

## Elements of the Spatial Organization of a Common Vole Population<sup>1</sup>

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Mackin-Rogalska R., 1979: Elements of the spatial organization of a common vole population. Acta theriol., 24, 14: 171—199 [With 2 Tables & 10 Figs.].

Spatial parameters of a population of common voles *Microtus arvalis* (Pallas, 1779) in relation to colonies of burrows, were studied two years for two populations of these animals living in isolated fields of alfalfa each one hectare in extent. The CMR method was used. Trapping sites were set up in the centre of each colony. As the number of colonies increased their distribution changed from random to evenly spaced. In the population where density was high than this change took place almost a year earlier than in the low-density population. Individuals exhibited a tendency to distribution in groups. The number of colonies of burrows occupied by individuals increased asymptotically as population numbers increased. The increase in the number of colonies occupied by females is greater than those occupied by males. The average number of individuals in an occupied colony also increases (in a straight line) with increase in population numbers. It is chiefly the adult individuals which take part in the process of settling up new colonies and settling deserted burrows, and females do this to a greater extent than males. The majority of the individuals entering the population (about 90%) increase the density of already existing colonies. Spatial penetration of voles varies with the season and is higher at times of low population numbers than when these are high. Males were found to move over larger areas than females, and the same applies to older individuals as compared with young ones. The greatest differentiation in individuals from the aspect of spatial penetration was found during the year preceding the year of maximum population numbers.

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### 1. INTRODUCTION

The common vole, *Microtus arvalis* (Pallas, 1779) exhibits cyclic fluctuations in numbers (Elton 1942; Skuratowicz, 1949; Dombrovskij, 1971; Adamczewska-Andrzejewska, 1974), and in years when its density is high its harmful effect on field crops is well known.

<sup>1</sup> Praca została wykonana w ramach problemu węzłowego 09.1.7., koordynowanego przez Instytut Ekologii PAN.

One of the important phenomena affecting variations in numbers of the common vole is the spatial organization of its population. Although a very large number of studies have been made of such organization (Karaseva, 1957, 1960; Reichstein, 1960; Spitz, 1964; Dub, 1969 and others), the results obtained are somewhat controversial. This applies to such questions as the tendency in the distribution of this species to form colonies in fields, the composition of individuals in colonies, the activity of individuals and their movements between colonies etc.

With the common vole, colonies consist of subterranean tunnels excavated in complicated systems of burrows with openings giving access to the exterior and with paths running between them (Bashenina, 1962; Poljakov, 1968). Descriptions are to be found in a large number of papers of the construction and complexity of the colonies and their simultaneous persistence in time (Naumov, 1954; Karaseva, 1957). Such colonies, units of space which can be relatively easily distinguished in the field, are occupied by definite groups of individuals.

The composition of individuals in colonies has been examined by means of unearthing colonies (Frank, 1954; Kratochvíl *et al.*, 1959; Bashenina, 1962) or flooding out the voles from their colonies (Andrzejewski & Gliwicz, 1969). According to many authors (Ognev, 1951; Kratochvíl *et al.*, 1959; Bashenina, 1962; Poljakov, 1968) the individuals occupying a colony constitutes a family. This is usually a female, or several females, with the young from one or sometimes several, litters (Frank, 1954). Males are more loosely connected with their colony (Kratochvíl *et al.*, 1959). As they participate in reproduction with a large number of females, they exhibit greater activity than the latter and their home range is more extensive (Naumov, 1956; Reichstein, 1960; Spitz, 1964; Dub, 1969).

The composition of a colony, defined by means of unearthing it or flooding out the animals from their burrows, gives a picture only of certain given moments in time, and omits the dynamic variations in the colony's composition, the degree of attachment of the captured individuals to their colony and the contacts taking place between individuals from different colonies. Variations in the composition of the colony depend to a considerable degree on the activity and migrations of individuals of this species.

The question of the activity, spatial penetration and attachment of individuals to their colony has been differently evaluated by different authors. According to many of them, common voles wander over the area in the vicinity of their colony and feed chiefly there, moving away

from the colony to maximum distances of 20 metres (Januszko, 1938; Karaseva, 1957; Bashenina, 1962; Ružic, 1967). Data are also to be found in literature pointing to the greater activity and periodical migrations of this species (Fenjuk, 1940; Karaseva & Kučeruk, 1954). Mackin-Rogalska (1975) has, however, shown that individuals of a common vole population are not closely connected with one colony, but wander over the area covered by several colonies and this area is larger in the case of males than females.

In addition to the question of activity and degree of individuals' attachment to their colony, the aspects most often analyzed in literature on spatial organization of rodent populations is the way in which individuals are distributed, the size of their home ranges and migrations of different individuals in a population (Reichstein, 1960; Spitz, 1964; Dub, 1969). Among those papers describing intrapopulation relations arising from differentiation of individuals in a population in respect of the extent of area occupied and penetration over this area, the aspect of the colony has been completely overlooked. The one exception is Dub (1969) who made a study of whether the centres of activity of the home range coincide with colonies and found that the activity centres of females were concentrated on the sites of their colonies.

The purpose of the present study was to evaluate the way in which space was used by common vole populations as their numbers increased, the tendency of individuals to gather in groups, intensity of their migrations over the area and movements of individuals between colonies, and also the composition of individuals in colonies and variations in time of the above parameters. The spatial parameters of the population were therefore examined in conjunction with colonies of burrows.

## 2. MATERIAL AND METHODS

The studies were carried out in two isolated populations of common voles living in one-hectare alfalfa fields in the neighbourhood of the Institute of Ecology, Polish Academy of Sciences at Dziekanów Leśny. The alfalfa fields, in their fourth year of cropping, were situated in flat ground, on medium brown silt muds with a sandy substrate. The two fields (A and B) were adjacent and were identical both in respect of formation of the surface and soil and food conditions. Each field was enclosed by wall of cement and gravel composition sunk to a depth of 60 cm below ground level and rising to a height of 60 cm above the ground. This wall prevented individuals from migrating between populations, and between the fields and the surrounding area. The normal cultivation operations to obtain good cropping (fertilization, harrowing, mowing) were carried out in both alfalfa fields.

The catch-mark-release method was used in these studies. The voles were caught

in living-traps baited with oats. Three traps were placed in wooden boxes measuring  $40 \times 40 \times 60$  cm, with the lid open, standing on four legs and at a height of a few centimetres above ground level. There was a hole on the bottom of the box for enter into the box. Boxes protected the traps and captured animals from unfavourable weather effects.

The boxes with their traps were placed in the centre of the area occupied by defined systems of burrows (colonies). The greatest accumulation of burrow holes was taken as the centre of the colony. When two colonies were situated so close together that it was difficult to distinguish between them they were treated as one colony. Accurate diagrams were made of the distribution of such colonies of burrows over the area of the fields (Fig. 1). If a change in the situation of

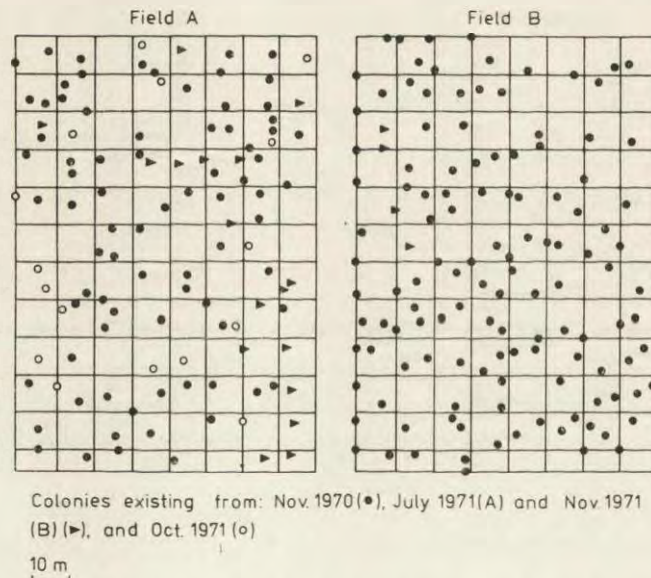


Fig. 1. Distribution of colonies of burrows over the study areas.

the colony centre was discovered, the trapping site (box containing live-traps) was appropriately shifted. It only rarely happened that the colonies shifted their position and even then it was only a question of several metres. New trapping sites were set up as new colonies appeared in the field, so that in effect the number of such sites agreed with the number of currently existing colonies.

The voles caught were marked individually by toe-clipping (Naumov, 1951), recording the number of previously marked individuals, their sex, date and place of capture after which the animals were released. Voles were trapped over the whole year, four times a week. The traps were inspected every 12 hours in the morning and evening on two successive days, ceasing such observations when temperature fell below  $-10^{\circ}\text{C}$  or rose above  $+28^{\circ}\text{C}$ .

