

Common Vole Numbers in Relation to the Utilization of Burrow Systems ¹

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Population dynamics of the common vole *Microtus arvalis* (Pallas, 1779), changes in the number of burrow systems, and their utilization were studied in perennial crops of different regions of Poland in 1970—1979. A multi-year cycle in common vole numbers was found. In the northern region of Poland, maximum peak numbers reached 350 individuals/ha, and in the southern region more than 1000 individuals/ha. An increase in common vole numbers in the multi-year cycle was positively correlated with the number of burrow systems. Highest increases in common vole numbers were observed in autumn, and lowest in spring. Per unit increase in the number of burrow systems, the rate of growth in common vole number increased in the years of peak numbers and decreased in the years of decline. The percentage of occupied burrow systems (colonies) and the number of individuals per burrow system increased with growing population size, but at a declining rate. Multi-year and annual changes in common vole numbers were more affected by changes in the number of occupied burrow systems than by changes in the number of individuals per system. Only in the periods of numbers decline, they mostly depended on changes in the density of colony members. The factors underlying differences in mean numbers of *M. arvalis* in different regions of Poland are discussed.

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1. INTRODUCTION

Besides food, the most important environmental factor for the common vole *Microtus arvalis* (Pallas, 1779) population is burrow system, where these animals spend most of their lives (Erkinaro, 1969; Lehman & Somersberg, 1980; Hoogenboom *et al.*, 1984), and where they nest and raise offspring (Frank, 1954; Pelikán, 1959). The underground system of burrows and corridors with outlets and runways connecting them, and together with the voles inhabiting it, is termed a colony. Burrow systems can cover an area from 0.5 to 2 m² (Leutert, 1983), or to

¹ Badania były wykonane w ramach problemów węzłowych 09.1.7, 10.2, 10.0.3.01, MR II/15 01.03.04, koordynowanych przez IE PAN.

3 m² (Formozov & Kiris-Prosvirina, 1937), or even 66 m² (Zlotin & Chodašova, 1974). The number of individuals in a colony ranges from several to a dozen or so (Bašenina, 1962), but individual animals can visit an area of several or even a dozen or so colonies (Mackin-Rogalska, 1975, 1979). Mostly females burrow (Pelikán, 1959). Burrows provide a good protection against predators, and also against low and high temperatures, heavy insolation, wind and precipitation. Agglomeration of many individuals in nests is advantageous, as it markedly lowers metabolic costs (Trojan, 1969a; Grodziński *et al.* 1977). Moreover, voles store food in colonies, thus burrow systems also function as storehouses (Bašenina, 1962).

As burrow entrances form clusters, it is relatively easy to distinguish neighbouring burrow systems. The relative ease in locating burrows and also runways of small mammals allows the study of relationships between population density and the number of burrows (Liro, 1974 for *Microtus arvalis*) or runways (Person, 1960 and Krohne, 1982 for *Microtus californicus*). Also the density of rodents was estimated from the number of runways (Lidicker & Anderson, 1962; Bowen, 1982) or burrow entrances (Zieliński, 1982 for different species of the genus *Microtus*). Romankowowa, Piekarczyk & Grala (1969) and Romankowowa (1970) calculated an index of crop endangering by the common vole from the density of the utilized burrow entrances. Attempts were also made to find a relationship between rodent density and the number of fissures in soil that could be used as shelters, or facilitate burrowing for *Mus musculus* (Newsome, 1969).

Hypotheses aiming at explaining the underlying reasons for cycling behaviour in populations of *Arvicolidae* (Krebs & Myers, 1974; Stenseth, 1977; Charnov & Finerty, 1980; Finerty, 1980) are not universal. Especially difficult issue is synchronous or asynchronous cycling of *M. arvalis* populations over large areas (Migula *et al.*, 1970; Straka & Gerasimov, 1971, 1977). Likewise, differential period of the cycle and variable amplitude of changes in numbers in the same phases of the multi-year cycle for different local populations have not been satisfactorily explained (Frank, 1957; Skuratowicz, 1957; Straka & Gerasimov, 1971, 1977; Bethge, 1982). Differences in the amplitude of multi-year cycling of *M. arvalis* in different regions of Bulgaria were found by Straka and Gerasimov (1971, 1977), and for northern and southern Poland by Adamczewska-Andrzejewska (1974); the questionnaire studies covering the whole Poland revealed the same phenomenon (Bandomir, Lehman & Tokarczyk, 1980). Adamczewska-Andrzejewska, Mackin-Rogalska & Nabagło (1982) suggest that the spatial utilization of the habitat is the most important factor accounting for multi-year fluctuations in *M. arva-*

lis. They take into account differences in the period of the cycle, resulting in asynchronous population dynamics.

Not only the population dynamics of the common vole was analysed (Adamczewska-Andrzejewska & Nabagło, 1977; Nabagło, 1981) but also individual differences in the attachment to burrow systems (Mackin-Rogalska, 1975), the rate of rebuilding destroyed burrows (Liro, 1974), and also changes in vegetation on and around the area of burrows (Ulehla *et al.*, 1974; Babińska-Werka, 1979; Leutert, 1983). Mackin-Rogalska (1979) has found a positive relationship between the population density and the number of occupied burrow systems in an isolated population of *M. arvalis*. This gave rise to a hypothesis that burrow systems are an important factor generating multi-annual cycling in the common vole populations (Adamczewska-Andrzejewska, Mackin-Rogalska & Nabagło, 1982).

The present paper is focused on the multi-year dynamics of the common vole population and burrow systems, and on the capacity of burrow systems. Emphasis is put on the effect of changes in the number of burrow systems and in the density of animals in them on seasonal and multi-year changes in numbers. The underlying reasons for differences in population levels between northern and southern regions of Poland are discussed.

2. STUDY AREA, METHODS, AND MATERIAL

The study was conducted on crop fields of State Farms located in two different types (regions) of the agricultural landscape of Poland (Fig. 1):

I — northern Poland (Gdańsk and Bydgoszcz districts) — a lowland with a small proportion of forests and mid-field woods, and alluvial soils formed on heavy loams or clay, typically characterized by a high cohesion (Uggla, 1983). Alfalfa crops 2, 3 or 4 years old, ranging from several to several hundred hectares were under study. They were harvested for green forage.

II^a — southern Poland (Opole, Wrocław, Legnica, Przemyśl, and Krosno districts) — a submontane region with crop field frequently surrounded by woods and uncultivated lands. The most common soil types comprised forest-steppe chernozem formed on loess or sandy loam, characterized by a rather high friability, and brown earths formed on loess and loess-like formations. The size of crop fields and management type were the same as in region I.

II^b — south-western Poland (Wałbrzych district in Lower Silesia) — a submontane area with a mosaic of crop fields interspersed with many tree-clumps, mixed woods, and uncultivated lands. The study pastures and alfalfa fields were much smaller than in regions I and II^a (no more than a dozen or so hectares). They covered brown soils formed on loess and loess-like formations. In regions I and II^a, the study was carried out in 1970–1975 in co-operation with County Plant Protection Stations. In region I, three to eight sites were surveyed, depending on the year, and in region II^a, four to eight sites. In region II^b, the study was con-

ducted in 1976—1979 on only one site, mostly on pastures, sometimes also on nearby alfalfa fields and pasture mixture.

