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Multi-Annual Fluctuations in the Size of a Population of the Bank Vole in European Part of the Soviet Union

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Data were analyzed on the dynamics of two neighbouring populations of *Clethrionomys glareolus* with a similar fluctuation pattern dwelling in broad-leaved forests north of the forest-steppe zone (54°45'N, 37°40'E). Censuses, using trap-lines, and investigation of the demographic structure were conducted simultaneously from April to October during 1966—1976 in Population 1 and during 1972—1981 in Population 2. On the basis of analysis of numbers, breeding and age structure all the observation years were divided into 4 groups corresponding to different types of population dynamics. These types differed substantially in the abundance of voles in June to August ("low", "moderate", "high" numbers and "peak"). In addition, they were characterized by different rates of changes in population size during the summer and winter and in other demographic parameters, *i.e.* duration of the breeding season, rate of population recruitement, ratio of the age groups and survival in different seasons. Multi-annual fluctuations in the size of the bank vole populations under study were complicated and differed from both the rigidly cyclic and the non-cyclic variants of population dynamics of *Clethrionomys*. Despite the comparatively low cyclicity index (0.26 and 0.32), the peak and subsequent crash of the population were well-defined. However, these peaks were repeated irregularly and three-year cycles associated with them ("peak" — "low" numbers — "high" numbers) were either consecutive or followed at intervals of 2 to 6 years. Most significant in the regulation of population processes under the given conditions were the dates of the onset of reproduction and the viability of the voles born in different demographic situations. Lengthening of the reproductive season to a whole year resulted in accelarated replacement of generations and in a rapid recovery of the population stock after a year of low numbers.

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1. INTRODUCTION

Number dynamics reflects both ecological properties of a species and conditions of its existence in a particular natural environmet. In a plastic species such as the bank vole (*Clethrionomys glareolus*) population dynamics vary greatly throughout its vast geographical range. This can be seen clearly by a comparison of the "European bank vole" (Bashenina, 1981) and the studies done by other authors (Petrusewicz, 1983; Bujalska, 1985; Henttonem *et al.*, 1985). Until recently most studies of this species have been mainly concerned with northern regions, while in the centre of the range the insular population has been largely dealt with (Koshkina, 1957; Ivanter, 1975; Wiger, 1979, 1982; Hansson & Henttonen, 1985; Bujalska, 1970, 1985 and others). In central Russia, with its sub-zones of broad-leaved forest and coniferous-deciduous forest, optimal for the bank vole, data concerning bank vole population dynamics is generally limited to relative numbers. There are few studies in this region where the population size of this animal is monitored on a multi-annual basis in combination with studies of population structure (Tupikova & Konovalova, 1971; Bernshtein *et al.*, 1987; Ivankina, 1987). We have studied the bank vole (*Clethrionomys glareolus*, Schreber, 1780) in hardwood forests of the European forest-steppe. The populations concerned were described in our previous studies (Zhigalsky & Bernshtein, 1986, 1989). This paper attempts to elucidate seasonal and multi-anuual population dynamics of the bank vole with special attention to demographic structure and to the major number fluctuation patterns under given conditions.

2. MATERIAL AND METHODS

The material was collected in the Tula Region (54°45'N, 37°40'E,) in the northern part of the forest-steppe zone at two isolated stations 25 km apart. The first station, 5 km^2 in area, was a plot of hardwood forest with a great variety of species, oak and linden predominating. The other station, 1 km^2 in area, was situated inside a large massif of old linden forest. The undergrowth and herbaceous vegetation were well developed in both areas.

Observations were conducted for 11 years (1966—1976) at the first station and for 10 years (1972—1981) at the second one. A total of 13.5 thousand bank voles were caught and examined during the study period. To determine relative numbers, the standard trap-line method was used, which is particularly informative when applied to forest rodents during the snow-free period of the year. Baited snap-traps (butter and oil) were set 5 metres apart in a line of 25 to 50 for one night. In this method numbers are estimated in relation to 100 trap-nights, *i.e.* as a percentage of catch. This index alone was used to determine the abundance. The censuses were made regularly in April, June, August and October, with 1500 to 2000 trap-nights during each month at the first station and with 500 to 800 trap-nights at the second station in accordance with their respective areas. In May, July and September additional censuses and captures were made (300 to 400 trap-nights). In winter no censuses were made, since their results are not comparable to the ones of the snow-free season.

The reproductive condition of the female was identified as being immature, pregnant, lactative or post-reproductive. During the first 6 days after fertilization when the embryos can not yet be seen in the uterus, pregnancy was identified by the presence of *corpora lutea* in the ovaries. Lactation was determined by the condition of the mammary glands. Repeated pregnancies and the number of litters in multiparous females were determined by coincidence the simultaneous occurence of pregnancy and lactation, and also by the number of dark (placental) spots in the uterus and involuting *corpora lutea* in the ovaries. The litter size was estimated only by the number of developed embryos.

The vole's age was determined by the development of molares (Tupikova *et al.*, 1968) and during the first 1 to 1.5 months of life by external traits (weight, moulting, *etc.*).

To distinguish years with the same pattern of seasonal dynamics factor analysis was used (Überla, 1977). Comparison of mean values and their increment, as well as the numbers and size of the litters, and also survival indices were determined by the Scheffe method of multiple comparisons (Glass & Stanley, 1970) and correlated fractions were compared according to McNemar (1947). The oak and linden seed production was scored on a five-point scale. Numerical data, not included in the tables, are given in the text, the sample size (n) being indicated. The significance level was in all cases assumed to be no less than 95%.

3. GENERAL CHARACTERIZATION OF POPULATIONS

In hardwood forests with a great proportion of linden and oak such as in the northern European forest-steppe, the bank vole is numerous, dominating the population of small mammals (Bashenina, 1981). At our stations it accounted for 85—95% of all the rodents taken. Average multi-annual numbers were very high: the number of individuals per 100 trap-nights in spring being 8.0 (CV 90%) and during the seasonal maximum 24.0 (CV 50%). An absence of profound depressions and many years with a high abundance also indicates very favourable conditions for the bank vole (Fig. 1).

The multi-annual dynamics pattern in both populations under study is similar. Numbers widely fluctuate annually, but in contrast to cyclic populations, it is difficult to determine any patterns in alternations of years with different number levels. The cyclicity index which in recent years has been used to evaluate density variation in different geographical zones (Henttonen *et al.*, 1985) is 0.26 and 0.32, respectively, in populations 1 and 2, and this index, too, characterizes them as noncyclic. In the cyclic *Clethrionomys* populations of Fennoscandia, this index exceeds 0.6. We attempted to group the years of observations on the principle of similarity of their demographic characteristics, using factor analysis. For criteria, parameters were used which play the most substantial role in the dynamics of the given population (Zhigalsky & Bernshtein, 1989): (1) number level; (2) rate of changes in numbers over consecutive periods; (3) involvement of females in breeding (proportions of immature and pregnant females; (4) age composition of the population (respective proportions of the individuals of 1—2, 3—6 and 7—12 months old). The factor analysis was conducted separately for April, June, August and October for each group of indices and for the total number of indices. All the years from 1966 to 1981 were considered in the same dynamics series, except the 5 years of parallel observations at the two stations. During these years (1972—1976), each population was considered to be a separate statistical point, since their rhythms did not coincide during this period (Fig. 1). A detailed description of factor analysis is given elsewhere (Zhigalsky, 1988).

As a result of the analysis four year groups were distinguished corresponding to different types of population seasonal dynamics:
I (low) — 1967, 1971, 1973*, 1976, 1978, 1981;
II (moderate) — 1969, 1970, 1974, 1975*;
III (high) — 1968, 1972, 1973, 1974*, 1976*, 1979;
IV (peak) — 1966, 1972*, 1975, 1977, 1980;
(hereafter* designates population 2 during the years of parallel observations on two plots).

