

Spatial Organization of a Bank Vole Population in Years of Small or Large Numbers

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Examination was made of the effect of differences in the numbers of a free-living island population of *Clethrionomys glareolus* (Schreber, 1780), on the elements of its spatial organization. Material obtained from studies on this population during the periods from 1966-1970 and 1972-1973 was used (In the second series the food supply was increased artificially for experimental purposes). Years of low level (1967, 1969), high (1966, 1968, 1970) and very high (1972, 1973) level of numbers were found to occur. It was found that in years with large numbers of bank voles individual home ranges are smaller than in years with low numbers. Both in peak years and years with low population numbers the home ranges of males are larger than those of females, and the hierarchy of successive entries into the population of generations is maintained in respect of the size of home ranges. Tendency to clumping distribution is always observed in spring, whereas in summer and autumn distribution may be either clumping or random. A positive correlation was found between the proportion of the youngest group of individuals and tendency to clumping distribution. The average number of individuals per trapping station does not significantly differ between years of high and low numbers. In all the study years (including those with supplementary food supply) higher density of bank voles is observed on the station in the optimum habitat, in comparison with the suboptimal habitat, although the increase in the number of individuals in the latter, together with increase in population numbers, was significantly greater than in the optimum habitat.

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1. INTRODUCTION

Populations of the bank vole, *Clethrionomys glareolus* (Schreber, 1780) may attain differing maximum numbers in different years. Cyclical occurrence of large numbers is often observed. In the case of the island population analyzed in the present paper, a high level of numbers occurs every other year (Gliwicz, 1975). It is interesting to ascertain whether and to what degree spatial organization depends on population numbers and what changes take place in it in years differing in respect of numbers. A large number of authors (Merkova, 1955; Kulicke, 1962; Nikitina & Merkova, 1963; Kucera, 1968; Zejda & Pelikán, 1969), who studied populations of the bank vole, found that in years with large

numbers the home ranges are smaller than in years when small numbers occur. Similar data have obtained for other species of rodents, e.g. for *Microtus pennsylvanicus* (Blair, 1940; Liduska, 1942) or *Peromyscus leucopus* (Stickel, 1960). There are also data pointing to the effect of population density on the way in which rodents are distributed over a given area, particularly in cases of areas of a mosaic character (Bock, 1972; Gubar, 1974). Overlapping of the effect of varying factors, such as different climatic conditions and differing abundance of food supplies in different years, and also seasonal variations in population numbers and consequent differences in age, sex and reproductive structure on spatial organization (Bujalska, 1970; Mazurkiewicz, 1971; Bujalska 1975; Andrzejewski & Mazurkiewicz, 1976) make it very difficult to grasp differences in the spatial organization of a population between years of low and high level of numbers of these animals.

The purpose of the present study was to try to discover whether a different level of numbers in different years affects the elements of the spatial organization of an island population of bank voles.

2. AREA, METHODS AND MATERIAL

The basis for the analysis consisted of material obtained from studies on a population of bank voles inhabiting an island 4 hectares in extent, situated in Bełdany Lake in northern Poland (53°40' N, 21°35' E). This population has for many years formed the object of a large number of studies, the results of which relate to variations in numbers, age and sex structure, and have been used in the present study (Gliwicz *et al.*, 1968; Bujalska, 1975 and others).

The island is covered by a tree stand composed of three phytosociological associations, 23% of the area being occupied by associations of *Circaeo-Alnetum* Oberdorfer, 1953 and *Salici-Frangulatum* Malc., 1929. The habitat is a wet one, with a high content of organic substances, and is preferred by the bank vole (Wrangel, 1939; Turček 1960; Chełkowska, 1969; Bock, 1972) to the remaining 77% of the area, which is occupied by *Tilio-Carpinetum* Traczyk 1962 (Traczyk, 1965).

The material analyzed originates from studies made from 1966—1970, when the population maintained itself from the natural food supply, and from 1972—1973, when this supply was supplemented by providing oat grains.

In each study year regular 7—14 day trapping series were carried out on the island (every six weeks), during which the entire island was covered by a grid of live-traps set at 15×15 m intervals. The method used for collecting data was based on the CMR principle. During years of supplementary feeding oats were laid out on trapping stations during the periods between trapping series.

