of precipitation in September.

An analysis of influence of all the four groups of factors on the numerical and structural characteristics of reproduction of the Udmurt population of the bank vole shows that the factors considered explain, as averaged for all population indices and the entire reproduction season, 86.2% of the reproduction characteristics variability. The least part of the explainable variance is typical of the fractions of overwintered pregnant females in the population in April and June and equals 62.3% (mean value for April–June), out of which 42.3% is due to the population state in September–October of the preceding year, 12.4% to the population numbers and structure in April, and 7.6% to the influence of weather conditions and yield of lime and spruce seeds in the preceding year. This means that their participation in breeding is determined not only by the population numbers and structure at preceding and current moments of time (although it is primarily connected with the action of these factors) but also by neglected effects, among which the most essential are, probably, those associated with food resources (productivity of phytocoenosis), impact of predators, etc. Changes in the fraction of current-year breeding females that take place throughout the reproduction season are due to largely to the population processes taking place in the population at the current moment of time (48.8%), are determined in 30% by the population prehistory, and only in 5.5% by weather conditions and stock of spruce and lime.

The variance of the fractions of sexually immature females is resolved still more in four factorial components. Sexual maturation of overwintered females in April depends chiefly on the first three factorial components (population demography in autumn of the preceding year and in spring, and also weather conditions in April) and is determined only in 4% by the abundance of spruce and lime seeds. The rate of sexual maturation of females from the age group of 3–6 months is connected weakly with changes in weather conditions and shows no relations to the abundance of food, but is determined greatly by endogenic factors (almost equally by the population prehistory and its demography at the time of analysis) (Table 27).

The intensity of sexual maturation of young animals in summer is connected mainly with the population state at the moment of analysis (about 60%), depends on the population prehistory (20.9%), is determined in 10% by weather conditions (in October the role of weather conditions increases to 28.2%), and depends very weakly on food abundance. Thus, the demographic situation at the end of the preceding reproduction cycle, the population numbers and structure in spring, and weather conditions in winter determine the reproduction intensity of adult females in spring. A similar distribution of the factorial loads was found for young females in October whereas throughout summer their sexual maturation is determined pri-

marily by the numbers and structure of the vole population at a given moment, and sexual maturation of adult females depends on the demographic situations at preceding moments of time.

Overwintered males of the bank vole attain puberty earlier than females do. Already in April practically all of them are sexually mature and therefore it was impossible to determine dependence of their sexual maturation on various factors using our material. According to our calculations, participation of current-year males in breeding is determined (up to 95%) by endogenic factors and, essentially, by the population demography (72.8%) at the moment of the time considered (Table 27). A weak dependence of sexual maturation of males on external conditions is probably due to the reduction of the behavioral reactions to environmental changes or to a higher physiological resistance of males (compared to females) to the action of various factors.

The above-given material suggests that the bank vole population in Udmurtia is controlled by the population structure and numbers at preceding moments of time, a particular situation in the population at a current moment of time, as well as weather and food conditions. However, considerable differences in the distribution of the operation intensity of the factors were revealed depending on age, functional group, sex, and the stage of the reproduction period. The population numbers and structure at preceding moments of time affect mainly "functionally" adult animals, determining their survival, reproduction intensity, and the rate of sexual maturation. In spring and in the first half of summer predominant are overwintered males and females, while in the second half (August- October) 3-6 months-old animals become the oldest in the population; it is already them that constitute the core of "functionally" adult group of animals which are influenced mainly by the population prehistory.

The numbers and structure of vole population (at the time of study) determine maximum changes in the reproductive potential of the youngest males and 1-2 months-old females practically in all summer months, although both survival and breeding of the animals of this age group are also controlled by preceding demographic situations, but their effect is much weaker and, probably, manifests itself in lower viability and reproduction intensity of the voles which were, during the period preceding high numbers, at the stage of embryonal (through their mother's reaction to high densities) and early postembryonal development.

Meteorological and food conditions are responsible for changes in the reproductive potential of the population and winter survival of the bank vole only at the beginning and at the end of the breeding season when they play the leading role in the population regulation. These factors do not affect population processes in summer months. Males are influenced very little by these factors.

4.1.3. Optimal and pessimal habitats in the taiga zone

It was shown in the chapter "General characteristics of the populations" that the population of spruce-lime forests on the Mari permanent study plot differs practically in all parameters from the population on other plots (as regards the population level, age structure dynamics, intensity and duration of reproduction

processes, and other parameters). The contrast is pronounced most on the young immature of the year 1968. The influence of various factors on the population processes was therefore analyzed only for these two contrasting areas. All the other biotopes occupy an intermediate position between the extremes.

Estimation of the effects of endo- and exogenic factors on the population processes has been described earlier and the correlations between various population characteristics and the factors acting upon them are similar to those observed on the Tula and Udmurt permanent study plots and therefore are not considered in this section.

Basic differences between the vole population in the young clearings and the population of the spruce lime forest consist in a lower level of the numbers throughout the reproduction season and in the absence of permanent population in the autumn-winter period (Figs. 6 and 7). In the spruce forest in April almost 90% of the study plot population are overwintered voles, whereas in the clearings these animals account for 30% only and 70% are young voles at the age of 1–2 months, which probably migrated to the clearings in spring. It is probably for this reason that the role of the population numbers and structure in autumn of the preceding year is so high (41%) in the clearings, whereas in the spruce-lime forests it is only 24% (Tables 28, 29). However, the spring population of immature voles is influenced most by meteorological factors: their contribution to the general variance is 50%. Feeding conditions (quantity of spruce seeds) are responsible for 2.5% of the general variance in immatures, while in primary forests their contribution attains 29%.

In April, the numbers of overwintered in the spruce-lime forest are determined by the operation of intrapopulation and external factors. The contribution of meteorological and feeding conditions into the variation of the abundance of adult voles is about 75% (Table 28): the contribution of weather conditions into the variance of the vole population in spring is 47% and that of feeding conditions (yield of spruce and lime seeds in the preceding year) accounts for 28.5%. Out of the population effects, the numbers of overwintered animals are connected only with abundance and population structure in autumn of the preceding year (24%).

Survival of voles in the autumn-winter period depends most on weather conditions: 57% of changes in survival is associated with their fluctuations. Another essential factor (29%) is the state of the population in October. Contributions of the population structure and numbers at a current moment of time and the stock of spruce and lime seeds into survival processes are insignificant: 6.6 and 3.2%, respectively.

In June the distribution of effects influencing the population in primary forests and in immature is other than in April. In this period the population processes determine the population numbers and structure at the current moment of time. In spruce-lime forests the population prehistory, as in the case of feeding conditions, influence little if at all the reproduction processes of voles of all age groups. In immature the role of preceding population situation is somewhat higher than in spruce forests but is lower than in April. In June weather conditions in both biotopes have a much lower effect than in April.

Table 28

Influence of the factors acting upon the bank vole population in Mari ASSR (spruce–lime forest)

Month	Population characteristics	Endogenic factors		Exogenic factors		Share of explainable variance
		preceding	current	climatic	food	
April	Number of overwintered voles	23.6	0	46.8	28.5	98.9*
	Winter survival	29.5	6.6	56.8	3.2	96.1
	Fraction of breeding overwintered females	7.7	67.3	0.2	0.3	75.5
June	Fraction of 1–2 month old breeding females	3.6	52.8	21.7	0	78.1
	Fraction of 1–2 month old sexually immature females	20.0	66.3	3.3	0	89.6
	Fraction of 1–2 month old sexually immature males	2.9	68.5	14.5	0	85.9
	Total fraction of breeding females	1.5	72.7	21.5	0	95.7*
	Total fraction of sexually immature females	5.1	61.7	20.9	0	87.7
	Total fraction of sexually immature males	23.6	47.3	14.8	0	85.7
	Number of 1–2 month old pregnant females	16.5	67.0	6.3	0	89.8*
August	Fraction of 1–2 month old sexually immature females	30.8	65.9	2.6	0	99.3*
	Fraction of 1–2 month old sexually immature males	4.4	59.7	27.4	0	91.5
	Fraction of 3–6 month old breeding females	16.6	65.8	13.3	0	95.7*
	Fraction of 3–6 month old sexually immature females	18.7	54.3	3.5	0	76.5
	Fraction of 3–6 month old sexually immature males	10.7	61.6	21.5	0	93.8*
	Total fraction of breeding females	16.6	58.7	16.0	0	91.3*
	Total fraction of sexually immature females	18.1	57.0	16.8	0	91.9
	Total fraction of sexually immature males	15.9	67.3	0	0	83.2*
October	Fraction of 3–6 month old breeding females	39.8	9.7	41.0	0	90.5*
	Fraction of 3–6 month old sexually immature females	12.2	58.9	19.6	0	90.7*
	Fraction of 3–6 month old sexually immature males	25.5	49.6	12.3	0	87.4*
	Total fraction of breeding females	48.7	0.8	37.0	0	86.5*
	Total fraction of sexually immature females	39.4	0.1	27.4	0	66.9
	Total fraction of sexually immature males	49.2	3.3	28.9	0	81.4

Figures denote the share of the explainable variance due to the contribution of each group of factors into the changes of the population characteristics. Explainable variances marked with an asterisk are values significant at $p=0.05$.

Table 29

Influence of the factors acting upon the bank vole population living in Mari ASSR (1968 clearing)

Month	Population characteristics	Endogenic factors		Exogenic factors		Fraction of explainable variance
		preceding	current	climatic	food	
April	Population numbers	40.6	0	49.6	2.4	92.6
	Winter survival	No permanent population during winter period				
June	Fraction of 1–2 month old breeding females	28.2	23.4	37.5	0	89.1*
	Fraction of 1–2 month old sexually immature females	6.9	20.2	4.8	0	31.9
	Fraction of 1–2 month old sexually immature males	15.1	81.0	2.8	0	98.9*
	Total fraction of breeding females	0.9	70.8	14.7	0	86.5
	Total fraction of sexually immature females	6.4	45.2	35.8	0	87.2
	Total fraction of sexually immature males	1.4	90.2	5.1	0	96.7*
	Number of 1–2 month old pregnant females	0.1	67.7	24.1	0	91.8*
August	Fraction of 1–2 month old sexually immature females	25.1	26.4	22.9	0	74.4
	Fraction of 3–6 month old breeding females	13.1	29.9	22.2	0	65.2
	Fraction of 3–6 month old sexually immature males	27.1	34.4	1.8	0	63.3
	Fraction of 3–6 month old sexually immature females	28.9	5.3	22.7	0	56.9
	Total fraction of breeding females	8.3	22.7	8.9	0	39.9
	Total fraction of sexually immature females	13.8	21.8	41.8	0	76.9
	Total fraction of sexually immature males	26.5	29.6	12.2	0	68.3
October	Fraction of 3–6 month old breeding females	9.2	33.3	49.7	0	92.2*
	Fraction of 3–6 month old sexually immature females	30.7	31.5	13.1	0	75.3
	Total fraction of breeding females	15.1	20.4	12.4	0	47.9
	Total fraction of sexually immature females	18.4	38.0	25.5	0	81.9

Figures denote the share of the explainable variance due to each group of factors responsible for changes in the population characteristics. Explainable variances marked with an asterisk are values significant at $p=0.05$.

The fraction of breeding females in spruce-lime forest in June is only 78% dependent on the operation of the factors analyzed, and 22% of the variance is due to unaccounted effects. As in the case of 3–6 months-old females, a basic contribution to the variation of the fraction of 1–2 months-old breeding females in primary forests is made by situations arising in the population at a current moment of time (Tables 28, 29).

The fraction of 1–2 months-old immature males in June in the spruce-lime forest and in the clearings is also determined mainly by the population numbers and structure in June (Tables 28, 29). The fraction of immature males and females correlates positively with the numbers of 1–2 months-old males and females in June and the amount of precipitation in April.

Voles 3–6 months of age account for about 20% of the population in both biotopes in June but in spruce forests this group of voles is always present in the population, while in immature it occurs only in the years of intensive winter breeding. It is therefore senseless to consider reproduction processes of 3–6 months-old voles.

The majority of papers dedicated to the analysis of the reproduction processes consider general characteristics of reproduction neglecting age-dependent peculiarities in the distribution of the effects produced by the operating factors. The total fraction of breeding females of all ages both in primary forests and in immature is determined mainly, as all of the above-discussed functions, by the population numbers and structure in June. However, some differences between the biotopes are noted as regards the distribution of effects produced by various factors (Tables 28, 29).

The intensity of breeding and sexual maturation processes of males and females on the entire territory of the Mari study plot are determined in the main by intrapopulation control mechanisms. Weather conditions can change the population only up to 15% and fluctuations in the yield of spruce and lime seeds do not influence significantly the reproduction activity of voles. Out of the group of the population factors, the reproduction processes of young females are affected mostly by overwintered voles. Current-year animals do not influence the reproduction of this year's breeds (only positive correlations were detected between the numbers of young animals and the degree of their participation in breeding). Overwintered females reproduce in June whatever the changes of the population numbers and structure on the stationary study plot and variations in weather conditions. Overwintered voles (32% of the total number) influence mainly sexual maturation of young females. The role of young animals is much lower (19%); an increase in the number of both young and adult voles leads to retardation of the sexual maturation of current-year animals.

Sexual maturation of males also depends on the numbers and the degree to which animals of all ages participate in breeding but the sexual maturation rate of males decreases most when the number of overwintered males and females rises.

The breeding intensity and sexual maturation of bank voles in June in spruce-lime forest and in immature differ insignificantly and some discrepancies refer mostly to quantitative estimates of the contribution made by various factors into the regulation of the population reproductive potential.

A seasonal peak of the bank vole numbers is observed in August on the entire territory of the Mari study plot. The breeding intensity of males and females lowers (the fraction of females to 25%, and that of males to 10%). The drop of the population reproduction potential in August is determined, on the one hand, by the seasonal peculiarities inherent in the reproduction processes of the bank vole and, on the other hand, intrapopulation control mechanisms that lower the breeding activity. If the reproduction attenuation is associated with seasonal peculiarities, changes in the physiological structure of the population (accumulation in the population of individuals with low reproduction potentialities in the second half of summer) should take place during cycle-determined transformations inherent in the population organization itself. If the reproduction attenuation is connected with the operation of the density-dependent control, the low rate of sexual maturation and small fraction of breeding females are due to high densities existing at that time. It is impossible to establish a strict line of demarcation between the effects of each method of control. However, explaining the general variance of e.g. the fraction of pregnant females, it is possible to estimate portions of this variance which are due to the action of a particular factor.

Reproduction processes taking place in August in spruce-lime forest and in immature are affected by the population processes at preceding moments of time, the population numbers and structure at the given time, and weather conditions. It is quite natural that the intensity of these factors is different and each population characteristic features its own distribution but the common point is an almost complete dependence of the reproduction activity on endogenic factors (Tables 28, 29). As distinct from the distribution of factorial loads in June, the role of the August population structure and numbers in the reproduction control is reduced by 10–15% in August and the influence of preceding population situations enhanced by the same amount.

A part of variance, for example, fractions of breeding females, associated with the operation of the factors being considered, can be related, with some approximation, to determined conditions. The other part of the variance associated with the operation of disregarded factors and random processes can be stochastically determined.

In August, the fraction of explainable variance reduces to 64% in the clearings and to 90% in the spruce-lime forest, this testifying unambiguously to reduction in the role of the groups of factors being analyzed in the regulation of reproduction processes and to rising of the role of disregarded factors and random fluctuations. Besides, while in June the reproduction potential of the population is determined mainly by the numbers and population parameters at the current time, in August there takes place a considerable rise in the contribution of preceding population situations and weather conditions (Tables 28, 29), which is most pronounced in the clearings. There the variability of the majority of the population characteristics is built up almost in equal parts of the effects due to changes in the population prehistory (20.4%), the population situation at the current time (24%), and changes in the weather conditions (20%). In the spruce-lime forest there also occurs a shift in the distribution of the factorial loads but the loading role is played

there by the population density and composition at the current time (16.5, 61.3, and 12.6% respectively).

In August, current-year animals constitute the major part of the population but the main contruction to the reproduction control is made by 3–6 month-old animals and by 1–2 months-old voles in clearings. Besides, 40 to 60% of the variability of the reproduction processes in the clearings is associated with the operation of disregarded and random factors. Sexual maturation of young females is largely blocked by the number of 1–2 months-old voles both in the forest and in clearings; however, apart from this, in clearings about 30% is considered by random factors. Sexual maturation of males both in the clearings and in the forest is influenced mainly by the number and reproduction activity of 3–6 months-old voles of both sex; also, as in the case of females in the clearings, the role of random factors rises.

The role of weather conditions enhanced in August, compared to June, and their effect on the fraction of breeding animals and sexual maturation is much higher for 1–2 months-old females than for 3–6 months-old animals. Out of the weather factors, monthly average air temperature fluctuations and monthly average amount of precipitation in June have the greatest influence in clearings, while changes in weather conditions of August are most essential in the forest. Changes in the air temperature have a greater influence compared to the amount of precipitation in clearings, while the opposite situation is observed in the forest. The different influence of weather conditions on the reproduction activity of the bank vole inhabiting clearings and forest is due to probably to different degree of protection of these biotopes.

On the Mari study plot the total numbers of the bank vole in October lower in all biotopes. The fraction of breeding females becomes smaller, too: of the total number of females, it accounts for 12% in the clearings and for 15 % in the forest. The fraction of sexually mature males reduces also at both sites and becomes equal to 2–5%. However, in spite of the equal reproduction activity of voles at both sites, the population age structures differ considerably (Figs. 6, 7). For example, the fraction of 1–2 months-old voles is 16% in the clearings and 34% in the forest. The considerable discrepancies in the population composition can be explained only by early termination of breeding in the clearings.

Young 1–2 months-old voles are not only few in the population but the fraction of breeding animals among them is small and therefore it is no use to analyze their participation in breeding because their contribution to the population growth is negligible. Reproduction of 3–6 months-old females is determined by three groups of factors but the distribution of factorial loads differ from that of August. The role of weather conditions rises in October equally for the clearings and the forest and attains 25–28%. The contribution made by the changes in the October population and the population structure lowers in the forest approximately by 40%, while that of preceding population situations rises by 20%. In the clearings the influence of the population prehistory on the reproduction processes is approximately the same in October and August (about 20%), while the role of variations in the population characteristics of October enhances. If we arrange the factors in the descending order of their effects, the major influence in clearings is due to

endogenic factors at the current time (30%), meteorological conditions (25%), and the population prehistory (19%). In the forest, the most influence is attributed to the endogenic factors in the preceding moment of time (about 30%), weather conditions (28%), and intrapopulation factors at the current time (20%).