To estimate common vole density, all the burrow systems were marked and counted on an area of 1 ha, and then entrances to the burrows were flooded until the underground corridors were filled with water (Andrzejewski & Gliwicz,



Fig. 1. Map of the study areas: Region I — northern Poland, Region IIa) — southern Poland, Region IIb — south-western Poland.

1969). The escaping voles were captured and counted. When the density of burrow systems was high, only 30 of them were flooded. The mean number of voles in the flooded burrow systems was then multiplied by the number of burrow systems per ha to get an estimate of the density of common voles. This method of numbers estimating can be used at low plant cover, when it is possible to observe all entrances to the burrows and all runways connecting them on the soil surface, and allowing catching the animals. Hence, the density of common voles was estimated on the plots with freshly mown alfalfa or on heavily grazed pastures. In 1971, on some fields of southern Poland (region II^a) where the densities reached 1500—2200 individuals/ha (Adamczewska-Andrzejewska, 1974), it was not possible to delimitate individual burrow systems. Numbers were then estimated by counting all flooded voles from an area of a known size.

On each occasion when the density of common voles was estimated, such variables were noted as the number of entrances to the burrows, the number of captured common voles, the number of common voles flooded but not captured, and the number of all burrow systems per ha. When burrow systems were counted on several 1-ha plots, mean value per ha was used to calculate *M. arvalis* densities.

The density of common voles on each site was estimated 3 or 4 times a year

over the study period: in spring (April or May), summer (June, July, August), including two estimates in some years, and in autumn (September, October, or November).

Linear, exponential, and logarithmic functions were fitted to each relationship, and those with the highest correlation coefficients were selected.

The material was divided into three groups according to the location of the study plots in the three regions earlier described¹. In total, the densities were estimated at 25 localities of Poland. A large proportion of crop fields under study was treated as replacement plots (e.g. because of ploughing), typically located in close vicinity. The total number of flooded burrow systems was 7669 in regions I and II^a, and 771 in region II^b.

3. RESULTS

3.1. Multi-year Changes in Numbers of Common Voles and Burrow Systems

The estimates of common vole numbers were grouped into three time intervals in each year: spring, summer, and autumn. Average densities of common voles per ha were calculated for each site in particular regions of Poland separately.

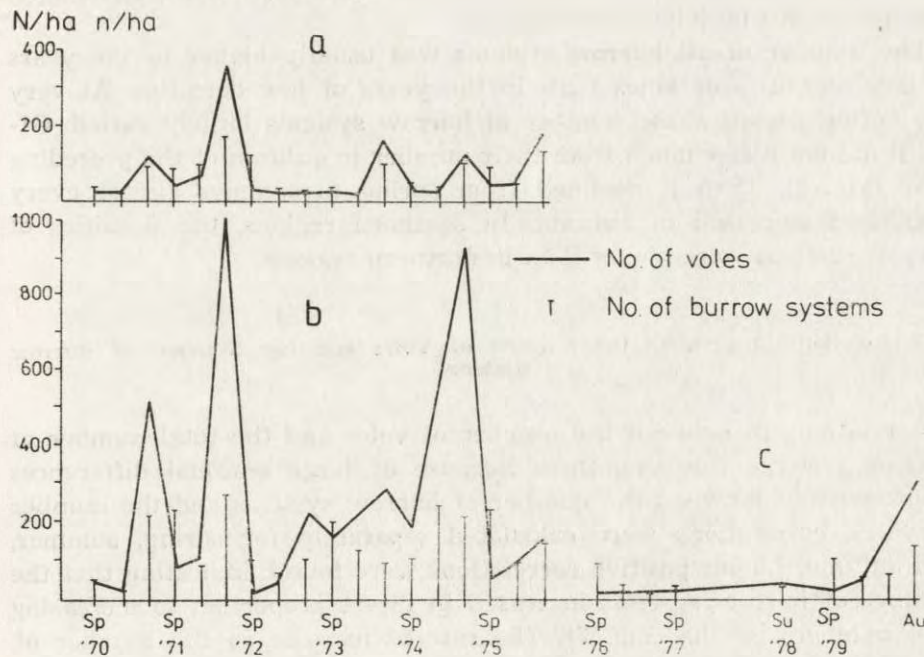


Fig. 2. Changes in numbers of *M. arvalis* (N/ha) and burrow systems (vertical bars, n/ha) in regions I (a), II^a (b), and II^b (c).

¹ a) Data from region I comprising ancient counties of Tczew, Pruszcz Gdański, Bydgoszcz, and Mogilno; b) data from region II^a comprising ancient counties of Brzeg, Nysa, Wrocław, Złotoryja, Jarosław, Lubaczów, Przemyśl, and Brzozów; and c) data from region II^b collected near Niemcza.

In northern Poland (region I) the observed densities of common voles were much lower than in southern Poland (Fig. 2). In southern Poland in the years of peak numbers, mean densities in autumn reached 1000 individuals/ha². In northern Poland, in the peak year of 1971 the mean density was 350 individuals/ha. In 1974, the population was low in this region. A much higher density was recorded in 1975. It is difficult to decide, however, whether or not this was a peak year. In southern Poland (region II^a), there were two distinct years of peak numbers, 1971 and 1974 (Fig. 2). They were followed by dramatic declines in 1972 and 1975, respectively. In each year, lowest numbers occurred in spring, then numbers increased over summer and autumn, and declined until next spring.

In Lower Silesia (region II^b), there occurred a small mammal community rich in species, and common voles frequently were a subdominant element in it (Adamczewska-Andrzejewska, Bujalska & Mackin-Rogalska, 1979a, 1979b, 1981). Very low densities of this species were recorded in 1976, 1977, and 1978 (Fig. 2). In 1979, the rate of population growth was very high from spring to summer, and in autumn the density of voles was almost 300 individuals/ha (Fig. 2).

The number of all burrow systems was usually higher in the years of high densities of voles than in the years of low densities. At very low spring densities, the number of burrow systems largely varied. Often it did not differ much from their number in autumn of the preceding year (Fig. 2). Then it declined from spring to summer almost every year, and increased in autumn. In southern regions, the densities of burrow systems were higher than in northern regions.

3.1.1. Relationship between the Number of Voles and the Number of Burrow Systems

A relationship between the number of voles and the total number of burrow systems was examined. Because of large seasonal differences in proportions between the number of burrow systems and the number of voles, correlations were calculated separately for spring, summer, and autumn. Linear positive correlations were found, indicating that the number of burrow systems increased in direct proportion to increasing vole numbers per ha (Fig. 3). The rate of increase in the number of voles with increasing number of burrow systems was highest in autumn, lower in summer, and lowest in spring. Differences among regression coefficients were statistically significant.

² In 1971, the highest densities obtained by another method (see study methods) reached 2000 individuals/ha, and these results are not shown in Fig. 2.

A similar, linear relationship was obtained for northern and southern regions of Poland (Fig. 3). But at the same increase in the number of burrow systems in any given season, the increase in the number of common voles was higher in southern than in northern Poland. That is, more voles could live in region II^a than in region I in the same number of burrow systems.

