

## Demographic Parameters and Variations in Numbers of the Common Vole <sup>1</sup>

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Adamczewska-Andrzejewska K. & Nabagło L., 1977: Demographic parameters and variations in numbers of the common vole. Acta theriol., 22, 31: 431—457 [With 2 Tables & 15 Figs.].

Observations were made for two years of the demographic variations in two enclosed populations (A and B) of the common vole *Microtus arvalis* (Pallas, 1779), by means of the CMR method. Variations in numbers followed a similar course in both populations, population A reaching a lower maximum number than B. Both populations were more numerous in the second study year (1972). The greatest rate of increase in numbers ( $r_N=0.23$ ) took place in May. Maximum increase was found in the number of individuals ( $\bar{r}_r=0.5-1.0/\text{week}/1 \text{ ♀}$ ) during the period from May to July. In the early summer period the rate of increase in numbers in the populations was found to be limited by the high degree of mortality among the youngest animals. During the reproductive period turnover was 60%—90% of the population per month. The ratio of females to males in the population varied from 0.25 to 2.35. The greatest percentage of females was observed during the period of intensive reproduction, and was correlated with the number of recruits to the population. The predominance of females results in higher recruitment and better survival. During the growing season over 60% of the population was formed by individuals which had spent less than one month outside the nest. During autumn of the year with higher numbers the populations were younger than was the case in the year with lower numbers. The more numerous population (B) was younger than the less numerous (A). During the reproductive period the females were older than the males. The study populations were in the phase of rapid population growth, which was accompanied in successive years by longer-lasting numerical predominance of females over males, prolongation of the reproductive period and better survival of new individuals.

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### I. INTRODUCTION

*Microtus arvalis* (Pallas, 1779) is a rodent living in agroecosystems, and variations in its numbers exhibit a considerable amplitude of fluctuation with outbreaks regularly occurring at intervals (Skuratowicz, 1957; Dombrowski, 1971; Adamczewska-Andrzejewska,

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1974). The economic significance of this species as a pest of agricultural crops is the reason so many studies have been made attempting to identify the cause of these fluctuations.

Studies made so far on cyclic populations of microtines have not as yet provided the solution to this problem, although it is known that the regulation of numbers in these animals is the result of a large number of overlapping mechanisms. These mechanisms act at both the population level, including physiological (Christian & Davis, 1964), or genetic and behavioural (Chitty, 1964; Krebs *et al.*, 1969; Krebs & Myers, 1974), the biocenotic level (Pearson, 1966; Lack, 1954) and the abiotic level (Poliakov, 1964, 1969; Prokofyeva, 1969). These mechanisms act under conditions of population overcrowding and bring about a rapid decline from the outbreak level of voles, but do not act sufficiently strongly during the periods preceding these outbreaks to maintain numbers at a given level.

Studies on *M. arvalis* have revealed considerable individual and population variation, depending on the season, time of birth and food conditions, which affect the growth of individuals and their life span (Spitz, 1966; Martinet, 1967; Martinet & Spitz, 1971). It was found that during the reproductive period the sex ratio changes in favour of females (Stein, 1955; Frank, 1954; Pelikán, 1959; Poliakov, 1964; Prokofyeva, 1969). In view of the fact that variations in sex ratio also occur in other species of microtines (Greenwald, 1957; Hoffmann, 1958; Batzli & Pitelka, 1971; Lidicker, 1973) and presumably in the common vole also. According to Stein (1953) and Poliakov (1964) this change acts as one of the mechanisms contributing to the regulation of numbers in this species.

The age structure of common vole populations may determine the reproductive rate of the population on the one hand, but it is also the resultant of reproduction and mortality and is thus an indicator of the simultaneous action of these two processes. For populations with considerable fluctuations in numbers, as in *M. arvalis*, this indicator may be of great importance in predicting numbers. Application of age structure as an index of population processes is appropriate however, only when age is assessed by a method not dependent on growth parameters which vary seasonally. Martinet (1967) described the age structure of free-living populations of *M. arvalis* on the basis of weight of the dry mass of eye lens. The calendar of capture method (Petruszewicz & Andrzejewski, 1962; Andrzejewski, 1969) also makes it possible to accurately trace changes in age structure simultaneously with changes in many other population parameters.

The purpose of this paper is to present the results of studies on the

demography, and the age and sex structure of two populations of common voles, living in close proximity but isolated from each other, in order to determine whether the simultaneous development of these two populations showed similar patterns. We have also attempted to discover in what way control of population numbers of the common vole takes place in years between outbreaks. Parameters making it possible to record this phenomenon are, for instance, the rate of variations in numbers analyzed in this paper and the turnover of individuals during a year in relation to changes in the sex and age structure of the populations.

## 2. STUDY AREA, METHODS AND MATERIAL

Two isolated populations (A and B) of *M. arvalis* were examined at Lomna near Warsaw from November 1970 to November 1972 inclusive. The populations were introduced there in November 1969 but preliminary studies carried out during the first year are not included in the present paper.

The common vole populations lived in two one-hectare alfalfa fields adjacent to each other. The area occupied by the fields was flat, with brown alluvial type soil. The experimental fields were adjoined on three sides by fields in which normal crop rotation, which included alfalfa, was applied, and on the fourth side they were bounded by other similar experimental fields used for studies on the vole. At the time at which the studies began alfalfa had been cultivated in the experimental fields for over three years, the succession of grasses, chiefly *Agropyron repens* L., in the crop being considerable. In consecutive study years succession intensified, despite the fact that normal agrotechnical operations necessary for obtaining good alfalfa crops were carried out in the field. Full NPK fertilization was applied, which made it possible to mow three times per annum at the following times, I — between June 10 and 20, II — between July 25 and August 5th and III — near end of September. Alfalfa was harvested in its green form, shortly after mowing. The fields were fenced with mouse-proof asbestos-cement tiles, 120 cm in height and sunk into the ground to a depth of 60 cm. This depth, as shown by Bashenina's observations (1962), is sufficient to prevent the rodents from digging underneath it. The fencing thus prevented the animals from migrating between fields, and consequently two isolated populations were formed, living under identical conditions of soil habitat, climate, food and penetration by predators.

Information on the two populations was obtained by the catch-mark-release method. Wooden boxes which constituted the trapping sites for the voles were placed on the surface of the fields. These boxes, measuring 40×40×60 cm, stood on legs 4 cm high and were closed from the top by a cover. There was an opening in the bottom of the box through which the voles could freely enter and leave. Three live traps baited with oats were placed in each box. As the trapping devices were protected from the effect of different weather conditions, we were able to continue studies almost uninterruptedly during the course of the whole year, even when the fields were covered with snow to a depth of 50 cm. Trapping of rodents was interrupted only on those days in which air temperature fell below -10°C, or rose above +28°C; in the latter case the traps were opened for the night only.

Throughout the whole study period the number and distribution of trapping sites depended on the spatial structure of the vole colonies. A group of burrows connected by paths has been termed a colony by Bashenina (1962). The largest aggregation of burrows of a given colony, situated most centrally in relation to the remaining burrows, determined its centre and boxes containing traps were placed in these sites. As new colonies were formed, new trapping sites were set up. Consequently 76 boxes were set up in field A and 37 boxes added in 1971, and in field B 125 and 4, respectively. A few colonies were formed on both fields at which boxes were not placed on account of their close proximity to other colonies.

The animals caught were marked individually by toe-clipping (Naumov, 1951). Each time the voles were caught they were weighed, and the number, sex and date of capture were recorded for each animal.

Trappings of these animals were made every week throughout the year, making four inspections of the traps at 12 hour intervals over a two day period each week. After the traps were closed a wheat rusk weighing 40 g was thrown into the boxes, and the remains of the rusk removed when the traps were set again. The size of the rusk prevented its being taken away through the hole in the box, so that it formed the food consumed by voles during the time the traps were not in operation.