It should be emphasized that in the given context the concept of seasonal population dynamics is broader than the one of seasonal number dynamics, since these types were distinguished by a set of traits including elements of population structure. Although this division is conventional, which is unavoidable in classification of natural phenomena, it provides insight into the regularities of population processes. In Sections 4—7 major demographic parameters in the years with different types of seasonal dynamics are described.

4. NUMBERS

The level and patterns of number changes in years with different types of seasonal dynamics are presented in Table 1 and Fig. 2. Classification of numbers into "low" (I), "moderate" (II), "high" (III) and "peak" (IV) was based on the average June-August value, which char-

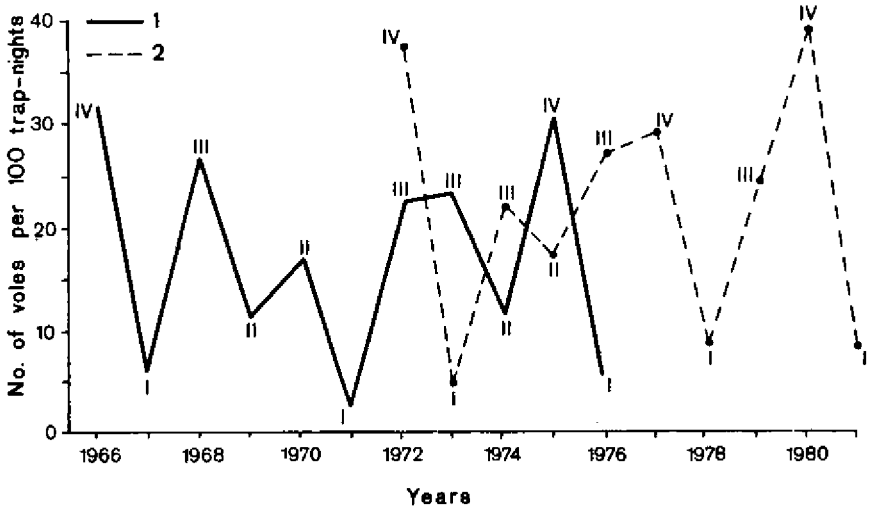


Fig. 1. Multi-annual fluctautions of number in the bank vole per 100 trap-nights (average values for June—August).

(1) Population 1; (2) Population 2. Roman numerals stand for the population dynamic type of a given year.

acterizes well the types distinguished: the extreme values of this index never overlap, while the moderate values differ significantly. Thus, an average summer number in itself can serve as a formal criterion for identification of the above types. These number definitions are hereafter synonymous with the respective types of population dynamics.

The April numbers were less informative. In April numbers varied widely in all the distinguished types and, therefore, in most cases it was impossible to predict the population's future. In early summer significant differences from the other types were found only in Types I and IV (average values in June, respectively, 2.4 and 14.4% of catch); Type II and Type III show no significant differences (8.7 and 6.1% of catch, respectively). In August similar numbers were recorded for Types III and IV, although they differed in principle in other population characteristics as will be seen below. Thus, during the entire snow-free season, high numbers were recorded only in "peak" years.

During all the years, except 1967 and 1971, numbers were minimal in spring, maximal values were in late summer, and then they declined again. The rates of growth during the first and second half of summer and also the pattern of decline during the autumn and winter for each dynamics type were fairly specific (Fig. 2). For "low" and "moderate"

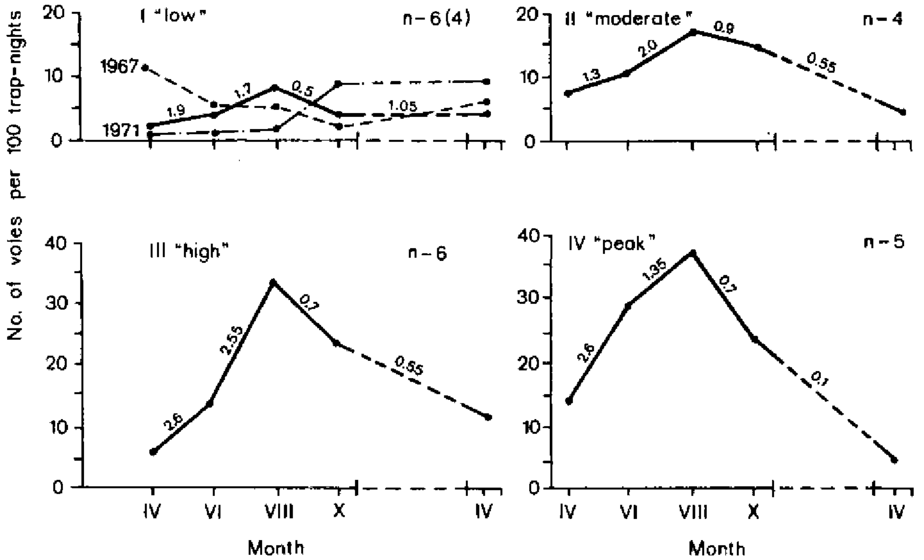


Fig. 2. Changes in bank vole numbers per 100 trap-nights during the annual cycle from April of one year to April of the next year depending on the type of populational dynamics (I—IV). The graphs show average number values for each type. n — number of years with a given type of population dynamics. Figures over the curve are factors of the numbers changed over the given period.

Table 1

Mean numbers (and ranges in parentheses) of bank voles per 100 trap-nights in relation to the types of population dynamics. See text for details of methods and denotations.

Type of dynamics	I (low)		II (moderate)	III (high)	IV (peak)	Significantly different types ($p \leq 0.05$)
Years	1967, 1973*, 1976, 1978 1981	1971	1969,1970, 1974, 1975*	1968,1972 1973, 1974*, 1976*, 1979	1966,1972* 1975, 1977, 1980	
Minimum numbers (April)	4.3 (2.3—11.6)	0.6	8.0 (5.3—11.4)	6.1 (3.9—9.1)	14.4 (7.0—23.7)	I—IV, III—IV
Maximum numbers (August)	7.8 (5.4—11.0)	9.0	17.2 (15.5—20.1)	33.7 (29.8—44.4)	37.7 (33.0—43.0)	all, except III—IV
Average numbers in summer (June—August)	6.8 (5.3—8.3)	1.9	14.2 (11.1—17.5)	24.3 (22.3—27.1)	33.8 (29.1—39.1)	all
Ratio of August:April numbers	2.8 (0.5—4.8)	15	2.1 (1.5—3.1)	6.0 (3.3—9.0)	3.3 (1.7—6.1)	I—III, II—III

numbers the factor of increment from April to June was much lower than for "high" numbers. During the peak years this value varied over a wide range depending on the initial numbers: at 7-8% of catch in April (1972*, 1975) the numbers increased 3.5-4.7 times by June, and at over 15% in spring (1966, 1977, 1980), only 1.4 to 1.7 times. During the second half of summer the highest rates of number growth were recorded for Type III, and the lowest for Type IV. As a result, by August numbers for these years became similar despite substantial differences in spring and in early summer. On the whole, during the spring-summer season the increment was greatest at "high" numbers: an average index is 2 to 3-fold higher than those in other types, differing from the latter significantly (Table 1).

The sharpest drop in numbers from autumn to spring occurred after the "peak" years (population crash). In other years numbers decreased during winter to a much lesser extent, and after the years of Type I it even somewhat increased (owing to undersnow breeding). The pattern of fluctuations during this period could not be determined due to lack of data from November to March.

Two "low" number years displayed atypical dynamics during the snow-free period (Fig. 2). In 1967, for a single time during the entire observation period from April to August the vole abundance did not increase but declined from 11.4 to 5.4%. But the sharpest drop of this value already occurred by May (to 4.1%) and subsequent seasonal dynamics differed from the usual to a lesser extent. In 1971 a reverse pattern was observed: with very low initial numbers (0.6%) it increased during the season by 15 times to reach maximum values only by October, and perhaps later. This low abundance in spring and its multiple increase during the year is more typical of the northern parts of bank vole range (Ivanter, 1975; and others).