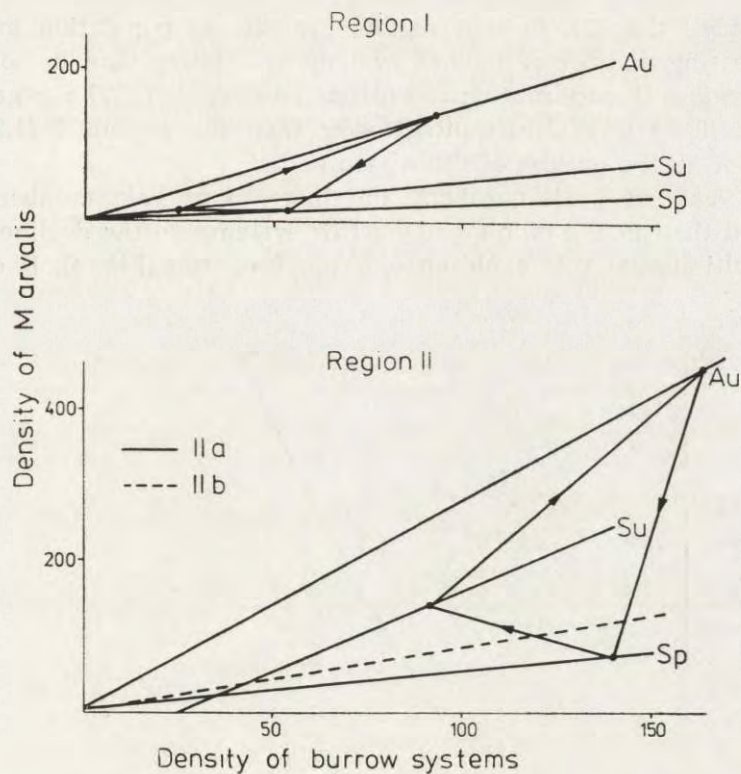


Fig. 3. Relationship between the density of burrow systems and the density of *M. arvalis* per ha.

Sp — spring, Su — summer, Au — autumn. Region I: $y=0.2178x+1.7848$, $r=0.72^3$ for spring, $y=0.5255x+4.1568$, $r=0.50^3$ for summer, $y=1.5781x-1.4738$, $r=0.86^3$ for autumn; Region IIa: $y=0.4465x+6.8098$, $r=0.63^3$ for spring, $y=2.1599x-55.1076$, $r=0.94^3$ for summer, $y=2.7216x+2.9513$, $r=0.77^3$ for autumn; Region IIb: $y=0.8704x-0.5941$, $r=0.47^1$. Points denote mean values. Statistical significance of the correlation coefficients: ¹ $P<0.05$, ³ $P<0.001$.

The trajectory connecting mean numbers of burrow systems and common voles in three periods for all the years pooled allows simultaneous observation of changes in the number of burrow systems and

voles over an average year. In both northern and southern Poland, the number of burrow systems decreased and the number of voles slightly increased from spring to summer, and both these parameters dramatically increased from summer to autumn (Fig. 3).

The relationship between the density of vole population and the number of burrow systems in Lower Silesia (region II^b) was estimated for all three periods of the season jointly, since the number of samples was too small (Fig. 3). In that region, the rate of population increase with increasing number of burrow systems was lower than in northern Poland (region I) and southern Poland (region II^a). The regression coefficient (0.89) was significantly lower than for regions I (1.2) and II^a (1.62) for all the periods of the season pooled.

In the years of peak numbers, the increase in vole numbers was more rapid than in the number of burrow systems. In the decline years of the multi-annual vole cycle an opposite was true (Fig. 4). It can be

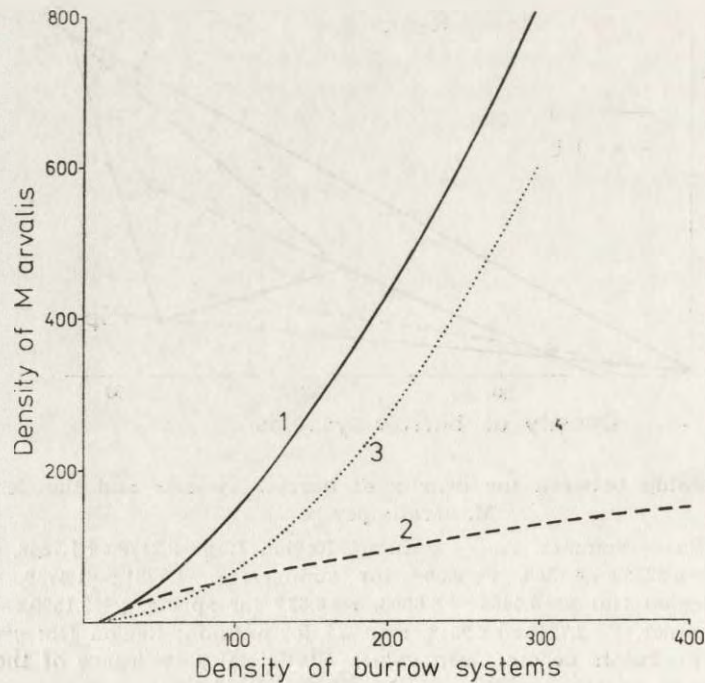


Fig. 4. Relationship between the density of burrow systems and the density of *M. arvalis* per ha in different phases of the multi-year cycle.

Phases: (1) peak numbers $y = e^{1.4833 \ln x - 1.7767}$, $r = 0.821^3$; (2) decline $y = e^{0.7297 \ln x + 0.0813}$, $r = 0.6669^2$; (3) increase $y = e^{1.9494 \ln x - 4.7325}$, $r = 0.9308^3$. Statistical significance of the correlation coefficients: ² $P < 0.01$, ³ $P < 0.001$.

stated, thus, that with increasing density of voles per ha in the years of peak numbers, the construction of new burrow systems is slowed down. In the years of decline, following the years of peak numbers, many burrow systems persists. Consequently, the density of burrow systems is frequently very high but a large proportion of them is not occupied by voles. Hence, unlike in peak years and in the years of increasing numbers, the increase in the number of burrow systems is not combined with an increase in the number of voles (Fig. 4).

3.1.2. Occupation of Burrow Systems by Individuals

Almost at any time some burrow systems are abandoned. A particularly low proportion of inhabited burrow systems, that is, colonies, was recorded in spring, when typically the densities of voles were low (Fig. 5). In summer and autumn, the proportions of colonies were higher than

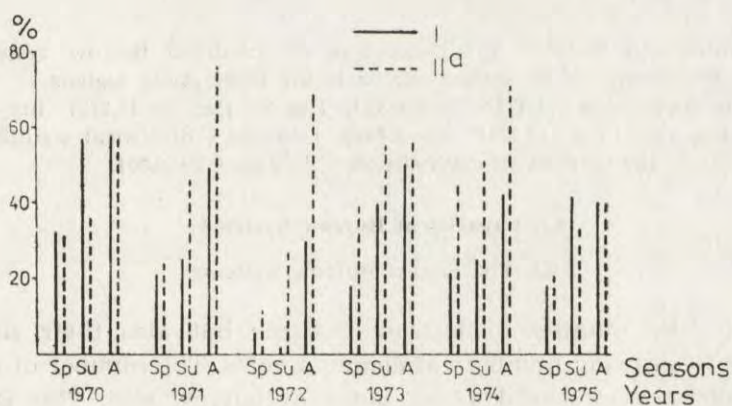


Fig. 5. Changes in the percentage of inhabited burrow systems (colonies) of *M. arvalis* in regions I and IIa. Sp-spring, Su-summer, Au-autumn.

in spring. In the years of declining numbers, that is, in 1972 in the two regions and in 1975 in region II^a, these proportions were also lower than in the other years. The percentage of inhabited burrow systems was thus different in successive phases of the multi-year cycle. A positive curvilinear relationship was found, that is, the rate of inhabiting burrow systems decreased with growing vole density on the plot (Fig. 6). These regressions followed a similar pattern in all the regions. But in region I, burrow systems were more intensely inhabited at lower

vole densities than in region II^a, and also the rate of inhabiting burrow systems began to decline at lower densities in region I.