During the whole study period a total of 412 inspections were made of traps in each field. The material obtained consisted of 16,854 captures of 2,731 individuals (field A) and 21,688 captures of 3,974 individuals (field B).

### 3. METHOD FOR ANALYZING MATERIAL

The material was analyzed by means of the calendar of captures method (Petruszewicz & Andrzejewski, 1962; Andrzejewski, 1969). This method permitted estimation of a large number of population parameters with sufficient accuracy, since the trappability of voles in the populations was low (average capture rate was 20% of the total population per inspection; Grunwald, 1975). All individuals caught for the first time were termed recruits to the population. Their number was the result of reproduction, nest mortality and mortality from the time they left the nest up to the age of first capture. The time from the first to the final capture was taken as the period of an individual's presence in the population. When an individual was not caught for a period of three months, it was considered to have died at the time of its final capture. All population parameters were calculated only from data on the trapped animals. Population numbers have consequently been slightly underestimated relative to actual numbers, as the time spent by the voles in the population before the first and after the final capture was not taken into account. It is possible that some of the individuals present in the population were never caught at all, which also lowers the true population numbers.

## 4. RESULTS

### 4.1. Variations in Numbers

Population numbers increases from May (1971) or April (1972) to October or November, when they reached their maximum values: 1971,

A — 227, B — 454; 1972, A — 386, B — 646 individuals<sup>2</sup>. Population numbers subsequently decreased in the remaining months of the year to lows recorded in April, which were similar in both years and populations: 1971, A — 55, B — 71; 1972, A — 59, B — 66 individuals (Fig. 1).

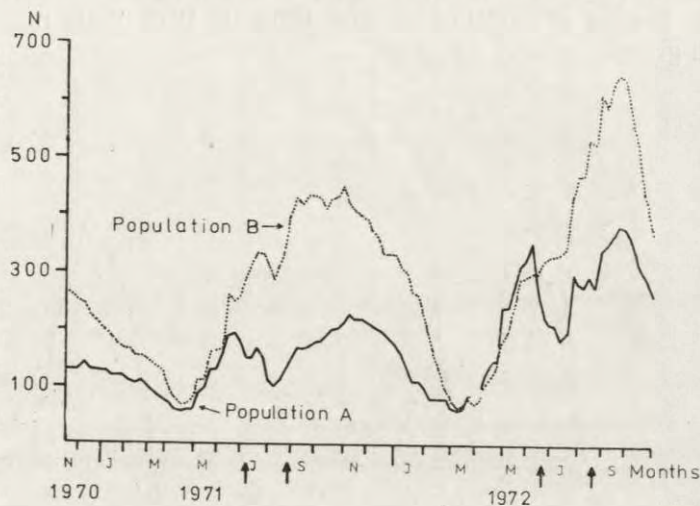


Fig. 1. Dynamics of population numbers of the common vole in successive study weeks. (Arrows below axis indicate time of mowing).

Weekly rates of variation in population numbers ( $r_{Nt}$ ) were calculated according to the following equation, and averages calculated for each month:

$$r_{Nt} = (N_{t+1} - N_t) / N_t$$

$N_t$  — populations in the given week;

$N_{t+1}$  — populations numbers in the following week.

These rates were similar for both populations and study years (Fig. 2). The most rapid increase in population numbers was observed during May 1971 and in April and May 1972. In June and July the rates were negative in population A. In August 1971 and in August and September 1972 there was an increase in the rates in both populations. From November to the end of March reductions in population numbers were increasingly rapid.

A greater reduction in the rate of increase in numbers was observed in the summer in both years, and lower maximum numbers in autumn in population A than in population B.

<sup>2</sup> Further increase in maximum numbers was found in 1973 in population A (539) and decrease in population B (328) in relation to the preceding years. The relevant data are being elaborated.

Higher maximum numbers in both populations during the second study year were due to the more rapid rate of increase in numbers in 1972 than 1971. Differences in the rate of increase in number in September were of particularly great significance here, when with a more numerous population at this time in 1972 than in 1971 there was also a greater rate of its growth.

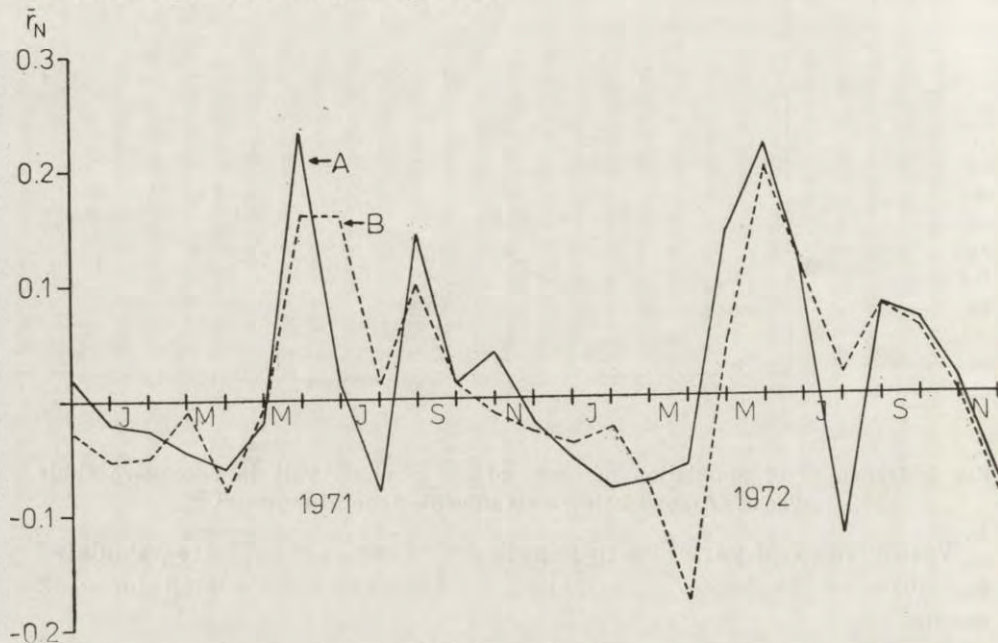


Fig. 2. Rate of growth of population numbers  $\bar{r}_N$  (average population increase/individual/week in month).

#### 4.2. Dynamics of Recruitment and Disappearance of Individuals

During the study period the average weekly number of recruits of the population in a month varied from 0.7 to 105.2 individuals (Table 1). Increase in the number of recruits lasted from April to the middle of the summer in 1971 and until autumn in 1972.

The weekly percentage of recruits to the population, averaged by month, was similar for both populations (Fig. 3). In the year with higher numbers (1972) the high percentage of individuals recruited to the population (over 15% a week) lasted two months longer than in the year with lower numbers (1971).

The number of recruits during a week per female present in the population four weeks earlier was calculated:

$$r_{rt} = N_{pt} / N_{\text{♀}} \text{♀}_{t-4}$$

$N_{pt}$  — number of individuals which were recruited into the population in a given week  
 $N_{\text{♀♀}t-4}$  — number of females present in the population for four weeks prior to the time of recruitment of individuals  $N_{pt}$ .

Table 1

Number of individuals recruited and disappearing during the course of one week (average per month).