In the spruce-lime forest, in October the fraction of breeding 3–6 months-old females, as well as the total fraction of breeding females, depends to a large extent on the reproduction activity of males and females in the preceding months, while the variations in the rate of sexual maturation of both males and females are due mainly to the total population numbers in August–October; these factors account for about 36% of the total variability. Reproduction processes in the clearings are determined by the same set of variables as those in the forest. Principal quantitative differences between the clearings and the forest show up in the reduction to 19% of the contribution made by the preceding population state in the clearings. In October, the numbers and structure groups of voles of 3–6 and 1–2 months-old exert practically the same influence on the reproduction activity of females. The contribution of this group of factors into the general variability is 31% in the clearings and 20% in the forest. As was already noted, in October the reproduction processes are progressively influenced by weather conditions, out of which changes in the amount of precipitation in September and, especially, in October incorporate all the effects of fluctuations in meteorological factors whose share is approximately the same in the forest and in the clearings and accounts for about 25% of the total variability of the reproduction characteristics.

In the clearings the role of random and uncontrolled effects rises to 26%, whereas in the forest it is about 16%. Estimates of the explainable variances are given in Tables 28 and 29.

Seasonal dynamics is clearly seen in the distribution of factorial loads. In spring, 50 to 70% of the variability in the bank vole demographic characteristics is explained by the influence of weather conditions and the yield of spruce and lime seeds. A rather large contribution is made by the autumn population numbers and structure. During this period the numbers, reproduction and winter survival of voles depend rather heavily on the external conditions, fluctuations and preceding population situations. The share of the explainable variance is maximum in April and accounts for 93 and 97% for clearings and the forest, respectively. In the phase of the maximum seasonal growth of the population (June–July), its growth rate is controlled mainly by endogenic factors (65–70%), out of which the population numbers and structure at the current time are most important (they are responsible for 55–60% of the total variability). The role of meteorological factors reduces in June to 12–18% and is maintained at this level up to the seasonal peak; by the end of the breeding season (October) it rises again to 25–27%. In the phase of the population growth the role of uncontrolled factors increases to 13 and 19% in the forest and in the clearings, respectively.

In August the population processes are influenced progressively by random factors: their contribution to the total variance rises to 35% in the clearings and to 10% in the forest. This was probably the cause of considerable changes in the distribution of factorial components in the clearings and in the forest. While in August 77% of the population characteristics variability in the forest was explained

by the operation of endogenic factors, their share in the clearings dropped to 44%. In the forest the leading role in the distribution of the contribution of effects is attributed to the population structure and numbers at the current time, while in the clearings the demographic situation in the population at preceding moments of time and at the current time and weather conditions took an almost equal share (Tab. 28, 29). These differences in the distribution of factorial loads in the forest and in clearings can be explained by a lower ecological capacity of the clearings and, consequently, by an earlier exhaustion of its resources and, hence, an earlier engagement of density-dependent control mechanisms that limit the reproduction and population growth processes. In October the role of random processes in the regulation of the bank vole reproduction remains to be high (16% in the forest and 26% in the clearings). The distribution of factorial components differs in these habitats. At the end of the breeding season the role of weather factors rises, while that of endogenic factors reduces to 56 and 49% in the forest and in the clearings, respectively. Out of the group of endogenic factors, the leading role in the forest acquired preceding states of the population and in the clearings – the demographic situation in the population at the current time.

4.2. DISTRIBUTION OF CONTRIBUTION OF INTRAPOPULATION AND EXTERNAL FACTORS IN THE PESSIMUM OF THE AREA

It was shown in Chapter 3 when describing the state of the bank vole population in true-moss spruce, mixed and deciduous forests of the Karelia study plot that as regards the set of characteristics the population phenomena in these habitats do not differ, except the reproduction intensity which is slightly higher in spruce forests (the fraction of breeding females there is approximately 10% higher). Therefore, to estimate the hierarchy of the affecting factors, only materials that characterize the population in true-moss spruce forests were analyzed.

The procedure of estimating the effects produced by the factors influencing the population phenomena has been described in the foregoing chapters. The population accounts of May bear a considerable portion of randomness owing to low population numbers. For this reason they may be used in the analysis of the mean values but may not be used for comparison of variances, and it is incorrect to utilize them as the basis for the estimation of the distribution of the effects produced by various factors. In comparison to the situation in May, the numbers level in September is the highest of all summer months. However, owing to some reasons, observations at that period of time were made only in separate years. This also makes impossible the use of the materials in the estimation of the distribution of factorial loads.

Reproduction of the bank vole in the Pre-Ladoga region starts approximately a month later than in other geographical zones and therefore June can be referred to the onset of the breeding season, whereas on other stationary study plots this is the period of maximum reproduction. In June, only overwintered voles and 1–2 month-old animals are present in the population. Overwintered animals account for 56% of the total population, practically all of them are sexually mature and participate in breeding. It is natural that 63% of the total offspring in the population is due to overwintered females (Figs. 9, 10). This group determines the popu-

lation growth processes and therefore it is interesting to consider its state as a function of endogenic factors (at preceding and current moments of time) and depending on changes in climatic and food conditions. The share of the variance explained by the operation of these factors is 98%, i.e. only 2% of the variability in the number of overwintered animals in June is determined by the operation of some other factors (Table 30).

Table 30

Influence of the factors acting upon the bank vole population (Karelia permanent study plot, true-moss spruce forests)

Month	Population characteristics	Endogenic factors at moment of time		Exogenic of factors		Share of explainable variance
		preceding	current	climatic	food	
June	Number of overwintered	17.8	0	79.9	0	97.7*
	Winter survival	3.9	0	87.8	0	91.7
	Fraction of 1-2-month-old breeding females	6.2	38.8	7.0	0	52.0
	Fraction of 1-2-month-old sexually immature females	41.2	29.6	11.9	0	82.7
	Total fraction of breeding females	15.6	66.9	5.4	0	87.9
	Total fraction of sexually immature females	4.6	74.5	1.4	0	80.5
	Total fraction of sexually immature males	54.7	22.5	13.2	0	81.4
	Number of breeding females	8.3	54.2	26.4	0	88.9
August	Fraction of 1-2-month-old breeding females	63.1	15.6	7.7	0	86.9
	Fraction of 1-2-month-old sexually immature females	12.6	31.0	48.9	0	92.5*
	Fraction of 1-2-month-old sexually immature males	33.8	21.6	28.1	0	83.5
	Total fraction of breeding females	35.7	19.9	28.2	0	73.8
	Total fraction of sexually immature females	20.0	41.5	27.6	0	89.1
	Total fraction of sexually immature males	28.1	37.8	19.5	0	85.4
	Number of 1-2-month-old breeding females	9.5	81.3	3.5	0	94.3*
	Number of 1-2-month-old sexually immature males	13.5	31.6	43.0	0	88.1*

Figures denote the share of the explainable variance due to the contribution made by each group of factors into changes of the population characteristics. Explainable variances marked with an asteriks are values significant at $p=0.05$

The population of overwintered animals in June is determined by fluctuations in weather conditions (80% of the controlled variance is explained by the operation of these factors), out of which the share of the explainable variance associated with fluctuations in the amount of precipitation and air temperature in September and October accounts for 35%, changes in weather conditions in April and May are responsible for 27% of the total variance, and the influence of meteorological conditions from December to February on the abundance of overwintered animals does not exceed 18%. Thickness of snow cover from January to March determines the number of overwintered voles for less than 1.5% but in the modification of winter survival the snow cover thickness from November to February is responsible for more than a half (48% out of 91.7%) of the total controlled variance. In all the cases an increase in the snow cover thickness results in lower mortality of voles in the autumn-winter-spring period. The second-rank factor that determines winter mortality is represented by weather conditions in September and October (it explains 24% of the variance) and only 20% of the total variance is due to the fluctuations in the amount of precipitation and air temperature from December to March. Feeding conditions affect very little, similar to the population numbers and structure in June, the abundance and survival of voles. The structure and stock of voles in autumn of the preceding year and determine survival of overwintering animals only in 4%, while the stock of voles in June – in 18%.

In June the reproduction intensity of voles of all ages is not limited. All of the overwintered and young females which attained puberty by that time participate in breeding. In the group of 1–2 month-old voles sexual maturation is determined chiefly by attaining the age of puberty by these animals, which is at a minimum at that time and is 25–30 days for some animals (Ivanter 1975). In June, the mean multiannual population of voles rises from 2 to 3%. Such insignificant changes in the population cannot have considerable consequences but, as is seen from Table 30, they are quite sufficient for a substantial reconstruction of distribution of the effects produced by the factors acting upon a population. In July, the population processes are influenced mainly by the population numbers and structure in that month. In July, overwintered animals account for 28% of the total vole population and all of them participate in breeding. The group of 1–2 month-old animals is the largest. They account for 72% but only 45% of the animals participate in breeding. Despite considerable differences in the numbers, the potential growth of the population is almost equally ensured by animals from both age classes.

All of the overwintered animals participate, as before, in breeding, while the reproduction activity of 1–2 month-old females (fraction of breeding females) is determined largely by the living conditions of the animals. A great part of uncontrolled variance is due probably to the fact that during the period of a rapid population growth recruitment of young animals to the breeding process is determined to a great extent by random combinations of the population endogenic properties and external conditions (in July the population responds even to small changes in the living conditions). The total population numbers in June have the most significant effect (39%) upon the reproduction of young voles. An increase of the total population results in a lower fraction of breeding young females. The contribution

of females into these processes can be estimated at 35% and that of males – only at 15%. In this case, we observe, most likely, some indirect or parallel process rather than a direct influence of the number of males on the reproduction activity of females. Weather conditions can be responsible for not more than 7% of the variability in the reproduction processes of females. The amount of precipitation in May and June as well as monthly average air temperature in July have a statistically valid influence on the reproduction activity of females in July. Out of all the considered indices of preceding states of the population, only the number of overwintered females in June has an inhibiting effect on the reproduction processes of young females.

Sexual maturation of current-year females in July is determined still greater by the numbers and composition of the bank vole population in July (endogenic factors of the current moment of time): the share of this group of factors in the explainable variance is 64%. While the fraction of pregnant and breeding females is influenced most by the general abundance of animals in July and the number of overwintered females among them, the fraction of sexually immature females in the population is related mainly to the number of 1–2 month-old females and males (the higher the abundance of young voles, the larger the fraction of sexually immature females among them). Changes in the number of young voles contribute in 41% to the controlled variance. Overwintered animals have a much lesser effect on the engagement of young females in breeding: the share of changes in the number of overwintered voles is close to 10%. Weather conditions (air temperature and amount of precipitation) in July, as well as the population history (population numbers and composition in June) influence very little sexual maturation of young females.

Sexual maturation of one- and two-month-old males is determined, as the reproduction activity of females of the same age, by endogenic factors. For males, the share of the explainable variance associated with these factors accounts for 71% (out of total 83%). While sexual maturation of females is affected mainly by the state and level of the population at the current moment of time, the greatest part of the variance (41%) in the case of males is due to preceding population situations (Table 30). Out of this group of factors, the most essential are the number of overwintered and young males and the total fraction of breeding females in June. Among the population indices typical of the current moment of time, the number of young males and females (22 and 30% of the variance are due to this group) influences mainly sexual maturation of males. Enhancement of the effects of preceding population situations compared to the influence of the composition and abundance of the population at the current moment of time is due to the fact that males respond much earlier to change in the density and associated population phenomena (by reducing the rate of sexual maturation and breeding participation intensity). It is quite probable that it is more expedient for the population to exclude males from the reproduction rather than females, yet preserving the total increase in the population.

Weather conditions influence insignificantly sexual maturation of males. The influence of weather conditions on all reproductive functions of young males and females does not exceed 10%.

The distribution of the factors that affect the total fraction of breeding and sexually immature males and females in the population is analogous in July to their distribution for one- and two-month-old voles.

In August the increase in the population numbers is up to 4% (Figs 9, 10). The population of the study plot comprises voles of three age groups: overwintered animals and 3–6 and 1–2 month-old voles. During this period the group of the youngest voles is the largest (over 85% of the total population). The reproduction activity of 1–2 month-old animals rises as compared to that in July (the fraction of breeding females becomes equal to 57 and that of males to 39%). The group of overwintered animals is the lowest in number (they account only for 2% of the population). The population of voles from early-summer litters is small, too (their fraction in the total population is 12%). Although all females of these age groups participate in breeding, their contribution to the population growth does not exceed 20% (Table 14). Changes in the total population numbers in August are therefore mainly due to either exclusion or inclusion of young females in the reproduction process.

Similar to the situation in July, breeding intensity of 1–2 month-old voles in August is determined largely by endogenic factors. However, while in July it was connected principally with the population numbers and structure in the same month, in August the most contribution to the variation of the reproduction activity is made by the composition and abundance of the animals at preceding moments of time. In particular, as the number of 1–2 month-old males and females increases in July, the fraction of breeding females in August is reduced (the variance explained by the operation of these groups of animals is 27%). The detected influence of the young vole numbers in July on the population reproduction in August has a well-interpreted biological sense: the higher the number of young animals in July, the more, young voles in August. These animals are at least a month older than those born in July, August, and could start breeding.

Sexual maturation of young voles and their engagement in breeding are blocked by older animals. The influence of the number of overwintered voles in July on the reproduction of young animals in August is lower and does not exceed 17%; the density in August can account only for 16% of the controlled variance. Weather conditions affect still less the reproduction of young animals.

While the fraction of breeding young females is determined to a great extent by endogenic factors with pronounced dominance of the preceeding population feature, the major part of other characteristics of the reproduction is not so susceptible to the influence of endogenic factors. For example, the fraction of sexually immature 1–2 month-old females is almost equally determined by endogenic and weather factors (44 and 49%). The greatest contribution is made by the population abundance and structure at the period of study. In the given case, the maximum regulating influence is due to current-year 1–2 month-old animals. The share of the variance explainable by the influence of these voles accounts for 28% out of 31% due to this group of factors. Overwintered voles and 3–6 month-old animals, along with the youngest animals, also inhibit the rate of sexual maturation of 1–2 month-old females, but their influence does not exceed 3%.

The influence of preceding population situations (population numbers and structure in July) can be estimated at 13% and practically the entire influence is due to the change that take place in the group of voles 1–2 month-old. Weather conditions, among them air temperature in July (24°C) and August (19°C) and the amount of precipitation in August, hinder rather intensively sexual maturation of young females; 49% of the explainable variance is due to weather conditions.

Sexual maturation of young 1–2 month-old males in August is influenced by preceding states of the population (their contribution to the total variance is 34%), population abundance and structure at the current period (22%) and weather conditions (28%). This means that the influence of random and uncontrolled factors is not more than 16%. Out of the population characteristics in July (history), variations in the number of young males and females affect most the rate of sexual maturation of young males (32 and 34%). In August, fluctuations in the number of young males are most effective (the higher the number of 1–2 month-old males in August, the larger the fraction of sexually immature animals among them). Air temperature in July (15.9°C) and August (8.2°C) and the amount of precipitation in August account on the total for 28% of the total explainable variance (83.5%).

The total share of breeding and sexually immature males and females is controlled by all the factors analyzed here. The distribution of their effects is given in Table 30. These indices include the reproductive functions of young voles considered earlier and therefore it is useless to interpret these relations again. All the reproduction indices common for the population are determined mainly by intra-population factors (their share in the total variance exceeds 50%) but, simultaneously, compared to July, the role of weather conditions (air temperature and the amount of precipitation in July and August) increases markedly (up to 27%).

Participation in breeding and sexual maturation of the bank vole in Karelia are determined by the state of the population at preceding moments of time, its state at the time of study, combined action of weather conditions, and biological features of seasonal generations. Each group of factors operate specifically in different phases of the reproduction cycle. At the beginning of the reproduction season the number of overwintered animals and their winter survival are determined by weather conditions and even in June their contribution to the total explainable variance reaches 85%. The population states in autumn of the preceding year exert a much weaker influence on the population processes, although in other populations of the bank vole weather conditions and the population composition in autumn produce almost equal effects.

Living conditions of the bank vole in the Pre-Ladoga region are far from optimum ones, a deduction which follows from a low population level, large fraction of breeding males and females, high mortality of the animals both in the autumn-winter and summer periods. In optimum zones, where the habitat capacity is rather high, it is a rather rare case that spring number are low, whereas in Karelia this situation occurs rather often. However, while a population dwelling in optimum biotopes can raise its numbers to very high values in one or two reproduction seasons, this is not the case in Karelia. One of the causes responsible for low spring numbers can be high mortality of voles in winter even in the years when the stock of the Karelia population rises by autumn: only one-third of the animals survive

winter. In favourable habitats (Tula region, Udmurt and Mari ASSR) about one-half of the animals survive the autumn-winter period. Besides, even at a sufficiently high reproductive potential during all summer months the population numbers cannot attain a high level owing to high summer mortality of current-year voles. On these grounds, the bank vole occurring in Karelia can be referred to the animals that control their numbers by the r-strategy since high reproduction activity is accompanied by high mortality. In other populations the numbers are controlled mainly through changing the fraction of breeding young voles. Most probably, severe climatic conditions, and poor forage supply to the voles in Karelia have a greater impact on their mortality than on the reproductive potential of the population. As a consequence, the role of weather factors rises substantially for the Karelia population, numbers and composition of the vole population in June affect little population phenomena of that month.

In July, the reproduction intensity is much more connected with changes in the intrapopulation processes. More than one-half of the variability in the reproduction activity of young voles is due to changes in the population numbers and composition in June (49% of 77% of the total controlled variance). Air temperature fluctuations and the amount of precipitation at this period influence insignificantly the population reproduction: the share of these factors in the total variance does not exceed 8%.

In August, the leading role in the variation of the population phenomena belongs, as before, to intrapopulation factors, although it is difficult to distinguish the most essential ones among them, because preceding and current states of the population predominate alternatively in the influence upon different population characteristics. From the total distribution of the operating factors, it is seen that the population abundance and composition at preceding and current moments of time and climatic conditions divide the entire explainable variance into three equal parts and therefore are no grounds to emphasize any of the groups. In the case of voles inhabiting the Tula, Udmurt and Mari stationary study plot, preceding population states undoubtedly dominate in August, while the role of weather factors is insignificant. In Karelia, climatic conditions determine one-third of the total variability of the reproduction activity at that period.