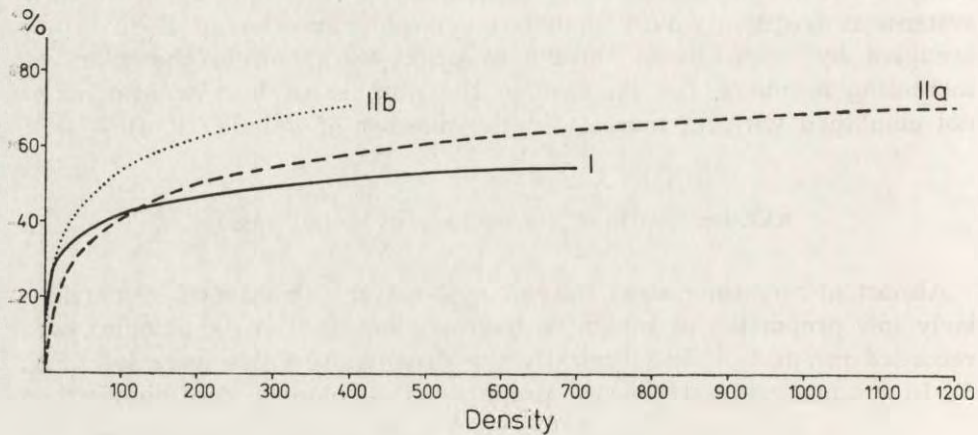


Fig. 6. Relationship between the percentage of inhabited burrow systems and the density of *M. arvalis* per ha in the three study regions.

Region I: $y = 6.6484 \ln x + 11.4741$, $r = 0.6132^2$; Region IIa: $y = 12.0751 \ln x - 14.4861$, $r = 0.8519^3$; Region IIb: $y = 12.4831 \ln x - 3.8466$, $r = 0.8066^3$. Statistical significance of the correlation coefficients: ² $P < 0.01$, ³ $P < 0.001$.

3.2. Capacity of Burrow Systems

3.2.1. The Size of Burrow Systems

Not only the number of burrow systems but also their size can increase with growing numbers of common voles. The number of entrances into burrows was used as an index of burrow size. This is based on the assumption that the higher the number of entrances, the larger is the distance between the two extreme ends of a single burrow system, thus the longer the underground corridors, and, consequently, the greater number of voles can potentially live there. This assumption is based on a statistically significant correlation between the colony size, as expressed by the distance between extreme entrances and the number of these entrances in a burrow system (Fig. 7). This analysis was done for unpublished data used for estimating damage to alfalfa by the common vole (Babińska-Werka, pers. comm.).

Mean number of entrances has been calculated for inhabited and abandoned burrow systems separately since their percentage varied. In all the regions, the number of entrances was statistically higher (t-Student test) for inhabited burrow systems, that is, for colonies, than for

abandoned burrows. The average number of entrances, as calculated for all the years pooled, declined from spring to summer and increased from summer to autumn in the three regions of Poland for both inhabited and abandoned burrow systems (Fig. 8). Seasonal differences in the number of entrances are statistically significant, and higher for inhabited than abandoned burrows. Spring burrow systems were typi-

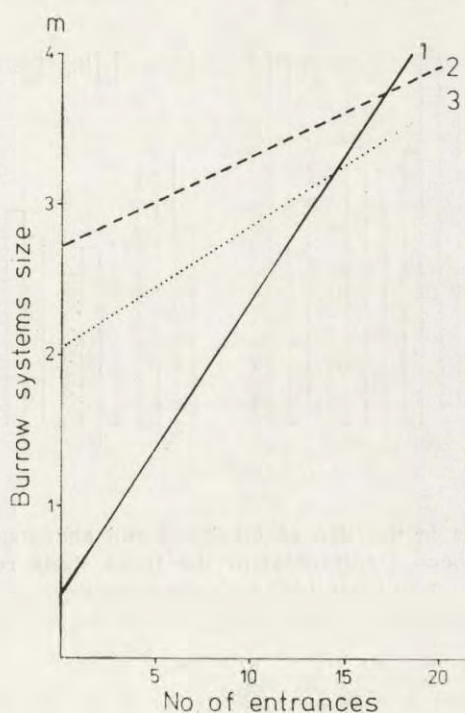


Fig. 7. Relationship between the number of entrances into a burrow system and its size, as measured by the distance between the extreme entrances (in metres), 1 — $y=0.1942x+0.420$, $r=0.7835^3$ before harvest; 2 — $y=0.0598x+2.7257$, $r=0.5253^3$ after harvest; 3 — $y=0.0830x+2.0334$, $r=0.6410^3$. Statistical significance of the correlation coefficients: $^3 P<0.001$.

cally represented by those from the preceding autumn, hence the number of entrances into them was similar to, and often even higher than in autumn burrows. It has also been found that the average burrow system in region I had a significantly lower number of entrances in all the seasons ($p<0.001$) than in region II^a. Changes in the size of burrow systems in the multi-year cycle did not correspond to changes in vole numbers. In the years of decline, the number of entrances was typically a little higher than in the years of peak numbers, e.g. in region I in 1972 and in region II^a in 1975 (Fig. 9).

A comparison of the size of burrow systems in region II^b for successive years show that the number of entrances was a little higher in the year of the highest numbers, that is, in 1979, as compared with other years (Fig. 10). In the years when it was possible to compare

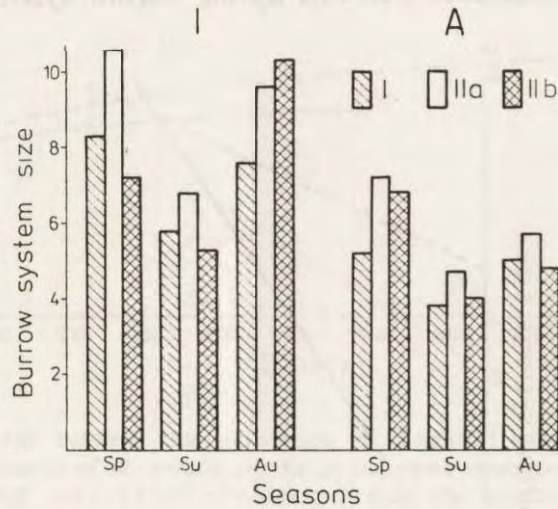


Fig. 8. Seasonal changes in the size of inhabited and abandoned burrow systems (measured by the number of entrances) in the three study regions (I, IIa, IIb), I — inhabited, A — abandoned.