Period Population	Recruitment				Disappearing			
	1970/71		1971/72		1970/71		1971/72	
	A	B	A	B	A	B	A	B
Winter period								
November	14.3	11.3	9.7	14.5	7.3	15.6	11.2	24.0
December	4.7	4.0	5.6	9.2	5.2	13.7	15.6	21.4
January	2.5	0.7	1.7	2.7	6.7	6.2	13.0	11.0
February	7.5	10.5	3.5	6.2	14.5	15.7	10.0	27.7
March	3.2	5.7	2.4	1.0	9.5	15.7	7.2	24.8
Summer period								
April	5.2	7.0	15.7	9.0	7.6	10.2	8.5	7.7
May	27.0	31.7	36.8	29.6	11.2	16.7	11.0	9.8
June	47.7	68.5	66.5	64.5	51.2	55.2	68.7	55.0
July	44.2	75.6	75.0	74.2	46.0	62.2	90.2	55.0
August	22.2	66.5	62.4	93.6	7.2	38.7	44.6	67.0
September	14.0	49.0	69.0	92.5	8.2	36.5	54.2	64.0
October	14.4	20.6	48.2	105.2	4.0	23.0	29.5	100.7

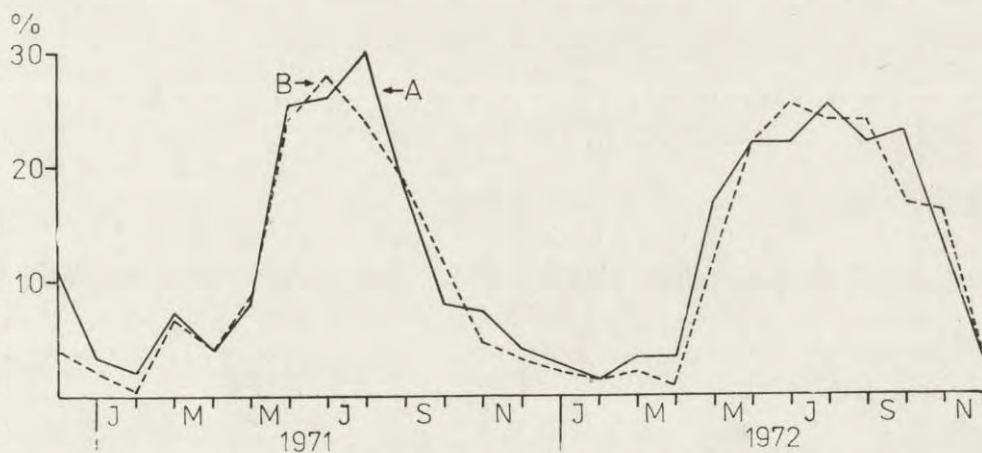


Fig. 3. Percentage of recruits in the population (weekly average in month).

This weekly index was averaged for successive months (Fig. 4). This index attained maximum values in May, June and July (0.5—1.0). In the second half of the summer this index was maintained at a level

of 0.2—0.4. The number of recruits per female did not exhibit statistically significant differences between the two populations or between years when checked by the *t* test.

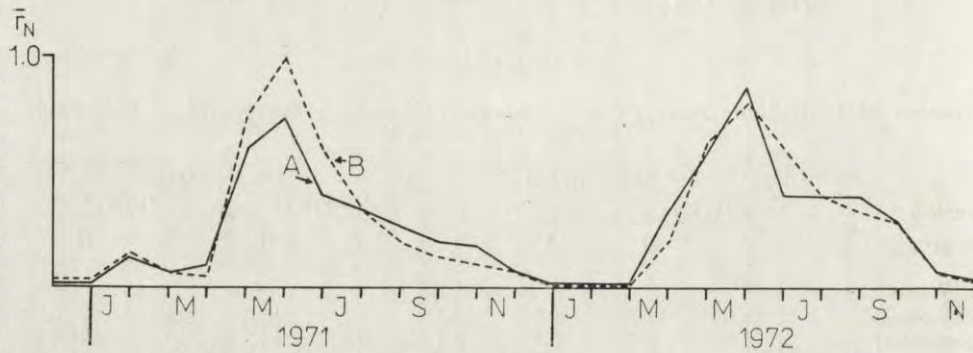


Fig. 4. Number of recruits in a given week per female, among females present in the population one month previously ( $\bar{r}_N$ ) (weekly average per month).

During the studies the average number of individuals disappearing weekly from the population varied from 5.2 to 100.7 (Table 1). From November to March the number of voles disappearing did not exceed

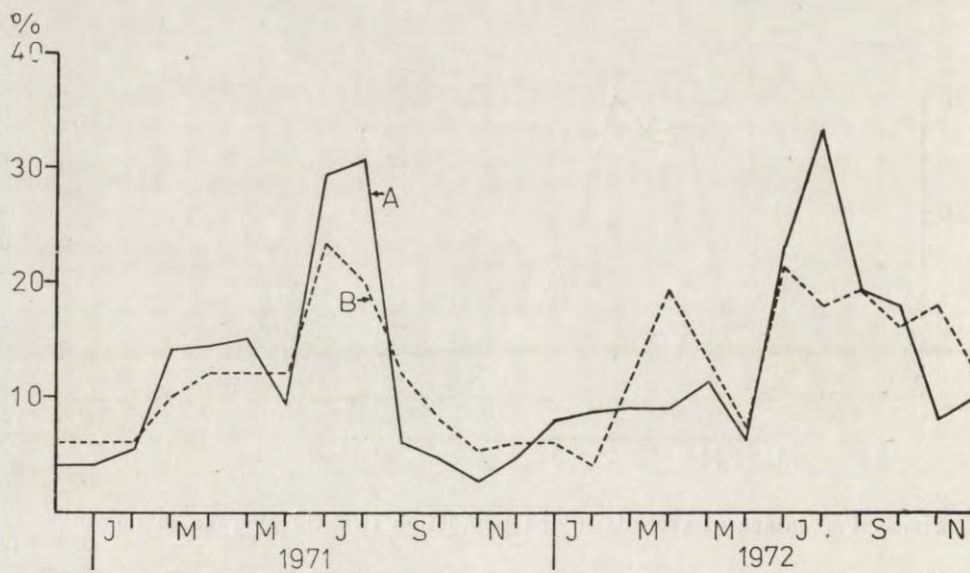


Fig. 5. Percentage of individuals disappearing from the population (weekly average in a month).



28 individuals a week. During the growing season the highest number of voles disappearing was observed in June and July. In addition in population *B* a large number of voles disappeared in the autumn of 1972 (Table 1).

The average percentages of individuals disappearing weekly from the population was calculated for successive month (Fig. 5). Intensive disappearance of individuals was lower but lasted longer in the year with higher numbers than in the year with lower numbers. The more numerous population was distinguished by a lower rate of disappearance than the less numerous population (Fig. 5).

Maximum recruitment and disappearance of individuals took place simultaneously in the populations. It was only in May, at the beginning of a high level of recruitment of individuals (22%—28% per week), that disappearance was maintained at a low level (6%—12% per week) (Figs. 3 and 5). This caused a more rapid rate of increase in population numbers in this month (Fig. 2). Despite the considerable percentage of recruits in subsequent months, rate of increase in population numbers decreased as the result of the high level of disappearance of individuals during this time (Figs. 2, 3, 4). In June and July, with a similar percentage of recruits in both populations, a greater percentage of individuals disappear from population *A* than from *B*. This difference accounts for the fact that a reduction in numbers took place in population *A*, whereas in population *B* there was only a reduction in the rate of increase in numbers during this time. In the year with greater population numbers (1972) disappearance of individuals from both populations during the period from April to July was less than in the previous year when numbers were lower. In the same year (1972), the period during which the percentages of both recruits to the population and of individuals disappearing from it were high, was prolonged by two autumn months.

#### 4.3. Sex Ratio

The numerical predominance of females in the populations began at the end of winter and as a rule continued throughout the growing season (Fig. 6). An exception to this generalization was population *A* in 1970/1971, in which numerical predominance of females occurred as early as November, but continued only until mid-August (Fig. 6). The average weekly ratio of females to males during a month varied from 0.78 (January 1972, population *B*) to 2.37 (June 1971 — population *A*; Fig 7). At the beginning of the growing season a higher percentage of female recruits than male recruits was observed in both populations

and study years. In addition more females than males were recruited during the winter reproduction period in 1971. In autumn there were as many, or even slightly more, male as female recruits (Fig. 8).