5. REPRODUCTION

5.1. Results

To describe reproduction, parameters were used which to a great extent reflect the strategy of population reproduction in different types of seasonal dynamics. Since the breeding activity of males did not limit the duration and rate of reproduction of the bank vole under given conditions (Zhigalsky & Bernshtein, 1986), we give data concerning only females. In addition to the common indices the relative numbers of breeding females (the number of pregnant females per 100 trap-nights) and the overall production of embryos were used. The latter index indicates a potential increment of the vole population over the breeding season (Christian, 1971; Okulova, 1975).

Embryo production was determined for each month separately by multiplying the numbers of all pregnant females (including females with not yet implanted embryos) by average litter size for this period. Subsequently the data obtained over the entire reproductive season were summed. This calculation was done separately for females of different times of birth, which made it possible to reveal the contribution of individual cohorts to the reproduction of the population. In estimating embryo production, the numbers of pregnant females, and the numbers and size of litters some additional evidence was used for May, July, and September. The beginning of the reproductive season was mainly determined by the age composition of the population in spring and in early summer and by the sexual condition of females in April. Direct observations of the reproduction of voles from November to March were only single.

5.1.1. Duration of Breeding Season

The breeding season in the study area varied widely. In most cases females were reproductively active for 4 to 6 months but the dates of this period were extremely variable in years with different types of seasonal dynamics. "Low" and "moderate" numbers of females with developed embryos at an age of 6 days were recorded not earlier than the third week of April and, occasionally, in early May. The dates of their appearance extended over two weeks. By contrast, during the "peak" years, reproduction began vigorously in early to mid-April. The only exception was 1980. In spring numbers of over 20 individuals per 100 trap-nights about 50% of females displayed no pregnancy traits in mid-April.

The earliest dates of the onset of breeding season were noted in the years of "high" numbers. Of the 6 years associated with this type of dynamics, the first pregnant females appeared in early April only in 1973. Judging by the population age composition in spring in other years reproduction proceeded fairly intensively as early as January-March (1972, 1976*, 1979) or continued from the autumn of the previous year (1967-1968, 1973*-1974*). In four cases intensive undersnow breeding was preceded by low numbers at the end of summer and in autumn, *i.e.* the years belonging to Type I, in combination with a good yield of linden and/or oak (4 to 5 points), and only in a single year (1975* - Type II) a sharp drop by October with an average seed yield (3 points).

During the "peak" years breeding stopped as early as July. At lower summer numbers it continued two to three months longer, and in some years, as already mentioned, it continued even in winter. As a result, the shortest breeding season (April-July) occurred during the "peak" years. By contrast, the longest season is characteristic of the years beloning to dynamic types I and III; in the former case owing to late cessation and in the latter case due to early onset of breeding.

5.1.2. Proportion of Breeding Females

During all years the observed proportion of breeding females was highest early in the season, when females of oldest age classes predominated and whose breeding activity was not associated with the abundance. While in April the proportion of pregnant females varied from 0 do 100% depending on the dates of the onset of breeding, from early May onward no barren females were encountered among overwintered ones or among those which were born in early spring. In addition, in spring the interval between the litters was reduced to a minimum: in April to May of the 140 lactating females caught 124 (80%) were pregnant again. By June, the proportion of immature young in the population increased, except for the peak years, when pregnant females constituted over 50% of the females.

At the end of summer and in autumn the breeding rate invariably declined, but years with different types of dynamics were markedly distinct in terms of this index (Table 2). At "low" numbers in August, over half of the females bred actively, and only in October the proportion of pregnant individuals among them dropped sharply. During the "peak" years, in August some rare pregnant females were recorded in only three cases out of five. In Type III years in late summer reproductively active females were encountered far more frequently than in Type IV years despite similar numbers of voles during this period (Tables 1 and 2).

5.1.3. Reproductive Activity of Young Females

The sexual maturation of young females was associated with the time of their birth and population density. Both these regularities are well demonstrated by our material (Fig. 3). All yearlings which were born before mid-April and the majority of females born in April or in May began breeding during the same season. Immature females from the second spring cohort were recorded only in those cases where the numbers were at a high level from spring (Type IV) and in 1968 (Type III), breeding continued from the previous year. But during these years by August less than half of the females born in April and in May remained immature. During other years the majority of voles born in spring produced offspring as early as the first two months of their life.

The yearlings born in summer matured at a slower rate and the limiting factor of density exerted a greater impact on them. At low numbers (Type I) about 50% of the females born in summer were breeding at an age of one to two months, and the other females during the next two months. During the years with high numbers in the course of the entire summer (Type IV), summer yearlings did not mature at all during the same season. In autumn the rates of sexual maturation sharply dropped during all the years and by October some females of the younger age class produced offspring, only when their numbers were low.

Overall, during the breeding season the proportion of yearling females that reached sexual maturity gradually declined from Type I to Type IV, constituting 73.4%, 58.3%, 49.7% and 19.8% (the number of individuals under study being 273, 920, 1989 and 1446; $p \leq 0.05$). Thus,

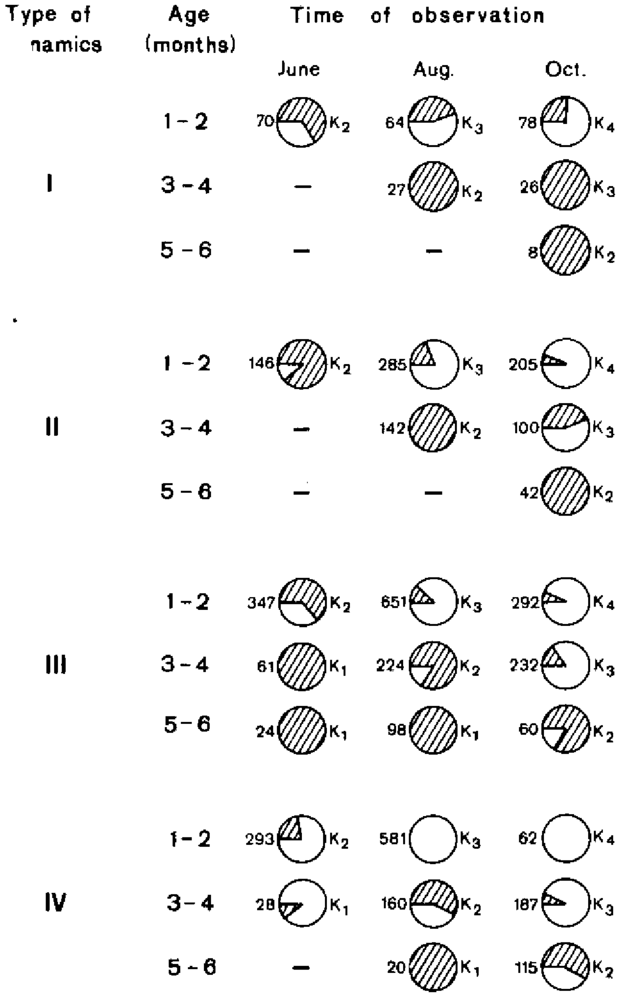


Fig. 3. Percentage of breeding yearling females of C. *glareolus* of different cohorts (hatched sector) as a function of the type of population dynamics.
Figures designate samples sizes, time of birth of the cohorts. K_1 — before mid-April; K_2 — mid-April—May; K_3 — June to July; K_4 — August—September.

in the autumn population at "low" numbers a relatively larger amount of breeding females was accumulated compared with all the other years; during the "peak" years their proportion was minimal (Fig. 3, Table 2).

Table 2
Percentage of breeding females of bank vole in relation to different types of population dynamics. Tf — total mature females, Pf — pregnant females (with embryos and/or with *corpora lutea*).