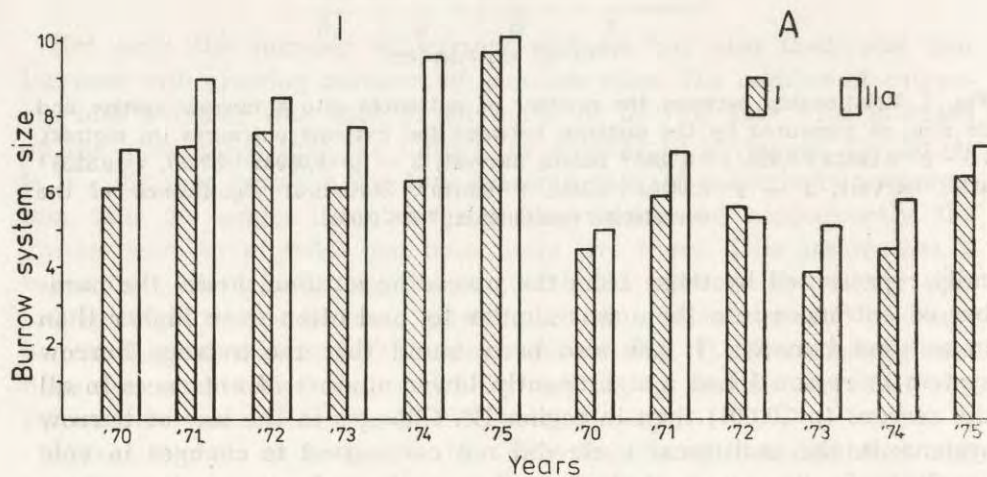


Fig. 9. Changes in the size of inhabited (I) and abandoned (A) burrow systems in northern (I) and southern (IIa) regions of Poland.

the size of burrow systems in alfalfa fields and pastures, larger burrows were found in alfalfa.

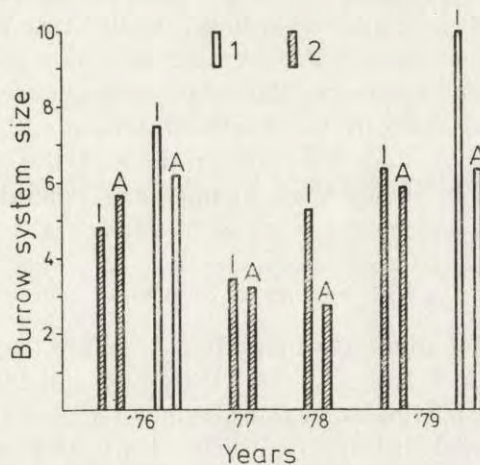


Fig. 10. Changes in the size of inhabited (I) and abandoned (A) burrow systems in region IIb in alfalfa (1) and in a pasture (2).

The size of inhabited burrow systems (colonies) depended on the density of vole populations. A statistically significant correlation between the vole density per ha and the mean number of entrances into a colony was found for northern areas in spring and autumn, and for southern regions only in autumn (Fig. 11). In northern Poland (region I), the

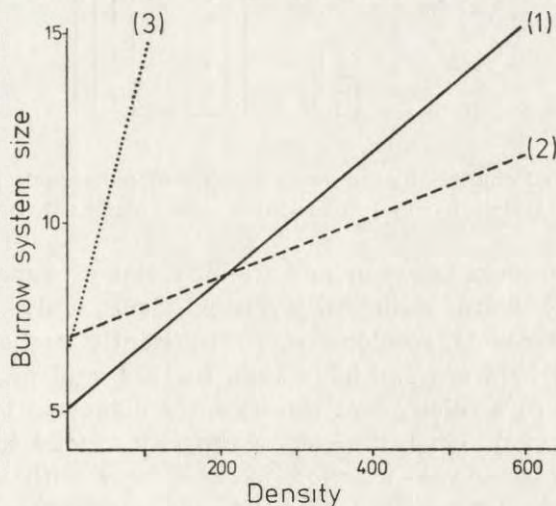


Fig. 11. Relationship between the size of inhabited burrow systems (colonies) and the density of *M. arvalis*: (1) autumn, region I, $y=0.0168x+5.0598$, $r=0.5501^2$; (2) autumn, region IIa, $y=0.0081x+6.947$, $r=0.4427^2$; (3) spring, region IIb, $y=0.0796x+6.538$, $r=0.4293^2$; $^1 P<0.05$, $^2 P<0.01$.

increase in the number of entrances into a colony was much higher in spring than in autumn at the same increase in the number of voles. A comparison of autumn regressions for the two study regions shows that the same increase in the number of voles per ha in the south requires a smaller increase in the colony size (as measured by the number of entrances) than in the north of Poland. In other words, these regressions indicate that in southern Poland the density of voles in autumn was much higher than in northern Poland at the same mean colony size expressed by the number of entrances.

3.2.2. Number of Voles in a Colony

The number of individuals inhabiting a colony (its capacity) increased from spring to autumn (Fig. 12). Differences between mean seasonal vole numbers in particular regions, calculated for all the years pooled, were statistically significant (*t*-Student test). The mean colony capacity in region II^a was significantly higher than in regions I and II^b in spring and autumn. In summer these differences were lower and statistically insignificant.

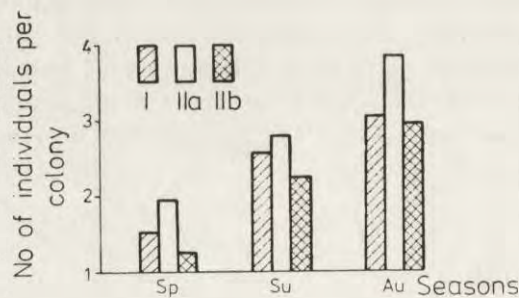


Fig. 12. Seasonal changes in the mean number of individuals per inhabited burrow system (colony) in the three study regions (I, IIa, IIb).

Most differences between mean annual colony capacities in the multi-year cycle were statistically insignificant. Only in region II^a the number of voles in a colony was significantly higher in 1973 than in 1972, and in 1974 it was higher than in 1975, and in region I the number of voles in a colony was significantly higher in 1973 and 1975 than in 1974 (Fig. 13). Thus, the colony capacity tended to be higher in the years with higher vole numbers, as compared with the years of lower vole numbers. Differences in the colony capacity between the two compared regions of Poland were small and most frequently statistically insignificant. Only in 1974 and 1975, differences in the colony capacity between northern and southern Poland were statistically significant. In

1974, it was higher in the southern region and in 1975 in the northern region (Fig. 13). This could be related to the occurrence of peak numbers in region II^a in 1974, and in region I most likely one year later. The colony capacity in region II^b in the multi-annual cycle cannot be compared because of an insufficient number of samples in 1977 and 1978.

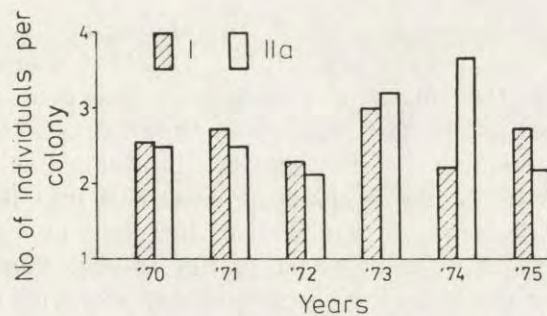


Fig. 13. Changes in the mean number of individuals per colony in regions I and IIa. Statistically significant differences at $P < 0.001$.

The mean colony capacity increased curvilinearly with vole density (Fig. 14). At lower vole densities, the mean colony capacity increased

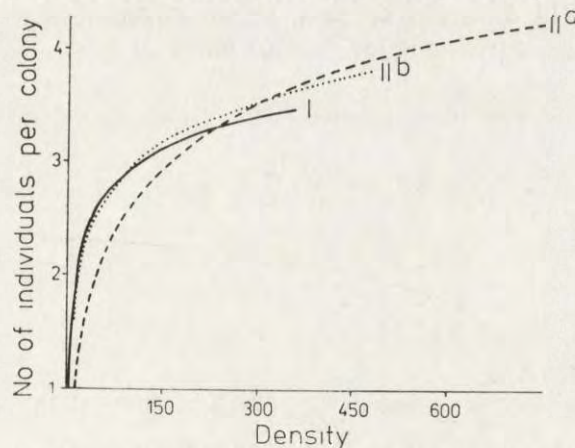


Fig. 14. Relationship between the number of individuals per colony and the density of *M. arvalis* in the three study regions.