In summer the response of males to all the effects is different from that of females. At the beginning of summer meteorological factors are decisive for males. In July, the influence of endogenic factors is higher than that of exogenic factors. The main endogenic factors being the population numbers and structure at preceding moments of time. In August, sexual maturation and reproduction activity of males are determined principally by intrapopulation situations at preceding moments of time and the period of study; however, the population history makes a little higher contribution to the variation in reproduction of males. Weather conditions in August affect reproduction of males to the same extent as that of females.

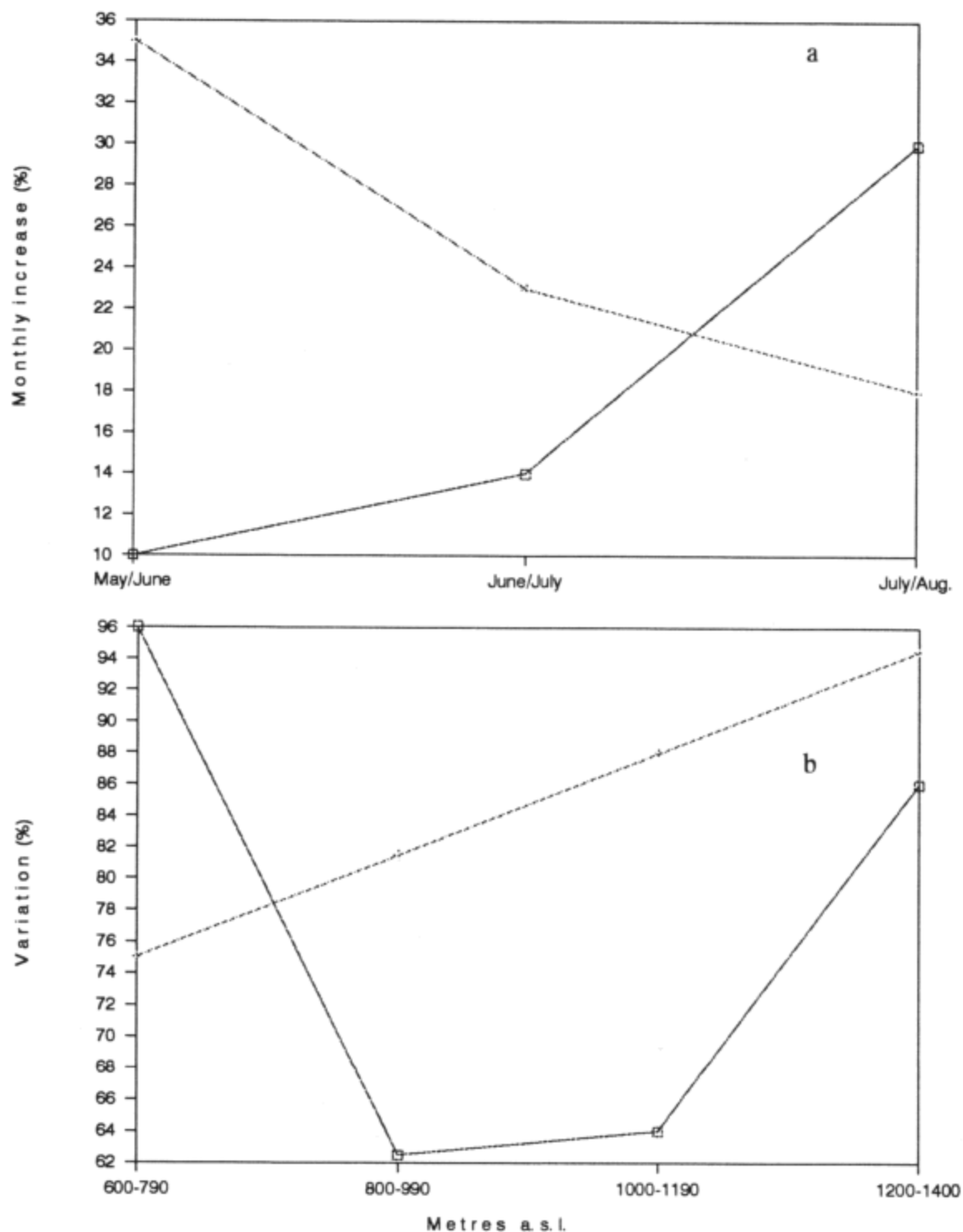
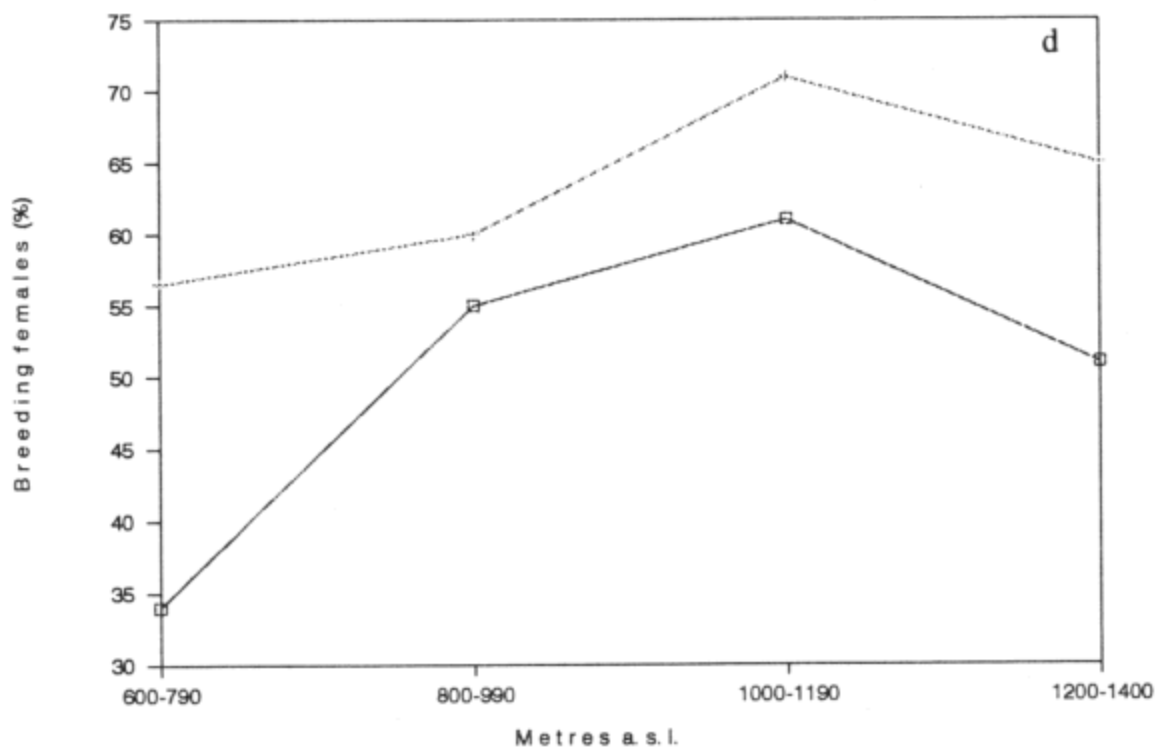
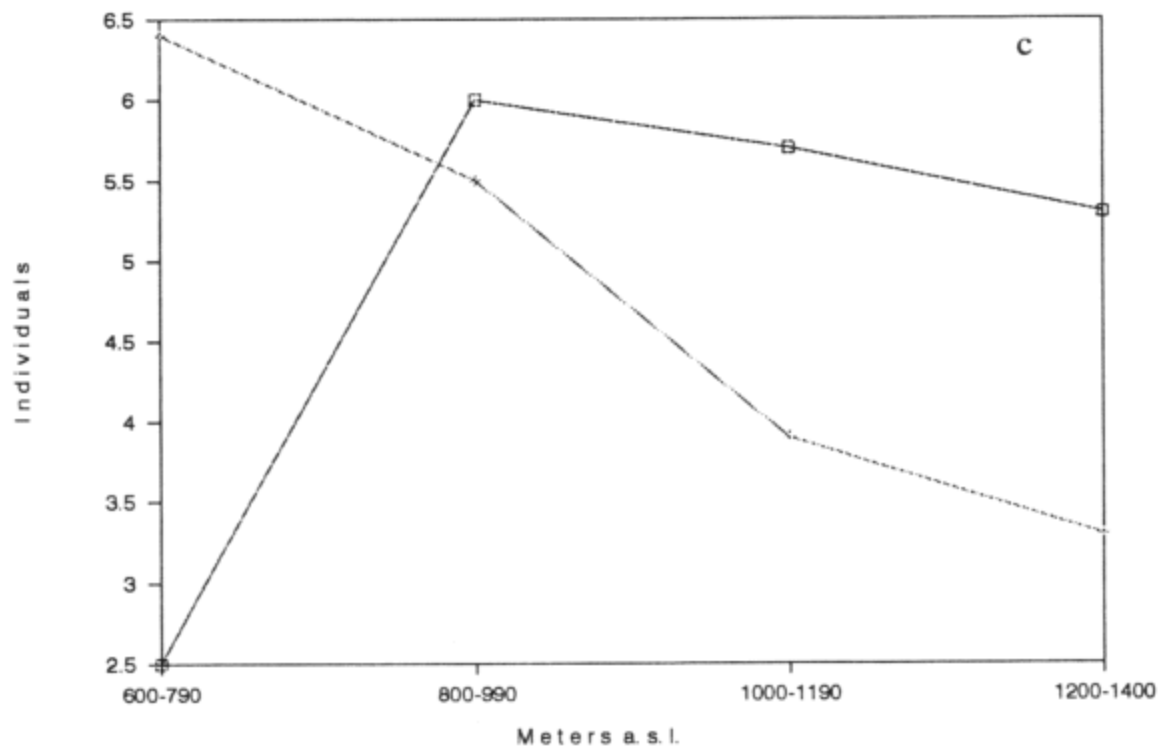


Fig. 11. Changes in time and space of certain basic population characters of *Clethrionomys rutilus* and *C. rufocanus* of Western Sayan permanent study plot. Black rectangles and continuous line – *C. rufocanus*, crosses and continuous line – *C. rutilus*. a – population growth rate, b – coefficient of variation of numbers caught, c – relative abundance (numbers caught per 100 trap-days), d – breeding fraction of the current year females



4.3. THE RATIO AND TOTAL INTEGRATED EFFECT OF INTRASPECIFIC AND INTERSPECIFIC INTERRELATIONS BETWEEN FOREST VOLES

It was shown in Chapter 3 that northern red-backed and grey red-backed voles inhabit the entire territory of the Sayan permanent study plot but their distribution over the territory is far from being uniform. The subbelt of mountain bilberry forests (600–800 m a.s.l.) presents the optimum regions for grey red-backed vole and the pessimal region for northern red-backed vole, while of mountain taiga coniferous forests (800–1200 m a.s.l.) is the optimal zone for northern red-backed and the pessimum zone for grey red-backed voles (Fig. 11). The estimation of the distribution of the effects produced by endo- and exogenic factors upon demographic characteristics of each species in these two regions is of considerable interest. Besides, the factors that determine the reproduction intensity of this or that species include the structure and numbers of the co-occurring species.

About 100 multiple linear regression equations were calculated to estimate the factors influencing reproduction of northern red-backed and grey red-backed voles that inhabit different sites of the Sayan permanent study plot. The relations between the population characteristics and endo- and exogenic variables are qualitatively the same as these for the bank vole and do not furnish a radically new information. For this reason we omit their detailed description.

In May, grey red-backed vole occurs in all study years only on the territory falling within the altitudes 600–800 m a.s.l. On the rest of the territory they are found in separate years only. Variability of the population characteristics at this period of time is determined only for 15–18% by the demographic situation in the population in autumn of the preceding year. It is actually independent of the population state in May, and depends for not more than 3% on the numbers and reproduction intensity of northern red-backed vole. The share of the explainable variance is 17 to 20% and the remaining 80% of variance is due to the operation of uncontrolled and random factors, out of which, probably, changes in weather conditions and food resources make the greatest contribution (Table 31). Only the autumn-winter survival is determined in 73% by the population state in autumn of the preceding year. Only 1% of the changes in survival of grey red-backed can be explained by fluctuations in demographic characteristics of northern red-backed vole.

In June, grey red-backed vole occurs throughout the territory of the study plot. In the region of optimum conditions 59% of the total variability (out of the total explainable variance of 71%) is due to endogenic factors. The changes in the population numbers being affected mainly by means of inverse density-dependent relations that lower the reproduction activity as the number and fraction of the own-species animals increase. Numbers, age structure and population organization of northern red-backed vole determine only for 12% the demographic processes of grey red-backed (Table 31). An extreme situation is observed in the subbelt of mountain taiga forests, where the population of grey red-backed vole drops sharply. In this altitude range habitats are pessimal. Here a maximum contribution to the changes in the reproduction intensity of grey red-backed is made by the structure and numbers of the northern red-backed vole population (40% out of the

Table 31

Influence of the factors acting upon the grey red-backed vole population (Western Sayan, 600–800 m above sea level)

Month	Population characteristics	Endogenic factors at moment of time		Contribution of sympatric species	Share of explainable variance
		preceding	current		
May	Total numbers	18.1	0	2.3	20.4
	Total fraction of breeding females	18.7	1.2	0.4	20.3
	Number of overwintered voles	14.3	0	2.8	17.1
	Winter survival	72.8	0	1.1	73.9*
June	Fraction of breeding current-year females	17.2	41.1	5.7	64.0
	Fraction of sexually immature current-year females	0	44.7	28.0	72.7
	Total fraction of breeding voles	5.1	59.5	7.3	72.0*
	Total fraction of sexually immature females	0	64.7	7.4	72.1*
	Total fraction of sexually immature males	5.3	57.4	12.3	75.0
	Number of breeding current-year females	4.1	70.3	11.7	95.1*
July	Fraction of breeding current-year females	31.5	15.2	22.7	69.4
	Fraction of sexually immature current-year females	28.0	23.5	15.1	66.6
	Total fraction of sexually immature females	51.3	10.3	24.4	85.9
	Total fraction of breeding females	23.6	44.9	7.9	76.4*
	Total fraction of sexually immature females	23.6	44.9	7.9	76.4*
	Total fraction of sexually immature males	29.7	36.7	16.3	82.6*
	Number of breeding current-year females	28.3	39.2	11.1	78.5
	Fraction of breeding current-year females	53.7	17.2	25.6	96.5*
August	Fraction of sexually immature current-year females	6.8	41.2	35.5	83.5*
	Total fraction of sexually immature males	45.9	11.5	9.8	67.2
	Total fraction of breeding voles	8.9	16.4	49.0	74.3
	Total fraction of sexually immature females	9.3	18.7	46.8	74.8
	Total fraction of sexually immature males	30.6	28.8	14.7	74.1

* Here and in Tables 32, 33, 34, 35 the explainable variances are values significant at $p=0.05$.

Table 32.

Influence of the factors acting upon the grey red-backed population (Western Sayan, 800–1 000 m above sea level)

Month	Population characteristics	Endogenic factors at moment of time		Contribution of sympatric species	Share of explainable variance
		preceding	current		
June	Total fraction of breeding females	0	11.9	48.2	60.1
	Total fraction of sexually immature females	0	11.0	48.8	59.8
	Total fraction of sexually immature males	3.0	43.7	23.6	70.3
July	Fraction of parous current-year females	19.9	31.7	26.6	78.2
	Fraction of sexually immature current-year females	17.9	56.1	2.8	76.8
	Fraction of sexually immature current-year males	11.1	49.1	9.0	69.2
	Total fraction of parous females	23.9	43.3	1.9	69.1
	Total fraction of sexually immature females	24.0	43.2	2.8	70.0
	Total fraction of sexually immature males	18.5	40.6	2.6	61.7
	Number of parous current-year females	13.8	22.1	19.0	54.9
August	Fraction of parous current-year females	64.0	6.3	3.6	73.9
	Fraction of sexually immature current-year females	42.8	16.0	12.5	71.3
	Fraction of sexually immature current-year males	35.9	22.9	3.4	62.2
	Total fraction of parous females	50.8	3.9	12.2	66.9
	Total fraction of sexually immature females	50.8	3.9	12.2	66.9
	Total fraction of sexually immature males	21.7	10.4	6.5	38.6

total 63% variance at altitudes 800–1 000 m a.s.l. and 41% out of 56% at altitudes 1 000–1 400 m a.s.l.) (Tables 31–33). The influence of the May numbers and structure of the grey red-backed vole population does not exceed 1% and that of the demographic situation in June is not more than 15–20%. Sexual maturation of young males in June in the optimum zone is determined mainly, as in the case of females, by the population abundance and its composition in June. At other sites, of greater importance is the demographic structure of the northern red-backed vole population but, as distinct from females, breeding activity of males is affected largely by the situation of grey red-backed vole in June. The interval from May to June is the time of maximum increase in the population of grey red-backed vole. In this period the population control processes become more ordered and

Table 33

Influence of the factors acting upon the grey red-backed vole population (Western Sayan, 1 000–1 400 m above sea level)

Month	Population characteristics	Endogenic factors at moment of time		Contribution of sympatric species	Share of explainable variance
		preceding	current		
June	Fraction of breeding current-year females	0	18.0	47.6	65.6
	Fraction of sexually immature current-year females	0	7.7	35.5	43.2
	Total fraction of breeding females	0	2.8	34.9	37.7
	Total fraction of sexually immature females	0	3.0	37.5	40.5
	Total fraction of sexually immature males	0	39.2	51.4	90.6*
	Number of breeding current-year females	0	29.0	29.4	58.4
July	Fraction of breeding current-year females	5.1	31.0	37.9	74.0
	Fraction of sexually immature current-year females	18.1	50.4	9.1	77.6*
	Total fraction of sexually immature males	10.5	69.8	5.7	86.0*
	Total fraction of parous females	31.9	8.3	13.9	54.1
	Total fraction of sexually immature females	31.9	8.4	13.9	54.2
	Total fraction of sexually immature males	12.0	56.0	21.2	89.2*
	Number of parous current-year females	32.5	41.1	14.6	88.2*
August	Fraction of parous current-year females	46.0	29.7	13.1	88.8*
	Fraction of sexually immature current-year females	24.5	65.0	7.3	96.8*
	Fraction of sexually immature current-year males	23.6	15.1	28.9	67.6
	Total fraction of parous females	36.0	58.3	2.1	96.4*
	Total fraction of sexually immature females	36.0	58.3	2.1	96.4*
	Total fraction of sexually immature males	35.8	52.3	4.8	92.9*

stringent. The role of uncontrolled and random effects lowers from 80% in May to 30–35% in June at all sites.