3. RESULTS

3.1. Size of the Home Range in Years of Low and High Population Numbers

The size of the home range was estimated by Wierzbowska's method (Wierzbowska, 1972), which has the advantage of making it possible to

carry out short trapping series of an individual (only two captures are needed) if the numbers of the group for which home range size is to be estimated is sufficiently large.

The size of the home range calculated for different cohorts (spring K_1 , early summer — K_2 , late summer — K_3) in all seasons in each year, was averaged for years with low (1967, 1969), high (1966, 1968, 1970) and very high numbers (1972, 1973). Population numbers are given in Table 2.

Analysis of the mean size of home range (Table 1; taking into account 6 captures of an individual) for males and females of different generations showed that the largest home ranges are those of individuals in years of low numbers, while in years with high and very high numbers they are correspondingly smaller. The decrease in the size of home ranges is greater between years of high and very high numbers (20—32.4%) than between years of low and high numbers (6.2—23.6%). The hierarchy of successive cohorts entering the population, in respect of home range size (the latter the cohort, the smaller the home ranges of its individuals), is maintained regardless of the population numbers. This is particularly clear in the case of males (Table 1).

Table 1

Average size of home range (m²) for males and females of different cohorts (K_1 — K_3 —spring, early- and late-summer) in years of different population numbers.

Cohort	Males			Females		
	low	high	very high	low	high	very high
K_1	1237.5	945.0	697.5	832.5	742.5	585.0
K_2	967.5	832.5	562.5	720.0	675.0	540.0
K_3	720.0	675.0	472.5	720.0	675.0	517.5

Differences in mean home range size for different cohorts depending on the population numbers in a given year also occur during the course of a season. Males reduce their home ranges to a greater degree when numbers increase than is the case with females. With females distinct reduction in home range size is not observed until very high numbers are reached (Fig. 1).

The effect of population density on the size of the home range was also examined by means of analysis of increase in the number of new capture sites of an individual, revealed during a given trapping series. In successive captures the number of sites revealed by the individual increases (Andrzejewski & Wierzbowska, 1970; Mackin-Rogalska, 1975). The average size of the home range calculated on this basis also increases.

It may be assumed that increase in home range size will be greater with increasing extent of the area over which the animals move, that is, their home range. On this account examination was made of increases in average home range sizes calculated on the basis of 2 and 6 successive captures. Increase was calculated in percentages, taking home range size calculated for two captures as a basis (Fig. 2).

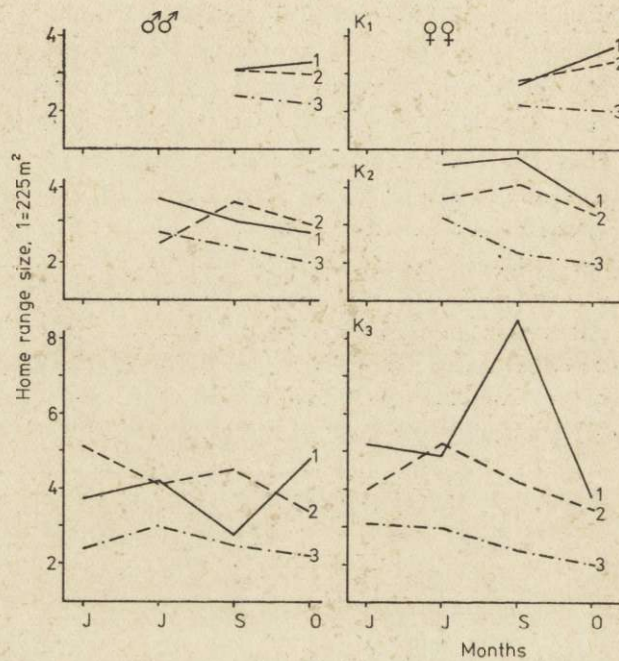


Fig. 1. Seasonal variations in average home range size for different cohorts (K_1-K_3) in years of low (1), high (2) and very high (3) numbers.