Type of dynamics		I (low)	II (moderate)	III (high)	IV (peak)	Significantly different types ($p \leq 0.05$)
April	N	110	183	223	191	
	Tf	31.5%	72.1%	95.1%	85.7%	all
	Pf	31.5%	72.1%	85.6%	82.7%	all
June	N	123	203	526	562	
	Tf	84.9%	87.9%	79.8%	54.6%	I—IV, II—III, II—IV, III—IV
	Pf	71.0%	71.8%	55.1%	32.3%	all, except I—II
August	N	98	456	1012	697	
	Tf	74.6%	51.8%	42.4%	24.0%	all
	Pf	56.6%	26.2%	17.5%	0.5%	all except II—III
October	N	130	354	631	427	
	Tf	45.2%	24.6%	22.0%	19.5%	all
	Pf	7.2%	5.0%	0	0	I—III, I—IV, II—III, II—IV

Table 3
Number of litters in breeding overwintered females of bank vole in April and May in relation to the type of population dynamics.

Type of dynamics	I (low)	II (moderate)	III (high)	IV (peak)	Significantly different types ($p \leq 0.05$)
		April			
Number of females	73	153	176	144	
Per cent females with					
1st litter	100%	100%	53.0%	84.0%	all except I—II
2nd litter	0	0	34.5%	16.0%	all except I—II
3rd litter	0	0	8.5%	0	I—III, II—III, III—IV
$\overline{X}$ litters per female	1.0	1.0	1.50	1.15	I—III, II—III, III—IV
		May			
Number of females	19	63	20	64	
Per cent females with					
1st litter	52.5%	35.5%	10.0%	11.0%	I—III, I—IV, II—III, II—IV
2nd litter	47.5%	64.5%	60.0%	78.0%	I—IV
3rd litter	0	0	30.0%	11.0%	all except III—IV
$\overline{X}$ litters per female	1.5	1.65	2.20	2.0	I—III, I—IV

5.1.4. The Number of Litters in Overwintered and Young Females

The number of litters produced by overwintered females and yearlings during the period of greatest breeding activity (April-June) largely determines the reproductive potential of the population. In our conditions it varied widely in different types of seasonal dynamics and was primarily associated with the dates of the onset of breeding (Table 3 and 4). The greatest number of litters in overwintered animals appeared in Type III years, since as early as April there were females with a second and even a third pregnancy, while in May their proportion was 90%. In the "peak" years, the majority of females produced a second litter in May, but those pregnant or lactating for the third time were encountered three times less frequently than in years with undersnow breeding. With "low" and "moderate" numbers in April only the first pregnancy was recorded in breeding females, and even in May from a fourth to a half females were still gravid or nursing their first litter. Since during these years, in May-April 44 to 89% (on an average 51%) of overwintered females died, many of them did not have enough time to produce or nurse the offspring. The majority of overwintered females that survived to June produced a second to third litter, but differences in the number of litters per female in years with different dynamics types remained fairly noticeable (Table 3).

Furthermore, the numbers of overwintered females were sharply reduced (in August on the average to 0.15 individuals per 100 trap-

Table 4
Number of litters in overwintered and young females of bank voles in June in relation to the type of population dynamics.

Type of dynamics	I (low)	II (moderate)	III (high)	IV (peak)	Significantly different types ($p \leq 0.05$)
			Overwintered females		
Number of female	44	41	78	108	
Per cent females with					
1st litter	18.0%	17.0%	0	2.0%	I—III, I—IV, II—III, II—IV
2nd litter	53.5%	44.0%	5.0%	49.0%	I—III, II—III, III—IV
3rd litter	28.5%	39.0%	95.0%	49.0%	I—III, I—IV, II—III, III—IV
$\overline{X}$ litters per female	2.10	2.20	2.95	2.50	I—III, I—IV, II—III
			Young females		
Number of females	42	110	299	130	
Per cent females with					
1st litter	93.0%	83.0%	67.0%	32.5%	all except I—II,
2nd litter	7.0%	16.5%	18.0%	67.5%	I—III, I—IV, II—IV, III—IV
3rd litter	0	0	15.0%	0	I—III, II—III, III—IV
$\overline{X}$ litters per female	1.05	1.15	1.50	1.65	all except I—II

nights). Some individual females that remained could theoretically produce the fourth and fifth litters, but could not contribute in any substantial way to recruitement of the population.

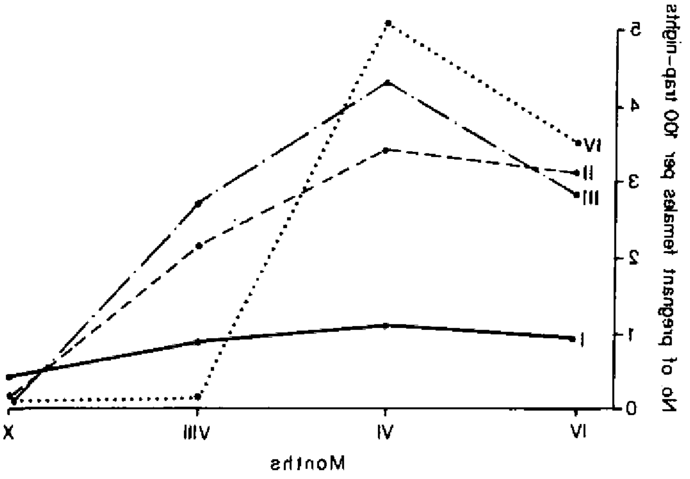
The number of litters produced by sexually mature yearlings at the beginning of summer is mainly associated with their age. In the years when breeding began late (Types I and II), the majority of young females in June were pregnant for the first time and the average number of litters did not exceed 1.15 (Table 4). At an early beginning of the reproductive season (Type III) 33% of breeding yearlings were pregnant or nursing the second or third litter at that time though the majority of them were May-born animals with the first pregnancy or lactation. During the "peak" years in June the females of the first spring generation, which already had second litters, predominated among mature young animals. In females born in May maturation was delayed. Hence, in such years only a third of the yearlings produced their first litter in June, and the average number of litters per breeding female was somewhat higher than at "high" numbers. During the second half of the season, the number of litters produced by yearlings was a function of their breeding activity and mortality in different years and was hard to determine.

5.1.5. Litter Size

The size of litter in the populations under study fluctuated in different years from 5.7 to 7.1 in overwintered females and from 4.9 to 6.4 in yearlings, on the average from 6.6 ± 0.03 ($n=604$) and 5.8 ± 0.05 ($n=560$). But variations of this index in different types of seasonal dynamics were less pronounced (Table 5). In overwintered females differences in the litter size over the season were insignificant, while in yearlings the largest litters were recorded in years with intensive population growth (Type III and the year 1971). The population density and physiological state of the females affected primarily the seasonal dynamics of the litter size. In the "peak" years the largest number of embryos in the overwintered animals occurred as early as the first pregnancy (April) and it markedly dwindled by June. During all the other years the litter size increased by the second or third pregnancy (June) and was only reduced by the second half of summer. Thus, a decrease in litter size was recorded during the period of reduction in breeding rate, which in the "peak" years took place 1.5—2 months earlier than usual. Despite the differences litter size was one of the most stable reproductive parameters and its fluctuations did not substantially affect recruitement.

Table 5
Average (±SD) litter sizes of bank voles in relation to the types of population dynamics.