In the second half of summer the growth rate of the grey red-backed vole population decreases in spite of the fact that the total fraction of breeding females rises. Most probably, mortality of young voles increases at that time on the entire territory and the effect is pronounced most in the pessimal region. As a result, distribution of factorial loads changes considerably in different zones. Participation in breeding and sexual maturation of young females occurring at the sites located at altitudes 600 to 800 m a.s.l. are determined primarily by the events that took

place in the population in June (32%). Major contribution is made also by July structure and numbers of northern red-backed vole (23%). As compared to June, the role of the July demographic situation drops to 15% (Table 31). Grey red-backed vole females occurring at 800 m a.s.l. are subject to rather considerable influences on the side of variation population groups – both of their own-species animals and northern red-backed vole, with the contribution made by either species being approximately equal. The role of preceding population situation in the regulation of the reproduction intensity of current year females rises compared to June but does not become decisive (Tables 32, 33).

In optimal habitats sexual maturation of young males is limited mainly by the numbers and composition of the *C. rufocanus* population in June and depends very weakly on the population abundance in July. Factorial components in reproduction of young males in pessimal habitats exhibits a quite different distribution. Here the main regulating function are the numbers and structure of the grey red-backed vole population in July. The influence of northern red-backed vole on sexual maturation of young males does not exceed 1%.

In August, the population of grey red-backed vole attains maximum seasonal values, the fraction of breeding females lowers, compared to July, by 5% on the average. It is preserved at a sufficiently high level (60%), while the population growth rates become minimum are only 15% per month (Fig. 11). At that period the reproduction activity of young voles living in the optimum biotope is determined in more than 70% by the operation of intrapopulation factors. The influence of northern red-backed vole is preserved at a level of 20–26%. However, when in July the influence of preceding demographic situations exceeds only slightly, at least for females, all the other effects, in August this group of effect has an absolute dominance over the others (Table 31).

In the subbelt of mountain taiga forests at altitudes over 800 m a.s.l. the fraction of breeding males and females is determined, as in the optimum zone, mainly by endogenic factors; the role of the sympatric species lowers and can be estimated at 20% (Tables 32, 33).

The distribution of the effects produced by the factors influencing the grey red-backed vole population is controlled at least by three components: seasonal (reproduction), quality of the habitat (optimal, pessimal), and intensity of the processes taking place in the population of the own and sympatric species. At the beginning of the breeding season (May in the case of grey red-backed vole in Western Sayan) the numbers, survival and participation in breeding are explained only in 33% by operation of the considered factors, out of which 31% is due to the factors connected with the population history. The remaining part of the total variance is associated with other disregarded and random effects, out of which (in analogy with the bank vole) weather and food conditions play the leading role throughout the permanent study plot.

The interval from May to June for grey red-backed vole is the time of maximum population increase. In this period differentiation of the factorial load distributions depending on the habitat quality is observed. Thus, in the optimal zone at a rather low fraction of breeding females (about 40%) and the lowest rates of the population numbers growth the main role is played by endogenic factors, while

in the pessimal zones – by the abundance and structure of the sympatric species. Such a division of factorial loads can be most probably explained by the fact that at altitudes 600–800 m a.s.l. grey-red-backed voles dominate in numbers and, besides, the habitats are optimal for them. Quite natural is that changes in the reproduction activity, especially of young voles, depend chiefly on the structure and numbers of grey red-backed at that period. In the territories located above the optimum zone the population of *C. rufocanus* lowers and that of northern red-backed vole rises and attains maximum values at altitudes 800–1 000 m a.s.l. The fraction of breeding voles increases to 60%, while the population growth rate lowers almost two-fold, a fact which is most likely due to increased mortality especially in unfavourable habitats. Northern red-backed voles dominate on this territory and an increase in their abundance represents the main factor that limits the population growth and reproduction activity of these animals.

In the second half of summer (July–August) the abundance of grey red-backed vole rises, the fraction of breeding current-year females increases, while its population growth rate becomes still lower. The response of the animals to changes in the population numbers and structure of animals of the own and sympatric species is the same in different zones. At this period is influenced mainly by intrapopulation factors. Only in the optimal regions (600–800 m a.s.l.) the contribution of northern red-backed vole into the demography of grey red-backed vole into the characteristics variability of the speaks attains 30%, whereas in pessimal habitats it does not exceed 10%.

As regards the set of population indices, the territory of the Western Sayan permanent study plot is divided for northern red-backed vole into the pessimal (mountain bilberry forests at altitudes 600–800 m a.s.l.) and optimal (mountain taiga forests at 800–1 200 m a.s.l.) regions. Let us consider the hierarchy of the effects influencing the population of northern red-backed vole in these regions. At the beginning of the reproduction period (May) the total numbers and winter survival are determined in 70% by intra-population factors and only 10% of variance of these characteristics is due to the processes that take place in the population of grey red-backed vole (Table 34). The data obtained are true only for the optimal region. Observations were not made in May in other zones.

From May to June, in favourable habitats in mountain taiga forests the numbers of northern red-backed increase, as does the fraction of breeding young voles: by June it equals 56% for females and 38% for males. The population of grey red-backed vole grows, too, and the fraction of breeding females even attains 70%; however, this species is the dominant (by a set of criteria) in this zone. It is probably for this region that the reproductive potential of northern red-backed (fraction of breeding animals and sexual maturation of young voles) is only 5–12% determined by the abundance of grey red-backed. The processes taking place in the northern red-backed vole population are affected most by the population numbers and structure of its own species at preceding and current moments of time, i.e. by endogenic factors. In habitats that are favourable for northern red-backed vole at altitudes 600 to 800 m a.s.l. the decisive role belongs to endogenic factors, while the influence of the sympatric species animals enhances there up to 18–27% (for various characteristics). An increase in the influence of one species upon the other

Table 34.

Influence of the factors acting upon the northern red-backed vole population (Western Sayan, 800–1 200 m above sea level)

Month	Population characteristics	Endogenic factors at moment of time		Contribution of sympatric species	Share of explainable variance
		preceding	current		
May	Total numbers	69.8	0	8.7	78.5*
	Winter survival	41.1	32.1	1.1	80.3*
June	Fraction of breeding current-year females	10.2	69.7	4.3	84.3*
	Fraction of sexually immature current-year females	18.8	46.7	12.2	77.7*
	Fraction of sexually immature current-year male	24.8	31.2	7.2	63.3
	Total fraction of breeding females	48.9	39.5	6.7	95.1
	Total fraction of sexually immature females	8.2	56.7	11.3	76.2*
	Total fraction of sexually immature males	0	21.8	26.9	48.7
	Number of breeding current-year females	6.1	74.5	6.4	87.0*
July	Fraction of breeding current-year females	32.2	5.5	3.3	41.0
	Fraction of sexually immature current-year female	33.4	4.5	11.1	49.0
	Fraction of sexually immature current-year male	15.9	15.8	5.3	37.0
	Total fraction of breeding females	30.8	4.8	16.5	52.1
	Total fraction of sexually immature females	49.1	9.9	4.4	63.4
	Total fraction of sexually immature males	15.1	1.5	9.3	35.9
	Number of breeding current-year females	43.9	20.7	10.4	75.1
August	Fraction of breeding current-year females	48.6	18.5	5.4	72.6
	Fraction of sexually immature current-year female	46.6	16.4	8.3	71.3
	Fraction of sexually immature current-year male	13.6	40.6	13.3	67.5
	Total fraction of breeding females	33.0	10.4	18.3	61.7
	Total fraction of sexually immature females	33.4	12.6	18.5	64.4
	Total fraction of sexually immature males	16.7	21.3	34.5	72.5*

Asterisks – explainable variance.

in the pessimal zone compared to the optimal zone is due probably to aggravation of competitive relations between northern red-backed and grey red-backed voles (Table 35).

In July, the share of variance explained by the operation of endogenic factors and by the influence of sympatric species reduces to 45% (from 25 to 63% for various characteristics) in favourable habitats and to 60% (from 40 to 70%) in pessimal zone, a fact which means that the birth-rate and mortality phenomena forming the population dynamics are determined to a greater extent by uncontrolled and random effects. Besides, while in June the structure and abundance of the own species at the moment of study played a considerable role among endogenic effects, in July the role of preceding situations rises markedly. The influence of grey red-backed on the demographic processes of northern red-backed vole is lower, as in other moments, in the optimal zone (800–1 200 m a.s.l.) compared to other zones, although in July the contribution of the co-occurring species

Table 35

Influence of the factors acting upon the northern red-backed vole population (Western Sayan, 600–800 m above sea level)

Month	Population characteristics	Endogenic factors at moment of time		Contribution of sympatric species	Share of explainable variance
		preceding	current		
June	Total fraction of breeding females	0	48.5	27.0	75.5*
	Total fraction of sexually immature females	0	49.2	26.2	75.4*
	Total fraction of sexually immature males	0	53.3	18.1	71.4*
July	Fraction of breeding current-year females	23.4	1.0	17.6	42.0
	Fraction of sexually immature current-year females	17.2	26.2	3.9	47.3
	Fraction of sexually immature current-year male	7.4	43.2	15.7	66.3
	Total fraction of breeding females	28.6	33.2	8.0	69.8
	Total fraction of sexually immature females	28.6	33.0	8.4	70.0
	Total fraction of sexually immature males	18.1	7.2	40.0	65.3
	Number of breeding current-year females	26.7	9.3	17.5	53.5
August	Fraction of breeding current-year females	28.8	27.6	25.4	81.8*
	Fraction of sexually immature current-year female	14.0	45.8	23.6	83.4*
	Fraction of sexually immature current-year male	33.0	23.0	25.6	81.6*
	Total fraction of breeding females	24.0	24.7	37.2	85.9*
	Total fraction of sexually immature females	24.3	24.5	37.1	85.8*
	Total fraction of sexually immature males	13.5	25.5	52.1	91.1*

Asterisks – explainable variance.

is reduced, compared to other months over the entire territory. From July to August little seasonal increases in the population of northern red-backed vole were noted on the entire territory of the study plot, a circumstance which should lead to lowering of the explainable variance and to enhancement of the share of random effects. However, by August the explainable part of the variance turned out to be larger than in the preceding months. This suggests an increase in the degree of ordering of the population processes and better quality of control of the reproductive potential and population abundance of northern red-backed. For the majority of the indices of the population functioning level the growth of the controlled part of the variance is due mainly to a rise in the contribution of the sympatric species (Tables 34, 35). In the pessimal region the role of grey red-backed vole becomes decisive among other effects, while in the optimal zone it approaches in efficiency to the effect of endogenic factors.

So, different combination of the habitat conditions (optimal and pessimal habitats), reproduction cycle phases, functioning level of the populations of the own and sympatric species (reproduction intensity and population growth rate) determine the hierarchy of the factors acting upon a population.

5. ZONAL AND BIOTOPIC PECULIARITIES OF THE FOREST VOLE POPULATIONS

5.1. NUMBERS AND THEIR VARIABILITY

The bank vole is widely spread over the territory of the Soviet Union. In the meridional direction it occurs from the northern taiga of the Kola peninsula to island forests of Ukraine and in the longitudinal direction the bank vole inhabits the European part of the USSR and part of Asia up to the river Enisei and Western Sayan mountains (Bashenina 1981). Basic habitats of the bank vole are situated in the forest zone. Our study deals with the features specific to the population dynamics of the bank vole in the taiga zone and the zone of broad-leaved forests. In addition, in the taiga zone the population was censused in primary and secondary biotopes, in the subzones of mid-taiga and sub-taiga forests. In each of these subzones the population structure and numbers are determined by the biotopic conditions, food and protection resources, on the one hand, and by ecological requirements of the animals, on the other.

The territories of the study plots are inhabited by bank and northern red backed voles, common field and striped field mice, grey red-backed voles, shrews and other small-number species. Judging by numbers and their variability, in summer the bank vole is the dominant species in all the habitats studied. According to multiannual observations, the fraction of this species in the population in different months of the snowless period and on different permanent study plots varies between 55 and 85%. Other species constitute only an insignificant part of the population. In all anthropogenic landscapes dominance of the bank vole lowers and other species become predominant during succession. Living conditions improve for grey red-backed vole in clearings and for mice in secondary mixed and deciduous forests. In addition to the fact that the bank vole dominates the popu-

lation on all permanent study plots, its numbers variability is lower than that of other species.

The bank vole population is most stable in primary forests (the total numbers variation coefficients oscillate there from 50 to 98%). In secondary forests the numbers variation coefficient rises to 65–137% (Tab. 36), this indicating probably to impairment of the living conditions and their lower stability for the bank vole. The numbers variability of other vole species and shrews is much higher and falls within 110 to 250% for various zones. Besides, variation coefficients of the bank vole population suffer changes in different months of the breeding season. At the onset of the breeding season the numbers variation coefficients are close in their values for primary forests of different zones; the coefficient value depends mainly on fluctuation in weather conditions that determine the onset of breeding in different years. In June, in the phase of the maximum population growth the numbers variability of the bank vole is at a maximum (except the Tula permanent study plot). During this period the strategy of the population consists in a maximum possible population growth rate. Most probably, in the phase of rapid growth a major part of the animals' energy resources is directed for sexual maturation and reproduction intensification, this leading to lowering of the protection functions of the organism and, as a consequence, even insignificant changes in external conditions and population state result in considerable variation in mortality and, hence, in large amplitude of the numbers fluctuations.

In August – September the seasonal peak of abundance is observed and it is at this period that the population of the animals is stabilized. An increase in the population stability by autumn is typical of the bank vole inhabiting different geographical points (Tupikova, Konovalova 1971, Bashenina 1981, Jensen 1982, Southern 1982, Petruszewicz 1983, Zhigalski et al. 1987). A decrease in the population variability during the seasonal peak is likely due to the fact that the abundance of voles reaches the upper limit characteristic of each permanent study plot and further growth of the population becomes impossible.

The number of individual species of forest mammals entering the population change considerably in different years, whereas the total number of animals which can find sufficient amount of food and good conditions for reproduction and breeding of the young is rather stable despite some differences in conditions of each particular year. A relative stability to the total numbers is connected with a limited capacity of the small mammals' habitat which is determined in each geographical zone by a set of conditions (climate, weather, food, composition of forest-forming species, availability of shelters, etc.) and exhibits a stability typical of the set. The ecological capacity of the biocoenosis determines, in turn, an adequate number of animals which can exist on the given territory. A decrease in the number of one species can be accompanied by an increase in the population of others, thus maintaining and stabilizing the optimum between the total abundance of the animals and the ability of the medium to ensure for their living. However, in this case, an extremely important task facing the population of small mammals is keeping their numbers at a level that does not exceed the limiting one for the given conditions. Therefore a decrease in the variability of the total population numbers is determined, on the one hand, by stability of the biotope capacity (sub-

Table 36

Numbers of forest voles (numerator) and their variability (denominator)

Species	Habitat	Demographic characteristics, %				Mean numbers over a season	Cyclicality index
<i>C. glareolus</i>	Tula study plot; oak-lime forests	April 11.1/90.9	June 15.0/66.5	August 24.3/50.9	October 20.3/51.0	17.7	0.37
	Mari study plot; spruce-lime forests	11.2/87.8	16.9/110.3	34.9/55.1	20.9/63.7	20.9	0.44
	birch forests	3.4/120.7	9.8/116.0	21.6/66.6	11.0/115.7	11.4	0.42
	regenerating 1957 clearing	5.2/89.4	12.8/96.7	23.0/68.4	18.2/74.7	14.8	0.43
	regenerating 1968 clearing	2.3/153.6	5.3/159.5	15.7/86.8	13.2/90.3	9.1	0.49
	Udmurt study plot; lime-fir-spruce forests	6.3/70.8	12.8/93.6	21.0/54.7	13.7/75.9	13.5	0.42
	Karelia study plot; true-moss spruce forests	June 2.0/98.9	July 2.8/102.7	August 3.8/72.8	September 9.2/107.1	4.4	0.8
	deciduous and mixed forests	1.3/135.5	1.8/113.9	4.1/136.5	7.7/126.5	3.7	0.84
<i>C. rutilus</i>	Western Sayan study plot; mountain bilberry forests	May 2.2/110.6	June 2.0/113.7	July 2.2/110.0	August 3.9/74.6	2.6	0.25
	mountain taiga coniferous forests	4.2/100.2	5.5/65.8	6.4/50.9	8.6/54.9	6.2	—
	Siberian stone pine-fir-true-moss forests	5.2/90.6	5.7/72.3	5.8/59.1	8.8/63.1	6.4	0.23
	true-moss Siberian stone pine forests	3.2/80.2	3.8/76.3	5.4/97.0	7.2/86.1	4.9	—
<i>C. rufocanus</i>	Western Sayan study plot; mountain bilberry forests	May 3.1/72.7	June 5.7/90.0	July 6.8/68.0	August 7.4/72.9	5.8	0.35
	mountain taiga coniferous forests	4.3/66.8	5.0/100.0	6.7/79.1	6.8/81.9	5.7	0.38
	Siberian stone pine-fir-true-moss forests	1.3/83.7	2.9/93.8	4.5/77.1	6.1/79.0	3.7	0.48
	true-moss Siberian stone pine forests	1.8/94.5	2.4/117.6	3.2/101.9	5.2/88.3	3.2	—

ject to variations in external conditions) and, on the other hand, by the efficiency of the intrapopulation mechanisms limiting the population growth.

Apart from seasonal component of the numbers variability, its geographical component is present as well. The amplitude of changes in the bank vole population increases in going from the south (zone of broad-leaved forests) to the north (mid-taiga subbelt) (Table 36). Some zoologists (Ivanter 1975, Hansson, Henttonen 1985) have come to a similar conclusion but the geographical component of the numbers variability was analyzed in sufficient detail by Hansson and Henttonen (1985) who give a list of 45 sites of multiannual observations made in Fennoscandia from 55.5' to 68' N. They showed rather convincingly that the numbers variation coefficients rise in going to the north but the given series contains some descriptions which do not obey the general regularities. For example, between 62 and 64' N the variation coefficients are within 96–120%, whereas according to the data obtained by Skaren (1972) for northern Fennoscandia (64') the variation coefficient equals 68%. There are habitats in southern Fennoscandia, where opposite shifts (increase of the variability level) were detected. Inadequate values of the variation coefficients in some geographical points against the background of their directional changes represent the main case of arguments on this point.