The percentages of females and males among individuals disappearing from the populations differed during the same period (Fig. 9). In both populations during the winter period the percentage of males disappearing was greater than females, except February 1971 (period of winter reproduction), when reverse relation was observed. A greater percentage of males disappearing from the population than females was observed up to June, maximum survival of females taking place in May. From July to October the percentage of females disappearing was greater than that of males. The percentage of females disappearing

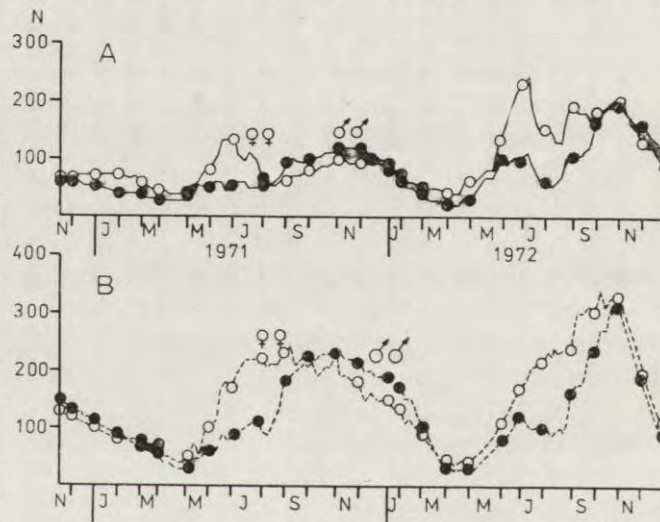


Fig. 6. Variations in numbers of females and males (separately for successive studies).

was greater than that of males only in population A in 1971, in June and July, but from August to October it was similar for both sexes (Fig. 9).

A check was made to see whether variations occurring in sex ratio during the growing season were correlated with variations in the percentage of recruits to the populations. It was shown that there is a low but significant correlation between these parameters ( $P < 0.01$ ; Fig. 10).

The average weekly percentages of females and males of the increase in numbers of the entire population were calculated for each month (Fig. 11). In accordance with the values of the percentage of recruits

and disappearing females and males during the some period, females formed a higher percentage in the increase in population numbers at the beginning of the growing season. Inhibition of the rate of growth of numbers in the middle of the summer affected both sexes. Further increase in population numbers during the course of the year was due chiefly to increases in the number of males. During the period of winter reproduction in population numbers males usually formed a higher percentage than females (Fig. 11).

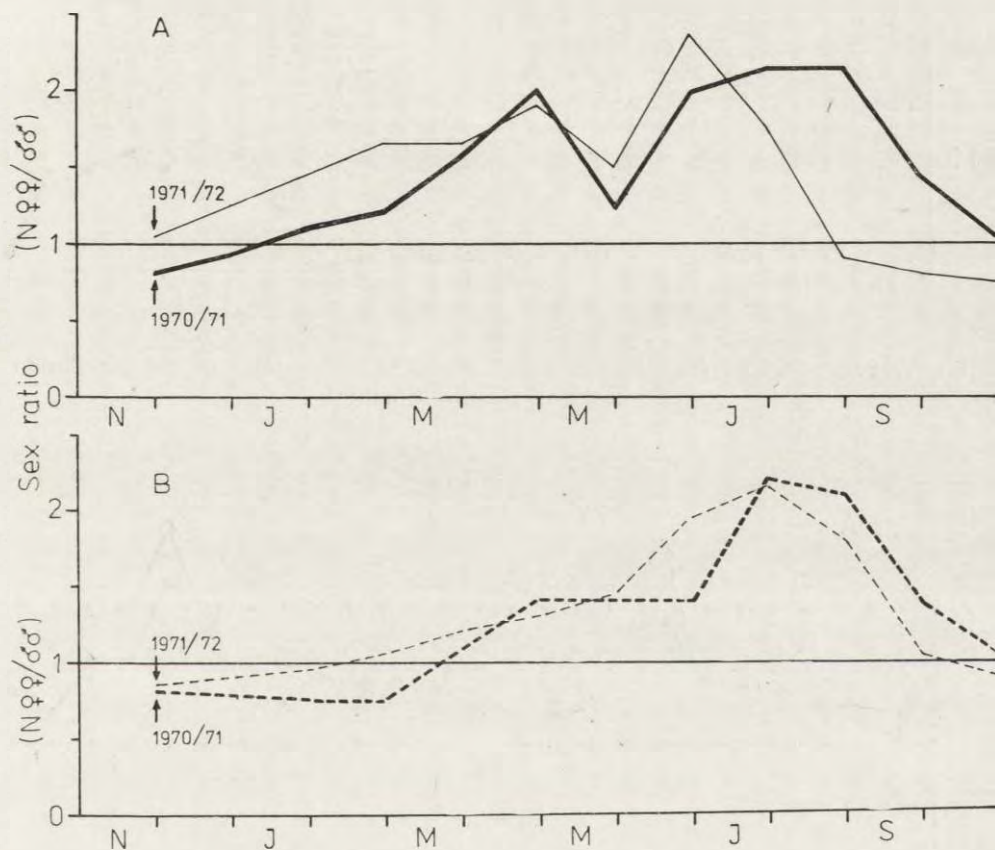


Fig. 7. Ratio of number of females to number of males in the population (weekly average in a month).

The variations in sex ratio in the populations were due both to the differential rates of recruitment and disappearance of the sexes during the same period. At the beginning of the growing season the rapid recruitment of females coupled with their slower rate of disappearance, resulted in a considerable numerical predominance of females in the

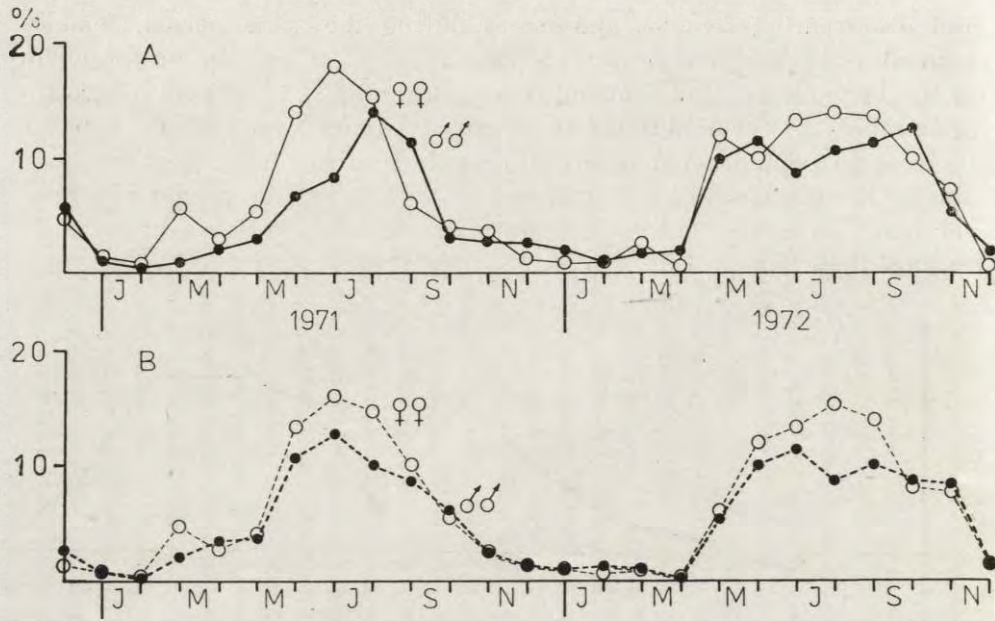


Fig. 8. Percentage of females and males recruited (separately) in the population (weekly average in a month).