Type of dynamics	I (low)						II (moderate)			III (high)			IV (peak)			Significantly different types
	1971			other years												
	N	$\overline{x}$	SD	N	$\overline{x}$	SD	N	$\overline{x}$	SD	N	$\overline{x}$	SD	N	$\overline{x}$	SD	($p \leq 0.05$)
							Overwintered females									
April—May	—	—	—	11	7.0	0.40	98	6.8	0.10	92	6.1	0.15	129	6.65	0.05	none
June	6	6.3	0.51	16	7.0	0.32	60	7.4	0.12	57	7.0	0.20	91	6.25	0.10	II—IV, III—IV
July—October	2	7.5	0.50	9	5.3	0.39	13	5.5	0.25	15	6.25	0.25	5	4.8	0.33	none
							Young females									
June	5	7.2	0.50	21	5.3	0.27	71	6.1	0.12	206	6.15	0.05	60	5.5	0.20	II—IV, III—IV
July—October	22	5.6	0.27	33	4.8	0.17	66	5.05	0.13	76	5.1	0.10	—	—	—	none
							During entire season									
Overwintered felmales	8	6.6	0.33	36	6.55	0.25	171	6.85	0.11	164	6.4	0.10	225	6.45	0.06	none
Young females	27	5.9	0.20	54	4.95	0.15	137	5.45	0.09	282	5.9	0.05	60	5.5	0.13	all except II—III, I(1971)—III



Fluctuations in bank vole population

Fig. 4. Changes in the numbers of pregnant females of *C. glareolus* from April to October as a function of the type of population dynamics (I—IV).

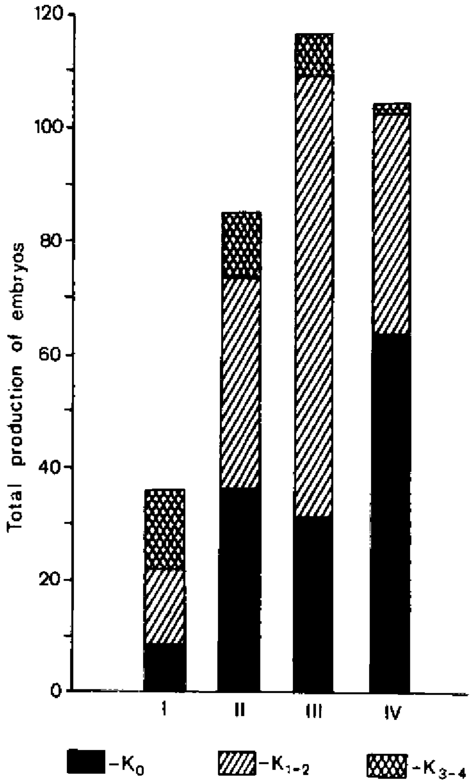


Fig. 5. Total embryo production in a population of *C. glareolus* over the breeding season and potential contributions of females of different cohorts to population recruitement as a function of the type of population dynamics (I—IV). K_0 — overwintered; K_{1-2} — born before June; K_{3-4} — born in June and later.

5.1.6. The Numbers of Pregnant Females and Potential Contribution of Females of Different Cohorts to Population Recruitement

The actual rates of recruitement during the breeding season are best understood by the numbers of pregnant females, since this index reflects not only the breeding rate, but also abundance at any one period (Fig. 4). Despite the fact that the proportion of reproductively active females in summer was inversely proportional to population density, in June as well as in spring, their numbers were significantly higher in the Type III and Type IV years compared with "low" numbers (4.3, 5.1, and 1.1 individuals per 100 trap-nights). Subsequently the numbers of pregnant females declined, but at varying rates, depending on the type of dynamics. During Type I years, the value of this index fluctuated only slightly during the season while during the "peak" years after the June maximum it dropped almost to nil by August. In other cases (Types II and III) the decline occurred slowly and by August the numbers of breeding females exceeded 3 to 4 times that at a low abundance (Type I).

In total the highest numbers of pregnant females over the breeding season were recorded in Type III and IV years (respectively 17.8 and 14.5 individuals per 100 trap-nights) and during Type I years this value was much lower (4.8). "Embryo production" over the season varied in accordance with the number of breeding females: from 114.0 to 34.5 at "high" and "low" numbers, respectively (Fig. 5).

The potential contribution of females of different cohorts to the recruitement also varied with types of seasonal dynamics. During the "peak" years which are distinguished by high spring numbers and early cessation of breeding, the offspring was largely produced by overwintered females, while in all other cases by yearling females. And, during the years with an early onset of breeding (Type III), the greatest role in recruitement was played by spring-born females, while at "low" numbers the contribution of spring and summer cohorts was fairly similar (Fig. 5). As a result, during the "peak" years, the wintering population members were mostly those of the first generation while in other years the ones of "grand-children", or "grand-grand-children", which may affect the future of the population.

5.2. Discussion

As follows from data given in this section, in the northern forest-steppe the population recruitement level of bank voles is largely determined by the extremely vari (from 4 months to a whole year) duration of the breeding season. All the other significant parameters (numbers, age composition of breeding females, number of litters and embryo production over the season) are associated with the duration of this season. Of particularly great importance were the dates of the onset of breeding, since under such conditions the population manifests its reproductive potential more successfully during the first half of the year. Judging by the rates of population growth, the reproductive success is greater the earlier the first litters appear.

Such great variations in the duration of the reproductive season due to the influence of winter and early spring months are characteristic of *C. glareolus* dwelling in deciduous and coniferous-deciduous forests of different climatic zones from the southwestern portion of the range to the Cis-Urals (Zejda, 1964, 1970; Smyth, 1966; Bernshtein *et al.*, 1980, 1987 and others). Like us, the majority of authors report that voles intensively breed under the snow usually after years with a good seed crop and low autumn numbers. In those zones and habitats where just one condition is lacking (*e.g.* a lack of rich forage resources in winter or stable high autumn population density) the breeding period is confined to the warm season. In these case negligible fluctuations in the dates of the appearance of the first litters in *Clethrionomys* are associated with the level of spring numbers and/or with the dates of snow melting (Tupikova & Konovalova, 1971; Ivanter, 1975; Koshkina & Korotkov, 1975; Ivankina, 1987).

In the region of our work the dates of the onset of breeding were not significantly related to these indices (Zhigalsky & Bernshtein, 1989). Rather, they appear to be determined by the previous history of the population and forage resources. There are reasons to believe that in addition to the small numbers of voles, intensive undersnow breeding is promoted by a great proportion of mature females in the previous autumn (Type I).

The level of reproductive activity of females during the summer months and the dates of the cessation of reproduction depend on the population density, which is generally characteristic of forest rodents. Particularly great is the impact of population density on the maturation of young females. The proportion of mature yearlings is invariably inversely proportional to the numbers. This phenomenon has been recorded many times and appears to be explained by rigid territoriality of adult females during the period of reproductive activity (Koshkina, 1965; Bujalska, 1970).

According to Bujalska (1970, 1985), in an insular population of the bank vole with a relatively constant and high density, females' territoriality leads to the stabilization of the number of females involved in breeding and the number of the offspring produced in different years. It is only the age composition of mature females during summer months that changes. There are reasons to believe that in this case, the population fully realizes its reproductive potential and annually there develops a saturation of the territories by breeding females. Presumably, this is partially explained by the effect of a bound population. In the study area a similar situation appeared to take place in spring and in early summer only at Types III and IV of population dynamics, *i.e.* in the years when breeding began not later than mid-April.

At low initial numbers and at later dates of the onset of breeding (Type I) the total numbers of pregnant females during all the months and the potential increment of the population (seasonal embryo production) were much lower than the upper limit for the given territory. This difference was not compensated by the higher reproductive activity of females during the summer-autumn season. A similar situation was observed by Ivankina (1987) in the bank vole population near Moscow. The total number of litters which females produced in an area of 4 hectares per breeding season at low *vs.* high density differed by more than four times. Apparently, this situation is more typical of open and less stable population of *Clethrionomys*.

It should be emphasized that in bank vole populations under study the general rate of breeding and particularly maturation of yearlings during the second half of summer are related to numbers during both the preceding period (June) and during the current period (August) (Zhigalsky & Bernshtein, 1989). It can be seen well in comparing Type III and Type IV years. Thus, the index of mid-summer numbers, which well differentiates all the types of seasonal dynamics is of definite biological significance. Under such conditions it characterizes individual years more fully than the numbers during the period of seasonal maximum and has a direct bearing on the regulation of breeding.