We have shown earlier then, along with a decrease in variability in going southward, the numbers variation coefficients can change over extremely wide limits on the same study plots but in different habitats. This is especially pronounced on the territory of the Mari permanent study plot. In spring the numbers variability in primary forests is almost twice as low as in clearings and even in autumn, when the total level of variability lowers, differences between primary and secondary habitats, though becoming smaller, persist.

A decrease in the bank vole population stability in going northward and in anthropogenic habitats is associated with a lower versatility of northern and disturbed biocoenosis. This agrees well with the existing opinion that an increase in the heterogeneity of the medium results in a higher stability of communities (May 1973, Goodman 1975, Puzachenko and Skulkin 1981).

To estimate the numbers variability level, the cyclicity index is used (Hansson, Henttonen 1985) along with the traditional standard deviation and variation coefficients. The cyclicity notion itself is interpreted rather freely in the population biology, although it has an unambiguous definition. Cyclicity is a regular and strictly recurrent alternation of population phenomena. In this context the cyclicity index does not reflect the duration of the interval between rises and falls in numbers but serves as a criterion for estimating the population variability of the animals. The cyclicity indices calculated for the bank vole populations considered here are given in Table 36. They rise synchronously with the variation coefficients in going from the south to the north. The cyclicity index is more stable compared to the standard deviation since it includes only the geographical component and is determined by climatic factors and total ecological capacity of the habitat typical of each latitudinal zone rather than by particular changes in weather conditions and the habitat capacity in each biotope. In different habitats of the Mari permanent study plot the difference in the variation coefficient values

of the spruce-lime forest and clearings attains 35%, whereas the cyclicity index only by 10%.

The problem of the causation of different levels of variability has been so far unsolved in many respects but, with increasing number of long-term stationary observations of individual populations, it becomes clear that the numbers fluctuations can be of purely seasonal character (Pokrovski 1967, Anderson 1970, Shvarts 1980) or they can show up as different increases in numbers, which do not fit regular cycles (Anderson 1970, Tensen 1982). Besides, as is seen from Table 36, cyclic (Karelia study plot) and acyclic populations of the bank vole exist within a single species. Myllymäki (1985) arrived to a similar conclusion. The variability amplitude depends on some factors: geographical location (Ivanter 1975, Kaikusalo 1982, Hansson, Henttonen 1985), wealth of habitats (Tamarin 1978, Krebs 1979), and migration flows (Lidicker 1978, Boonstra, Krebs 1979, Abramsky, Tracy 1980). The majority of investigators single out, however, three basis groups of factors that determine the variability level of the bank vole population.

One of the explanations of the variability gradients obtained can be latitudinal differences in the predator-vole interrelations. The most important element of this hypothesis is the availability of several alternative species of preys and the ability of predators to change their diet from voles which are few at a given moment (not bringing their population to critically low numbers) to numerous species. The species distribution and abundance of preys can be determined by the quality and capacity of the medium, degree of anthropogenic changes (Angelstam et al. 1984), heterogeneity (Hansson 1977, 1979), and productivity of phytocoenosis (Abaturon 1984). Most of these characteristics correlate negatively with the degree of adversity of the living conditions and therefore the closer to the north the area inhabited by a population, the larger the amplitude of the vole numbers fluctuations.

No less convincing is the hypothesis that explains the variability level fluctuations on the basis of relations between the rodents and productivity and quality of plants (Laine, Henttonen 1983). It is impossible however to give preference (as regards control of the variability amplitude) either to predators or to food resources proceeding from the currently available data. If voles followed only the rhythms of vegetation whose cyclicity is pronounced most, one could expect asynchronous fluctuations of sympatric species owing to specific preference given by different vole species to forage plants. Instead, numbers of all species change synchronously on all the permanent study plots: correlation coefficients are positive everywhere and exhibit high values. In northern Fennoscandia the rise and lowering of the population level also occur synchronously for all species (Hansson and Henttonen 1985).

Weather conditions in northern regions, particularly in Karelia, are characterized as unstable. Warm periods in winter can be replaced by severe frosts and in summer cold periods with rains (not a rare case). All this, along with the other factors considered, can determine the variability level.

Scientists have long been discussing the causes responsible for fluctuations in the vole population and the role played by intrapopulation (physiological stress,

genetic and behavioral polymorphism) and external (climate, food, predator impact) factors. However, it is customary to assume (Ivanter 1975, Koshkina, Korotkov 1975, Krebs 1979) that external factors are more important in northern regions and endogenic factors are more essential in southern regions (Ryszkowski et al. 1973, Ivakina 1987).

Seasonal dynamics of the bank vole is of the form typical of small mammals inhabiting temperate zone (Tupikova, Konovalova 1971, Zejda 1973, Hansson 1974, Ivanter 1975, Christiansen 1983). The bank vole numbers are low at the beginning of the breeding season, rise gradually in summer, reach maximum values by the end of summer, and lower again in autumn. During the autumn-winter period the population of the animals decreases and in spring 30 to 60% of voles born in the preceding year are left in the population. Two periods are clearly seen in the seasonal dynamics: growth (April–August) and drop (from the seasonal peak to spring of the following year). Geographical differences in the seasonal dynamics of the bank vole manifest themselves in the numerical fluctuations and in a much later termination of breeding in the north. Analogous changes of the seasonal dynamics are noted in the succession series in going from primary forests through all development stages of the communities to clearings of different standing (Table 36).

An increase in the vole population in the southern parts of the area and in primary forests is accompanied by a decrease in the population increments during the reproduction period (from spring to the seasonal maximum). Negative correlations arise between the total numbers of the population and the value of its seasonal increment: the higher the vole numbers, the lower the increment. In the zone of broad-leaved forests of the Tula study plot and primary subtaiga forests of the Mari and Udmurt study plots the seasonal increase of the population is 2.1 - 3.3-fold, while on the Karelia study plot and in secondary forests of other territories the population increase is much higher and varies between 4.6– and 6.8–fold. The population growth is influenced most by the spring numbers: the higher the abundance of voles in spring, the more the vole numbers approach the level that is limiting for the given conditions, and the lower increase of the population brings it closer to the maximum level. A different picture is observed at low spring numbers. In this case the difference between the spring and critical populations is larger and the population can raise its abundance during the reproduction season by more fold. The lower limit of the population increase is at a minimum level, below which mortality starts to dominate over reproduction. The upper limit of the population increase is set by the habitat capacity; violation of the upper limit disturbs the equilibrium between the population numbers and the regeneration rate of the environmental resources (Freeland 1974, Zhigalski 1982, 1984, Abaturov 1984).

Low spring numbers of the bank vole secondary biotopes and northern parts of the area may be due to low ecological capacity of the medium (small number of shelters, severe weather conditions, shortage of food, etc.), though none the less important may be high winter mortality of the animals, which is caused by worsening of the vole living conditions and a great impact of predators in secondary forests and in the north. In all southern populations living in primary forests, the

Table 37

Breeding intensity of current-year voles (numerator: females; denominator: males)

Species	Habitat	Fraction of breeding animals, %				Winter survival
		April	June	August	October	
<i>C. glareolus</i>	Tula study plot;					
	oak–lime forests	33.3/90.0	52.7/46.0	30.6/22.4	24.2/2.0	46.9
	Mari study plot					
	spruce–lime forests	–	67.5/36.5	20.4/5.9	12.6/3.2	48.3
	birch forests regenerating 1957 clearing	–	61.8/27.9	18.8/6.3	19.8/0	28.6
	birch forests regenerating 1968 clearing	–	50.0/57.1	26.1/5.0	12.3/0	17.4
	Udmurt study plot					
<i>C. rutilus</i>	lime–fir–spruce forests	55.0/59.3	38.8/27.1	17.4/8.4	6.5/0.2	47.5
	Karelia study plot	June	July	August	September	
	true–moss spruce forests	36.9/87.0	44.4/72.7	56.8/38.9	21.9/3.8	31.3
	deciduous and mixed forests	12.9/98.9	54.4/99.4	33.3/70.0	51.4/1.1	22.7
<i>C. rutilus</i>	Western Sayan study plot	May	June	July	August	
	mountain bilberry forests	–	28.3/94.5	32.4/18.7	42.3/20.3	50.8
	mountain taiga coniferous forests	–	54.8/36.3	62.8/46.6	49.5/31.3	43.9
	true–moss Siberian stone pine– fir forests	–	53.6/33.3	63.3/38.2	65.7/32.1	53.2
	true–moss Siberian stone pine forests	–	59.4/51.5	46.3/41.6	63.1/36.1	40.1
<i>C. rufocanus</i>	Western Sayan study plot					
	mountain bilberry forests	–	44.4/7.4	66.7/31.3	60.5/31.0	37.7
	mountain taiga coniferous forests	–	51.0/13.7	68.7/24.8	53.8/20.5	56.9
	true–moss Siberian stone pine– fir forests	–	72.2/9.7	67.9/28.8	68.1/33.2	19.2
	true–moss Siberian stone pine forests	–	59.3/0.2	64.6/21.1	68.2/24.6	31.1

autumn–winter period is survived by 47–48% of the animals born in autumn of the preceding year (Table 37). According to the data of Tupikova and Kononova (1971), in southern taiga lime forests mortality of the bank vole from September to June was about 74% and varied for different ages from 10 to 83%, this being in agreement with our idea. On the Karelia study plot and in southern secondary forests winter survival of the voles is much lower and varies between 17 and 31% (Table 37).

Although the phenomena of the numbers variations of the southern populations in secondary forests and northern populations in primary and secondary forests are outwardly similar, these variations are realized in different ways. High rates of the population increase in the first half of summer and its slow drop in the second half of summer in secondary forests for southern populations cannot be explained by changes in the reproduction activity, because the fractions of breeding females are approximately the same both in primary and secondary biotopes. Breeding stops early there and in August not more than 25% young females participates in reproduction. The detected differences in the rates of the population growth and fall are probably due to the fact that in secondary habitats the vole population rises not only at the expense of reproduction of the settled population but also as a result of the flow (that increases in early summer) of young animals from primary to secondary habitats, where the population density is much lower. As the bank vole moves to the north, the reproduction season becomes longer: in August over 50% of young females still participates in breeding and even in September the fraction of breeding females is larger than in southern populations (Table 37) despite the fact that weather conditions in autumn are much worse for northern populations than for southern ones. This means that low numbers levels encourage a delay in the termination of breeding equally in southern and northern populations. Proceeding from this, it may be stated with a great degree of validity that in southern populations living in secondary forests high population increments are determined mainly by migration flows of young animals from primary to anthropogenic habitats, whereas in northern populations the population increments are due to an extended reproduction period and general enhancement of the reproduction activity of young voles.

5.2. DURATION OF THE REPRODUCTION SEASON

At different geographical points varies over sufficiently broad limits. In the majority of cases reproduction-active females occur during 4 - 6 months but the terms of the reproduction onset and termination differ markedly: the variation coefficient is of the order of 80%. In medium latitudes females with implanted embryos appear at the beginning of April and the term of their appearance are extended approximately for two weeks. In some years winter-late autumn (November-December) and sometimes early-spring (February-March) breeding is noted on the Mari, Udmurt and Tula permanent study pots and in 1985 breeding persisted throughout the autumn-winter period in Udmurtia. The all-year-round breeding is noted also in other parts of the area; however, it is observed irregularly only in the years with mild winters and adequate food resources (Zejda 1966, Bernshtein et al. 1975). In these latitudes mass reproduction of the bank vole stops as a rule in late August - mid-September but in some years it terminates already in July and sometimes even in October reproduction-active females are present in the population.

In the Karelia population of the bank vole the reproduction period is shorter, which is characteristics in general of northern altitudes (Viro 1974, 1974a, Hansson 1974, Ivanter 1975). However, differences in the terms of the breeding termination from year to year within a single population exceed the geo-

graphy-induced terms. The terms of the breeding termination vary to a greater extent than the terms of the breeding onset and, as is rightly noted by N.V. Tupikova, E.A. Konovalova (1971) and E.V. Ivantseva (1975), apart from the phenologically determined decrease of the reproduction intensity and complete termination of breeding in the second half of summer, they depend also on the population numbers level. If the numbers are high, breeding stops already in July and if the numbers are low, pregnant females are caught in September–October (Koshkina 1967, Wiger 1979, 1982).

In all the populations considered the onset of the reproduction season is determined by a combined action of endogenic factors. On the Udmurt permanent study plot their effects are disturbed as follows: 31.6% of the total variability in the terms of the breeding onset is due to the population numbers and structure at the end of the preceding reproduction cycle; 16% is connected with the numbers of different sex-age groups in spring; 45.6% is determined by weather conditions in the autumn-winter period (from November of the preceding year to March of the following year); and only 6.4% can be attributed to changes in food resources. In the Karelia population in the north distribution of the factorial components determining the breeding onset does not exhibit principal differences from the population, except that the effects of weather conditions variation rise to 54%.

5.3. AGE COMPOSITION.

The age composition depends directly on the terms of the breeding onset and termination, as well as on the variation of the reproduction process intensity throughout summer. The age structure is one of the most essential population indices. It is formed as a result of reproduction and mortality but the age structure itself determines to a great extent the direction and intensity of these processes, being subject to considerable variations both in different geographical habitats and within a single reproduction cycle.

Over a single reproduction season the bank vole population changes almost completely and only few animals live for about two years. In medium-latitude regions, in spring at the beginning of a new reproduction period populations comprise almost 90% of overwintered animals and only 10% is due to current-year early-spring and winter litters (Table 38). On damaged territories, in going from early to later succession stages, the fraction of overwintered voles reduces. In fresh 1968 clearings, overwintered animals account for 29% of the population, while 71% is due to current-year 1–2 month-old voles (Table 38). In fresh 1975 clearings, permanent population is about altogether in April and it is only in separate years that single individuals are found. Predominance of young voles on disturbed territories is connected not with the intensification of reproduction at these sites (Table 37) but with migration of young voles from primary regions of the permanent study plot, where the numbers of the young are rather high in spring. The territory is divided between the animals inhabiting the study plot: the most optimal regions are occupied by adults and pessimal zones are inhabited by the young. This redistribution of habitats is controlled directly by the hierarchic status of different-age voles (Bujalska 1973, Shilov 1977, Kutenkov 1979, 1980, Lidicker 1978).

Table 38

Estimates of the age composition of forest voles (numerator: fraction of 3–6-month-old voles in the population; denominator: fraction of 1–2-month-old animals)

Species	Habitat	Age structure, %			
Bank vole	Tula study plot;	April	June	August	October
	oak–lime forests	5.4/11.7	8.0/62.0	28.4/65.0	54.7/42.9
	Mari study plot				
	spruce–lime forests	–/11.3	20.1/55.6	32.7/62.5	65.5/32.5
	secondary birch forests	–/18.1	10.2/65.3	33.8/60.2	80.9/19.1
	regenerating 1957 clearing	–/29.5	14.1/62.5	37.4/54.8	70.9/29.1
	regenerating 1968 clearing	–/29.4	18.9/64.2	34.4/60.9	82.7/15.9
	Udmurt study plot				
	lime–fir–spruce forests	3.2/11.2	7.0/72.7	9.5/85.7	33.8/64.2
	Karelia study plot	June	July	August	September
	True–moss spruce forests	–/44.4	–/72.5	12.2/85.7	24.9/74.2
	deciduous mixed forests	–/50.8	–/67.8	14.0/83.3	31.4/66.7
Total fraction of current-year voles					
northern red-backed	Western Sayan study plot	May	June	July	August
	mountain bilberry forests	–	35.7	37.5	68.2
	mountain taiga coniferous forests	–	20.0	60.7	74.1
	true–moss Siberian stone pine–fir forests	–	12.3	55.1	68.4
	true–moss Siberian stone pine forests	–	26.3	47.8	74.3
grey red-backed	Western Sayan study plot				
	mountain bilberry forests	–	40.3	65.7	72.5
	mountain taiga coniferous forests	–	40.3	65.3	72.8
	true–moss Siberian stone pine–fir forests	–	32.1	64.4	73.2
	true–moss Siberian stone pine forests	–	43.7	54.9	74.3

On the Karelia permanent study plot breeding starts later and therefore up to mid-May only overwintered voles are trapped (Ivanter 1975). In June, young animals appear, whose fraction does not exceed 50%, whereas on more southern study plot their fraction is close to 70%. In northern populations of the bank vole the fraction of current-year animals decreases proportionally to the reduction in their numbers (low number of females is associated with a lesser offspring) and general level of their reproduction (Table 37, 38).

In August, the fraction of the young in the population is independent of the latitude and varies from 94 to 98% for different geographical regions. In August, overwintered voles account for 6% of the mid-taiga populations and only

for 2% in northern populations. In spite of insignificant differences in the ratio of current-year and overwintered animals in these zones, their numbers differ more than ten-fold (Richter, Geiler 1972, Ivanter 1975). For this reason, in the north of the area adult females do not influence appreciably the distribution of home ranges and reproduction activity of young females, while in the south they can influence markedly the vital activity of young voles (Ivanter 1975, Gliwicz 1983, Ivakina 1987). For example, the influence of overwintered animals and voles from early-summer litters on sexual maturation and reproduction activity of young animals on the Tula and Mari study plots is rather high, whereas in Karelia the influence of overwintered animals is very low.

Of interest is the existence of differences in the ratios of the numbers of current-year voles from first generations and animals born in late summer in different geographical ranges. Here an increase in the fraction of trapped voles from late-summer litters is rather clearly seen as the populations move from the south to the north, which is undoubtedly connected with changes in reproduction activity. High reproduction activity of the Karelia population is accompanied by a large fraction of voles from late-summer litters.

Numerous investigations show that seasonal generations realize different reproduction strategies and therefore their numbers ratio at a particular moment of time determines largely the population dynamics (Olenov 1964, Pokrovski 1967, Brown 1973, Bujalska 1975, 1977, 1983). Animals born during summer come from different parents: those from the first and second generations represent the offspring of overwintered voles; the third and fourth generations are born by overwintered voles and individuals from the first generation. The fourth generation consists completely of the offspring of current-year individuals (first and second generations), while the last, the fifth, generation comprises offspring of the second, third and fourth generations. Partially the fourth and practically all the fifth generations do not reproduce in the year of their birth and give the first litter in spring of the following year, thus representing the basis of another reproduction cycle. The principal function of the animals from first spring litters is to ensure a maximum population increase. Animals from first spring generations are distinguished for the highest rate of growth and sexual maturation and practically all of them die, as a rule, by autumn. Voles born in mid-summer represent the population reserve which is engaged in breeding in the years with small numbers and in the periods unfavourable for the population (Olenov 1981). Finally, animals born in late summer-autumn are characterized by a delay in sexual maturation and inhibition of the growth and development processes. Demands of these animals are lower, while resistance to unfavourable effects is higher, and therefore their mortality in the autumn-winter period is lower compared to that of sexually mature animals from early litters (Ivanter 1975, Ivakina 1987).