I: $y = 0.4201 \ln x + 1.0138$, $r = 0.7224^3$, IIa: $y = 0.8155 \ln x - 1.1186$, $r = 0.8142^3$, IIb: $y = 0.5635 \ln x + 0.3624$, $r = 0.9281^3$, $^3 P < 0.001$.

at a higher rate than at high densities. In the northern region, the increase in the vole density per colony firstly occurred at a higher rate than in the southern region, and then the rate of increase progressively declined. In the southern region, the decline in the rate of density

increase per colony with growing vole population density was less violent. In region II^b, the increase in the colony capacity followed a similar pattern as in region II^a.

3.2.3. Colony Capacity in Relation to Colony Size

The relationship between the density of vole population and the mean colony size, described in Section 3.2.1, suggests that there is also a relationship between the colony size and the number of individuals in this colony in local populations at a given time instant. It follows from the calculated regressions that the greater the number of individuals in a colony, the greater is the number of entrances into it, and that in most populations the number of entrances increases at a declining rate with growing number of individuals in the colony. The most typical function describing declining increases in colony size with the increasing number of individuals in this colony is of the form $y = A + B \ln(x+1)$, where x is the number of individuals in a colony, and y is the number of entrances into the colony. This is illustrated in Figure 15 for a vole population at Zapałów (region II^a) in the autumn of 1970. Such regressions were calculated for 155 local populations in different years of the cycle and in different seasons. Large differences were found in the course of these regressions for various sites.

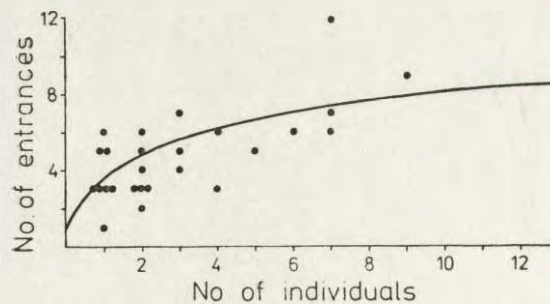


Fig. 15. Relationship between the number of entrances and the number of individuals in a colony (Zapałów — autumn 1970 — region II^a) $y = 1.0411 + 2.97 \ln(x+1)$, $r = 0.6705$, $P < 0.001$.

The number of entrances rapidly increased, reaching a maximum value of 7, when the number of individuals in the colony increased from

1 to 2—3, and the colony with only 6 entrances was sufficiently large to accommodate 7 individuals. It seems thus that 1—3 individuals are capable of making a burrow system for 7 and more individuals (Fig. 15).

3.3. Changes in the Density of Burrow Systems and in the Colony Capacity in Relation to Population Dynamics of the Common Vole

The number of colonies can increase with growing vole population size as a result of establishing new burrow systems or resettling temporarily abandoned burrow systems, and/or the number of individuals in a colony can increase. Consequently, the number of voles in the population fluctuates as a product of changes in the number of burrow systems per ha and changes in the colony capacity. In this study, plots were shifted in successive years (e.g. because of ploughing), and mean values from several sites were used. Hence, the value of this product shows only tendencies in vole number changes, and allows elucidation of the dominant process.

To see whether the rate of these processes was identical, the rate of changes (increases or decreases) in the following parameters was examined: 1) density of voles per ha, 2) density of inhabited burrow systems (colonies) per ha, and 3) mean colony capacity. These parameters were compared for spring and summer, and for summer and autumn of each study year in regions I and II^a, where the number of data was sufficient. In this way, characteristics of changes occurring in the first and the second half of the growing season were obtained. The rate of changes was calculated as N_t/N_{t-1} , where N_t is the value of a parameter in period t (summer or autumn), and N_{t-1} is the value of a parameter in period $t-1$ (spring or summer, respectively). The comparison of the rate of change in the density of colonies and in the colony capacity shows that the relative importance of these processes clearly depends on the season (Fig. 16). In the

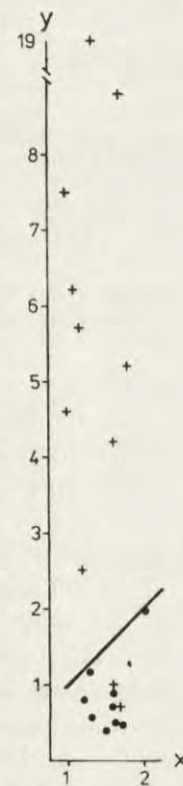


Fig. 16. Comparison of the rate of change in the number of individuals per colony (x) and the rate of change in the density of colonies per ha (y) in the first and the second half of the growing season, points — spring-summer, crosses — summer-autumn; along the diagonal line the two rates are equal.

period spring-summer, when the population growth rate is typically low, the number of individuals in a colony increased at a higher rate than the number of colonies. In the second half of the growing season, when the number of voles largely increases (growth rate varied from 2 to 41.8), the process of establishing new colonies was much more intense than an increase in the density of voles in individual colonies. An opposite situation was observed only in the southern region in the periods spring-summer of 1973 and 1974. This could have been related to a higher rate of population increase in the first than in the second half of the season in those years there.

Table 1

Indices of changes in the number of the common voles, inhabited burrow systems, and in the number of individuals per burrow system in the period autumn-spring of the next year for successive years.

Region I					
Period	70/71	71/72	72/73	73/74	74/75
Numbers of voles/ha	0.197	0.034	1.605	0.078	0.231
Number of inhabited burrow systems	0.330	0.079	3.250	0.192	0.360
Number of voles per burrow system	0.542	0.422	0.516	0.429	0.664
Region II ^a					
Period	70/71	71/72	72/73	73/74	74/75
Numbers of voles/ha	0.126	0.017	0.635	0.405	0.060
Number of inhabited burrow systems	0.419	0.058	1.162	0.894	0.323
Number of voles per burrow system	0.497	0.305	0.825	0.396	0.198

An identical comparison of changes in the number of colonies and colony capacity was made for the period autumn-spring of the next year. Generally, the compared parameters decreased with declining population size at that time (Table 1). In region I, the number of colonies declined at a higher rate than the colony capacity, except in the winter of 1972/73, when the population size increased, and so did the number of colonies, whereas the number of individuals in a colony was reduced by half. In region II^a, a decrease in the population size was accompanied by a similar decrease in the value of the parameters compared, or a decrease in the colony capacity was a little higher. Only in the winter of 1971/72, that is, after peak numbers, the number of colonies was reduced at a very high rate as compared with the colony capacity.

In the two periods treated jointly, that is, in the period spring-autumn, generally changes in the number of colonies were greater than changes in the colony capacity. This was not the case only in 1973 and 1975 in region II^a, when changes in the density of colonies went in oppo-

site direction to the changes in the population size, or their number increased at a lower rate than the colony capacity (Table 2).

Table 2

Indices of annual changes in the number of common voles, inhabited burrow systems, and in the number of individuals per burrow system in successive study years. incr. — increase. decl. — decline.