6. AGE AND WEIGHT COMPOSITION OF THE POPULATION

The age composition of the population depends directly on the dates of onset and cessation of breeding as well as the rate of this process during the season (Table 6). In spring the population in the majority of cases consisted of overwintered voles, mainly 7 to 10 months old. An exception was Type III years. In April there were yearlings of different age classes, and during the years with the most intensive undersnow breeding (1968, 1974*), 43 to 47% of the voles were 1 to 4 months old. During the summer the proportion of overwintered voles naturally decreased and by August it was only during the "peak" years that overwintered individuals constituted about 10% of the population. Of them, only separate individuals survived to autumn, and hardly any survived another winter.

By October the difference in the age composition of yearlings in years with different types of dynamics became particularly noticeable.

Especially distinguishable were the "peak" years when the young of early generation constituted the basis of the autumn population. In other years their number is 2 to 3 times less than that of the one to two months old (Type I and Type II) or similar (Type III).

The growth of yearlings in the populations under study did not discontinue during the second half of summer with an increased population density and delayed maturation. Thus, during the years of "peak" and "high" numbers, the population that went under the snow consisted of larger individuals than in the years of "low" and "moderate" numbers. In the former case the weight of animals was 18.04±0.1 (n=1208), while in the latter case, 16.4±0.05 (n=918). Within these groups the differences were not significant, while inter-group differ-

Table 6
Age structure of bank vole population in relation to different types of population dynamics.

Age groups	April	June	August	October
		Type I (low)		
Number of voles	307	280	241	246
Per cent voles in				
age class 1— 2 months	—	62.1	80.9	76.5
3— 6 months	—	—	13.6	22.0
7—16 months	100	37.9	5.5	1.5
		Type II (moderate)		
Number of voles	461	454	994	730
Per cent voles in				
age class 1— 2 months	—	68.7	62.6	64.1
3— 6 months	—	—	32.2	34.4
7—16 months	100	31.3	5.2	1.5
		Type III (high)		
Number of voles	519	1102	2449	1186
Per cent voles in				
age class 1— 2 months	8.0	60.5	66.8	46.7
3— 6 months	18.6	14.4	28.5	50.9
7—16 months	73.4	25.1	4.7	2.4
		Type IV (peak)		
Number of voles	559	1085	1582	824
Per cent voles in				
age class 1— 2 months	—	64.7	68.9	14.9
3— 4 months	5.0	3.8	21.8	82.6
7—16 months	95.0	31.5	9.3	2.5
Significantly different types ($p \leq 0.05$)				
Age class 1—2 months	I—III, II—III, III—IV	all except I—III, I—IV	all except III—IV	all
3— 6 months	all except I—II	all except I—II	all	all
7—16 months	all except I—II	all except II—IV	I—IV, II—IV, III—IV	none

ences were significant. The weight of overwintered animals increased gradually from the years of "low" numbers to the "peak" years (on the average over April to August in Types I, II, III and IV: 22.3±0.3, n=318; 24.5±0.4, n=716; 26.0±0.2, n=614; 26.1±0.2, n=517). All the types of dynamics except Type III and IV differed significantly in terms of this index. Thus, in the given conditions the Chitty effect, *i.e.* an increase in the weight of adult individuals during the peak phase, was manifested during all the years with high numbers at the end of the breeding period.

The great weight of both overwintered individuals and yearlings in dynamics Types III and IV appear to be indicative of a good condition of the population during the summer period in these years.

7. SURVIVAL

7.1. Results

Data on the survival of bank voles under different types of seasonal dynamics are presented in Table 7. The survival index of yearlings is a ratio of the number of yearlings at the end of the breeding season to embryo production during that season. In other cases the values are obtained by comparing the numbers of a given group at the end and at the beginning of each period. Embryonic mortality was not taken into account, since it did not exceed 1% during all the years of observations.

The most intensive mortality of both overwintered individuals and yearlings in spring and summer of the current year was recorded at "low" and "moderate" numbers (according to our method of estima-

Table 7
Survival (%) of bank voles in different period of life in relation to the types of population dynamics.

Type of dynamics	Current year		Autumn-winter to follow	Second year of life April-August
	Overwintered April-August	Young April-end of breeding		
I (low)	5.2^1 33.3^2	10.9^1 25.4^2	58.1	33.6
II (moderate)	11.2	22.5	41.5^3	25.0
III (high)	29.5	28.5	35.4	15.8
IV (peak)	23.0	40.0	7.4	5.2
Significantly different types ($p \leq 0.05$)	I^1—III II—III	I^1—III I^1—IV,II—IV III—IV	I—IV, II—IV, III—IV	I—III, I—IV, II—IV

^{1} all years, except 1971; ^{2} 1971; ^{3} all years, except 1970/71.

tion the index of survival of yearlings in such cases is somewhat lower than actual due to an increased mortality of pregnant females). An exception was 1971 when a manifold increase in numbers was accompanied by high survival values (Table 1 and 7). The mortality of overwintered individuals during the Type III and IV years did not differ significantly, since data vary widely. Yearlings survived best of all during the "peak" years.

A quite different picture is observed during the autumn and winter and during the second summer of life. Of the animals that were born during the "peak" years 5 to 12% survived by spring (on the average 7.4%) and by the end of the second summer less than 6% of the spring stock. In the voles that were born during the years of "low" and "moderate" numbers the mortality during these periods was 5 to 8 times lower. Only after 1970 (Type II) by spring 3% of the voles of the preceding years remained, which will be discussed in the following section. The years of "high" numbers are intermediate in this respect, but they differ significantly from the "peak" years (Table 7).

As a result of the regularities revealed, the spring numbers of overwintered individuals after the years relating to Types I and IV of the dynamics were similar despite 5 to 6-fold differences during the preceding summer and autumn. And at the end of the second year of life the animals born during the "peak" years were far less abundant than during all the other years (0.3 and 1.5-2.2%, respectively, of the total animals trapped). The highest numbers of overwintered individuals during the entire season were noted after Type III years (Fig. 6).

We compared the survival of voles over the autumn and winter with their numbers during the preceding summer and the crops of linden and oak (Fig. 7). After the "peak" years even when the forage resources were good, mortality was far higher than in other years. When the abundance was low this value was stably high. After the transition years, the percentage of individuals that survived to the spring varied widely with no definite pattern. In some individual years the abundant crop of seeds appeared to have promoted successful overwintering when autumn numbers were high (Type III, 1979) and poor yields led to increased mortality (1968, Type III, 1970, Type II). However, the relationship between survival over the autumn and winter and the numbers during the preceding summer is more conspicuous (Fig. 7). During the warm season of the year, rains combined with a sharp drop in the temperature may occasionally increase the mortality of females and their litters, though our data failed to show the consequences of such events.

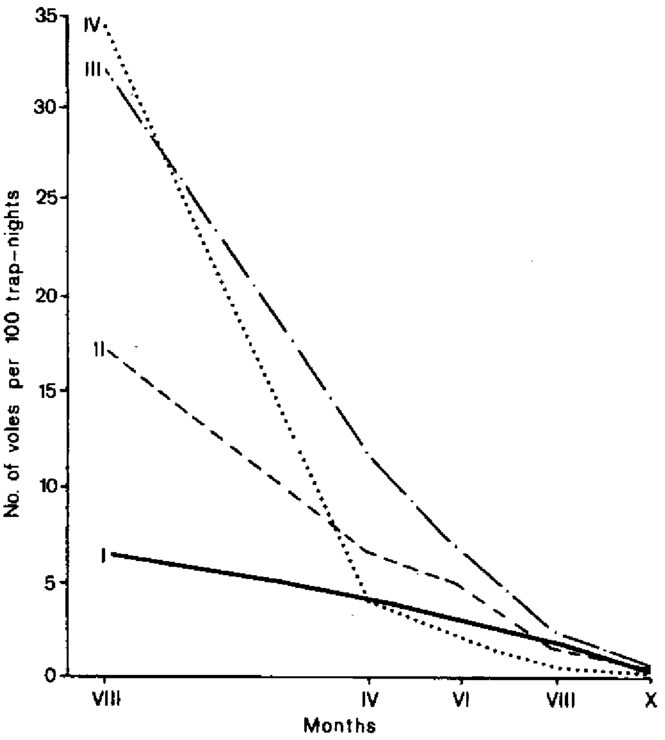


Fig. 6. Changes in the numbers of *C. glareolus* per 100 trap-nights over the autumn-winter season and the second summer of life as a function of the type of population dynamics (I—IV).