To evaluate the "generation effects", we used a simulation discrete model (Shvarts et al. 1976, 1977). Computer-aided experiments, which were made for, changes in the mortality rate of young individuals and, also, for partial or complete exclusion of various generations from reproduction, allowed us to classify the influence of seasonal generations and showed that the first generation plays a special role in the population dynamics, while the fourth generation is next

in importance. Different mortality and birth rates of these generations lead to greatest alternations in the population structure and its numbers dynamics. If the fourth, along with the fifth, generation delivers the first offspring only in spring of the following year, the numbers variation rate increases approximately two-fold. So, the population has an additional reserve for raising its numbers in the following year; the reserve is determined however not only by the initial number of rodents by spring but also by the conditions of the year. For example, if favourable conditions occur in early summer (high survival of the young from first litters), the population numbers rise. If favourable conditions occur in mid-summer, the population numbers either remain unchanged or increase a little. Favourable conditions in late summer do not encourage an increase in the population.

In northern populations a considerable part of young voles, which must go in winter, are sexually mature and participate in breeding, a situation which results in their lower vitality and enhanced mortality during the autumn-winter period. As a consequence, spring numbers are maintained at a low level from year to year. Besides, small number of overwintered females give birth to proportionally small number of the young and, owing to unstable weather in those regions, especially in early summer, mortality of voles from first litters rises. As a result, the already low numbers of the first-generation animals which reached puberty become still less and the seasonal dynamics is determined by overwintered and first-generation voles. Another possible cause of low numbers in Karelia can be due to the fact that the bank vole inhabited the Pre-Ladoga regions relatively recently and therefore it had not time to develop an adequate system of adaptive reactions to more severe and varying living conditions.

A different situation takes place in medium-latitude populations. There not only the spring population in primary biotopes is high but also the number of animals from first generations is higher, while more favourable and stable weather conditions encourage high survival of young animals. A favourable combination of population characteristics enables the population to reach high numbers levels. Certainly, one cannot disregard an enhanced ecological capacity of the habitats but it is so far impossible to estimate the contribution made by each of these components. As with northern population, the spring numbers in disturbed medium-latitude sites are low, a fact which is due to the absence of permanent population during the autumn-winter period. Young animals which come to these biotopes (from the first generation) are sufficiently numerous and therefore bring large offspring; mortality of the animals and their offspring is low and by August the population reaches the threshold numbers which are adequate to the ecological situation in each biotope.

In medium-latitude populations of small mammals wintering animals prove for continuity of the population, young voles ensure seasonal increase of the population, and their offspring forms the group of animals which serve as the basis for another reproduction cycle. Depending on the population location, season and the numbers level, females from different age groups change their reproductive contribution dependently on the changes in the population numbers. At the beginning of another reproduction cycle the population growth processes are con-

nected with the activity of overwintered voles and starting from the period of intensive breeding current-year animals contribute more and more to the potential increase of the population. In June, in medium-latitude populations of the bank vole up to 70% of the offspring is due to this year's breeds, with the major part of the offspring coming from youngest voles (Tupikova, Konovalova 1971, Bujalska 1975, 1975a, 1985, Bronson 1985, Gliwicz 1975, 1983, Ward, Reed 1985, Ivankina 1987). At that time in Karelia the population grows mainly at the expense of overwintered voles and therefore about 70% of this year's breeds is the offspring of overwintered animals and 30% of this year's breeds is due to young 1–2 month-old animals (Ivanter 1975) (Table 39). In August, in northern populations a major part of this year's breeds are the offspring of two-month-old voles, while on southern study plots the main increase in the population is ensured by animals from first summer generations (3–6 months old). It is only at the end of the reproduction period that on all the territories considered the population growth is determined chiefly by 3–6 month-old voles.

Table 39

Estimated contribution of differenage voles into the potential increase of the population (%)

Age	Tula study plot (oak-lime forests)	Mari study plot		1957 clearing	1968 clearing	Udmurt study plot (lime-fir-spruce forests)	Karelia study plot	
		spruce-lime forests	secondary birch forests				true-moss spruce forests	deciduous and mixed forests
April							May	
7-16	87.0	100.0	100.0	100.0	100.0	70.0	100.0	100.0
3-6	-	-	-	-	-	-	-	-
1-2	13.0	-	-	-	-	30.0	-	-
June							June	
7-16	39.0	24.7	18.4	24.4	21.1	42.5	62.5	82.6
3-6	14.0	27.5	18.4	22.3	26.3	12.7	0	0
1-2	47.0	47.8	63.2	53.4	52.6	44.8	37.5	17.4
August							August	
7-16	20.4	25.0	19.2	40.6	18.2	25.3	3.0	5.8
3-6	63.1	70.0	73.1	56.3	81.8	49.5	17.4	32.7
1-2	16.5	5.0	7.7	3.1	0	25.2	79.6	61.5
October							September	
7-16	14.3	23.1	0	0	12.5	7.9	0.1	5.4
3-6	78.0	69.1	75.0	95.0	87.5	92.1	84.5	58.9
1-2	7.7	7.7	25.0	5.0	0	0	15.4	36.0

The differences detected in the dynamics and distribution of contributions made by different-age animals into the population growth in various geographical zones are due to variations in the terms, at which the population numbers approach the limiting level. As a result, on medium-latitude plots young animals are excluded earlier from reproduction and their influence in the population growth processes does not exceed 10% already in August, while in the Karelia population of the bank vole such a situation takes place much later. Owing to this, in late September - early October a part of young 1-2 month-old voles continue breeding and since their number is large, their offspring are numerous, too (Table 39). In primary and secondary forests within a permanent study plot the dynamics of the reproduction significance of different-age animals is identical and is synchronized by simultaneous seasonal variations in reproduction in these biotopes.

Sexual maturation of males and their participation in breeding are controlled by the same effects as these of females (age, reproduction cycle phase, geographical latitude of occurrence). At the onset of the reproduction season the fraction of sexually immature males in all populations in different biotopes does not exceed 10% but by autumn it rises to 98% and only few animals participate in breeding (Tab. 37). In autumn, males stop breeding earlier than females do (spermatogenesis attenuates and gonads degenerate) and it is quite probable that, along with seasonal determination of these phenomena, a decrease in sexual activity of males is due to their higher sensitivity to changes in intrapopulation situation and especially to the numbers rise (Ivanter 1978, Bolshakov, Kubantsev 1984).

5.4. SEX RATIO

The role of the sex structure in the general system of the population numbers control and causes responsible for its changes have been long a subject of laboratory and field studies no unambiguous answer has been found so far to these questions. The observed inequality of sexes can be due to the existing methods of selective trapping, seasonal specifics of the population, biological cycle stage, population numbers, habitat character, and some other reasons (Myers and Krebs 1971a, Bolshakov and Kubantsev 1984). Besides, it is impossible to draw a strict demarcation line between the causes responsible for shifts in the sex structure (especially proceeding from results of field observation), which can take place either as a result of sex-differentiated mortality of the animals or as a consequence of a greater number of males or females born by females which are influenced by exo- or endogenic factors (Ivanter 1978, Hansson 1978, Bujalska 1983).

We studied the sex ratio of bank vole for three age groups and therefore only tertiary and quaternary ratios were analyzed, although it is not always possible to rigorously distinguish between them (Bujalska 1983). From spring to autumn a considerable rearrangement of the sex structure is observed among overwintered animals. At the beginning of the reproduction season males predominate in all habitats. In different geographical points their fraction varies from 60 to 76% but by September-October it lowers to 20-25% (Ivanter 1975, Bujalska 1983, Ivankina 1987). Dominance of males in spring can be explained

by higher winter mortality of females and partially by trapping selectivity of males owing to their high mobility. In autumn, on the contrary, females predominate, which is probably due to the fact that males, which are more mobile in spring and summer, die on a greater scale than females do (Ivanter 1975, Bolshakov, Kubantsev 1984, Ivankina 1987, Bujalska 1983). During the breeding season (April–October) mortality of overwintered males is 70% and that of overwintered females is about 50% and therefore 15% of females and only 2–3% of males are left in the population by autumn. During the autumn–winter period an opposite picture is observed: mortality of females is higher (60%) than that of males (40%).

In going from the north to the south, the sex disbalance in the group of overwintered voles is still more pronounced. This is probably due to the fact that females living in the north are more subjected to unfavourable conditions than the females inhabited the Tula, Udmurt and Mari permanent study plots. On the Karelia permanent study plot the bank vole population contains 76–79% of males, whereas in medium-latitude populations in spring the fraction of males equals 60–68% (Table 12, 15). The succession series (from young clearings to radical forests) shows up a directional increase in the fraction of females, and in 10–15 year-old clearings females are even more numerous than males (Table 12). The difference in the sex structure of the bank vole populations in different biotopes may arise from migration processes.

The sex structure of current-year voles also suffers changes during the breeding season, while its modification associated with the geographical latitude is limited only to 1–2 month-old animals, among which males predominate in northern populations and females – in medium-latitude populations. Despite the fact that these changes are valid in some cases, they are so insignificant that can hardly influence considerably the population processes. Even in April, when small shifts in the sex ratio are noted, a hypothetical levelling of the numbers of males and females could increase the population only by 17%.

An analysis of the demographic structure of the bank vole population shows that the structure, as in other species, is closely connected with the numbers dynamics. At the same time, the population structure and its numbers are always the result and the cause of changes in the living conditions of the animals, their physiological state and genetic structure, while the population density acts as a reproduction control mechanism. In population with low numbers, reproduction and, consequently, the population growth are limited only by seasonal phenomena. As a result, up to the end of the reproduction period the largest age group in the population is represented by young 1–2 month-old animals. When the vole population is large, reproduction is inhibited, apart from the seasonal limitation, by density-dependent control mechanisms (smaller litter size, delay in sexual maturation of young animals, lower fraction of breeding animals, shorter breeding season). In such populations the population growth stops in the second half of summer and this is reflected in rising of the mean age of the population.

At high and low population numbers the group of animals going to winter and serving as the basis for another reproduction cycle differs in composition. In

the former instance it is made up of animals from first summer generations, while in the latter case it consists of young voles from autumn generations. Each of these groups has its own specific, physiological and genetic structure and also exhibits different resistance to external and intrapopulation factors (Olenov 1964, Pokrovski 1967).

5.5. RANKING OF THE EFFECTS PRODUCED BY ENDO- AND EXOGENIC FACTORS

The bank vole, as other representatives of the order Rodentia, is characterized by cyclic changes in the numbers and demographic structure of the population (Henttonen et al. 1984, Hansson and Henttonen 1985). Acyclic populations are also found (Hansson 1971, Fuller 1977, 1977a, Bashenina 1977, Krebs 1979, Mihok, Fuller 1981, Tensen 1982). However, cases of cycles with a regular amplitude and frequency are extremely rare both in cyclic and acyclic populations. It is customary to assume that cyclic populations are controlled by intrapopulation mechanisms, while acyclic populations are regulated by external factors; however, a combined action of biotic and abiotic factors cannot be excluded (Hansson, Henttonen 1985). Besides, it has been universally accepted now that at optimal sites of the area intrapopulation factors play one of the leading roles in the control of the numbers whose changes are almost independent of the variations in weather and food conditions (Koshkina 1974, Southern 1979, Poulet 1985), whereas in the pessimal zone an increasing part is played by external factors, for example, greater thickness of the snow cover in northern Fennoscandia (Merritt 1981, Henttonen, Hansson 1984), better food conditions (Tast and Kalela 1971, Andrzejewski 1975, Laine and Henttonen 1983, Alibhai 1985), effect of predators (Tast and Kalela 1971, Henttonen et al. 1977), interspecific competition (Henttonen and Hansson 1984), and heterogeneity of the medium (Hansson 1977, 1979). It is assumed that in different geographical regions the degree of domination of various effects can alter. Some investigators think that in southern regions the numbers fluctuations are due to the impact of predators (Pulliainen 1981, Kaikusalo 1982), while in northern regions the principal part is played by external factors, in particular thickness of the snow cover and severity of climate (Tast and Kalela 1971). Clearly it is impossible to describe responses of the population by the action of a single factor, although results obtained with the use of this approach lend themselves to check-up and interpretation. As we see, population processes are determined by simultaneous operation of all factors whose efficiency depends on the habitat conditions.

We made quantitative estimates of the effects produced by the factors using a screening procedure which included at the final stage a multiple regression analysis with expansion of the total explainable variance into parts proportional to the contribution of each effect. Methodically similar approaches were exploited in some papers (Ivanter 1975, Volkov and Ershov 1978, Spitz 1982, Myllymäki et al. 1985, Okulova 1986, Kudryashova and Kudryashov 1988) but they were concerned mainly with the estimation of the relationship between the total population numbers and climatic factors. The multiple regression analysis is used as a rule for prediction and therefore its final aim con-

sists in quantitative description of the relationship between variable and a great number of independent variables.

Parameters of the multiple regression equations can be calculated in two ways. In one case, use is made of short time series of observations performed in numerous different habitats. The main drawback of this approach is that the description obtained reflects geographic or biotopic peculiarities of the population reactions rather than the chronographic component (Myllymäki et al. 1985). The other approach uses long-term investigations carried out at a single site and makes it therefore possible to analyze the real influence of endo- and exogenic factors on the population dynamics.

Most close to the estimation of the factors affecting a population were N.M. Okulova (1986) and E.V. Ivantsev (1975) who found valid correlations between population characteristics and the factors acting there upon for some species of forest voles. However, the obtained estimates of the correlations are not partial correlations but include also all other factors (in the form of interactions) and they cannot therefore serve as an estimate of the relative influence produced by a particular factor. Our procedure uses partial correlations and makes it therefore possible to obtain relative estimates of the effects produced by each factor.

The reproduction intensity, sexual maturation, survival and total level of the population numbers of the bank vole, northern red-backed and grey red-backed living at all the six different-quality sites of the area are determined by the population structure and numbers of their own species at preceding and current moments of time, state of the sympatric-species populations, meteorological conditions (monthly average air temperature, amount of precipitation, and thickness of snow cover), food conditions (yield of seeds of basic forest-forming species), and biological feature of seasonal generations. In different phases of the reproduction cycle each group of factors operates in a specific way. At the beginning of the breeding season weather conditions are decisive for the number of overwintered animals and their winter survival. Their contribution to the total explainable variance rises in going from the south to the north. In the optimum area of the bank vole occurrence - in the zone of broad-leaved forests (Tula permanent study plot) and the taiga zone (subtaiga, southern taiga) - weather conditions in the autumn-winter period can account for 37 to 52% of the variation in demographic indices in April (Table 40). In the pessimum area - in the subzone of mid-taiga forests (Karelia permanent study plot) - the role of climatic factors is much greater: The state of the spring population is determined 83% by these factors. Both in the optimum and pessimum of the area weather conditions operate most efficiently in "bottleneck" periods of the population. The fact itself that the numbers level and survival of overwintered voles during the autumn-winter period depend on changes in weather conditions is known. Moreover, it has been discussed more than once that it is precisely the population "bottleneck" periods that determine survival of animals (Chernyavski and Tkachev 1982, Okulova 1986, Kudryashova and Kudryashov 1988) but the enumerate papers do not contain the procedure of quantitative relative estimation of the efficiency of the factors affecting a population; they only state the presence of such relations.

Table 40

Estimated influence of the factors acting upon reproduction of the bank vole

	Month	Factors				Share of explainable variance
		Endogenic		Exogenic		
		preceding	current	climatic	food	
Tula study plot	April	39.1	0.0	33.7	21.4	94.2*
	June	4.6	73.2	11.3	0.0	89.1*
	August	66.0	6.0	13.8	0.0	85.8
	October	35.9	4.4	56.0	0.0	96.3*
Mari study plot	April	23.4	6.2	53.4	14.6	97.6*
Spruce–lime forests	June	1.5	72.7	21.5	0.0	95.7*
	August	16.6	58.7	16.0	0.0	91.3*
	October	48.7	0.8	37.0	0.0	86.5
	Clearing	April	39.4	0.0	48.7	3.0
June		0.9	70.8	14.7	0.0	86.5
August		8.3	22.7	8.9	0.0	39.9
October		15.0	20.4	12.4	0.0	47.9
Udmurt study plot	April	38.8	8.3	43.7	3.3	94.0*
	June	0.0	72.0	0.1	0.0	72.1
	August	31.2	56.3	1.4	0.0	88.9*
	October	32.9	56.5	7.1	0.0	96.5*
Karelia study plot	June	12.3	0.0	83.3	0.0	95.6*
	July	15.6	66.9	5.4	0.0	87.9*
	August	25.7	19.9	28.2	0.0	73.8

* Values significant at $p=0.05$.

On the Karelia permanent study plot the spring population of bank voles is also determined by weather conditions, out of which the share of the explainable variance associated with fluctuations in the amount of precipitation and air temperature in September and October equals 36%, changes in weather conditions in April and May are responsible for 29% of the total variance, while the effect of meteorological conditions during the period of established snow cover (December – February) with respect to abundance of overwintered voles does not exceed 19%.

In the optimum zone variability of the population characteristics at the beginning of the breeding season is at least in 50% determined by fluctuations in weather conditions, especially in November and March (35% out of 50%), when snow cover is formed and disappears, while only 15% of the population characteristic variance can be explained by changes in weather conditions during the period of established snow cover.

By analogy with the differences detected in the efficiency of weather conditions at the center and periphery of the bank vole area, one might expect similar reactions of populations living within a single latitude zone at optimal and pessimal sites. We saw on the example of the Mari permanent study plot that contributions made by weather conditions into the formation of the spring numbers and winter survival of the bank vole are rather close (53.4 and 48.7%) for radical spruce-lime forests (optimal habitat) and clearings (pessimal biotope). On these grounds one may state that the degree to which weather conditions influence the bank vole population in spring is not connected with the biotope protectiveness level, its food resources and other ecological conditions (habitats quality) but with global climatic phenomena characteristics of each geographical latitude. Thus, Karelia is characterized by a high degree of cyclicity accompanied by a high level of weather conditions variations. In winter, warm periods are frequently replaced by frosts and snowfalls, a fact which, on the one hand, determines high mortality of the animals and, on the other hand, established a more stringent dependence of the population processes on fluctuations in winter air temperature, amount of precipitation and snow cover thickness. In the central regions of the Russia climate approximates the continental one, weather conditions vary to a much lesser extent, and besides, catastrophic phenomena (sudden thaws and frosts) are infrequent, this probably determining a lower dependence of the population processes on weather factors.