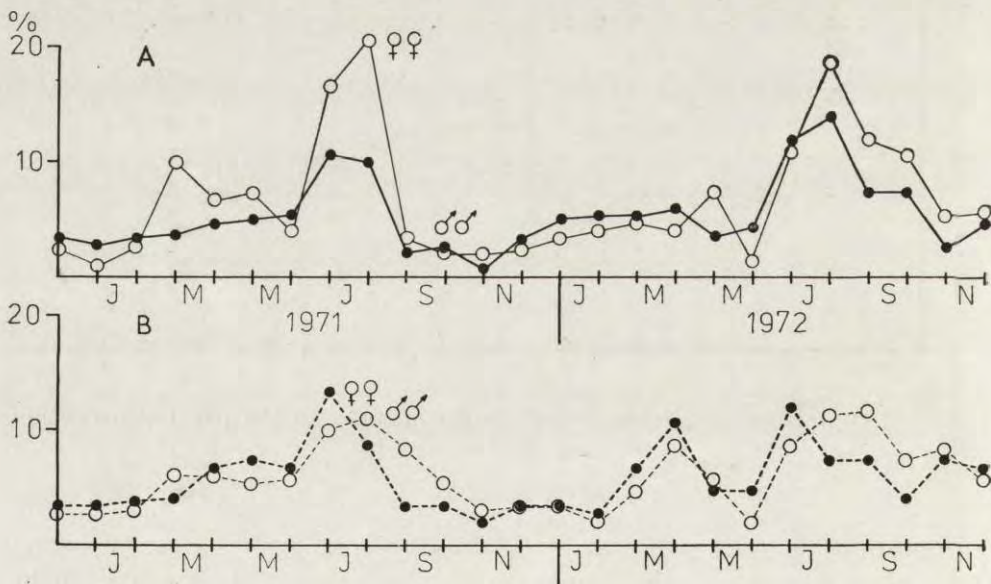


Fig. 9. Percentage of disappearing females and males (separately) in the population (weekly average in a month).

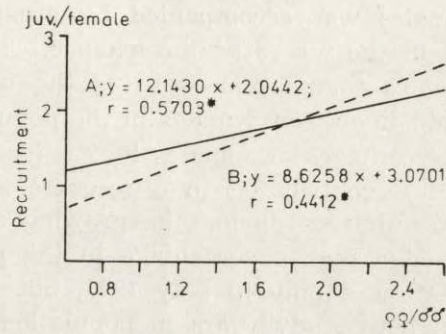


Fig. 10. Relation of percentage of recruits to sex ratio in populations. \*Level of significance  $\tau=0.01$ .

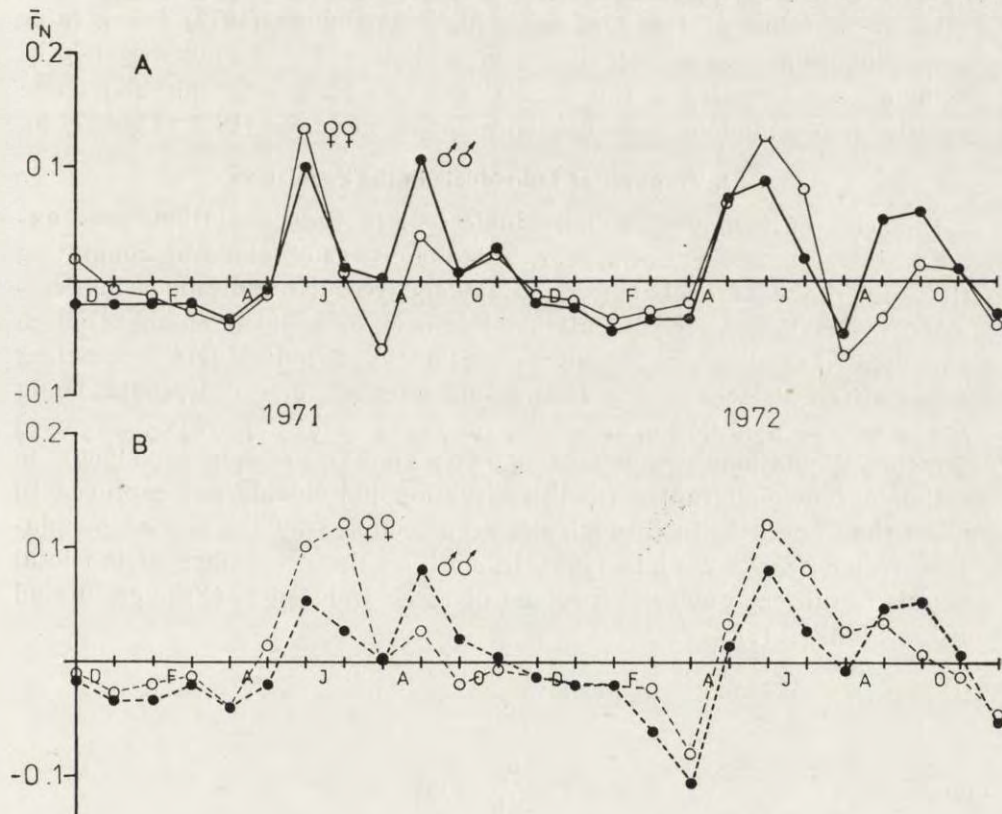


Fig. 11. Percentage of females and males (separately) in increase of population numbers (weekly average in a month)

population. Towards the end of the growing season similar recruitment of females and males was accompanied by greater disappearance of females, and brought the sex ratio into balance. The greater percentage of disappearing males than females during the winter again initiated the numerical predominance of females in the population.

The different percentages of females in the increases in numbers of populations *A* and *B* contributed to differences in the numerical dynamics of these populations during the growing season. It was found that females formed a higher percentage in the growth of population numbers of population *A* only in May 1971, but in population *B* — in May and June. In both study years in population females formed the higher percentage of the summer reduction in numbers, whereas in population *B* the percentage of females of the increase in numbers was never negative during this time (Fig. 11).

In the autumn of the year with higher numbers (1972) the greater percentage of female recruits than males and the numerical predominance of females in the populations was maintained for about one month longer than in the year with lower numbers (1971; Figs. 7, 8).

#### 4.4. Turnover of Individuals in the Population

Intensity of turnover of individuals ( $q_N$ ) in the populations was examined over the course of a year. This index was obtained by computing the percentage of exchanging individuals (recruits + disappearing animals) in relation to the population numbers in a given month. Due to the great variation in the life expectancy of individuals originating from different generations (from one week to one year, data being analyzed) the modified equation (1) for turnover of individuals was used for the calculations, instead of Petrusiewicz's equation (1966), to estimate flow »migrants« (in this situation individuals not captured in more than one month) through the area occupied by the settled population (Andrzejewski, 1963). In addition the percentage of the total population in each month composed of these »migrants« ( $E$ ) is calculated using equation (2).

$$(1) \quad q_{Nt} = \frac{(a_t + b_t) - b_{at}}{N_t} \times 100$$

$$(2) \quad E_t = \frac{b_{at}}{N_t} \times 100$$

where:

$a_t$  — number of individuals recruited into the population within the given month,  
 $b_t$  — number of individuals which disappeared from the population within the given month,

$b_{at}$  — number of individuals which were recruited into the population and disappeared from it within the given month,

$N_t$  — population numbers in the given month.

Monthly turnover rates were lowest in the winter (20%—40%) and highest in the summer (80%—90%) (Fig. 12). During the first year of the experiment rapid turnover of voles lasted in both populations from April to August. During this time from 60% to 90% of the population was exchanged per month. In the second study year the period of rapid exchange of voles in the populations lasted until October.