It was found that increase in home range sizes with increase in the number of captures is greatest in years of low numbers, and is correspondingly lesser in years of high and very high numbers, although these differences are not always statistically significant, (*t*-Student test used for comparisons). Thus for males, for which increase in home range size was on an average 76% with low numbers, 31.4% with high numbers and 15.9% with very high numbers, a statistically significant difference was found between years of very high numbers and years with low numbers ($p > 0.05$) and between years with high and low numbers ($0.01 < p < 0.001$). No statistically significant difference was found in the increase in home range size between years of high and very high numbers. For females increase in home range sizes was respectively 43.1%, 48.3% and 12%. A statistically significant difference

Table 2

Variations in numbers and mean population density per 1 ha for periods 1966—1970 and 1972—1973.

	1966	1967	1968	1969	1970	1972	1973
April	56	68	70	69	29	140	313
June	152	160	332	147	85	121	692
July	302	171	368	142	280	396	1066
Sept.	268	175	364	170	316	460	1076
Oct.	166	178	225	141	221	500	918
Avg. density	104.9	84.4	161.4	72.8	116.2	178.9	451.7

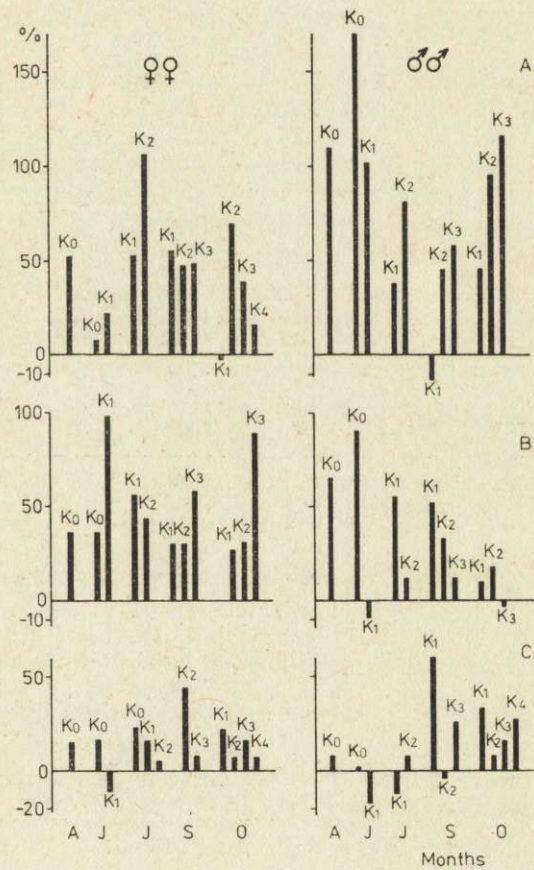


Fig. 2. Increase in average home range size of males and females of different cohorts (K_0-K_4) in different trapping series during years, of low (A), high (B) and very high (C) numbers.

was found between years of very high numbers and years with low and high numbers ($0.1 < p < 0.05$).

3.2. Description of Spatial Penetration by Individuals of a Population

A detailed analysis was made of variations in the dispersion of bank voles depending on population numbers, for three selected years varying in respect of numbers (Table 3).

Table 3

Variations in numbers of cohorts (K_0 — old adults, K_z — winter, K_1 — K_4 — spring, early- and late-summer, autumn for 1967 (low) 1966 (high) and 1972 (very high).

	K_0	K_z	K_1	K_2	K_3	K_4	N
April							
1967	68						68
1966	56						56
1972	48	92					140
June							
1967	36		124				160
1966	38		114				152
1972	21	36	64				121
July							
1967	12		92	67			171
1966	31		80	191			302
1972	16	24	33	323			396
Sept.							
1967	8		53	52	62		175
1966	6		50	167	45		268
1972	11	17	24	215	193		460
Oct.							
1967	2		36	37	33	70	178
1966	1		32	111	16	6	166
1972	6	14	20	209	162	89	500

3.2.1. Intensity of Visits to Different Trapping Stations

Distribution of captures in particular trapping station was analyzed. Attention was directed to whether intensity of visits to different trapping stations differed in years of low, high and very high numbers (Fig. 3).