Food conditions, especially in winter period (yield of seeds of basic forest-forming species), limit the population numbers in the optimal zone, their influence for different study plots varies between 3.0 and 21.4%. Food conditions practically have no limiting effects on the population of the Karelia permanent study plot. Most likely, in the pessimum of the area, where the abundance of voles is low, food requirements of the population agree well with the environmental resources.

Apart from weather and food conditions, demographic characteristics of the population in spring are determined also by the population numbers, age structure and reproduction intensity in autumn of the preceding year, i.e. by the qualitative composition of the population, which existed at the end of the preceding reproductive cycle. In the optimum of the area the state of the population in preceding autumn determines 23 to 40% of the total variability in the spring numbers and survival level of the animals, while in the pessimum its contribution does not exceed 11%.

The last group of effects influencing a population includes the population numbers and structure at the moment of study (density-dependent factors). In spring, the population numbers are low and therefore the contribution of these factors to the vole population control does not exceed 8% for all the plots studied. As we saw, one of the reasons of low spring populations is high mortality of voles during the autumn-winter period (Koshkina 1967, Ivanter 1975, Fuller 1979, Safronov 1983, Bujalska 1985, Okulova 1986, Zhigalski and Bernshtein 1986, 1989). In the Karelia population, winter is survived by about 30% of animals, while in favourable habitats (Tula, Udmurt and Mari permanent study plots) about one half of the animals going to winter survive.

Differences in the level of winter mortality in optimal and pessimal sites of the area result in considerable differences in the spring numbers, a fact which in combination with structural rearrangements in the vole population in autumn of the preceding year defines seasonal dynamics of the population. It should be noted in addition that irrespectively of the geographical latitude of the habitat, low reproduction activity of voles in spring is preceded by high autumn numbers, considerable number of voles from early-summer litters, and large fraction of non-breeding animals at the end of the preceding reproduction cycle. This combination of population characteristics is typical of periods with high numbers (Ivanter 1979, Bujalska 1985, Okulova 1986, Zhigalski 1988). The impact of numbers and low air temperatures lead to the situation, where a group of animals with a low reproductive potential and high mortality level are selected in the population. It is impossible to follow exactly the genetic relations between these phenomena on the basis of our materials. However, we can reasonably believe that the population structure in autumn of the preceding year determines the functional level of the population in spring.

In the phase of rapid growth (first half of summer, up to the seasonal peak) and in the period of relatively low numbers the share of explainable variance lowers and the influence of random factors rises in all the five populations of the bank vole being analyzed. Even on Karelia study plot (in the pessimum of the area) 50% of the total variance of the population characteristics is due to density-dependent factors operating at a given time, though it was assumed earlier that under unfavourable conditions (at the northern boundaries of the area) exogenic factors should have a maximum effect (Ivanter 1975, Merritt 1981, Henttonen, Hansson 1984). During this period reproduction of overwintered voles is not limited, while the participation of current-year 3–6 month-old females in breeding is determined chiefly by endogenic factors, out of which the leading position belongs to the total numbers of overwintered animals, number and fraction of pregnant females, i.e. of the animals which have their own home ranges. The role of current-year voles in the control of the population reproduction activity is much lower. While the fraction of breeding females is determined mainly by the population numbers and structure at a current moment of time, sexual maturation of young voles is defined by the population state both at current and preceding moments of time.

The mechanism through which high current densities influence the sexual maturation rate of young voles has received an adequate study in the population biology (Ivanter 1975, Chernyavski and Tkachev 1982, Shilov 1984, Bujalska 1985, Ivankina 1987) and is well known, whereas the mechanism through which the sexual maturation rate changes as a function of fluctuations in the population numbers and structure at preceding moment of time should be discussed on the assumption basis only. Under the action of various preceding demographic situations a differentiation in the growth and development of young females takes place (Jaszczak 1974, 1975, McCarty, Southwick 1979, Medvedev et al. 1983, Hansson 1984, Ingeborg and Yonathan 1985) and, as a result, selective advantage is given to some genotypes, this leading prob-

ably to changes in the ratio of rapidly and slowly maturing females (Chitty 1967, Krebs et al. 1973, Krebs 1978).

In the phase of rapid growth (May, June and July), weather conditions influence very little the population processes; their contribution to the reproductive activity variance for various habitats lies within 0.1 to 21.5% (Tab. 40), with both pessimal habitats located within a single geographical zone and peripheral zones of the bank vole area inclusive.

During the seasonal peak (August in the medium latitudes and June in Karelia) and a regular seasonal drop in the reproduction activity, the role of the population situations in preceding months rises, along with high regulating efficiency of changes in the population structure and abundance at the moment of study. Young 1–2 month-old voles are affected to a greater extent by changes in the population numbers and structure in June and July than by variations in these parameters at the moment of study. Besides, the influence of preceding states of the population on the voles from early-summer litters is much higher than on animals of later offspring. At that time the basic control function belongs to the total abundance and numbers of breeding voles (mainly 3–6 month old) and also to the age composition and reproduction activity of females in June and July. The amount of precipitation and air temperature also influence the population state but their contribution is, as in June and July, insignificant and for various characteristics of populations living in different geographical zones is not more than 16%; even in the pessimum of the area the contribution of these parameters to the total variance is equal to 5% (phenologically, June in Karelia is similar to August in the middle zone). No significant quantitative differences were found in the distribution of contribution made by preceding demographic situations, state of the population at the current moment of time, and weather conditions during the seasonal numbers peak into the formation of the structure and abundance of voles.

In the second half of summer (after the seasonal peak) the population strategy consists in reduction of the reproduction activity and formation of the group of wintering animals which serve as the basis of another reproduction cycle. Therefore, the reproduction processes are affected at that time, apart from the effects described above, by a decrease in sexual maturation of voles, which is associated with biological features of animals born in late summer (Shvarts et al. 1976, 1977, Gliwicz 1983, Bujalska 1983).

It is quite obvious that the seasonal lowering of the reproduction activity is determined in the main by the reproductive potential, while a high numbers level and autumn condition only speed up the process. By the end of the reproduction season sexually immature animals from late-summer litters are accumulated in the population and therefore the potential population growth is due principally to overwintered animals and voles of early-summer generations (3–6 months old). This causes, probably, a still greater decrease in the role of the population numbers and structure at the current moment of time and a considerable rise in the influence of preceding population states. However, this hierarchy of the factorial loads within the group of endogenic factors is typical of the bank vole living in radical habitats of the optimum of the area (Table 40). In the pessimal zone and in secondary (poor) habitats the vole numbers do not reach high level at the end

of the reproduction period, breeding time in the population is longer, and, probably, it is for this reason that the role of density-dependent mechanisms (at the current moment of time) in the regulation of the demographic processes intensity is still sufficiently high. Besides, variation in weather conditions, food resources, number of sympatric species, and other characteristics of the environment enhance in autumn, a circumstance which is reflected in turn in reduction of the fraction of the explainable variance and increased influence of random factors on the reproduction activity. In the second half of summer and especially in autumn changes in air temperature and amount of precipitation again have a perceptible effect on the reproduction processes, determining both their intensity and sexual maturation of young voles. The increase in the effect of weather conditions is practically independent of the habitat type and its geographical location.

Response of current-year males to changes in preceding and current states of the population, weather and food conditions differs slightly from that of females. The greatest changes in the distribution of effects produced by the operating factors are associated with an increase in the contributions made by the population numbers and structure at the preceding moments of time and a lower role of density-dependent mechanisms at the current moment of time. Activity of males depends on fluctuations in air temperature and amount of precipitation to a somewhat greater extent than that of females. However, the most important factors regulating activity of males in all the bank vole populations studied remain to be, as in the case of females, endogenic factors.

Reactions of northern red-backed and grey red-backed voles to endo- and exogenic factors are qualitatively similar to those observed in the bank vole populations and the distribution of the effects produced by these factors is determined by the habitat conditions (optimal or pessimal), reproduction cycle phase, and the functioning level of the population of the own and co-occurring species (breeding intensity, age structure, numbers variation rate). Spatial distribution of northern red-backed and grey red-backed on the territory of the Sayan permanent study plot serves as a good biological model for investigation of interrelations between two co-occurring species, because one and the same territory has zones optimal for one species and pessimal for the other, and vice versa.

At the beginning of the reproduction cycle the decisive factors are the population numbers and structure at the end of the preceding reproduction season, and weather conditions of wintering. The species influence each other insignificantly (10%, maximum) and the mutual influence does not depend on the habitat quality (Table 41). Already in June (the period of mass reproduction), however, both northern red-backed and grey red-backed respond differently to changes in the demography of the own and sympatric species depending on the habitat quality. In optimal zones the decisive role belongs to the processes that take place in the own-species population at the current moment of time. In pessimal regions the fraction of the explainable variance lowers and the influence of the sympatric species increases several fold. In the case of grey red-backed living in unfavourable habitats, up to 40% of the controlled variance is due to the effect of northern red-backed. Intrapopulation processes remain to be of primary importance for

Table 41

Seasonal and altitudinal distributions of the effects produced by the factors acting upon reproduction of forest voles in Western Sayan

Species	Month	Endogenic factors		Contribution of sympatric species	Share of explainable variance	Altitude above sea level, m
		preceding	current			
<i>C. rutilus</i>	June	0.0	48.5	27.0	75.5*	600–800
	July	28.6	33.2	8.0	66.3	
	August	24.0	24.7	37.2	85.9*	
	May	45.6	22.7	9.1	77.4*	800–1200
	June	48.9	39.5	6.7	95.1*	
	July	30.8	4.8	16.5	52.1	
	August	33.0	10.4	18.3	61.7	
<i>C. rufocanus</i>	May	18.1	0.0	2.3	20.4	600–800
	June	5.1	59.5	7.3	72.0*	
	July	23.6	44.9	7.9	76.4*	
	August	8.9	16.4	49.0	74.3*	
	June	0.0	11.9	48.2	60.1	800–1000
	July	23.9	43.3	1.9	69.1	
	August	50.8	3.9	12.2	66.9	
	June	0.0	2.8	34.9	37.7	1000–1400
	July	31.9	8.3	13.9	54.1	
	August	36.0	58.3	2.1	96.4*	

* Values significant at $p=0.05$.

northern red-backed inhabiting that region, although 24% of the explainable variance is connected with the influence of *C. rufocanus*.

At altitudes over 800 m the numbers level of grey red-backed differs little from that of northern red-backed but that region is the optimal zone (low variability level) for the latter species. Naturally, a greater part of nesting sites convenient for breeding is occupied by females of the dominating species, a fact which, in the final analysis, determines the dependence of the reproduction activity of grey red-backed on changes in demography of northern red-backed. Similar changes in the distribution of effects from factorial loads are observed for northern red-backed living in the region optimal for grey red-backed at altitudes 600 - 800 m (Table 41).

In July and August, during a sharp drop in the growth rates of grey red-backed population in pessimal biotopes, endogenic factors become most essential: their specific weight in the control of the population phenomena increases to 55–80%. At that period, the role of endogenic factors for northern red-backed living in the pessimal zone is preserved at the same level but, simultaneously, the effects of

preceding and current population situation become equal. Besides, by August, i.e. the time of maximum increases in the population of northern red-backed, this species is subject to an increasing influence of grey red-backed (decrease in breeding intensity and longer time of sexual maturation).

In August, the role of northern red-backed in the reproduction processes of grey red-backed voles rises, too. Note that while in other months such phenomena were observed only in the pessimal region, in August the basic effect shows up in the zone optimal for *C. rufocanus*.

Let us analyze the causes underlying the mechanism that determines the level of interrelations between co-occurring species. One of the causes is as follows. When the study plot was colonized by forest voles, its territory was divided between the voles either as a result of competitive relations or in accord with biological features of the species. Zones optimal for each species (numbers at a maximum, numbers variability at a minimum) established themselves. So, we have currently a historically established spatial structure of the population.

In the zone optimal for one species, the other species is controlled, in addition to other factors, by the numbers and structure of the population of the first species. This effect is pronounced most in the period of maximum increases in the population of the dominating species and can attain 40% of the total control effect, though its magnitude is insufficient to change radically the population dynamics of the sympatric species. Positive coefficients of the correlation between changes in the numbers of northern red-backed and grey red-backed are indicative of synchronous and correlated multiannual dynamics of both species. This suggests in turn that co-occurrence of the voles of two species does not aggravate competitive relations but results in spatial and time division of the living space according to biological features of each species. It is probably for this reason that the main purpose of changes in the level of interspecific relations in the population dynamics of northern red-backed and grey red-backed voles consists not in complete suppression of the reproduction processes of the sympatric species but in partial reduction within the limits sufficient for maintaining the spatial structure of the population of each species so that northern red-backed and grey red-backed are not transformed into antagonistic species.

In the phase of rapid growth, the population numbers are brought to the level adequate to the existing conditions by means of density-dependent mechanism to form another physiological and genetic structure. At the next stage of the regulation process the entire inhabited territory is redistributed between the animals entering different functional groups. However, both at the first and, especially, second stages of the regulation all responses of the population to changes in its living conditions are realized with a considerable delay, this not allowing the population to react promptly to fluctuations in living conditions. Using a simulation mathematical model, we analysed in detail causes and effects of delay responses of the northern red-backed and grey red-backed populations to particular influences (Zhigalski 1982, Benenso and Zhigalski 1982).

As was already noted, numbers of forest voles are controlled by several circuits and if one classifies feedbacks according to the delay magnitude, the "density-sexual maturation time" relation features a minimum delay (18 days, maximum). A

further progressive increase in the delay corresponds to the following relations. "density – mortality of animals from junior age groups" (18–20 days), "density – number of breeding females" and "density – time span between successive matings" (57–60 days). Some discrepancies between the dynamics of the model and natural populations are mainly due to a delay in the response of the model population to particular effects. In natural populations of forest voles this delay is compensated partially by a rapid change of biologically specific seasonal generations and re-arrangement of the population genotype structure. It may therefore be assumed that numbers of forest voles are controlled not only by density-dependent regulation mechanisms (quantitative changes in population characteristics) but also at the expense of changes in the qualitative composition of the population – different ratio of genetic, behavioral and physiological intrapopulation groups which are realized during regulation of the vole population.

In the term of the system analysis, density-dependent feedbacks from a system whose function is to fit the population numbers and structure to varying habitat conditions, which is realized indirectly via changes in demographic characteristics of the population. To study resistance of the forest vole population to particular changes in external conditions, some computer experiments were made using a simulation mathematical model (Zhigalski and Shubin 1981, Zhigalski 1982, 1984). In one case external conditions remained unchanged, in the other case they changed in cycles with a period of two and three years (duration of the periods corresponds to periodicity of changes in external conditions (Drozdov and Grigoriev 1971)). While in the last instance external conditions changed randomly but with a mean duration of the period equal to 2.7 years. Changes in external conditions were simulated in the model by variations in "critical numbers"; if the latter are exceeded, density-dependent feedbacks are "engaged", bringing the population numbers and structure to the level adequate to the environmental conditions.

In the first variant, where the critical numbers were kept constant, there appeared stable two-year fluctuations in the structure and numbers, which are due only to the processes that take place in the population itself (Fig. 12). During the first five years a structure, which is adequate to new living conditions, is formed in the population (this interval reflects, most probably, the rate of the population adjustment to new environmental conditions). In variants 2 and 3 the fluctuation periodicity set up also on the fifth year. But while in the second variant the fluctuation period of the population demographic parameters was two years, in the third variant it became equal to three years. In the last two cases the population was "accustomed" to the new rhythm after a five-year period and intrinsic two-year cyclicity was replaced by a three-year cyclicity of external conditions (variant 3). Even when the critical numbers varied randomly (mean cycle duration of 2.7 years), the population "followed" fluctuations in the external conditions (fluctuation period of the population characteristics was also close to 2.7 years; Table 42).