The percentage of individuals which were registered in the population for a period shorter than one month exhibited similar variations over the course of a year to the turnover rates among animals registered for longer than a month (Fig. 12). The least number of such voles was

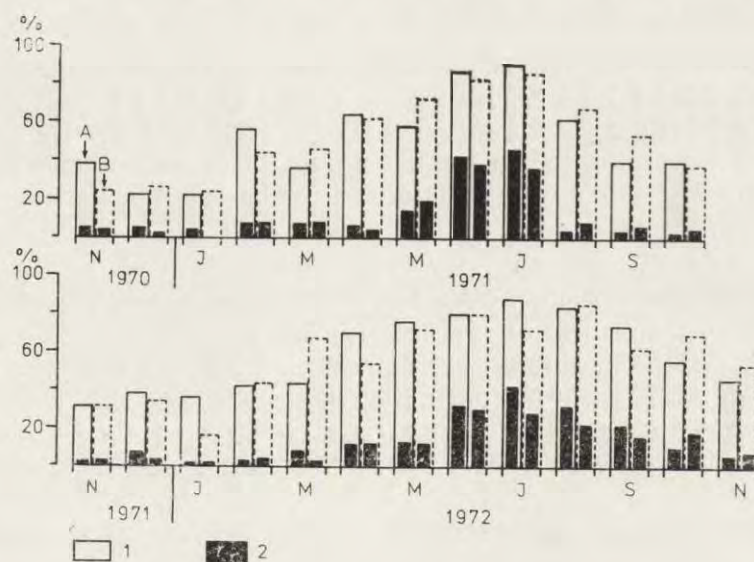


Fig. 12. Turnover of individuals in populations.

1 — percentage of individuals exchanging in a population during the course of one month ( $R_t$ ); 2 — percentage of individuals which were recruited to or disappeared from the population during the course of one month ( $E_t$ ).

observed in the study populations in autumn and winter (0—10%), and the most in summer (almost 50%). During the first study year percentage of individuals caught for a period shorter than one month was greater than 10% only in May, June and July. Although there were fewer such individuals the following year in May, June and July than the first year, the period of highest percentages occurred from April to October. No significant differences were found between populations

(except for July) in the intensity of turnover and the percentage of individuals caught over a period shorter than one month.

Increases in turnover rates and percentages of individuals caught for a period shorter than a month occurred during the periods of intensive recruitment of new rodents. In both populations in the year with higher numbers (1972) a lower percentages of transients were observed, from May to July. This shows that the young individuals had a better chance of survival during this time.

#### 4.5. Age Structure

Individuals from the study population were divided into four groups according to the age at which they were caught for the first time. The first group (class *A*) included individuals captured for the first time; the second (class *B*) — known to be alive between the second and fourth week after initial capture; the third (class *C*) — animals known to be alive during the second to third months, inclusive; the fourth (class *D*) — all individuals caught over a period longer than three months. The age structures (according to the class) for both sexes were then calculated for weekly and monthly time intervals in the two populations and in both years (Fig. 13).

Recruits consisted mainly of young animals weighing from 10—15 g, which for the population described gave their age as 1—1.5 months when estimated by the method of dry weight of eye lens (Adamczewska-Andrzejewska, 1973). Older individuals were, however, also caught for the first time which, judging by their body weight, were up to three months old.

The age structure of the common vole population underwent considerable changes during the course of a year (Fig. 13). During the winter the predominant part of the population consisted of individuals assigned to Class *D*. The percentage of voles in this class gradually increased from November to March. From April rejuvenation of the populations took place. During the period of intensive recruitment of new individuals the populations consisted chiefly of voles up to one month old (over 60%). The representation of the oldest age class in populations during this time fell to only a small percentage. A reduction in the percentage of recruits to the populations took place simultaneously with an increase in class *C*. Voles in this class predominated during the autumnal peak in numbers. The course of variations in age structure over the annual cycle showed differences between the two populations, between sex and between successive study years.

The age structures of females and males were compared in the two



populations and in different years. Age classes were analyzed in three time periods independently for each year: 1) May—August; 2) September—November; 3) December—April. Differences in age structures of the populations were checked for significance using the  $F$  test. It was found that a significant difference in the age structure of the populations

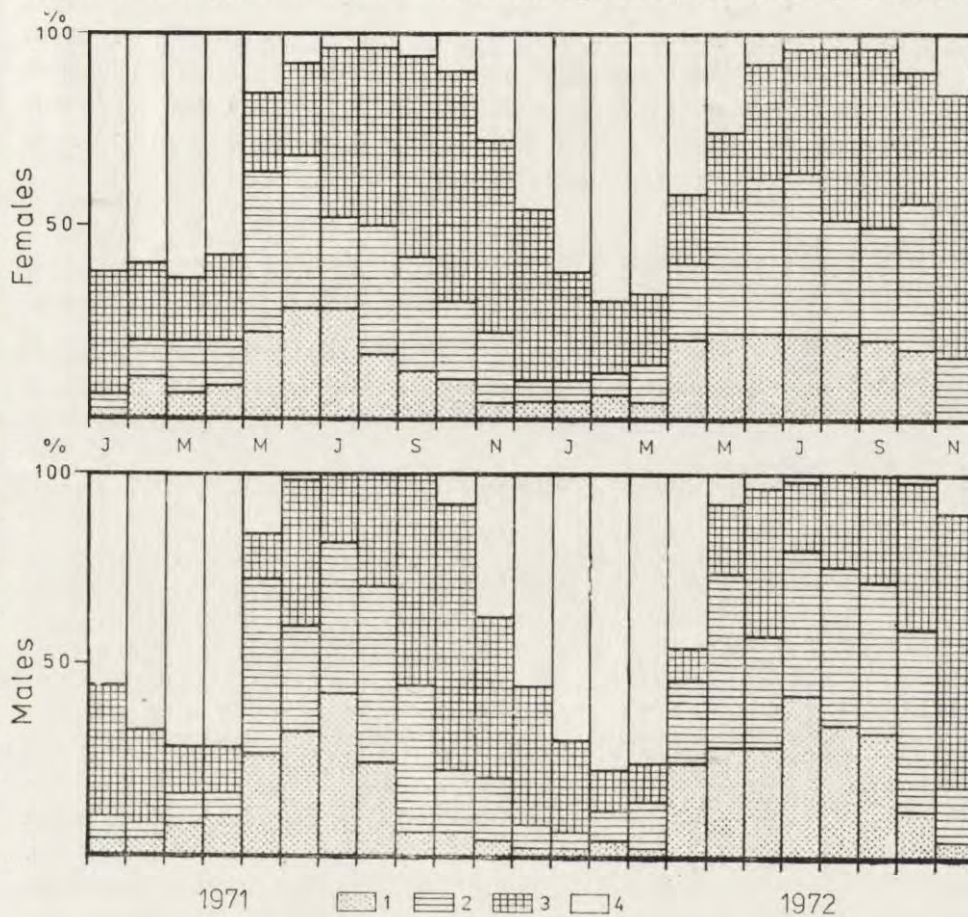


Fig. 13. Age structure in population A. Shaded fields indicate weekly average in a month of the participation of individuals in the given age class in the population: 1—recruits, 2—one week to one month; 3—month to 3 months, 4—above 3 months.

occurred during the autumn period (from September to November; Table 2). Only females in population B failed to exhibit significant changes in age structure between 1971 and 1972. In all other cases the groups were older in the autumn of the year with lower density (1971);

than in the autumn of the year with higher density (1972). At the same time the population *A* (lower density) was older than population *B*.

Differences in the age structure of females and males from the same populations were compared by means of the *t* test for the reproductive period from April to September, but combining the first and second age classes. During this period the percentage of the youngest males in the population was significantly higher (except for population *A* in 1971), than that of the youngest females ( $P < 0.001$ ). In older age classes this percentage changed in favour of females, but statistically significant differences occurred only among individuals in age group three in population *B* in 1972 (maximum density).

Table 2

Differences in age structure between various groups of individuals in the study populations.

Groups compared	Months, year	$\chi^2$
♀♀ <i>A</i> — ♀♀ <i>B</i>		10.9861 *
♂♂ <i>A</i> — ♂♂ <i>B</i>		30.9134 **
♀♀ <i>A</i> — ♂♂ <i>B</i>	Sept.—Nov. 1971	16.2034 **
♂♂ <i>A</i> — ♀♀ <i>B</i>		23.6052 **
♂♂ <i>A</i> — ♀♀ <i>B</i>	May—Aug. 1972	8.1243 *
♂♂ <i>A</i> — ♂♂ <i>B</i>		8.8142 *
♀♀ <i>A</i> — ♀♀ <i>B</i>	Sept.—Nov. 1972	12.9308 **
♂♂ <i>A</i> — ♀♀ <i>B</i>		26.3025 **
♂♂ <i>A</i> 1971 — ♂♂ <i>A</i> 1972		16.4462 **
♀♀ <i>A</i> 1971 — ♀♀ <i>A</i> 1972	Sept.—Nov.	13.9356 **
♂♂ <i>B</i> 1971 — ♂♂ <i>B</i> 1972		19.3067 **

\* Statistically significant differences, with accepted level of confidence 0.05; \*\* Statistically significant differences, with accepted level of confidence 0.01.