It was found that the proportion of stations visited by a given number of individuals, in this case males, is similar, particularly in years of low and high numbers. In a year of very high numbers there is an increase in the proportion of stations with a number of individuals close to the average. The average number of males per trapping station is also very similar, — 11.5 ± 4.8 individuals per station when numbers are low, 11.4 ± 4.6 with high numbers and 10.1 ± 3.4 with very high numbers. In the case of females there is a shift in the distribution,

together with increase in numbers, in the direction of increase in proportion of stations with a larger number of individuals, and also increase in the average number of individuals per station: 7.6 ± 3.1 ; 9.3 ± 4.8 ; 10.5 ± 3.9 . At the same time a positive correlation was found ($p > 0.001$) between the number of females and males caught on the same trapping stations.

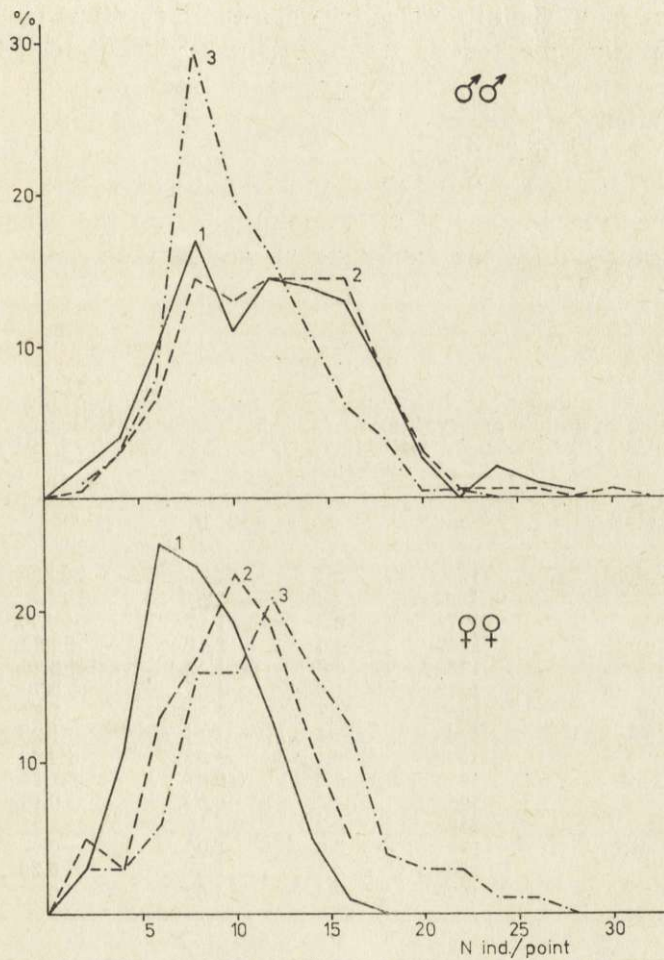


Fig. 3. Distribution of trapping stations depending on number of individuals caught on them during a year of low (1), high (2) and very high (3) numbers.

3.2.2. Spatial Distribution of Individuals in a Population

Analysis was made, of the distribution of the numbers of individuals caught in different trapping stations in successive trapping series. The type of spatial distribution of individuals in a population in a given trapping series was examined by means of the following equation:

$$V = \frac{\sigma^2}{\bar{x}}$$

where: σ^2 — variance of number of individuals caught on different
 \bar{x} — average number of individuals on station.

When the value $V=1$, distribution is random, value $V < 1$ indicates even distribution, $V > 1$ — clumped distribution.

The significance of the difference between the theoretical and empirical distributions was checked by means of the *t*-Student test, using the

following equation
$$t = \frac{V-1}{\sqrt{\frac{2}{S}}}$$

where *S* defines the number of all trapping sites on the island. Distribution significantly different from random occurs with value $t > 1.971$ (Table 4).

Table 4

Average number of individuals per trapping station (\bar{x}), values of index and values of *t*-Student test. Statistically significant differences with level of $P=0.05$ indicated by plus signs.