Year	1970	1971	1972	1973	1974	1975
Phase of the multi-year population cycle	incr.	peak	decl.	incr.	incr.	peak
Numbers of voles/ha	19.35	13.89	0.26	29.18	7.20	8.16
Number of inhabited burrow systems	8.39	5.25	0.17	12.04	3.79	4.32
Number of voles per burrow system	2.80	2.22	1.67	2.54	1.55	1.78
Region II ^a						
Year	1970	1971	1972	1973	1974	1975
Phase of the multi-year population cycle	incr.	peak	decl.	incr.	peak	decl.
Number of voles/ha	24.83	12.96	12.73	1.97	8.53	2.68
Number of inhabited burrow systems	8.32	3.67	6.11	0.61	3.44	1.31
Number of voles per burrow system	2.22	3.00	1.97	1.97	3.30	2.17

In the phases of depression, the rate of increase in the number of individuals in a colony was higher than that of the number of colonies in two cases, and in one case a reverse was true. In the years of population increase, the rate of increase in the number of colonies was higher in four cases, and the rate of increase in colony capacity was higher in one case. All the years of peak numbers were characterized by a higher rate of increase in the number of colonies than in the colony capacity (Table 2).

This analysis shows that generally, the number of colonies accounts more for changes in the population size than the colony capacity, especially in the periods of rapid population growth. In the periods of low population growth and number declines, changes in the density of voles in a colony may be of greater importance.

4. DISCUSSION

Observation of long-term changes in numbers and the accompanying changes in population and environmental parameters in the multi-annual cycle is one of the ways of elucidating the mechanisms underlying cyclic fluctuations and differences in population levels. This paper analyses

long-term changes in numbers of common vole populations, along with the number, size, and utilization of burrow systems. Cyclic fluctuations in the number of common voles, known from the literature (Frank, 1957; Skuratowicz, 1957; Adamczewska-Andrzejewska, 1974; Straka & Gerasimov, 1977, and others) was clear cut in the study regions because of high peaks in 1971 in the northern and southern regions of Poland and in 1974 in southern Poland. The other study years were the years of decline or increase in numbers. Though the cycle in various regions was synchronous only in part. In the two regions the population increased in 1970, reached a peak in 1971, and declined in 1972, but the next peak in 1974 was clear only in southern Poland (region II^a). In northern Poland it is difficult to decide whether it occurred in 1975 or perhaps in 1976, when the study was not continued in this region. Asynchronous cycling over large areas and irregular mass appearance of the common vole was observed by Migula *et al.* (1970) and Straka & Gerasimov (1971). Similarly, Schindler (1972) and Myllymäki (1977) observed this in *Microtus agrestis*. On the other hand, Ryszkowski (1983) found almost totally synchronous cycling for common voles occurring in four different crops forming a mosaic within a crop-land. Thus, cycling is not always synchronous over large areas. Krebs & Myers (1974) suggest that similar weather conditions can synchronize cycles from time to time. Adamczewska-Andrzejewska, Mackin-Rogalska & Nabagło (1982) described a hypothetical cycle in a mosaic of crop fields and on a macrogeographic scale, specifying factors accounting for differentiation of its phases among local populations, and also conditions for synchronous cycling.

The number and complexity of burrow systems (colonies) of the common vole has been considered as a basic factor determining the multi-year cycle of this species, on the basis of biological and ecological premises (Adamczewska-Andrzejewska *et al.*, 1982). These authors have assumed that the population density and the density of burrow systems are interrelated by a positive — positive feedback. It follows from the hypothetical course of the population cycle that the number of burrow systems should increase with increasing vole population, and this, in turn, should stimulate a further increase in the population.

This paper shows that there is a linear relationship between the vole population size and the number of burrow systems in the multi-year cycle. Seasonal differences in this regression are characterized, and also simultaneous changes with time in the mean number of burrow systems and mean vole numbers. Seasonal and annual differences may be important for estimating and predicting the number of voles from the number of burrow systems. According to the hypothesis (Adam-

czewska-Andrzejewska *et al.*, 1982), the rate of increase in the number of burrow systems with population density should decline. The present study shows that such a decline in the growth rate of burrow systems when a threshold vole density is exceeded takes place in the years of peak numbers. This is indicated by the curvilinear form of the regression curve in the years of peak numbers in southern Poland. In the years of decline, this increase was not slowed down. The density-dependence in the increase in the number of the colonies can result from an aggressive behaviour of adults of the same sex, or from the aggressive behaviour of the family groups (de Jonge, 1983), forcing animals to burrowing new systems. A decline in the growth rate of the number of colonies with increasing number of common voles in an isolated population, and a tendency towards a uniform distribution of colonies which may provide evidence for aggressiveness of their inhabitants, was found by Mackin-Rogalska (1979). An increase in the number of common voles with increasing number of burrow systems was significantly higher in the southern region (II^a) than in the northern region (I). This could have been due to differences in the size of burrow systems (as measured by the number of entrances) in the compared regions. An average burrow system, both inhabited and abandoned, had less entrances in northern than in southern Poland. These differences can be related to the type of soil. Soils of the northern region were characterized by a greater cohesion, as compared with soils of the southern region (Uggla, 1983). Thus, it is very likely that burrowing was more difficult in the northern region.

Burrow systems are relatively persistent and can be used by several generations. In perennial crops, they can be used even more than one year (Ružic, 1967; Grulich, 1980). From time to time, some burrow systems are successively abandoned, temporarily or permanently for unknown reasons. Temporary abandonment and resettlement of burrow systems was described by many authors (Karaseva, 1957; Bašeni-na, 1962; Ružic, 1967; Mackin-Rogalska, 1979). Inhabited and abandoned burrow systems differed in size. In all the study areas, the number of entrances into a burrow system, indicating its size and complexity, was greater in inhabited than in abandoned burrows. Similarly, Zie-liński (1982) has found that the number of entrances into inhabited burrows of *Microtus brandti* was greater than into abandoned burrows.

The size of the space occupied by burrows, as indicated by the number of entrances, depends on the soil type, crop type, height of plant cover, and the season (Panteleev, 1983). For example, in this study, burrow systems occupied larger areas in alfalfa than in the pasture. Also Ryzkowski (1983) emphasized preference of common voles for

alfalfa, where colonies are particularly large. Thus, low numbers of common voles in pastures of Lower Silesia can be explained by a lower capacity of colonies in pastures as compared with alfalfa. However, a fine-grained mosaic of crop fields surrounded with woods and a high proportion of mid-field woods suggest that also predation and migrations could have been more important in this region.

The proportion of inhabited burrow systems (colonies) increased with increasing population size. This proportion was a net result of establishing new colonies, abandoning old colonies, and resettling of temporary abandoned burrow systems. With increasing population size, the percentage of colonies increased at a declining rate, tending to a stable level, as indicated by the curvilinear regression. Mackin-Rogalska (1981) has found a similar relationship for the percentage of space occupied by *M. arvalis* and the population density in agroecosystems of Lower Silesia.

When the density of the population increases, not only new colonies are established and the abandoned colonies reoccupied, but also the number of individuals in already existing colonies may increase. This process can be approximated by a curvilinear regression of the number of individuals in a colony on the population density per ha. When a threshold density is exceeded, the number of individuals in a colony increases at a declining rate to a steady state. This is understandable because the capacity of a colony is limited, and sometimes there is no more space for extending the burrow system as neighbouring burrow systems are closely packed.