7.2. Discussion

Survival as well as breeding reflects the population state, and determines its dynamics. In the populations of *C. glareolus* under study mortality in different seasons and in different demographic situations differed considerably. To a great degree, it is affected by previous and existing numbers. On the whole, survival during the first year of life is directly, and during the autumn and winter, inversely related to the average summer numbers in the year of birth. As a result, the individuals that were born during the second half of summer and in autumn when the numbers were low remain in the population for the longest time, while the shortest life span is the one in the yearlings that were born in summer during the "peak" years.

During the first months of "peak" years, young stand the greatest chance of survival owing to the good condition of the parents and also due to a maturation delay that results in a decrease of mobility of yearlings and a decline of competition. An unfavourable effect of high

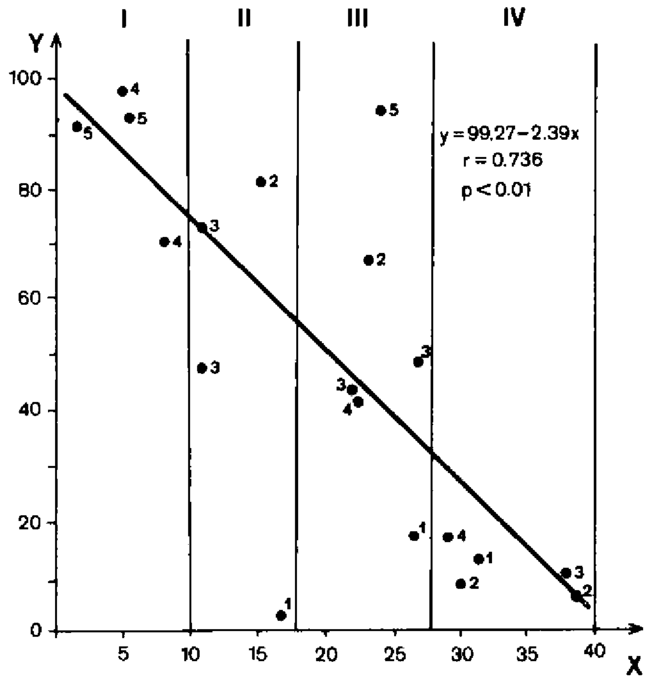


Fig. 7. Relationship between survival in the bank vole over the autumn-winter period (y) and the average numbers (x) under different crop yields.
1—5 — crop of seeds of linden an oak in grades; Roman numerals stand for types of population dynamics.

numbers in these cases begins to manifest itself not earlier than October, but it may be sharply expressed. Interestingly, in winter and during the second summer of life the young animals born in the Type IV year were characterized by a considerably higher level of mortality than the ones born in the Type III year despite similar numbers and body weight at the end of breeding season. Hence, these indices in themselves do not determine the population's viability. At the same time a small weight of yearlings in combination with small numbers appear to promote their successful overwintering after Type I and II years, other things being equal. Survival during this period can also be affected by the age and origin of the animals. As was already mentioned, during the "peak" years, individuals of the first cohorts born by overwintered females predominate in autumn, and in other younger individuals, *i.e.* offspring of yearlings of the first and second generation.

An increased mortality of the voles born and matured in overdense populations has been noted (Chitty, 1960; Wiger, 1979 and others). This may be due to the physiological stress developing in animals under such conditions. According to Ivashkina (1987) in *Microtus oeconomus* a depressed state of the population caused by an increased stress level continues from autumn during the "peak" year to the end of the next summer (a year of minimal numbers). The lowest level of stress in these voles was recorded during the spring-summer period in the "peak" years and during the entire phase of increasing numbers, which is close, in terms of demography, to Type III of seasonal dynamics in our classification. Judging by the survival indices, a similar dynamics of the population's physiological state is characteristic of *C. glareolus* in our study area as well.

The exogenous factors effected survival of the bank vole in the northern forest-steppe mainly during the autumn-winter period (Zhigalsky & Bernshtein, 1989). The forage appear to make this value very variable after the years of "moderate" and "high" numbers. By contrast, in the extreme variants (Type I and IV) their effect was less noticeable and mortality during the winter remained relatively stable.

8. RELATIONSHIPS BETWEEN MULTI-ANNUAL FLUCTUATIONS OF POPULATIONS AND TYPES OF THEIR SEASONAL DYNAMICS

Analysis of fluctuations of numbers of the bank vole during the observation period revealed a number of pecularities. There was a special sequence pattern in the alternation of years with some types of seasonal dynamics (Table 8). Type IV was invariably followed by Type I and subsequently by Type III. Each of these transitions was determined by the population's previous history, *i.e.* its demographic structure and, possibly, by its genetic composition during the preceding period. During Type IV years the animals that wintered were large individuals which were born mostly by overwintered females during the first half of summer when density was high. This combination of traits led the population to a crash, which is characteristic of the peak phenomenon to a greater extent than population parameters. As a result by the next

Table 8
Sequence of years with different types of population dynamics.

Type of dynamics	Number of observation	Frequency of transitions to type:				
		I	II	III	IV	?[1]
I	6	—	—	4	—	2
II	4	1[2]	1	1	1	—
III	6	—	3	1	2	—
IV	5	5	—	—	—	—

[1] last years of observations; [2] 1971.

spring numbers dropped to a minimal level, and overwintered individuals and their offspring were not able to recover their abundance rapidly. The poor condition of the populations in the years of "low" numbers manifested itself in a later onset of breeding and in poor survival of both overwintered animals and yearlings during the entire summer, and, as a consequence, retaining of numbers at a low level to the end of the season. At the same time sexual maturation of the surviving offspring was very intensive. During the summer and autumn the involvement of females in breeding was higher than in other years, in contrast to the situation in voles and lemmings under more profound depressions. In autumn the population in these cases mainly consisted of 1 to 2 month old animals which were grand-children and grand-grand-children of overwintered females. They had a relatively small weight, overwintered successfully and bred under the snow. This was undoubtedly promoted by good crops of linden and oak, which accompanied all the Type I years. As a result, after such years the numbers in April were equal to or exceeded the autumn values and the population was in good physiological condition, recruitement proceeding rapidly to the middle or end of summer, and mortality among those overwintered and young was relatively small. This led to a high growth of the population up to maximal values (Type III). However, transition from "high" numbers to the "peak" was recorded only 2 times out of 6. The years with "moderate" numbers were also repeated in no definite pattern (Table 8).

During all the years of observations (a total of 21 years) the above-described sequence pattern of the alternation of Types IV-I-III were only recorded three times (1966-1968; 1972*-1974*; 1977*—1979*) and another two years "low" numbers after the "peak" were at the end of observations (1975—1976 and 1980—1981). It can be seen that such cycles were repeated irregularly or followed directly one after another (if the year of "high" numbers immediately turned into a "peak") or had intervals of 2 to 6 years alternating with years of "high", "moderate" or "low" numbers in various combinations.