Common vole populations were formed in the autumn of 1969, releasing 150 individuals on each field. The material analyzed in this paper was obtained over a two-year study period, from November 1970 to October 1972, during which period

98 trapping series (weeks) were carried out in each field, achieving a total of 16,133 captures of 2681 individuals marked in field A and 20,065 captures of 3889 individuals marked in field B.

### 3. RESULTS

#### 3.1. Variations in Numbers of Populations A and B

The material collected was examined by means of the calendar of captures method (Andrzejewski & Petruszewicz, 1962; Andrzejewski, 1969). Population numbers were estimated on the basis of the presence of individuals belonging to the trappable part of the population, counting their period of presence in the population from the first to the final trapping. Thus in accordance with the calendar of captures method, numbers in each week consisted of: the number of individuals caught (newly-marked or marked previously), and number of individuals not caught in the given week, but present in the population, as shown by previous trapping and that carried out in later weeks. The mean value obtained from numbers in the different weeks of a month was taken as numbers for the given month.

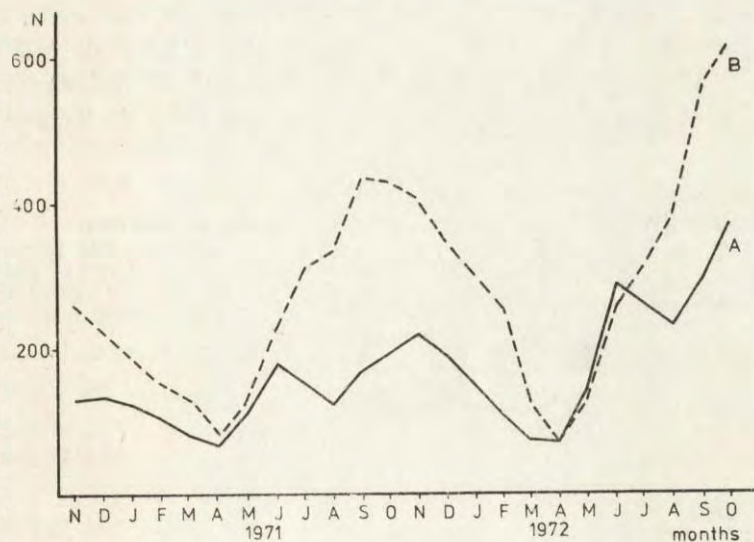


Fig. 2. Variations in numbers in populations A and B.

Numbers in the two populations increased from April to autumn, then decreased up to April of the following year (Fig. 2). In population A, two peaks of numbers occurred in both years, in June and in autumn. Only one peak of numbers was, however, observed in population B —

in September or in October. In both years maximum numbers for population *B* greatly exceeded numbers of population *A*. Minimum numbers occurred in both populations in April in both the first and the second study year, and were very similar (Fig. 2). The numbers of the two populations were higher in the second study year than in the first. In 1973, as stated by Adamczewska-Andrzejewska & Nabagło (1977), in population *B* in which density was greater, there was a decline in numbers, and in population *A* — with lower density — peak numbers occurred. On the basis of numbers of the study population in subsequent years, Adamczewska-Andrzejewska & Nabagło (1973) suggest that there must have been a shift of one year in the phases of the numbers. So the year of maximum numbers in population *A* would be 1973 — the year after completion of collection of material for the present studies, and in population *B* — in 1972 — the second year of these studies.

### 3.2. Spatial Distribution of Colonies and Individuals

#### 3.2.1. Spatial Distribution of Colonies of Burrows

New colonies, *i.e.* new groups of burrows, were repeatedly formed in both fields during the study period. As old colonies existed simultaneously the total density of colonies increased. At the start of the studies (November 1970) there were 78 colonies in field *A*, but 97 by July 1971 and from October 1971 up to the end of the experiment (October 1972) there were 113 separate colonies (Fig. 1, Table 1). In

Table 1  
Density and index of aggregation of colonies of burrows.

| Period of time       | Number of colonies of burrows | The mean number of colonies per 1 are | $V = \frac{S^2}{\bar{x}}$ | Level of statistical significance differences between <i>V</i> and 1 |
|----------------------|-------------------------------|---------------------------------------|---------------------------|--|
| Field <i>A</i>       |                               |                                       |                           |  |
| Nov. 1970—June 1971  | 78                            | 0.833                                 | 0.747                     | NS   |
| July 1971—Sept. 1971 | 97                            | 1.010                                 | 0.608                     | 0.01 > <i>P</i> > 0.001  |
| Oct. 1971—Oct. 1972  | 113                           | 1.177                                 | 0.567                     | 0.01 > <i>P</i> > 0.001  |
| Field <i>B</i>       |                               |                                       |                           |  |
| Spring 1970          | 75                            | 0.781                                 | 0.859                     | NS   |
| Nov. 1970—Oct. 1971  | 125                           | 1.302                                 | 0.546                     | 0.01 > <i>P</i> > 0.001  |
| Nov. 1971—Oct. 1972  | 129                           | 1.344                                 | 0.493                     | 0.01 > <i>P</i> > 0.001  |

NS — non significant

field *B*, however, the majority of the colonies were formed during the time preceding the study period, *i.e.* before November 1970. It was only in November 1971 that there were four new colonies and for the remainder of the study period there were 129. Some of the new colonies

were formed in sequences at relatively slight distances from each other (Fig. 1). No great changes were found in the situation of colonies in the two fields during the study period. The shifts occurring from time to time in the centre of the colonies as the result of new burrows being excavated, revealed after the fields had been harrowed, did not alter the picture of spatial distribution of the colonies of burrows.

In order to define what interaction took place between colonies in the study fields evaluation was made of the index of grouping of trapping sites, since their position corresponded to the position of the centre of the colony, on each study area on the basis of the equation:  $V = S^2/\bar{x}$  where:  $S^2$  — variance in number of sites/colonies in squares  $10\text{ m} \times 10\text{ m}$ ,  $\bar{x}$  — average number of colonies in these squares. If the distribution of the colonies is random, then it should be in accordance with Poisson's distribution, for which  $S^2 = \bar{x}$ , that is,  $V = 1$ . Where  $V > 1$ , the distribution is clumped, while where  $V < 1$ , the distribution is even.

The size of the sample, or squares in which the character of distribution of number of colonies was examined, would appear to be aptly chosen. This is shown by the value of the average number of elements examined in a sample (about 1.0) in relation to the size of the elements examined (Tarwid, 1960).

Analysis was made of distributions of the number of colonies in periods differing in respect of density of colonies in the fields. The significance of differences between the analyzed distributions and random distribution was examined by the method of analysis of significance of differences between the value of the index of clumping ( $V$ ) and unity.

During the initial period (October 1970 — June 1971) no significant differences were found in field *A* between the distribution of number of colonies in squares  $10\text{ m} \times 10\text{ m}$  and the random distribution (Table 1). As from July 1971 the distribution of colonies of burrows in field *A* was even. Changes in the spatial distribution of colonies of burrows in field *B* took a similar course to that in field *A*. During the period preceding the studies (spring 1970 — own data) there was random distribution of colonies gradually changing to even distribution (Table 1).

Despite the identical conditions in both populations and their simultaneous establishment in 1969, in population *B* (with higher density) even distribution of colonies over the surface of the alfalfa field took place almost a year earlier than in population *A* (with lower density).

### 3.2.2. Concentration of Individuals' Visits to Colonies

One of the ways of presenting spatial organization is to analyse the degree of concentration of individuals in different places in the area,

which makes it possible to describe the population's tendency to gather in groups, and the intensity of contacts between individuals included in its composition (A n d r z e j e w s k i & G ł o g o w s k a, 1962). It would appear particularly interesting to examine the grouping of individuals for a species forming colonies of burrows, the distribution of which exhibited a tendency to evenness.