In southern Poland, burrow systems were larger and the rate of their colonization, as expressed by both the number of individuals per colony and the proportion of inhabited burrow systems, was lower and levelled at higher population densities than in northern Poland. These differences, in our view, accounted for differential population levels of the common vole in the regions compared.

Analysing the processes of establishing new colonies and density increases in single colonies with increasing population size in different years, it has been found that they vary with the season. In spring, the rate of increase in the number of individuals in single colonies is higher than the rate of increase in the number of colonies. In the second half of the growing season, when the rate of common vole numbers increase is much higher than in spring, new colonies are established at a higher rate. This may be related to reproduction and to the fact that the first spring litters remain in their mother colonies. With increasing number of litters, individual colonies become overcrowded, and dispersal becomes intense. Voles of earlier litters, which are already

capable of burrowing, establish new colonies. The process of establishing new colonies or an increase in the vole density in individual colonies in both annual and multi-annual cycle depend on the level of population density (Fig. 17). Both these processes are density-dependent but the increase in the number of individuals in single colonies declines, whereas the increase in the number of colonies intensifies with increasing population size. Also the space occupied by the vole population extends as the number of burrowing systems and their size are

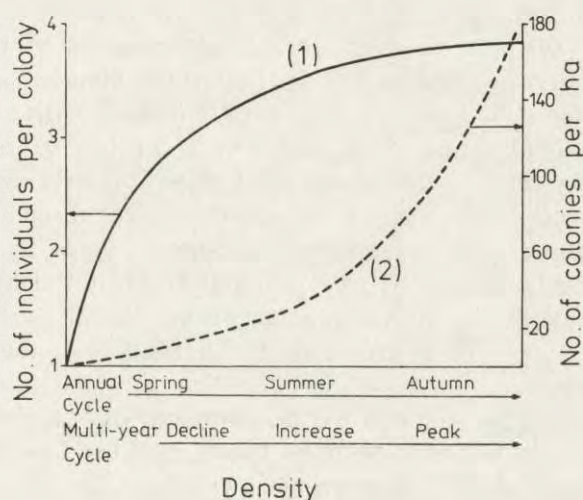


Fig. 17. Schematic representation of changes in the density of individuals per colony (1) and the number of colonies per ha (2) with an increasing density of *M. arvalis* per ha over the annual and multi-year cycle.

increasing. One can easily imagine that in the year of peak numbers, the distance between individual colonies declines gradually until they become contiguous and no more space is available for new settlers. This is accompanied by heavy damage to plant cover and soil caused by abundant burrows and corridors, including damage to crops (Babińska-Werka, 1979). If all the colonies become overcrowded simultaneously, this being indicated by slowing down the increase in the number of individuals per colony with growing population size, increased migration to other crops may be expected, along with increased vole mortality. As a result of increased dispersal, genetic heterogeneity of the population may increase, which accounts for changes in survival of individual voles, observed at higher population densities (Dobrowolska, 1983). According to the Chitty-Krebs hypothesis (Krebs & Myers, 1974), these processes determine decrease in number and, consequently,

the phase of decline. A high rate of establishing new colonies in the common vole, especially from summer to autumn, implies that this is a highly expansive species. Hence, it markedly increases in numbers and colonizes many crops over the growing season and in successive years of the cycle, and due to this it predominates rodent communities in agroecosystems, especially in autumn and in peak years (Adamczewska-Andrzejewska, Bujalska & Mackin-Rogalska, 1981).

To sum up, it should be reemphasized that the results of this study, including long-term changes in vole numbers in different regions of Poland, and the accompanying changes in the number, size, and capacity of burrow systems, as well as interrelationships in these changes, indicate that burrow systems are an important element accounting for cyclic fluctuations in common vole populations. Further investigations are needed to explain in detail differences in the course of number cycles for many local populations, and their underlying mechanisms, taking into account sex ratio and age structure of common voles in individual colonies, and to explain multi-year cycles in crop mosaics. The results of this study and experimental tests of the hypothesis proposed by Adamczewska-Andrzejewska *et al.* (1982) such as manipulating the abundance of burrows in the habitat (*e.g.* their destructing or providing artificial burrows), will enrich the understanding of the importance of burrow systems to the common vole cycles not only on the local scale. The understanding of the mechanisms determining long-term fluctuations of the common vole is not only of theoretical but also of economic importance, as this species causes heavy damage to agriculture (Tahon, 1969; Trojan, 1969b; Spitz, 1977; Babińska-Werka, 1979).

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LICZEBNOŚĆ NORNIKA ZWYCZAJNEGO A WYKORZYSTANIE SYSTEMÓW NOR

Streszczenie

Wieloletnie zmiany liczebności populacji *Microtus arvalis* (Pallas 1779) i systemów nor oraz stopień wykorzystania ich na uprawach wieloletnich, zbadano w 25 miejscowościach trzech rejonów Polski. W latach 1970—1975 badania prowadzono na wielkołanowych polach lucerny w północnym (I) i południowym (II^a) rejonach Polski, różniących się wyraźnie poziomem zagęszczenia *M. arvalis*. W latach 1976—1979 badaniami objęto pola pastwisk i mieszanek pastewnych agro-

ekosystemu o dużym stopniu mozaikowości, w rejonie południowo-zachodniej Polski (II^b).

Liczebność nornika wykazywała cykliczne wahania z wyraźnymi fazami wzrostu, szczytu i spadku. Wzrost liczebności *M. arvalis* w cyklu wieloletnim skorelowany był dodatnio z liczbą systemów nor (Ryc. 3). W roku szczytu liczebności, ze wzrostem liczby systemów nor tempo przyrostu liczebności *M. arvalis* rosło a w roku depresji malało (Ryc. 4). Proces zasiedlania systemów nor przez osobniki w cyklu wieloletnim, wyrażony procentowym udziałem systemów nor zamieszkałych, zależał dodatnio od zagęszczenia norników, a tempo wzrostu udziału systemów nor zajętych malało (Ryc. 6).

Systemy nor *M. arvalis* w rejonie I były istotnie mniejsze niż w rejonie II^a (Ryc. 8). Na uprawach lucerny stwierdzono większe systemy nor niż na pastwisku (Ryc. 10). Liczba osobników zamieszkujących system nor (kolonię) wzrastała od wiosny do jesieni i była istotnie większa w rejonie II^a niż w rejonach I i II^b (Ryc. 12). Ze wzrostem zagęszczenia populacji *M. arvalis* w cyklu wieloletnim, liczba norników w systemie nor wzrastała w zmniejszającym się tempie (Ryc. 14).

W kształtowaniu wieloletnich i rocznych zmian liczebności nornika zwyczajniego, większą rolę odgrywały zmiany liczby zamieszkałych systemów nor w porównaniu ze zmianami liczby osobników w systemie, zwłaszcza w okresach wzrostu i szczytu liczebności (Ryc. 16, Tabele 1 i 2). Natomiast do spadku liczebności nornika mogły się przyczyniać w większym stopniu zmiany liczby osobników w systemie nor niż zmiany liczby systemów nor na polu. Zmiany liczby i wielkości systemów nor oraz stopnia ich wykorzystania (udział systemów zamieszkałych i liczba osobników w systemie) towarzyszące cyklicznym wahaniom liczebności *M. arvalis* w różnych rejonach Polski, pozwalają sądzić o przyczynach różnic w poziomach liczebności i przebiegu cyklu nornika w tych rejonach.