An exception to the general pattern was the year 1971 when increased mortality of voles from autumn to spring and an exceptionally low level of numbers in April for a single time followed the year of Type II rather than Type IV of seasonal dynamics. During that period there was a general depression of numbers of forest rodents in most of Central Russia. It was presumably caused by extreme weather conditions at the beginning of spring throughout the entire region (early melting of the snow cover followed by rains and cold) in combination with poor crops with poor crops of seeds. Excessively high rates of population recruitement at our station, from spring to autumn 1971 in contrast to other years of Type I suggest that the low number level in this case was not a cause of the demographic situation during the preceding period nor of a bad condition of the animals.

9. GENERAL DISCUSSION

In the majority of studies devoted to *Clethrionomys* two extreme variants of their population dynamics are considered, *i.e.* cyclic, which is peculiar of voles of northern Fennoscandia, and relatively stable populations which occur in optimal habitats of the central part of the range. The former is distinguished by a greater amplitude of density fluctuations over the years and a certain sequence pattern in the alternation of cyclic phases (*e.g.* Koshkina, 1957; Wiger, 1979; Hansson *et al.*, 1985; Henttonen *et al.*, 1985). In the latter variant, the density at the end of summer-autumn period is invariably relatively high and its seasonal fluctuations are pronounced (Tupikova & Konovalova, 1971; Koshkina & Korotkov, 1975; Bujalska, 1985 and others). The populations of *C. glareolus* under study were in between these extreme variants. They had a complicated fluctuation pattern and a highly dynamic structure, which appears to be generally characteristic of forest rodents of the temperate climate. The diversity of demographic situations in the given conditions is characterized by the four types of seasonal dynamics of the bank vole population, on which our analysis of populational processes during the observation period was based.

Average values, cyclicity index and some other population parameters were similar in the bank vole from the study area to the members of this genus dwelling in the most favourable conditions (*e.g.* Bashenina, 1981; Henttonen *et al.*, 1985; Okulova, 1987). However, in contrast to the well-balanced populations of *Clethrionomys* from the optimum range, the northern forest-steppe bank vole is characterized by a no less-pronounced multi-annual population dynamics than seasonal dynamics and the population peak phenomenon is undoubtedly present. This is manifested in structural and physiological shifts, whose consequences are felt throughout the entire subsequent year, rather than in the high summer-autumn density.

These peaks trigger off brief three-year cycles with sequentially alternating types of seasonal dynamics ("peak" - "low" numbers — "high" numbers). The decline following a peak was invariably of a crash type. But owing to a prolonged breeding season and a quick change of generations, which promotes renewal of the population, and, presumably, selection of respective genotypes (*e.g.* Krebs & Mayer, 1974), the period of relative depressions lasted no more than a year. Population size reached maximal values by the end of the next breeding season. However, the years of "high" numbers were not followed by a crash, since the population exhibited a drastically different structure than the one during the "peak" years. In terms of certain demographic parameters this type of seasonal dynamics is similar to a growing phase, which is followed by a peak in cyclic populations. But in the given conditions no such regular transition was recorded. This explains why such three-year periods are repeated here irregularly, following each other either consecutively or at 2 to 6-year intervals.

A rigid sequence pattern within the above cycles gives reason to believe that it is largely based on some intrapopulation mechanisms. The external conditions appear to affect the sequence pattern of the years with "moderate" and "high" numbers and also the frequency of the repetition of the peaks. The effects of weather and forage on the population vary and are clearly associated with its state. An indirect support of this is that the demographic situations of two adjacent populations during the years of parallel observations (1972—1976) did not coincide. A qualitative evaluation of this differentiation effect is beyond the scope of the present study. Our observations suggest that under given conditions the exogenous factors themselves result in a disruption of the multi-year dynamics of population processes in *C. glareolus* only under some exceptionally unfavourable conditions (1971).

The intrapopulation regulation of the bank vole density in the northern forest-steppe operates in a different way than in the well-balanced populations of *Clethrionomys*, where the peak phenomenon and its consequences are not pronounced, and the breeding season confines itself to the snowless period only. In such cases, the basic mechanism for the relatively stable density is the regulation of sexual maturation of the yearlings. As already mentioned, this process is presumably based on the territoriality of reproductively active females, limiting the total number of individuals involved in breeding and the productivity of the population as a whole (*e. g.* Bujalska, 1985).

In the populations under study the rate of maturation of young females was also regulated by summer density. However, during the years with a late onset of breeding and increased mortality during the spring-summer period (Types I and II) intensification of sexual maturation of yearlings did not results in a accelerated recruitement or in a considerable increase in population size over a single season. Hence, the greatest impact on the autoregulatory processes under the given conditions were the dates of the onset of the reproductive season and survival of the voles in different periods. Both these parameters are related to the population conditions at the beginning of the reproduction season which is manifested in its potential for further growth, rather than with spring abundance. The population condition, in turn, is determined by the structure and density during the previous years, and, only to a certain extent, by the wintering conditions (Zhigalsky & Bernshtein, 1989).

It follows from the above, that the dynamics of population processes in *C. glareolus* of the northern forest-steppe showed the following characteristic features:

(1) High variability over the years in the majority of demographic parameters, as reflected in four well-pronounced types of population seasonal dynamics.

(2) A wide range of fluctuations of the length of reproduction season (from four months to a whole year) and the noticeable effect of this index on population recruitement.

(3) The presence of a population peak and related three-year cycles against the background of a relatively high density and a comparatively low rate of its fluctuation in late summer and in autumn.

(4) A rigid sequence pattern of seasonal dynamics (IV-I-III) within the three-year cycles in combination with irregularity of the repetition of these cycles.

This pattern of population dynamics with variations is fairly typical of *C. glareolus* in forests with a predominance of broad-leaved species where the dates of the onset of breeding may vary within a wide range (*e.g.* Bernshtein *et al.*, 1987). Hence, in the study of population processes and the mechanisms of their regulation in those parts of range of the bank vole, more attention should be given to the demographic situation in the preceding periods as well as to the role of undersnow breeding in the maintenance of the population size.

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WIELOLETNIE WAHANIA LICZEBNOŚCI POPULACJI NORNICY RUDEJ Z EUROPEJSKIEJ CZĘŚCI ZWIĄZKU RADZIECKIEGO

Streszczenie

Przeanalizowano dane na temat dynamiki liczebności dwu populacji *Clethrionomys glareolus* zamieszkujących lasy liściaste północnej strefy lasostepu. Odłowy na liniach przeprowadzono od kwietnia do października w latach 1966-76 w populacji I i w latach 1972-81 w populacji II. Na podstawie analizy liczebności, rozrodu i struktury wiekowej populacji wszystkie lata odłowów podzielono na 4 grupy odpowiadające czterem typom dynamiki liczebności, różniącym się liczebnością nornic w okresie od czerwca do sierpnia (niskie, średnie, wysokie i szczytowe liczebności). Dodatkowo, wyróżnione typy dynamiki liczebności charakteryzowały się innym tempem zmian wielkości populacji latem i zimą, długością okresu rozrodczego, przeżywalnością i innymi parametrami demograficznymi.

Obserwowane wieloletnie wahania liczebności populacji nornicy rudej różniły się zarówno od wyraźnie cyklicznych, jak i od niecyklicznych populacji *Clethrionomys*. Mimo stosunkowo niskiego wskaźnika cykliczności (0.26—0.32) wyraźnie były szczyty i następujące po nich gwałtowne spadki liczebności. Jednak szczyty te występowały nieregularnie i trzyletnie cykle "szczyt-niska liczebność-wysoka liczebność" następowały po sobie bądź też oddzielone były 2—6-letnimi interwałami czasu.

Najważniejszymi czynnikami wpływającymi na dynamikę liczebności nornicy rudej były: czas rozpoczęcia rozrodu w danym roku i żywotność nornic urodzonych w różnych stanach liczebności. Obserwowane niekiedy wydłużenie rozrodu do całego roku przyspieszało wymianę generacji i powodowało szybki wzrost liczby nornic po roku niskiej liczebności.