In analyzing distributions of the number of individuals on a trapping site, using the above-mentioned index of clumping, only one capture of each individual on a given site was taken into consideration, in order to avoid an increase in the index of clumping caused by repeated captures of a given individual on the same site. In addition, analysis of the index of clumping for the first captures gives its relatively constant value, despite the increase in the time for which the traps were accessible (A n d r z e j e w s k i & G ł o g o w s k a, 1962). This was of importance in the analyses made here, since on account of the relatively low

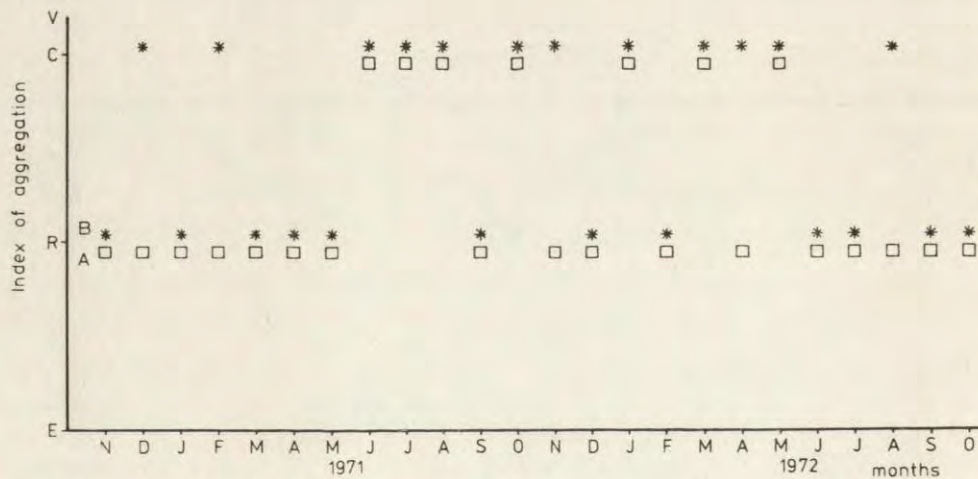


Fig. 3. Index of tendency to congregate ( $V=S^2/\bar{x}$ ) of populations A (□) and B (\*) V, index of aggregation; C, clumped distribution; R, random distribution; E, even distribution.

trappability of the common vole (Grunwald, 1975) tendency to clumping was calculated for monthly intervals of time, in order to ensure a better chance of revealing individuals in all the colonies they visited.

The tendency of individuals in colonies of population B to gather in groups was statistically significant (*i.e.* differed significantly from



Poisson's distribution) more often than in population A in twelve months of the two-year study period, whereas in population A this figure was seven months (Fig. 3). In the remaining months the distribution of individuals in colonies was of a random character.

No significant difference was found in the index of clumping between females and males, or a relation between the numbers in a population and its tendency to gather in groups.

Analysis of changes in grouping between different generations of individuals revealed statistically significant grouping of individuals in the first month of life in the trappable part of the population. As the individuals grew older, their tendency to gather in groups decreases.

### 3.3. Establishing Colonies and Increase in Density of Individuals in the Colony Depending on Population Numbers

Even distribution of colonies in a field does not necessarily result in even distribution of the number of individuals in colonies. On the basis of the presence, *i.e.* of individual captures on trapping sites it proved possible to distinguish occupied and unoccupied colonies. This term has been used, as colonies are relatively lasting in time and their relative resistance to destruction, despite harrowing of fields, results in their being re-occupied, or revisited, after being deserted for a time (K a r a s e v a, 1957; B a s h e n i n a, 1962; R u ž i c, 1967). Thus in addition to the process of formation of new colonies of burrows there is also re-occupation of old colonies which had temporarily remained unoccupied. In both cases, however, this is a process capable of illustrating the establishment of colonies of individuals, understood as groups of individuals occupying a common system of burrows, or wandering over its area.

Examination was made to discover whether the phenomenon of establishment of colonies of individuals understood in this sense depends on population numbers. For this purpose the correlation was calculated between population numbers in each month and the number of colonies occupied by individuals of this population, *i.e.* the number of trapping sites on which at least one individual was caught, at least once in a given month.

The relation examined takes a curved line (Fig. 4). In both populations the course of regression curves points to increasingly smaller increase in the number of colonies occupied as numbers increase by the same number of individuals, that is, this increase tends to zero. When the course of such relations is compared for females and males it can be seen that with the same increase in numbers, the number of colonies occupied by

males increases to a far lesser extent than the number of colonies occupied by females (Fig. 4). In addition, after a certain number of males has been exceeded, the number of occupied colonies ceases to vary or attains an almost constant value. The above relations show that after exceeding a certain threshold of numbers of males further colonies are set up chiefly by females. Using the *F* test significant differences

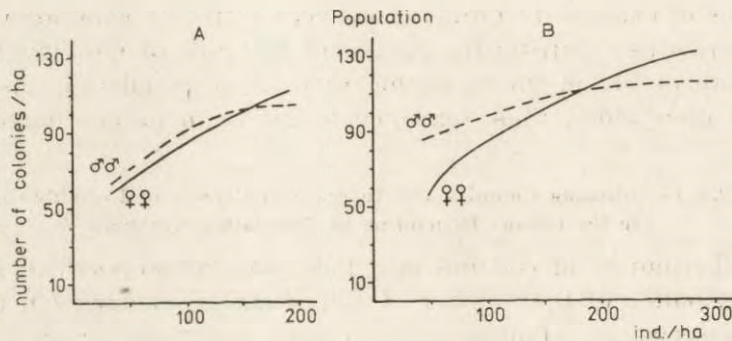


Fig. 4. Relation between population numbers and number of colonies occupied.

Population A: ♀♀  $-y=40.5563+0.5088x-0.0007x^2$ ,  $R=0.7118$

♂♂  $-y=38.9323+0.7229x-0.0020x^2$ ,  $R=0.4864$

Population B: ♀♀  $-y=35.2151+0.5445x-0.0007x^2$ ,  $R=0.6877$

♂♂  $-y=74.0828+0.2946x-0.0005x^2$ ,  $R=0.2688$

were, however, found between the course taken by regression curves only in population B ( $0.05 > P > 0.01$ ), while differences in population A were not significant, although they tended in the same direction. In population B the coefficient of curvilinear correlation between the number of colonies occupied and numbers of individuals is significantly higher for females than for males ( $P=0.05$ ).

Together with an increase in population numbers, not only the number of occupied colonies increased but also the average number of individuals in these colonies (Fig. 5). This is a straight-line regressions relation. The fact that the course of straight line regressions are not parallel for females and males indicates a greater increase in the average number of females than males in an occupied colony, with increase in numbers of individuals (Fig. 5). This difference is significant ( $0.05 > P > 0.01$ ) for population B, but not significant for population A.

With an increase in numbers, the increase in the number of occupied colonies may be due to occupation of empty colonies or setting up new colonies by recruits (the individuals caught for the first time), or previously-recruited individuals.

Recruits may in turn:

- participate in setting up new colonies
- occupy empty colonies
- occupy frequented colonies.

It was found on the basis of places in which first captures were made that percentage of recruits setting up colonies does not exceed 10%,

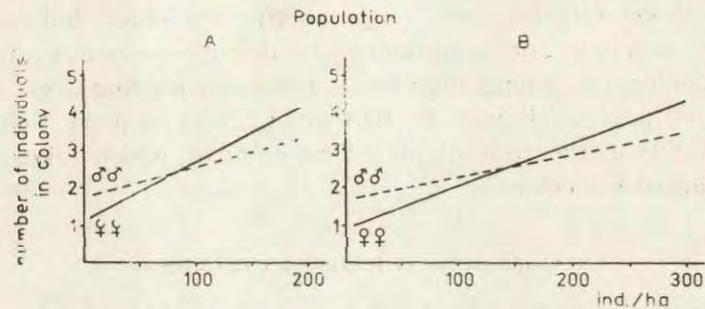


Fig. 5. Relation between population numbers and number of individuals in an occupied colony.

Population A: ♀♀  $-y=0.0151x+1.130$ ,  $r=0.7957$   
 ♂♂  $-y=0.0080x+1.742$ ,  $r=0.4530$   
 Population B: ♀♀  $-y=0.0112x+0.8837$ ,  $r=0.8464$   
 ♂♂  $-y=0.0061x+1.6300$ ,  $r=0.6320$

and therefore more than 90% of these individuals settled in frequented colonies. At the same time the percentage of recruit females setting up colonies in field A was significantly higher (4.69%) than the percentage of males (2.89%), with probability of  $0.05 > P > 0.01$ . In field B, however, these differences were not significant. The sex ratio was not found to affect the above differences in the case of newly-recruited individuals. Since simultaneously the number of colonies occupied by females increased more with increase in their numbers it may be assumed that the initiating role in setting up colonies is played by females.

Calculation was also made of what percentage among newly-established colonies and re-occupied colonies during the whole study period was formed by colonies set up by recruits. Participation in setting up colonies was evaluated on the basis of captures of individuals in new-established and newly-occupied colonies. When both recruits and older individuals were caught in the same colony, it was taken that such a colony was set up or occupied by both groups of individuals. In this case also the percentage of females was greater than that of males:

- in field A — ♀♀ — 27.38%, ♂♂ — 13.69% (N=168)
- in field B — ♀♀ — 20.56%, ♂♂ — 18.76% (N=386)

The value of these percentages shows that the majority of the colonies (about 70—80%) were set up by older individuals (previously marked). This may perhaps have been due to the greater percentage formed by previously-marked individuals in the population (on an average over 60%).