In order to make a comparison as a whole of differences in age structure of the populations in successive years the combined age structures for both populations and sexes were calculated (Fig. 14). Differences in the representation of different age groups for successive months in both years were checked by the *t* test. It was found that the representation of the age groups distinguished differed statistically during the period from August to November. During this time the percentage of individuals in the populations in classes *A* and *B* was greater in the year with higher numbers (1972) than in the year with lower numbers (1971). It was only in August 1972 that the representation of the second age group was smaller than in 1971. The third and fourth age groups were found to form a smaller percentage of the population in the second year of the experiment.

To sum up, during the breeding season the percentage of young males

in the age structure of the population was greater than that of females. Differences in the age structure in both populations and successive study years occurred only in the autumn. In the year with higher numbers in autumn the population was younger on the average than the population in the year with lower numbers.

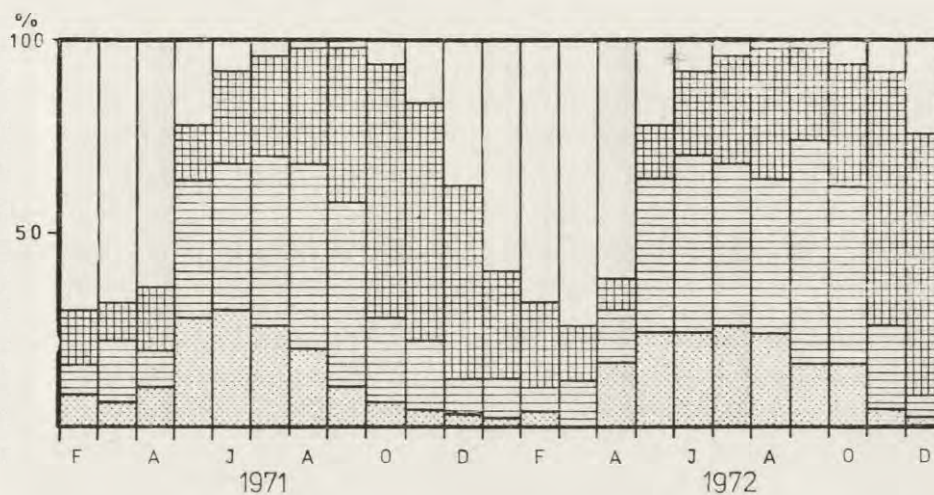


Fig. 14. Average age structure for both populations and sexes in a year with low (1971) and high (1972) density. Symbols for percentage of the different age classes as for Fig. 13.

#### 9. DISCUSSION

These studies show that with differences in numbers between the two population the direction taken by demographic parameters was identical during same period in both populations. A similar phenomenon for the three enclosed populations of *M. townsendi* was observed by Le Duc & Krebs (1975). In the present study the extent of reduction in rate of increase in numbers in the middle of summer exerted a marked influence on the dynamics of population numbers over the course of a year. In particular, when there was a considerable reduction of females during this time, population numbers were lower in autumn (population A). Inhibition of the rate of increase in population numbers in the middle of summer was caused by a rapid disappearance of individuals, which was accompanied by an equally rapid recruitment of new individuals. It may be that predators played an important part in increasing mortality in the population during this time, since they could more easily penetrate into the study area after the alfalfa had been mown.

Easy access of predators to their prey over a long period of time is, according to Pearson (1966), the principal factor causing cyclic mass irruptions. In this case the exposure of the field after the alfalfa had been mown lasted too short a time to cause fluctuation in population numbers. The problem of the causes of mortality in captive populations is not, however, solved. This mortality might equally well be due to the fact that emigration was rendered impossible. It is known that migratory tendencies have a fundamental role in controlling population numbers (Petrušewicz & Andrzejewski, 1962; Lidicker, 1962, 1973; Spitz, 1966; Wojciechowska, 1970; Mazurkiewicz, 1972) and it may be that in the case of the vole, it also plays the part of a co-ordinator of phases in the population cycle in large areas. Confirmation of the potential emigratory capacities of the common vole is provided by the maximum activity of voles in these populations in June (Mackin-Rogalska, 1975). In open population part of the individuals would probably settle in out lying areas with poorer habitat characteristics. Thinning of population density by emigration to open areas replaced by mortality in enclosed areas. Predators may also have contributed to the mechanism, understood in this sense, increasing mortality in the population. Migrants remained longer in the exposed area and were thus more likely to fall victims to predators.

The increased mortality among individuals was accompanied in summer by rapid recruitment of new voles. This quick turnover of individuals points to the considerable capacity for regeneration of *M. arvalis* populations, which permits of rapid replacement of disappearing individuals. This capacity for regeneration makes it difficult to develop techniques for limiting population. Morris (1972) found in an enclosed population of *M. pennsylvanicus* that after 50% reduction brought about by endrine, the population increased its numbers within two months to the level of the control population to which poison had not been administered.

The numbers of the two populations increased during successive study years. Data on subsequent years show that in 1973 population *A* reached peak numbers, while population *B* went through a phase of depression. On the strength of such dynamics in numbers it might be concluded that there is a shift of one year in the phase of the cycle in population *A* in relation to population *B*. As shown by studies on other rodent species exhibiting fluctuations (Kalela, 1957; Hoffmann, 1958; Krebs, 1964, 1969, 1970; Bätzli & Pitelka, 1971; Krebs & Myers, 1974) the populations examined here should differ in 1972, for example with respect of duration of the breeding season, percentage of sexually active females, occurrence of winter breeding in accordance with phases

of the cycle. Similar regularities were found for free-living populations of *Microtus arvalis* (Adamczewska-Andrzejewska, 1974). In the present studies, on the other hand, prolongation of the period of recruitment of new individuals into the population was found in both populations in the autumn of 1972 compared to the preceding year, and a longer-lasting numerical predominance of females over males. In addition, winter breeding took place in both populations in 1970/71 and did not occur in the winter of 1971/72. No phenomena characteristic of the phase of peak numbers were thus found in 1972 in population B, but rather characteristics typical of the phase of increase in numbers, which similar were in both populations.

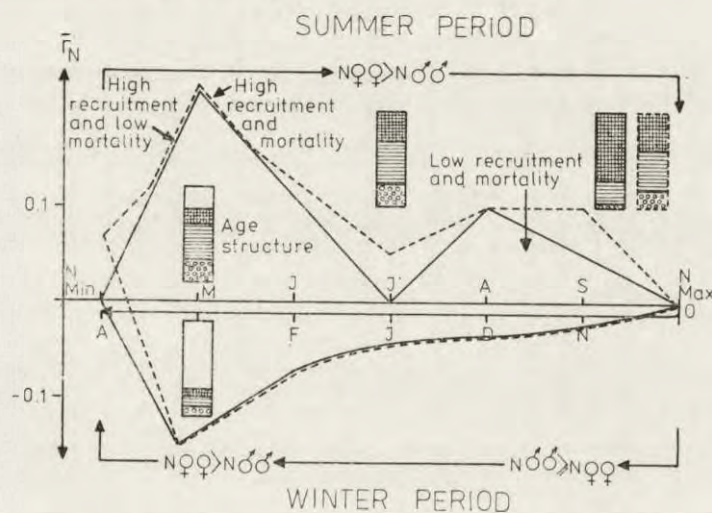


Fig. 15. Diagram of variations in rate of growth of numbers and the variations accompanying them in sex ratio, recruitment and disappearance and also age structure in a population of *M. arvalis* over the course of a year, solid line—year of low numbers, broken line—year of high numbers. Percentage of the different age classes (%) in the population at selected moments of time is indicated in columns. Height of column indicates 100%. Symbols for age classes as for Fig. 13.