In all the experiments the value of the critical numbers is higher than that of the spring numbers. This phenomenon can be observed only when regulation mechanisms keep the spring numbers efficiently from year to year at a level approaching the permissible one for given conditions. In variants 1, 3 and 4, the

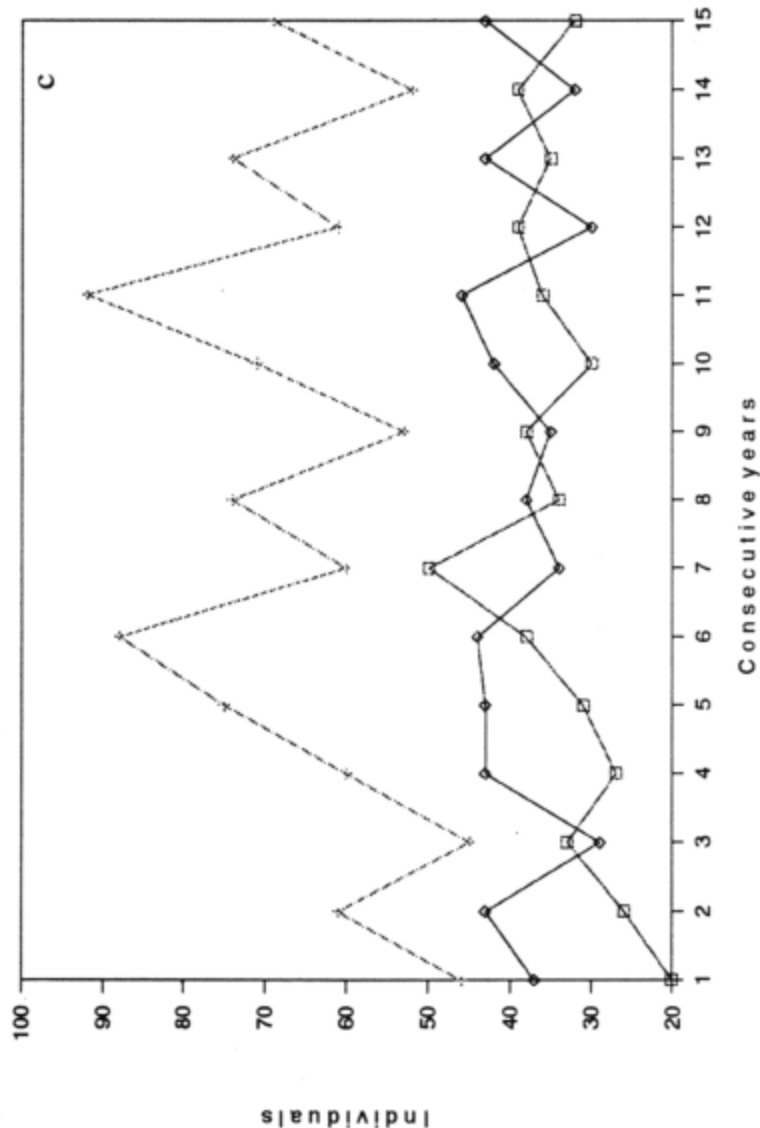


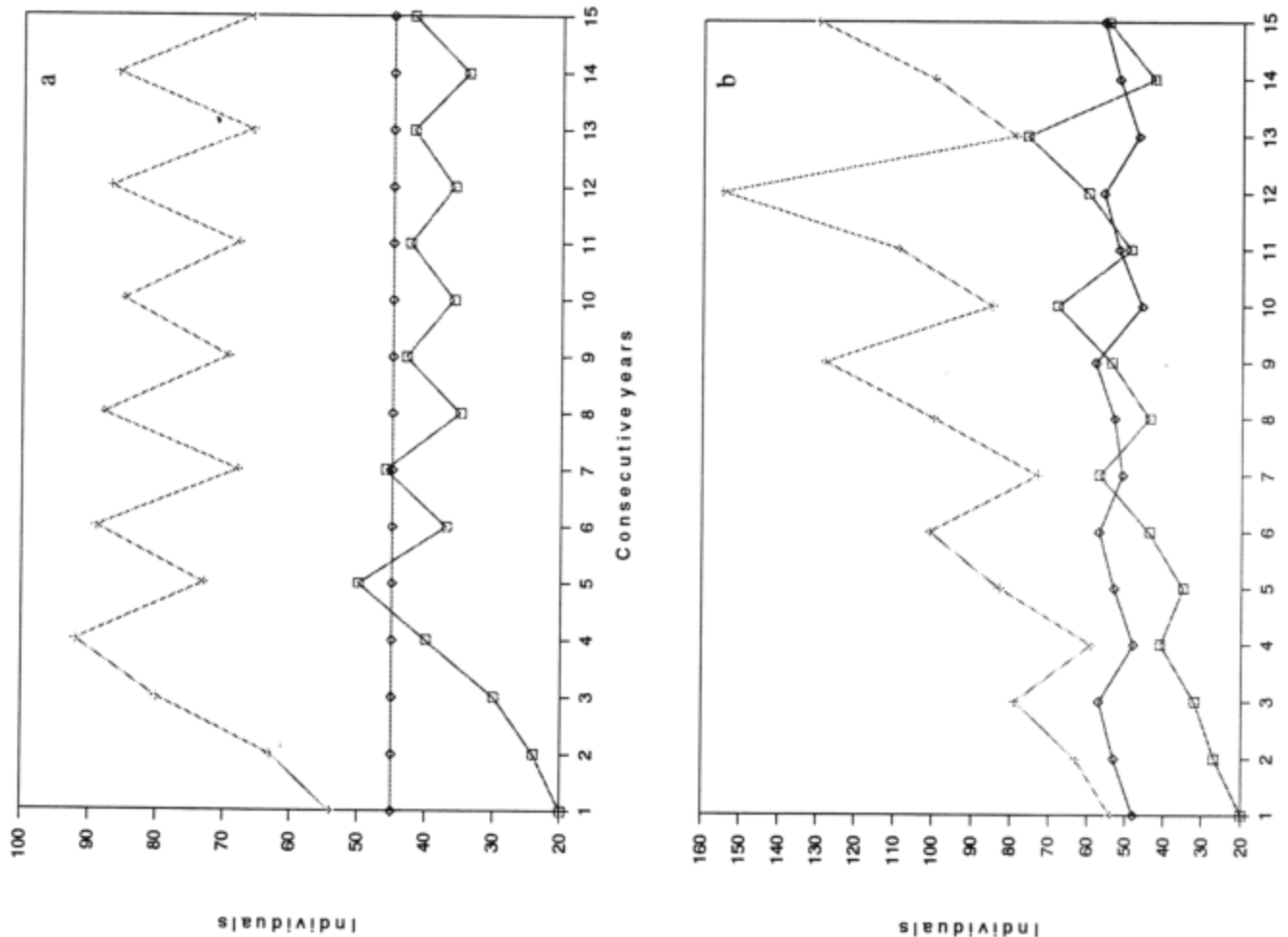
Fig. 12. Dynamics of the spring, autumn and critical numbers. Black rectangles and continuous line – spring numbers, crosses and continuous line – autumn numbers, dashed line – critical numbers. Critical numbers: *a* – constant, *b* – vary with a period of 3 years, *c* – vary at random.

to the external conditions. Besides, strengthening of correlative relations between various parameters can be reasonably considered as an increase in the ordering of the population control mechanism and their greater correlation. It is only high correlation of the population processes and their high degree of ordering that enable a population to respond to changes in external conditions in a shortest time (with only an insignificant misadjustment) (Table 42). It should be noted that a high correlation of the population processes in the second variant is due to the coincidence of the periods and phases of the external and internal cyclicity (high capacity of the environment always coincides with high reproduceability and low

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critical numbers are 1.1 times as high as the spring numbers, and in variant 2, 1.6 times. A greater difference between the critical and spring numbers in the second variant suggests that population mechanisms control the numbers more strictly and determinately. A more stringent regulation is caused by coincidence of the periods and external processes; as a result, the internal two-year cyclicity is synchronized by external cyclicity. This exactly leads to an optimal relationship between the population structure dynamics and habitat conditions dynamics. A similar conclusion is true also for the value of the seasonal peak numbers. In all the experiments, except the second one, the seasonal peak numbers exceed the critical numbers 5.3-fold, while in the second experiment, 3.8-fold.

In the first variant, variability of the population characteristics is at a minimum and depends only on changes in population processes (external conditions are constant here). In the other experiments, environmental conditions variation coefficients vary from 18 to 43%. One might think that with such a great variability of the external conditions, variability of the population characteristics should rise, too (in case the population "follows" passively the external conditions). However, total variability of the population characteristics does not equal a simple algebraic sum of the external and internal variability and therefore it is much less than it could be in the case of simple adding-up (Table 42). Intrapopulation control mechanisms and, specifically, density-dependent ones dampen partially the effect of oscillations in the environment. Variability of the population characteristics (at a considerable variability of external conditions) is rather small (up to 20%, whereas in the case of passive summation it could attain 50–60%). In variants 3 and 4, variation coefficients of the spring and autumn numbers are equal to 21%, out of which intrinsic population variability accounting for 11% and 10% is due to external factors, this totalling to slight more than 40% of the total variability. At the same time, fluctuations of the critical numbers (environment) account for 99% of the value in variant 1, i.e. population mechanisms reduce almost two-fold the effects due to changes in external conditions. In this context, the second variant is of interest: here the critical numbers variation coefficient is at maximum (34%) and the variation coefficients of the spring and autumn numbers, seasonal peak numbers, and the number of current-year voles over the entire breeding season are low and their values are close to those of intrapopulation coefficients.

This picture can be observed only when density-dependent feedbacks exhibit high impact which does not allow the population to change its structure and numbers over wide limits. Put another way, population mechanisms of control (in the second variant) bring the population most efficiently to the level that is adequate to the external conditions. Besides, strengthening of correlative relations between various parameters can be reasonably considered as an increase in the ordering of the population control mechanism and their greater correlation. It is only high correlation of the population processes and their high degree of ordering that enable a population to respond to changes in external conditions in a shortest time (with only an insignificant misadjustment) (Table 42). It should be noted that a high correlation of the population processes in the second variant is due to the coincidence of the periods and phases of the external and internal cyclicity (high capacity of the environment always coincides with high reproduceability and low

Table 42

Estimates of basic population characteristics and their correlation

	Mean	Standard deviation	Variation coefficient	Period duration	Correlation coefficients			
					1	2	3	4
variant 1								
1. Critical numbers	45	0.09	0.2	–				
2. Spring numbers	41.9	4.8	11.4	2	0.18			
3. Autumn numbers	78.8	9.3	11.8	2	–0.11	–0.95		
4. Total number of current-year voles	552	28.9	5.2	2	–0.64	–0.23	0.16	
5. Seasonal numbers peak	235	17.3	7.4	2	–0.06	–0.94	0.99	0.75
variant 2								
1. Critical numbers	69	23.2	33.7	2				
2. Spring numbers	43.9	5.7	13.2	2	–0.99			
3. Autumn numbers	84	11.2	13.3	2	0.98	–0.95		
4. Total number of current-year voles	543.8	50.4	9.3	2	0.96	–0.92	0.99	
5. Seasonal numbers peak	297.5	31.3	11.7	2	0.94	–0.89	0.97	0.97
variant 3								
1. Critical numbers	68.4	18.5	27.1	3				
2. Spring numbers	61.1	12.2	20.1	3	–0.48			
3. Autumn numbers	118.5	23.1	19.5	3	0.93	–0.31		
4. Total number of current-year voles	711	195.5	27.4	3	0.96	–0.47	0.97	
5. Seasonal numbers peak	353	33.2	16.0	3	–0.09	0.71	0.71	
variant 4								
1. Critical numbers	39	7.1	18.3	2.7				
2. Spring numbers	25.6	7.6	21.3	2.8	–0.47			
3. Autumn numbers	68.8	13.7	19.9	2.7	0.67	0.21		
4. Total number of current-year voles	445.3	85.3	19.2	2.7	0.64	0.2	0.92	
5. Seasonal numbers peak	208	33.3	16.1	2.7	0.72	0.17	0.96	0.83

variant 1 – critical numbers are constant,

variant 2 – critical numbers change every two years,

variant 3 – critical numbers change every three years,

variant 4 – critical numbers vary randomly.

mortality of the population). In the third variant, in spite of cyclic changes in environment, the rate of coincidence of favourable conditions and the population capabilities is much lower, this resulting in a lower correlation coefficient. The coincidence rate decreases still more in the fourth variant and, as a consequence, the characters are correlated still less.

Thus, if the northern red-backed population existed under stable conditions, two-year fluctuations of its numbers and demographic structure would arise. The period of these fluctuations is determined by the birth-rate-mortality ratio and, also, by feedback intensity. It is most probably different for different species and habitats. In the model developed using data due to T.V. Koshkina and Yu.S. Korotkov (1975) for northern red-backed vole, the numbers fluctuation period is three years (Zhigalski 1982), while in the model that uses data obtained by L.R. Michurina (1974) and V.S. Surkov (1976) for grey red-backed, it equals two years. Clearly it is an ideal case which was necessary only to show that endogenic cycles exist in the population, whose periodicity is probably not so stable as the one obtained for the model population. In all the cases where environmental conditions changed, the population adapted itself rather rapidly to a new rhythm and all its characteristics changed following periodicity of the external conditions. The closer are the period of changes in external conditions and that of the intra-population fluctuations and the more pronounced in the periodicity of external conditions, the higher are the correlation and ordering of the population processes, allowing the population to react as fast as possible to changes in environment. The last point is a mandatory pre-requisite for survival of a population which colonized a new territory, where its mechanisms of adjustment of the structure and numbers to more arduous conditions of living are inadequate (Ivanter 1975). In case of random variations in external conditions, no regular fluctuations in the population parameters are present; "global" maxima and minima of the numbers are due in some cases to the coincidence of favourable environmental conditions and high reproduceability of the population or, elsewhere, to low capacity of the environment and low reproduceability. One should not forget about all the intermediate variants, where either external or internal factors limit the population growth (Fig. 12).

The regularities, which were found by us in model experiments agree well with our field observations and are confirmed by the data obtained by other investigators. This makes us believe that our findings are not only of theoretical character but can be of practical significance as well.

6. CONCLUSIONS

The population dynamics is an integrated indicator of the population state and represents the final result of the interaction between the population and the environment.

In all the populations of the bank vole, *C. rutilus* and *C. rufocanus* studied, the reproduction intensity of the animals in spring, their survival in the autumn-winter period, and the total population numbers are connected chiefly with the demographic situation in the population in autumn of the preceding year and win-

tering conditions (food and weather), no matter what part of the area the population inhabits. The influence of wintering conditions upon survival and spring reproduction is noted for other species of small mammals: tundra and field voles, Norway lemming.

During the breeding period the reproduction processes are determined mainly by internal factors. It is only at the beginning of the period, when a considerable part of the territory is free, that migration flows can play the role of an efficient numbers regulator. However, in the course of reproduction, submarginal biotopes are filled gradually, the flow of migrants reduces sharply and, as a result, intrapopulation mechanisms become dominant in the regulation processes on the entire territory occupied by the population. In that period weather conditions do not influence significantly the population processes, except catastrophic and anomalous phenomena.

In the second half of the breeding season (after the seasonal peak) the population strategy is to lower the sexual maturation rate of this year's breeds and to form a group of animals which go to winter and serve as the basis for another reproduction cycle. Therefore seasonal phenomena determine essentially sexual maturation rate of the young, while the reproduction intensity of adults is, as before, connected with the population density and structure. The influence of weather conditions on the reproductive potential of the population rises again by autumn.

Thus, numbers of forest voles are controlled by many factors, out of which the most essential are the demographic composition of the population at preceding and current moments of time, the state of the population of sympatric species, and weather and food conditions of the winter period. The hierarchy of their contributions to the variations in the population numbers and structure is determined by the habitat quality, location of the population in the area, and the season. Using a multi-factor ideology of the population dynamics, regulation of the population numbers can be presented as follows. The spatial structure of the population and, in particular, the home range size provide the framework of the population regulation. At low levels of the vole population abundance the area of home ranges is at maximum, while their "packing" density is low, as is the frequency of contacts between the animals; as a result, the population reproduction is not limited by anything, survival of voles is at a high level, and the population grows at a maximum rate possible for the given conditions. This situation is typical of the onset of the breeding season and of population with low numbers. In the course of reproduction the population numbers increase, the "packing" density of home ranges rises, the number of contacts between individuals grows, antagonistic relations are aggravated, and the stress level rises, this leading in turn to lower vitality of voles and impairment of reproduction (longer sexual maturation time, changes in estrous cycle, inefficient fertilization, resorption of embryos) and as a result of these processes, reduction in the population growth rate.

The populations of the forest voles studied are affected to a rather great extent by density-dependent mechanisms: they are responsible for up to 70% of the variance explaining the population processes, except winter period and the onset of the breeding season, where the contributions made by endo- and exogenic

factors into the numbers regulation are approximately equal. Even in the pessimism of the area, where the vole population is not very high, intensity of the population processes is determined mainly by intrapopulation factors. In this connection, the significance of migration in the dynamics of small mammals should be reviewed since, in addition to the genetic (informative) aspect, it is of secondary importance. Emigration and immigration flows do not exceed the level over which they can influence considerably the population numbers and structure. At the first stage of the numbers regulation the response of the population to a distribution balance between the habitat capacity and the population abundance is eliminated basically by means of density-dependent mechanisms.

At the second stage, under the action of intrapopulation mechanisms (selective elimination and reduction of reproduction activity) a reconstruction takes place in the population structure, which adjusts the population processes to another functional level and, furthermore, can present a cause of transition from strictly territorial to group pattern of life, with establishment of a new hierarchy that allows the population to maintain its numbers at a higher level at the same resources.

Thus, maximum effects produced by factors acting upon small mammals are separated in time. During the autumn-winter period and at the beginning of the breeding season a greater part is played by exogenic factors, while during the reproduction cycle, endogenic factors. External factors (meteorological conditions, food resources, impact of predators, competition, etc.) determine the upper limit of the density level that is optimal for the given conditions. The function of intrapopulation mechanisms consists in bringing the numbers to a level adequate to these conditions. The population represents a "follow-up" which transforms continuously its structure and numbers in accord with the varying conditions of the habitat.

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7. STRESZCZENIE

ANALIZA CZYNNIKÓW WPŁYWAJĄCYCH NA DYNAMIKĘ POPULACJI GRYZONI

Przeprowadzono wieloczynnikową analizę procesów określających liczebność i strukturę populacji trzech gatunków gryzoni leśnych. Wieloletnie badania prowadzone w 5 rejonach usytuowanych w różnych częściach geograficznego zasięgu poszczególnych gatunków stanowiły empiryczną podstawę przeprowadzonej analizy. Wykazano, że podczas sezonu rozrodczego procesy demograficzne w populacjach badanych gatunków zależą przede wszystkim od czynników wewnątrzpopulacyjnych. Te ostatnie są jednak modyfikowane przez okoliczności związane z lokalizacją populacji w areale gatunku, a także przez jakość zasiedlanego biotopu. Czynniki

zewnętrzne, jak pogoda i pokarm, oddziałują najsilniej w okresach sezonowych zmian klimatycznych, to jest na przełomie jesieni i zimy oraz zimy i wiosny. Analiza wieloletniej dynamiki populacji symetrycznych gatunków gryzoni dowiodła, że na rozrodność każdego z nich ma wpływ liczebność i struktura populacji obu gatunków. Przedstawiona koncepcja podziału czynników na zewnętrzne i wewnątrzpopulacyjne tworzy system wzajemnie uzupełniających się czynników, który pozwala na stosunkowo pełne i precyzyjne wyjaśnienie prawidłowości obserwowanych w dynamice populacji leśnych gryzoni.

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This paper is aimed at multifactorial analysis of processes affecting abundance and population structure of 3 vole species inhabiting forests. Long-term studies in 5 sites located in different parts of the geographical range of the species involved have provided the empirical data. It is shown that during the breeding season demographic processes in the vole populations basically depend on intrinsic factors. The latter, however, are influenced by circumstances related to the location of the population within the species geographical range, as well as to the habitat quality. Extrinsic factors, like weather and food conditions, are the most effective in so-called transitory seasons, that is autumn-winter and winter-spring. The analysis of multi-annual population dynamics of 2 sympatric vole species shows that reproduction is influenced by the abundance and population structure of both of them. The presented concepts of intrinsic and extrinsic factors make a complementary system allowing for a rather full and precise evaluation of regularities in population dynamics of forest voles.

KEY WORDS: rodents, populations dynamics, external and internal factors.

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