To sum it may be stated that population increase causes on the one hand establishment of colonies, understood both as settlement of empty colonies and establishing new ones, chiefly by older individuals — particularly females, and simultaneously density increases in already existing colonies, the young individuals (recruits) playing a greater part in this second process. It may be that newly-recruits leave their native colonies later than the time of their first capture, which takes place at the age of about 6 weeks.

#### 3.4. Composition of Individuals in Colonies

Using a suitable modified calendar of captures (A n d r z e j e w s k i, 1969), for each trapping site, that is, colonies of burrows, an estimate of the number of individuals caught on this site during two-month time intervals in the study period was made. This number fluctuated from zero to over twenty individuals. The numbers of individuals from trapping sites with the same number of individuals was next totalled, obtaining in this way the distribution of number of individuals caught on trapping sites with a given number of individuals of 2, 3, 4, ... n, with division into males and females and into different generations. Individuals marked during the last two months were taken as the youngest generation, individuals marked during the two preceding months as the middle generation and the remaining individuals as the oldest generation.

The range of distribution, that is, differentiation of colonies in respect of size (number of individuals occupying and/or visiting a colony) and also differentiation of the percentage of different categories of individuals (sex, generation) varied with the seasons. Particularly sharply-defined differences were found between the winter-spring period and summer-autumn period. In winter there is less differentiation and small colonies predominate. At the same time the oldest individuals form the majority in colonies. In summer the range of variation is greater, and the number of medium size colonies is largest, while colonies with high or low numbers are in the minority (Fig. 6). Sex and age structure of the colonies does not vary proportionately to their size.

In order to ascertain whether colonies with a small or large number of individuals differ in respect of the composition of their individuals,

distribution of numbers of individuals in colonies was divided into two-month time intervals, in the way closest to the median, *i.e.* into two parts as equal as possible (in respect of the total number of individuals

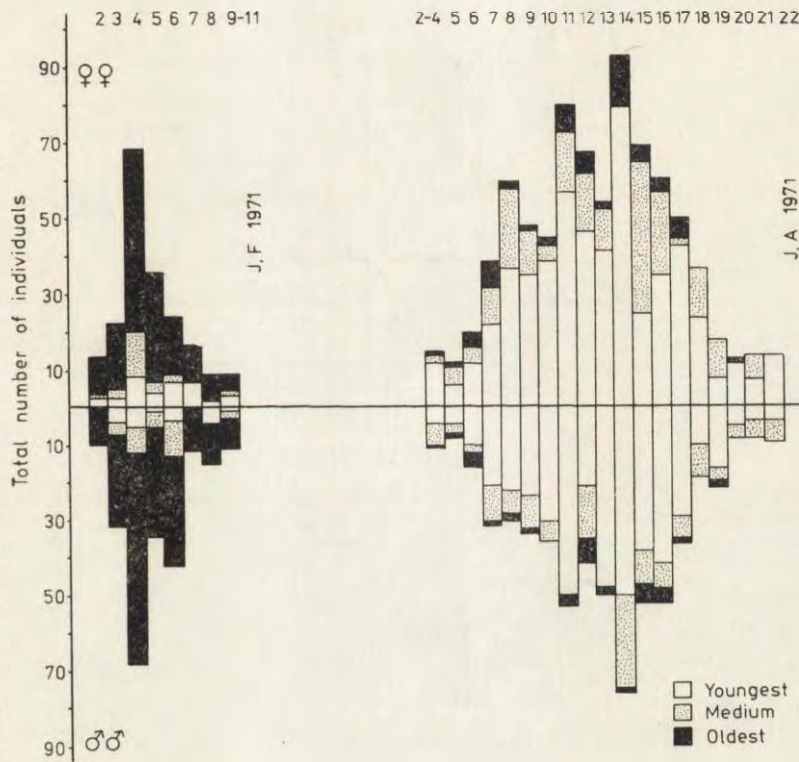


Fig. 6. Composition of individuals in colonies in selected periods of the year in population B.

Figures above the bars show numbers of individuals in colonies. The height of the bars indicate the number of animals caught.

caught in colonies) (Fig. 7). No significant differences were found between the percentage of females and males in small colonies (below the median) and large colonies (above the median). Analysis of the percentage of different generations in these two groups showed that in the majority of periods in large colonies (above the median) the percentage of youngest individuals (recruits), in comparison with the other generations, was greater than in small colonies (below the median). The greater percentage of young individuals was connected in certain periods with the smaller percentage of the oldest individuals, and in other periods with the decreased participation of individuals in the middle age

group. Statistically significant differences in the percentage of the youngest individuals occurred in both populations in spring (in March-April) in both years. In population A, characterized by lower numbers

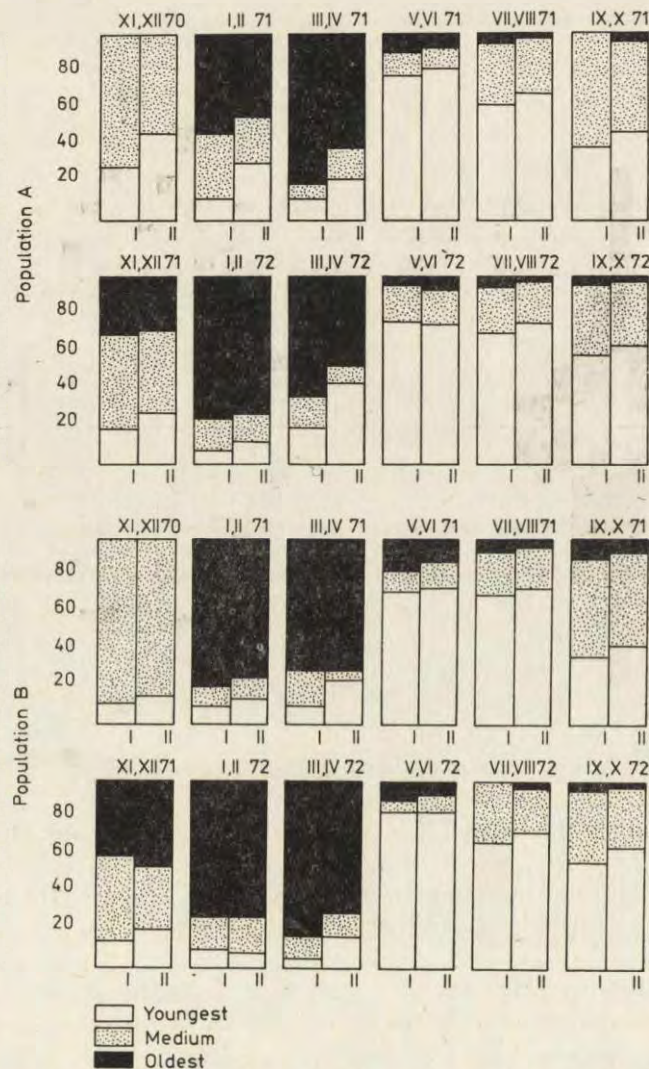


Fig. 7. Composition of individuals in colonies with low (I) and high numbers (II). Symbols as for Fig. 6.

than in population B (Fig. 2), significant differences occurred more often during the winter-spring period, while in population B this occurred during the summer-autumn period.

The higher percentage of young individuals in large colonies may

be connected with the tendency to form groups, resulting from those individuals remaining in their native colonies, and also in the greater mutual tolerance of individuals in these colonies and hence the easier acceptance of new individuals into large colonies.

### 3.5. Exchange of Individuals in Colonies

#### 3.5.1. Index of Spatial Penetration of Individuals

Analysis of successive captures of marked individuals from May to October 1971 in population B showed that common voles visit many colonies during the course of their lives (Mackin-Rogalska, 1975). Differences were found in the number of colonies visited between females and males and between individuals born in spring, summer and autumn.