Month	Year	\bar{x}	<i>V</i>	<i>t</i>
April	1967	2.3	4.34	+29.30
	1966	1.4	2.61	+14.10
	1972	2.3	1.79	+6.90
June	1967	4.0	1.71	+6.20
	1966	3.8	1.42	+3.70
	1972	1.6	1.09	0.79
July	1967	4.8	0.79	1.86
	1966	7.1	1.14	1.23
	1972	5.1	1.53	+4.60
Sept.	1967	5.4	0.87	1.14
	1966	4.5	0.98	0.18
	1972	5.3	1.15	1.31
Oct.	1967	3.6	1.00	0
	1966	4.1	0.97	0.26
	1972	6.2	1.00	0

It was found that in all the study years clumped distribution of individuals in the population occurs in spring. In summer and autumn either clumped or random distribution is observed. No relation was found between the type of distribution and population numbers. The proportion of young individuals in a population affects the character of distribution of individuals in summer and autumn (Fig. 4). If comparison is made of the distribution of individuals in different years, but at analogical periods of the population's life, and with similar level

of numbers, distribution in space will be clumped when there is a large proportion of young voles (the youngest group of individuals) and random if the numbers of adult voles are similar to those of young voles (Table 3, Table 4). Other causes are responsible for the occurrence of clumped distribution in spring, when the population consists only of adult

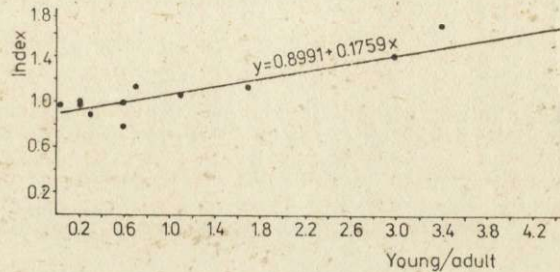


Fig. 4. Relation between index of tendency to grouping V and ratio of young to adult voles.

individuals. This is the effect of the way males move over the area, since they are characterized by large home ranges clumped (Mazurkiewicz, 1971), while females during this period exhibit tendencies to even distribution (Bujalska, 1970).

3.2.2. Effect of Population Density on Use of an Optimal and Suboptimal Habitat by Individuals

As mentioned in section 2 — 23% of the area of the island consists of a wet habitat, which is distributed in several fairly small patches surrounded by dry habitat. Black (1972) in analyzing this same population found that the bank vole prefers a damp habitat (here termed optimum) to a dry one (suboptimum). She also showed that increase in population density causes the voles to occupy the dry habitat (suboptimum), and that in years with high population numbers nearly equal use is made of the two habitats. In years of low population numbers, however, use of these two habitats depends on the habitat humidity (level of the water table and amount of rainfall). With great humidity approximately equal use is made of the habitats, but with low humidity there is a decided preference for the wet habitat.

Examination was therefore made of the relation between total population numbers and intensity of the use made of the optimal and suboptimal habitat by these bank voles. The average number of individuals per trapping station was calculated in both habitats, in successive trapping series, in years with different population numbers. An attempt was also made at estimating the intensity of the use made of the two habitats during the course of a whole year. For this purpose

the number of individuals caught in a given station during five trapping series (a whole year) was added together and the average annual number per station calculated (Table 5).

It was found that in all the years analyzed lower density was observed on the station in the suboptimal habitat, as compared with the optimal. Increase in numbers during the year causes an increase in the

Table 5

Average number of individuals per trapping station (\bar{x}) and standard deviation (S.D.) in successive trapping series and over the course of a whole year in the optimum and suboptimum habitats in different years. Average number of individuals per trapping point with highest population numbers in a given year is boldfaced.