On the basis of the variations observed in recruitment and disappearance of individuals over the course of a year in populations which were in the growth phase, it is possible to draw conclusions about certain population processes controlling numbers (Fig. 15). Increase in population numbers during the growing season was caused by:

1. A one month delay in the increase in mortality in the spring relative to the increase in recruitment of new individuals,
2. The numerical predominance of females over males,

3. A greater percentage of females than males in the older age classes,
4. A prolongation of the period of rapid recruitment of new individuals.

The rate of growth in population numbers during the growing season was hampered by:

1. An increase in mortality among the individuals,
2. A reduction in the number of recruits per female,
3. A reduction in the proportion of females in the population.

During the winter, disappearance of males was more rapid than that of females, which resulted in an increase in the proportion of females in the population in the spring (Fig. 15).

A delay in the increase in mortality in relation to the increase in recruitment of new individuals is an important element controlling population numbers. Owing to the low mortality among young animals in spring, the populations were supplemented within a short time by young, rapidly maturing individuals, which successively replaced old adults as they died.

The significance of sex ratio to the rate of increase in population numbers in microtines has not as yet been determined. In the study populations of *M. arvalis* we have shown a straight line relationship between rate of recruitment of young animals and numerical predominance of females over males. Myers & Krebs (1971), Krebs & Myers (1974) did not, however, find a straight linear relationship between sex ratio and population parameters in *M. pennsylvanicus* and *M. ochrogaster*, but consider that if such relationships exist they do not act directly.

The studies we made and also those by a large number of other authors (Stein, 1953; Frank, 1954, 1956; Pelikán, 1959; Prokofyeva, 1969 and other) show that in populations of the genus *Microtus* the greatest numerical predominance of females over males occurs during the breeding season. In the opinion of many researchers sex ratio in populations of *M. arvalis* changes during the earliest period of the voles' life. Stein (1953) found a numerical predominance of females over males during the breeding season due to older males ousting the younger. On completion of the breeding season the percentage of males in the populations increases. This result was confirmed by Frank (1954) and Pelikán (1959). According to Frank (1956) females predominate among embryos, but on account of the high and differentiated natal and postnatal mortality males predominate among the young animals. Kubantsev *et al.*, (1970) found more males than females in litters and a change in this ratio in adult animals in favour of females. Myers & Krebs (1971) in discussing the

problem of differentiation of sex ratio on the basis of Fisher's theory and the theory of genetic variations (Tamarin & Krebs, 1969), using captive and free populations of *M. ochrogaster* and *M. pennsylvanicus* as examples, found that predominance of females was maintained even with a larger number of male recruits to the population, due to the greater mortality among males during this period. In our studies the greatest numerical predominance of females over males was due to a larger number of new female recruits to the population and more rapid disappearance of males. Increase in the percentage of males took place after the breeding season had ended, owing to a lower mortality among males than females. Differentiation of the sex ratio thus took place both before the first capture (among very young animals) and during the course of our recording of their presence in the population. The mechanisms operating here may have been analogous to those referred to above.

The common vole is characterized by very great variation in the age structure of the population over the course of a year. This is confirmed by the data obtained by Martinet (1967) for three free populations of *M. arvalis*. During the growing season the population is very young and consists chiefly of individuals initially captured less than three months previously. This structure is due to the very high mortality rate among the youngest individuals during the first half of the summer. In autumn, recruitment and mortality of young animals decrease, and consequently ageing of the population takes place. With a prolonged period of intensive recruitment of young individuals in the autumn, however, mortality in the youngest age class is almost as high as at the beginning of the summer. In this case the population is younger over a longer period of time. Annual variations in the ratio of females to males in the populations was connected, for example, with the different viability of the various age groups of both sexes. Reduction of young males during the period of intensive recruitment of new voles into the population took place more rapidly than recruitment of young females. According to Martinet (1967) males of *M. arvalis* mature more slowly than females and during the growing season almost 100% of the males over one month old are sexually active. It is therefore chiefly the sexually immature males which are eliminated. In our results the greater percentage of females than males in the oldest age group also points to the greater life expectancy of females, which would agree with the results obtained by Bashenina (1962). Pelikán (1959) showed that from April to August sexually adult females from over 90% of the female population, and Martinet (1967) that about 100% of the females are more than one month old. This kind

of age structure is thus evidence of the existence of mechanisms controlling the sex ratio and maintaining optimum conditions for reproduction of the population, by eliminating young males.

A further process increasing population numbers was prolongation of the recruitment of new individuals in autumn. Despite the small number of recruits per female, a rapid increase was observed in the density of voles during this time due to high population numbers with numerical predominance of females over males.

Inhibition of the rate of growth of population numbers in the middle of the summer and in autumn (Fig. 15) was brought about by various factors. A reduction in the rate of growth of numbers in the summer was due to an increase in mortality, primarily among the youngest individuals. In autumn, on the other hand, the number of recruits per female gradually diminished until complete cessation of breeding occurred. In addition, as a result of the better survival rate of males than females during this time the sex ratio equilibrated in the population. The above processes contributed significantly to a reduction in the level of the autumn peak of population numbers and to the formation of an equal number of overwintering individuals of both sexes.

The studies presented here provide grounds for assuming that the variations taking place in population structure during the outbreak phases of the cycle, stimulating the increase in numbers, are controlled by population factors. Inhibition of the increase in numbers during the same time may be caused not only by population factors, but also by habitat factors.

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PARAMETRY DEMOGRAFICZNE A DYNAMIKA LICZEBNOŚCI  
NORNIKA POLNEGO

Streszczenie

Przy pomocy metody CMR rejestrowano przez dwa lata zmiany demograficzne dwóch (A i B) zamkniętych populacji *Microtus arvalis* (Pallas, 1977). Zmiany liczebności w obu populacjach przebiegały podobnie. Populacja A osiągała niższą liczebność maksymalną (Ryc. 1). Obie populacje były liczniejsze w drugim roku badań (1972). Największe tempo wzrostu liczebności ( $r_N=0.23$ ) występowało w maju (Rys. 2) dzięki intensywnemu przybywaniu nowych osobników i lepszej przeżywalności populacji. Maksymalny przyrost liczby osobników ( $\bar{r}_r=0.5-1.0/\text{tydzień}/1\text{♀}$ ) notowano od maja do lipca (Ryc. 4). W okresie wczesnoletnim stwierdzono w populacjach zahamowanie tempa wzrostu liczebności spowodowane dużą śmiertelnością najmłodszych (Ryc. 5, Tabela 1).

W sezonie rozrodczym rotacja wynosiła 60%—90% populacji na miesiąc (Ryc. 12).

Liczbowy stosunek samic do samców w populacji wahał się od 0.25 do 2.35. Największy udział samic obserwowano w okresie intensywnego rozrodu (Ryc. 7), korelował on z liczbą osobników przybywających do populacji. Przewaga samic wynikała z większego przybywania i lepszej przeżywalności. Jesienią wyrównanie stosunku płci powodowała większa śmiertelność samic.

W okresie wegetacyjnym ponad 60% populacji stanowiły osobniki młodsze niż jeden miesiąc życia pozagniazdowego (Ryc. 13). Jesienią, roku o wyższej liczebności, populacje były młodsze niż w roku o niższej liczebności (Ryc. 14). Populacja liczniejsza (B) była młodsza od mniej licznej (A). W okresie rozrodczym samice były starsze od samców.

Badane populacje znajdowały się w fazie wzrostu liczebności, której w kolejnych latach towarzyszyła dłużej utrzymująca się przewaga liczbowa samic nad samcami, oraz wydłużenie okresu rozrodu i lepsza przeżywalność nowych osobników.