If the combined sum of all individuals caught on all trapping sites is divided by the number of all individuals in the population caught

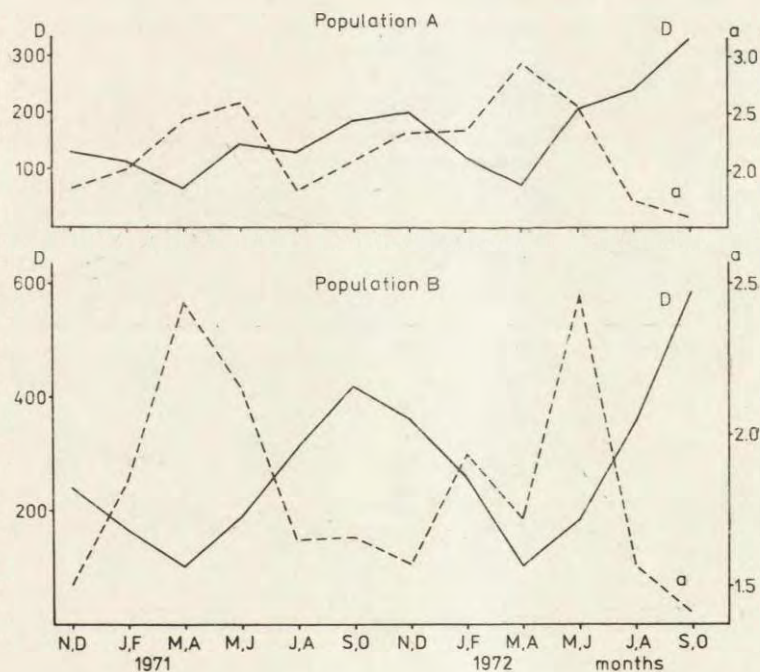


Fig. 8. Index of penetration (a) and population density (D).

in successive two-month periods of time, we obtain the average number of colonies visited by an average individual. This number can form an indication of the penetration by common voles of the study area and also an idea of the degree of exchange of individuals between colonies.

The index of penetration, calculated in the way described above, increases in population *A* from November-December 1970 to May-June 1971, then falls in July-August, to rise again up to March-April 1972, after which it again falls (Fig. 8). In population *B* the average number of colonies visited increases up to March-April 1971, and decreases until the autumn, rising from November-December to reach a peak in May-June 1972 (Fig. 8). In population *A* the peak value of the index of penetration occurred in May-June during the first study year, and in March-April during the second year, *i.e.* at the time of lowest numbers in that year. The opposite was the case in population *B*, where the peak took place in March-April, occurring during the first study year when numbers were lowest, and in May-June in the second year. Simultaneously these peak values in population *B*, in both years, fail to differ from each other ( $a=2.46$ ), while individuals in population *A* exhibited a slightly higher degree of peak penetration during the second study year ( $a=2.94$ ) than in the first ( $a=2.59$ ).

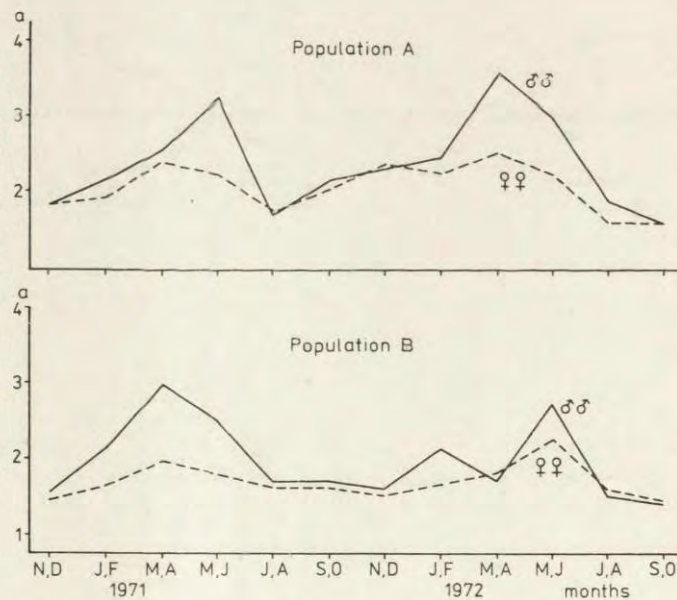


Fig. 9. Changes in the index of penetration of males and females in population *A* and *B*.

Calculation was made in a similar way of the index of penetration of the area separately for females and males, and for the young animals (recruits) and the remainder. In both populations males exhibited significantly higher average number ( $0.05 > P > 0.01$ ) of colonies visited



than females (as was found by the Student *t* test method for combined variables) (Fig. 9). These differences were slight during the autumn period but considerable differences occurred in May-June 1971, March-April and May-June 1972 in population *A*, and in population *B* in March-April, May-June 1971, in January-February and May-June 1972. During periods with the greatest difference in penetration a male visited on an average one more colony than females.

In both years and populations the older individuals visited significantly more colonies ( $0.05 > P > 0.01$ ) than recruits in successive two-month periods (Fig. 10). Differences between young and old individuals

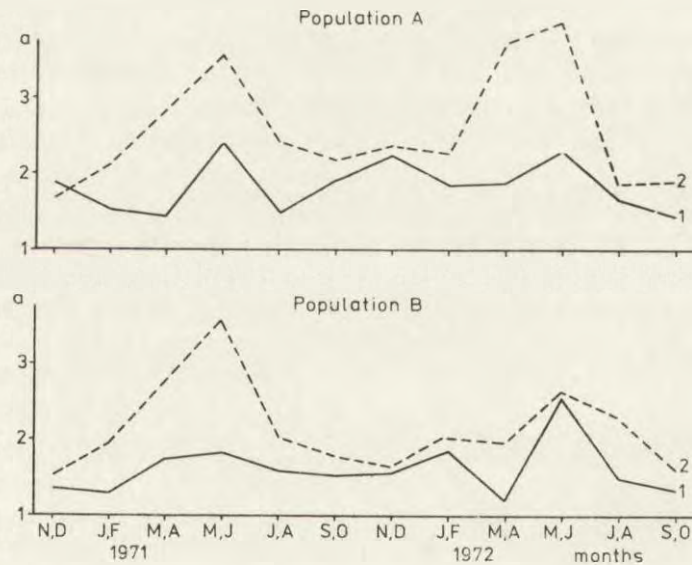


Fig. 10. Changes in the index of penetration of newly-marked individuals (1) and older individuals (2) in population *A* and *B*.

were also greater in the second study year in field *A*, but during the first year in field *B*.

Greater differentiation of individuals in the population in respect of spatial penetration occurred in both populations during the year preceding maximum numbers (in population *A* — 1972, in population *B* — 1971) in the long-term cycle of these populations. A high coefficient of penetration points to intensive exchange of individuals in the colonies and to intensive contacts taking place between individuals from different colonies, and hence to the very labile nature of their composition.

### 3.2.5. Degree of Attachment to Colonies ( $h/m$ ) during Periods of Low and High Spatial Penetration

Not only the spatial penetration of individuals in a population but also their attachment to a given colony, or conversely, intensity of changing colonies during the course of successive captures, affect exchange of individuals in the colonies.

Examination was made of the degree of attachment individuals to a colony in two chosen periods: when penetration was either low or high in both population *i.e.* in November-December 1970 and May-June 1971. For this purpose calculation was made of the ratio of individuals caught in the same colony to the number of individuals caught in another colony for successive pairs of captures (1—2, 2—3, 3—4, ... *etc.*) of different groups of individuals. If the given capture (beginning with the second) was in the same colony, it was defined as  $h$ , if in a different one — as  $m$ . Calculation was next made of the average ratio of  $h/m$  for all pairs of captures (since no regular changes in it with a definite trend were found as successive captures of individuals took place). The higher the ratio of  $h/m$  calculated in this way, the greater the degree of individuals' attachment to given places (Petrušewicz & Andrzejewski, 1962; Reimov *et al.*, 1968), or the greater the constancy of home ranges (Chełkowska, 1978). Conversely, the lower  $h/m$ , the smaller the degree of attachment to the colony and hence the more frequent the moves to other colonies and the greater the spatial penetration.

The coefficient  $h/m$  was higher in autumn (November-December) than in summer (May-June) (Table 2). These differences (examined by the Student  $t$  test) were statistically significant. It may be concluded from the higher value of  $h/m$  in females than in males during the summer that females are more attached to one place. In the autumn, however, the  $h/m$  ratio is similar in both males and females (no statistically significant differences were found). At the same time differences in the degree of attachment to colonies in summer and autumn are greater for males than for females (statistically significant).

Ratio of  $h/m$  was calculated also for recruits (youngest) and the remainder (older) during these same periods. Differences between values of indexes for both groups of individuals were slight and not statistically significant, either in summer or autumn. Similarly for the whole population and in the two sexes separately the index  $h/m$  in both young and old individuals is significantly greater in autumn (Table 2).