	Optimum		Suboptimum	
	\bar{x}	S.D.	\bar{x}	S.D.
	1967 (low)			
April	3.56	2.09	1.98	1.91
June	5.68	2.38	3.60	2.64
July	5.23	2.23	4.47	2.21
Sept.	6.05	2.24	5.37	2.03
Oct.	4.48	1.59	3.28	1.92
Whole year	22.46	6.59	17.89	6.44
	1966 (high)			
April	2.08	2.41	1.32	1.72
June	3.85	2.63	3.75	2.00
July	7.46	3.32	6.93	2.82
Sept.	5.21	1.81	4.46	2.07
Oct.	4.51	1.78	3.91	1.48
Whole year	23.18	7.34	20.32	6.82
	1972 (very high)			
April	2.23	1.86	2.63	1.61
June	2.54	1.48	1.28	1.17
July	5.59	2.97	4.93	2.74
Sept.	6.31	2.83	4.86	2.32
Oct.	7.31	1.84	6.08	1.99
Whole year	23.46	6.98	19.59	5.09

average number of individuals on the trapping station in both categories of habitat. In both habitats the highest average number of individuals on a station occurs during the period when the population attains maximum numbers in a given year. It does not, however, differ significantly when years with different maximum numbers are compared. Similarly the average annual number of individuals per station is almost constant, regardless of population numbers but is different in the two habitats (usually lower in the suboptimal habitat).

In order to determine whether increase in population numbers affects the increase in number of individuals caught in the two of habitats

groups of individuals were distinguished for each trapping series in successive years, which made use either entirely or partly (where recorded at least once) of the optimal habitat, and the group of individuals using the suboptimal habitat only. Calculation was next made for each of two successive series in increase in population numbers, in accordance with the equation:

$$Z_p = \frac{N_{t+1}}{N_t}$$

and increase in number of individuals using the optimal habitat (Z_o) and suboptimal (Z_s). The relation between increase in numbers of the whole population and increase in the number of individuals in each of the habitats was then examined (Fig. 5).

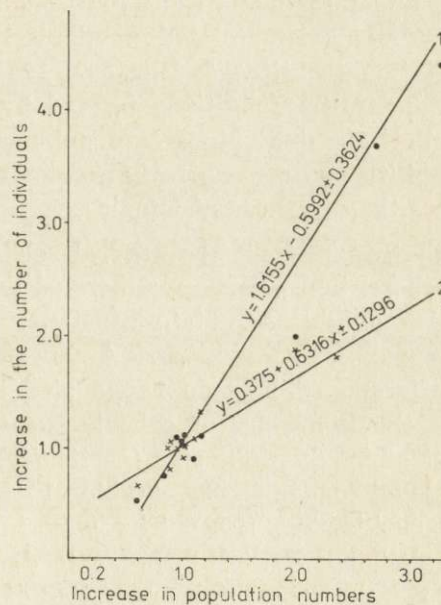


Fig. 5. Relation between increase in the number of individuals in an optimum habitat (1) and suboptimum (2) and increase in population numbers.

It was found that increase in population numbers causes a significantly greater increase in the number of individuals in a suboptimal habitat than in the optimal habitat ($p > 0.001$), even though, as shown above, density per station in this habitat is higher than in the suboptimal habitat.

4. SUMMING-UP AND DISCUSSION OF RESULTS

The results presented show that population numbers primarily affect the range of spatial activity of an individual. When numbers are high the range decreases, as is shown by reduction in the average size of home ranges (Table 1) and tendency to quicker establishment of the size of home ranges, together with increase in the number of captures of an individual (Fig. 2). The more distinct effect of the increase in numbers on the size of the home ranges of males as compared with females is remarkable (Table 1, Fig. 1). This is probably connected with the different way in which males and females made use of space. Similar data were obtained for bank voles by Zejda & Pelikán (1969), Andrzejewski & Wierzbowska (1970), Mazurkiewicz (1971), Andrzejewski & Mazurkiewicz (1976/1976). Males are distinguished by considerable mobility (Smirin, 1963; Zejda & Pelikán, 1969), consequently increasing both likelihood and frequency of contacts with females, whereas the latter exhibit low mobility and their home ranges are chiefly defined by their food requirements and are often isolated, particularly during the period of gestation and lactation (Nikitina & Merkova, 1963; Radda, 1968; Bujalska, 1970, 1973). Under the conditions formed by high numbers the chances of contact between individuals are enhanced, which causes a decline in males' mobility and consequently greater reduction in the size of males' home ranges than in those of females.