The differences discussed in the tendency to use of several colonies ( $h/m$ ), or its converse, that is, the degree of attachment to colonies, are in agreement with differences in the average number of colonies visited

(coefficient of penetration) during the same periods, and particularly in summer. Conclusions may therefore be reached on the basis of a high index of penetration during summer, as to intensive exchange of individuals in colonies and contacts between individuals from different

Table 2

Degree of attachment of common vole to colony (*h/m*) in summer and autumn.

| Period of time  | ♀ ♀ + ♂ ♂ | Recruits | Older | <i>P</i> | ♀ ♀   | ♂ ♂   | <i>P</i> |
|-----------------|-----------|----------|-------|----------|-------|-------|----------|
| Population A    |           |          |       |          |       |       |          |
| Nov., Dec. 1970 | 0.881     | 0.790    | 0.934 | NS       | 0.894 | 0.934 | NS       |
| May, June 1971  | 0.514     | 0.449    | 0.429 | NS       | 0.611 | 0.312 | 0.01     |
| <i>P</i>        | 0.01      | 0.05     | 0.001 |          | 0.01  | 0.001 |          |
| Population B    |           |          |       |          |       |       |          |
| Nov., Dec. 1970 | 1.120     | 1.377    | 1.110 | NS       | 0.978 | 1.130 | NS       |
| May, June 1971  | 0.475     | 0.493    | 0.393 | NS       | 0.670 | 0.326 | 0.01     |
| <i>P</i>        | 0.001     | 0.01     | 0.001 |          | NS    | 0.001 |          |

*P* — level of statistical significance of differences tested by Student *t* test; NS — nonsignificant

colonies during this period. The spatial penetration of common voles examined in this paper and the intensity of their movements over the area in successive captures, and also the very small number of individuals constantly making use of one colony (Mackin-Rogalska, 1975), confirm the assumption that the composition of individuals in colony is labile.

#### 4. DISCUSSION

The elements examined of the spatial organization of a population of common voles, providing evidence that the individuals composing the population wander over an area which covers the area of several colonies, give rise to some doubt as to exactly what is meant by the term colony.

In literature so far published the concept of a colony is used to mean two things. In the case of the common vole term colony is used to mean a more or less complex system of burrows connected with each other by a network of paths (Karaseva, 1957; Bashenina, 1962; Ružic, 1967; Poljakov, 1968). Such a colony is inhabited by one or several females with their young (Frank, 1954). Similarly constructed systems of burrows with a nest of *Reithrodontomys* sp. (Naumow, 1954; Kulik, 1955; Karaseva, 1957; Lobacev, 1967) and *Ochotona* sp. (Darskaja, 1957) are termed colonies. The concept of a colony, by which is meant a group of burrows as distinct

from other analogical groups of burrows and single burrows in the case of forest rodents is also encountered (Opuszyński & Trojan, 1963).

On the other hand, under agrocenosis conditions, particularly in alfalfa crops, when the density of the common voles is high (more than 150<sup>00</sup> individuals per 1 hectare), colonies are often connected with each other and it is then impossible to distinguish separate colonies (Adamczewska-Andrzejewska, 1974). Similarly connected colonies were found by Ružic (1967) in pastures several years old. In habitats which are not typical of the common vole this animal does not form colonies (Nikitina *et al.*, 1972).

The concept of a colony also means a group of animals, often very closely connected with each other and sharply divided from population units of a different type from them. Such colonies are found in marmots and other species of rodents living in colonies (Formozov, 1948; Armitage, 1962, 1973, 1975). »Compact colonies« in *Clethrionomys rufocanus* (Kalela, 1957) in turn form examples of application of the concept of colonies of animal to non-colonising species.

In the present study typically isolated systems (colonies) of burrows were found to occur. Despite the isolation of colonies of burrows, no isolation was observed between groups of individuals caught on different trapping sites corresponding to the colonies.

The spatial activity of individuals measured by the average number of colonies visited was from about 1.5 to 3—4 colonies (Figs. 8, 9). Males exhibited a particularly high degree of penetration in comparison with females, and older individuals in comparison with newly-recruited individuals. The above index of penetration and the tendency to change colonies during the course of successive captures was expressed by the ratio  $h/m$  (Table 2), which makes it possible to reach conclusions as to contacts between individuals from different colonies of burrows and as to the exchange taking place between some of the individuals in colonies. The composition of individuals in colonies is therefore variable on account of the exchange between individuals due to their spatial penetration and the demographic rotation of the population, examined for the same common vole populations by Adamczewska-Andrzejewska & Nabagło (1977).

Differentiation found between individuals in respect of penetration, depending on sex and age, resulted in the composition of individuals visiting different colonies of burrows failing to constitute a simple reflection of sex and age structure but being, as it were, modified by this differing degree of spatial activity. The labile structure of the composition of individuals in colonies, owing to their lack of close attachment to these colonies (Mackin-Rogalska, 1975), makes it difficult to

define this composition accurately. The numbers of individuals in colonies in successive periods of time describe the differentiations of colonies of burrows in respect of extent and degree of penetration of the colony area by the individuals. It is possible that some of these individuals inhabited a given colony. These numbers varied from zero to over twenty individuals. It is thus not a group closely connected in time and space, and consequently it is difficult to term the group of individuals which within a given time visited a given colony of burrows a »colony«, since these are not strictly isolated groups. It would even seem that with intensive penetration there may be persistence of the composition of individuals between colonies of burrows over the whole field. Individuals linking colonies of burrows would thus be chiefly exchanging individuals, *i.e.* animals with a high penetration index (possible potential migrants) and individuals only visiting neighbouring colonies from time to time. According to Opuszyński & Trojan (1963), contacts between forest rodents from different colonies of burrows take place in two ways, *i.e.* by means of contacts between individual attached to the colonies and their immediate neighbours, and also by means of what are known as ubiquitous individuals contacting rodents from a large number of burrows, even those at some distance away.

It may be concluded, on the basis of the periodically occurring tendency of individuals in the population to form groups and this particularly marked tendency in young voles, that ties between neighbouring colonies are not uniformly strong. Thus a colony of common voles is perhaps a group of individuals from several systems (colonies) of burrows connected with each other not necessarily as the result of direct contacts (by touch or sight), but more by a wealth of acoustic or chemical information carried out or left in the area by individuals (Sewell, 1967; Ropartz, 1968; Anderson, 1970; Stoddart *et al.*, 1975).

It is next necessary to consider what is the biological sense of the common voles building colonies of burrows, unlike the single burrows of forest rodents. It may be that this is a form of transformation and differentiation of a homogeneous habitat of cultivated fields in comparison with the rich and varied forest habitat. In addition a system of burrows in a habitat exposed for a long period of time provides greater safety and makes it easier to escape from predators. It is for this reason that burrow systems are more greatly developed during the periods when plant cover is low (Kraseva, 1957).

Thus, if the term colony is to be applied, it is necessary to define exactly what we understand by this term. In the case of the common

vole this concept should be limited more to colonies of burrows. Individuals inhabiting a colony of burrows and penetrating its area can hardly be termed a colony of animals (voles). It may be that a separate term should be introduced (e.g. »co-users«) to define animals using colonies of burrows.

The formation of a colony of burrows leads, as their density increased, to even distribution of colonies over the study fields (Fig. 1). The evenness of distribution, pointing to the effect of competition or antagonism in animals, manifested in territorialism (Cole, 1946; Dice, 1952; Gerard, 1970), provides grounds for concluding that relations of this type exist between individuals setting up colonies of burrows. Bernstein (1974) drew the conclusion that old colonies have a negative effect on formation of new colonies, from the fact of even distribution of ant colonies. It may be assumed from the fact that even distribution of colonies of burrows occurred a year earlier in field *B* than in field *A*, that effects of this type were stronger in population *B*. The time at which they take place may therefore occur at different times during the population's development.

Some elements of territorialism in the common vole, according to many authors, occur in females during the reproduction period (Frank, 1954; Naumov, 1956; Reichstein, 1960). This is a characteristic feature of other rodent species (Kalela, 1957; Bujalska, 1973). A second factor, in addition to territorialism, ensuring isolation and even distribution of colonies of burrows, may be the fact that they are occupied by many successive generations which, according to Naumov (1954), ensures their persistence in time. Even colonies deserted for a certain period were re-occupied by individuals. Repeat occupation of old colonies has also been found by Karaseva (1957), Bashenina (1962) and Ružic (1967). Evenly distributed isolated colonies of burrows are not uniformly penetrated by individuals, as is shown by the periodical tendency to gather in groups in both populations (Fig. 3), and also the tendency to congregate exhibited by the youngest individuals.

Establishment of new colonies and occupation of deserted colonies take place in proportion to population numbers. As numbers increase the number of occupied colonies, that is those used by individuals, increases asymptotically, *i.e.* it tends to reach a certain constant degree of density (Fig. 4). The asymptotic character of regression curves in both populations is particularly strongly expressed in the case of males, which may mean that after certain numbers are reached, it is chiefly females which take part in further establishment of new, and in occupation of deserted, colonies. Confirmation of this hypothesis is provided

by the significantly higher participation in this process of newly-recruited females than males. The above data point to the role of females as initiators in forming colonies. Also, according to Kratochvíl *et al.* (1959), females set up new colonies or construct new burrows as additions to old colonies, while their progeny usually remains in the old colony. Development of colonies by digging new burrows was found in the study fields when population numbers were high (Liró, 1974).

The question therefore arises as to what the number of colonies would be with the very high densities encountered under natural conditions, *e.g.* 1,500 individuals per 1 ha, in which case Adamczewska-Andrzejewska (1974) considers that colonies are connected with each other. Do all colonies become connected by means of new colonies continually being formed, or are the final number of colonies formed earlier and further development (enlargement) of the burrow system leads to their connection? Judging by the even distribution of colonies of burrows, interactions presumably occur between the individuals making use of them which prevent connection and cause isolation of colonies. It would therefore appear that development of already existing colonies of burrows is responsible to a greater degree for their becoming connected when population densities are very high.

Many of the elements of a population's spatial organization depend on its numbers, *e.g.* the size of home ranges and the degree to which they overlap (Andrzejewski, 1967; Mazurkiewicz, 1971; Andrzejewski & Mazurkiewicz, 1976). In the present study a positive relation was found between the number of occupied colonies, and also density of individuals in a colony, and the populations numbers of voles, but absence of a relation between numbers and the degree to which the population congregated. The spatial activity of voles measured by the average number of colonies visited exhibited the reverse changes over the yearly cycle to changes in population numbers. Greatest penetration of the area was observed during the spring-summer period, but in autumn (September-October), *i.e.* during the period of greatest numbers, it was far lower (Fig. 8). This would thus point to a negative relation between numbers and activity.

The differences found in spatial penetration between males and females and between age groups contribute to differentiation in the size of home ranges (Naumov, 1956; Reichstein, 1960; Spitz, 1964; Dub, 1969). Particularly great differences between males and females during the reproduction period are probably connected with the participation of females in reproduction, since gestating and lactating females do not move far away from their burrows (Karaseva, 1957) and their home ranges are small in comparison with those of sexually

inactive females (Mackin-Rogalska, 1975). On the other hand, males taking part in reproduction with several females penetrate, according to Kratochvíl *et al.* (1959), over the area of several colonies, hence the range of male embraces the home ranges of several females (Karaseva, 1955). The greater degree of penetration and of changing colonies ( $h/m$ ) found in these studies may also point to the greater migratory tendency of males (Naumov, 1956).

Differences in spatial penetration between recruits and older individuals are due to their different age. Mazurkiewicz (1971) found in relation to *Clethrionomys glareolus* (Schreber, 1780) that the home range of individuals which entered the population early in the yearly cycle was more extensive.

Spatial differentiation was not uniform in the two study years in the above groups of individuals. Particularly great differences occurred in population B. In 1972 differences in the average number of colonies visited between males and females and between young and older individuals were far smaller than in the preceding year. This was due to reduced spatial penetration by males and older individuals, and greater penetration by females and young individuals, than in the preceding year. It is difficult to find an explanation for this type of change in the spatial structure of the population, consisting in levelling up differences between individuals, since the basic feature of population organization is the difference in the importance of its elements (Petrusewicz, 1965). It may be that the change in spatial organization, pointing to disturbance of intrapopulation relations, caused the occurrence of a greater degree of maximum density in the longer-term cycle of this population. Changes in intrapopulation relations affect the numbers of voles and *vice versa*, but gradation years, in comparison with other phases of population dynamics, are characterized even by disturbances of these relations, that is, of population organization (Wojciechowska, 1969). The phenomenon of disappearance of differences between different categories of individuals (changes in spatial structure was not found in population A, but maximum density was not reached in population A until 1973) (Adamczewska-Andrzejewska & Nabağło, 1977). The year preceding maximum numbers in the long-term cycle (1971 — in population B, 1972 — in population A) was characterized by great differentiation of individuals in respect of the size of area penetrated, particularly in spring (March-April). This may have been caused by the relatively high percentage of potential migrants in the population, since a high degree of migratory tendency is a characteristic feature of a common vole population the year before gradation (Wojciechowska, 1969).



The parameters of spatial organization described here for a common vole population were examined in an enclosed population (isolated), *i.e.* where migration was impossible which, in accordance with literature on this subject, may lead to the occurrence of higher densities (Petrusewicz & Trojan, 1963; Petrusewicz, 1963; Petrusewicz *et. al.*, 1963; Krebs *et al.*, 1969). Isolated populations are deprived of one of their regulating mechanisms of emigration (Lidicker, 1973). Mortality, the only factor (apart from reduction in reproduction) reducing numbers under natural conditions, may be replaced by dispersion (Myers, 1974). Populations living in open cultivated fields are however also to some extent isolated by the vicinity of species of crops not used by common voles, by roads and shelter belts, but this is a far less strict isolation than in the case of the study populations. It would appear useful to carry out studies on the spatial structure of common vole populations under conditions of open cultivated fields, particularly from the aspect of the relation between the vole's migrations between crops and the change in the spatial organization of populations supplying migrants.

**Acknowledgements:** My sincere thanks are due to Dr. R. Andrzejewski for his supervision of subject matter during the course of these studies and for his assistance during the writing of this paper; Professor K. Petrusewicz, Dr. K. Andrzejewska, Dr. J. Gliwicz, Mgr L. Nabagło, Dr. W. Walkowa-Kotowa and Dr E. Rajska-Jurgiel for their searching evaluation and critical observations which were of great help to me during correction of the text.

#### REFERENCES

1. Adamczewska-Andrzejewska K. A., 1974: Prognozowanie zmian zagęszczenia nornika polnego (*Microtus arvalis* Pall.) w oparciu o pogłębioną analizę populacji. Biul. IOR, 57: 393—400.
2. Adamczewska-Andrzejewska K. A. & Nabagło L., 1977: Demographic parameters and variations in numbers of the common vole. Acta theriol., 22: 431—457.
3. Anderson P. K., 1970: Ecological structure and gene flow in small mammals. Symp. zool. Soc. Lond., 26: 299—325.
4. Andrzejewski R., 1967: An attempt at empirical verification of the relation between density and average coverage of the home range and their values. Ekol. pol., A, 15: 743—753.
5. Andrzejewski R., 1969: Analiza wyników połowów drobnych ssaków metodą „Kalendarza złowień”. Zesz. Nauk. IE PAN, 2: 1—104.
6. Andrzejewski R. & Gliwicz J., 1969: Standard method of density estimation of *Microtus arvalis* (Pallas 1779) for the investigation on its productivity. Small. Mammal. Newslett. 3: 45—53.
7. Andrzejewski R. & Głogowska J., 1962: The influence of the layout of traps and length of time for which they remain set on the distribution of capture of small rodents. Ekol. pol., A, 10: 285—295.