It would appear that apart from the general relation between size of home range and numbers, that a large numbers of the analyzed features of spatial organization exhibit a certain constancy, both during years of peak and of low population numbers. Amongst these features we may include the differences in home range size between males and females. In addition the hierarchy of cohorts successively entering the population in respect of home range size (particularly of males), occurs regardless of the level of numbers (Table 1, Mazurkiewicz, 1971; Andrzejewski & Mazurkiewicz, 1976). The way in which individuals of a population are distributed would appear to depend chiefly on the age structure of the population. A high proportion of the youngest group of individuals resulted in clumping distribution (Fig. 4).

Results regarding intensity of visits made to different trapping stations also deserve particular attention. It was found that the average number of individuals which »pass through« the trapping station is similar in both the optimal and suboptimal habitat, and does not significantly differ in years of low and high numbers. It was also found that despite the fact that differences between maximum numbers in different years are fairly considerable (178, 302, 500 individuals) average numbers per trap-

ping station do not differ significantly (Table 5). It seems that the stable average number of voles per station can be maintained, despite differences in numbers, only under conditions of a marked tendency to increase home range size when numbers are low, and to reduce this when numbers are high. It may be that the phenomenon of maintenance of a constant level of contacts between individuals takes place here. Limitation of spatial capacity (station) is not directly conditioned by food, as when it was experimentally supplemented this did not affect the maximum number of individuals on a station. Furthermore differences in average density per station between the optimal and suboptimal habitats are also maintained. In all the study years, both with the natural food supply and with its experimentally increased amount, higher density is observed on the station in the optimal habitat as compared with the suboptimal. The level of contacts would thus also depend on the properties of the habitat. Despite the significantly greater increase in number of individuals in the suboptimal habitat in relation to increase in the number of individuals in the optimal habitat, the values of the two habitats for these rodents do not become equal with an increase in population numbers.

In conclusion the statement may be risked that regardless of whether home range size depends directly on population numbers or on abundance of food (Mazurkiewicz, 1978), its reduction or enlargement will be limited in order to maintain a defined level of contacts between the individuals in a population.

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ORGANIZACJA PRZESTRZENNA POPULACJI NORNICY RUDEJ
W LATACH NISKIEJ I WYSOKIEJ LICZEBNOŚCI

Streszczenie

Zbadano wpływ różnego poziomu liczebności wolnożyjącej wyspowej populacji *Clethrionomys glareolus* (Schreber, 1780) na elementy jej organizacji przestrzennej. Podstawą analizy był materiał uzyskany z badań tej populacji w latach 1966—70 i 1972—73 (w drugiej serii przy eksperymentalnie zwiększonej bazie pokarmowej). Wyróżniono lata niskiej (1967, 69 r.), wysokiej (1966, 68, 70 r.) i bardzo wysokiej (1972, 73 r.) liczebności (Tabele 2, 3).

Stwierdzono, że w latach wysokiej liczebności areały osobnicze są mniejsze niż w latach niskiej liczebności (Tabela 1, Fig. 1). Natomiast zarówno w latach szczytu jak i niskiej liczebności populacji areały osobnicze samców są większe niż samic zachowuje się też hierarchia kolejnych wchodzących do populacji kohort pod względem wielkości arealów osobniczych. Sposób rozmieszczenia osobników populacji zależy przede wszystkim od struktury wiekowej (Fig. 4). Średnia liczba osobników na punkt połowu nie różni się istotnie między latami niskiej i wysokiej liczebności. Ograniczenie pojemności przestrzeni (punktu) nie jest uwarunkowane przez pokarm, gdyż eksperymentalne jego zwiększenie nie wpływało na maksymalną liczbę osobników w punkcie (Tabela 5, Fig. 3). We wszystkich badanych latach obserwuje się wyższe zagęszczenie nornic na punkt w środowisku optymalnym w porównaniu z suboptymalnym, choć wzrost liczby osobników w środowisku suboptymalnym był istotnie większy niż w optymalnym (Fig. 5).

Dyskutowane są relacje między liczebnością i pojemnością środowiska dla gryzoni a wielkością areału osobniczego i sposobem użytkowania przestrzeni przez osobniki populacji.