8. Andrzejewski R. & Mazurkiewicz M., 1976: Abundance of food supply and size of the bank voles home range. *Acta theriol.*, 21: 237—253.
9. Armitage K. B., 1962: Social behaviour of a colony of the yellow bellied marmot (*Marmota flaviventris*). *Anim. Behaviour*, 10: 319—331.
10. Armitage K. B., 1973: Population changes and social behaviour following colonization by the yellow bellied marmot. *J. Mammal.*, 54: 842—853.
11. Armitage K. B., 1975: Social behaviour and population dynamics of marmots. *Oikos*, 26: 341—354.
12. Bashenina N. V., 1962: Ekologia obyknovennoi polevki, nekotorye čerty ej geografičeskoj izmenčivosti. *Izd. Mosk. Univ.*: 1—309. Moskva.
13. Bernstein R. A., 1974: Seasonal food abundance and foraging activity in some desert ants. *Amer. Natur.*, 108: 490—498.
14. Bujalska G., 1973: The role of spacing behaviour among females in the regulation of reproduction in the bank vole. *J. Reprod. Fert., Suppl.*, 19: 465—474.
15. Calhoun J. B., 1963: The ecology and sociology of the Norway rat. *Publ. Hlth. Serv. Publ. Wash.* 1008: 1—288.
16. Chełkowska H., 1978: Variations in numbers and social factors in a population of field voles. *Acta theriol.*, 23, 11: 213—238.
17. Cole L. C., 1946: A theory for analysing contagiously distributed populations. *Ecology*, 27: 329—341.
18. Darskaja N. T., 1957: Blohi daurskoi piščuhi. *Fauna i ekol. gryz.*, 5: 163—169.
19. Dice L. R., 1952: Measure of spacing between individuals within a population. *Contr. Lab. Vert. Biol. Univ. Mich.*, 55: 1—23.
20. Dombrovskij V. V., 1971: Zakonomernosti kolebania čislennosti obyknovennoi polevki v Moskovskoi oblasti v sviazi s landšaftnymi osobnostiami territorii i hoziaistvennoi dejatel'nostju čeloveka. *Fauna i ekol. gryz.*, 10: 199—215.
21. Dub M., 1969: Movements of *Microtus arvalis* Pall. and a method of estimating its numbers. *Zool. listy*, 20: 1—15.
22. Fenjuk B. K., 1941: Instinkt doma u gryzunov. *Priroda*, 3: 51—58.
23. Elton Ch., 1942: Voles, mice and lemmings. *Oxford Univ. Press*: 1—496. London.
24. Formozov A. N., 1947: Očerki ekologii myševidnyh gryzunov — nositelei tuljaremii. *Mat. po gryz.*, 7: 42—69.
25. Frank F., 1954: Die Kausalität der Nagetier-zyklen im Lichte neuer populationsdynamischer Untersuchungen an deutschen Microtinen. *Z. Morph. u. Ökol. Tiere*, 43: 321—356.
26. Gerard G., 1970: Modeles de repartition spatiale en ecologie animale. *Biometrie-Praximetric*, 11:
27. Grunwald A., 1975: Changes in trappability of common vole. *Acta theriol.*, 20: 333—341.
28. Janusko P. A., 1938: Smertnost' polevok (*Microtus arvalis*) v usloviah stepnyh raionov Predkaskazia i vlijanie na nej hiščnikov. *Zool. Ž.*, 17: 102—112.
29. Kalela V., 1957: Regulation of reproduction rate in subarctic populations of the vole *Clethrionomys rufocanus* (Sund.). *Ann. Acad. Sci. fenn. Ser. 4A (34/40)*: 1—60.
30. Karaseva E. V., 1955: Mečenie naziemnyh mlekopitajuščih v SSSR. *Biul. MOIP, Biol.*, 60: 31—42.

31. Karaseva E. V., 1957: Sezonnye i stacialnye osobennosti stroenija nor i kolonij obyknovennoi polevki srednej polosy SSSR. Mat. po gryz., Fauna i ecol. gryz., 5: 67—75.
32. Karaseva E. V., 1960: Osobennosti stacialnogo raspredelenija obyknovennoi polevki i značenie različnyh stacij v nej žizni v centralnyh oblastiah RSFSR. Fauna i ecol. gryz., 6: 27—59.
33. Karaseva E. V., 1971: Ekologičeskie osobennosti mlekopitajuščih — nositeli leptospiry grippotyphosa i ih rol v prirodnyh očagah leptospiroza. Fauna i ecol. gryz., 10: 30—144.
34. Karaseva E. V. & Kučeruk V. V., 1954: Izučenie podvižnosti obyknovennyh polevok s pomoščiu mečenia zverkov. Mat. Ecol. Konf., Tez. Dokl., 3: 80—83.
35. Kozakiewicz M., 1976: Migratory tendencies in population of bank voles and description of migrants. Acta theriol., 21: 321—338.
36. Kratochvíl J. 1959 [Ed.]: Hraboš polni, *M. arvalis* Pallas 1779. Cesk. Akad. Ved: 1—359. Praha.
37. Krebs Ch. J., Keller B. L. & Tamarin R. H., 1969: *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in Southern Indiana. Ecology, 59: 587—607.
38. Kulik I. L., 1955: Nekotorye osobennosti podvižnosti bolših peščanok v sviazi s izučeniem prirodnyh očagov infekcij. Sb. »Prirodnaja očagovost boleznej čeloveka i krajevaja epidemiologia«. Medgiz.
39. Leonteva H. N., 1969: Ispolzovanie nor bolšoj peščankoi i ej dinamičeskaja plotnost. Zool. Ž., 48: 414—425.
40. Lidicker W. Z., 1973: Regulation of numbers in an island population of the California vole, a problems in community dynamics. Ecol. Monogr., 43: 271—302.
41. Liro A., 1974: Removal of burrows by the common vole as the indicator of its numbers. Acta theriol., 19: 259—272.
42. Lobacev V. S., 1967: Osobennosti ispolzovania nor-kolonij bolšimi peščankami. Biul. MOIP., Biol., 72: 21—27.
43. Mackin-Rogalska R., 1975: Attachment of the field vole to its colony. Bull. Pol. Acad. Sci., Cl. II, 12: 813—821.
44. Mazurkiewicz M., 1971: Shape, size and distribution of home ranges of *Clethrionomys glareolus* (Schreber 1780). Acta theriol., 16: 23—60.
45. Myers J. H., 1974: Genetic and social structure of feral house mouse populations on grizzly island, California. Ecology, 55: 747—759.
46. Naumov N. P., 1951: Novyj metod izučeniija ekologii melkih lesnyh gryzunov. Fauna i ecol. gryz., 4: 3—21.
47. Naumov N. P., 1954: Tipy poselenii gryzunov i ih ekologičeskoe značenie. Zool. Ž., 33: 268—289.
48. Naumov N. P., 1956: Mečenie mlekopitajuščih i izučenie ih vnutrividovyh sviazei. Zool. Ž., 35: 3—15.
49. Nikitina N. A., Karulin N. S. & Zenkovic N. S., 1972: Sutočnaja aktivnost obyknovennoi polevki i ej territorija. Biul. MOIP, Biol., 77: 55—64.
50. Ognev S. J., 1951: Očerok ekologii mlekopitajuščih. Mat. k pozn. fauny i flory SSSR, 26, Izd. MOIP: 1—251.

51. Opuszyński K. & Trojan P., 1963: Distribution of burrows and elements of the population structure of small forest rodents. *Ekol. pol. A*, 11: 339—352.
52. Petruszewicz K., 1963: General remarks on the productivity of confined populations. *Ekol. pol. A*, 11: 617—626.
53. Petruszewicz K., 1966: Dynamics, organization and ecological structure of population. *Ekol. pol. A*, 14: 413—436.
54. Petruszewicz K. & Andrzejewski R., 1962: Natural history of free-living population of house-mouse (*Mus musculus* Linnaeus) with particular reference to grouping within the population. *Ekol. pol. A*, 10: 85—122.
55. Petruszewicz K. & Trojan P., 1963: The influence of the size of the cage on the numbers and density of a self-ranging population of white mice. *Ekol. pol. A*, 11: 611—616.
56. Petruszewicz K., Prus T. & Rudzka H., 1963: General remarks on the productivity of confined populations. Density and size of medium in populations of *Tribolium*. *Ekol. pol. A*, 11: 603—610.
57. Poliakov V. K., 1966: Vrednye gryzuny i borba s nimi. Izd. Kolos, Lenin-grad: 104—112.
58. Reichstein H., 1960: Untersuchungen zum Aktionsraum und zum Revierverhalten der Feldmaus, *Microtus arvalis* (Pall.). *Z. Säugetierk.*, 25: 150—169.
59. Reimov R., Adameczyk K., & Andrzejewski R., 1968: Some indices of the behaviour of wild and laboratory house mice in a mixed population. *Acta theriol.*, 13: 129—150.
60. Ropartz P., 1968: The relation between olfactory stimulation and aggressive behaviour in mice. *Anim. Behav.*, 16: 97—100.
61. Ružic A., 1967: Study of the effect of rodents (*Rodentia*) upon perennial artificial meadows. *Archiv Bioloskih Nauka* 19, 3—4: 147—167.
62. Sewell G. D., 1967: Ultrasound in adult rodents. *Nature, London*, 215: 512.
63. Skuratowicz W., 1949: Uwagi o pojawach gryzoni polnych w Polsce w latach 1945—1955. *Ekol. pol. B*, 3: 3—16.
64. Spitz F., 1964: Etude des densites de population de *Microtus arvalis* Pall. a Saint-Michel-in-L'Herm (Vendne). (2). *Mammalia*, 28: 40—75.
65. Stoddart D. M., Aplin R. T. & Wood M. J., 1975: Evidence for social difference in the flank organ secretion of *Arvicola terrestris*. *J. Zool., Lond.*, 177: 529—540.
66. Tarwid K., 1960: Szacowanie zbieżności nisz ekologicznych gatunków, drogą oceny prawdopodobieństwa spotkania się ich w połowach. *Ekol. pol. B*, 6: 115—130.
67. Wojciechowska B., 1969: Fluctuations in numbers and intrapopulation relation in *Microtus arvalis* (Pall.) population in agrocenoze. [In: »Energy flow through small mammal populations«, eds K. Petruszewicz L. Ryszkowski]. Państw. Wyd. Nauk.: 75—79. Warszawa.

Accepted, November 16, 1978.