

The Role of Habitat Isolation in Formation of Structure and Dynamics of the Bank Vole Population

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Examination was made of variations in numbers, rate of exchange of individuals, sex structure and sexual activity, trappability and spatial organization of a local population of bank voles, *Clethrionomys glareolus* (Schreber, 1780), inhabiting an isolated patch of wooded land forming a habitat island. The results obtained were compared with analogical results for an control open population. The animals were trapped in live-traps, using the CMR method from 1977—1979 in three 10-day series in each calendar year (spring, summer, autumn). Lower density, slower rate of exchange of individuals, smaller percentage of sexually active animals and greater trappability were found in the local population as compared with the open population. A constant degree of overlapping (regardless of density) of home ranges caused by reduction in the mean size of area together with increase in density was shown to occur, whereas no such relation was found in the control population. It is assumed that habitat isolation, by means of limiting the animals' migration (chiefly immigration) causes the rate of exchange of individuals in the population to slow down, and this affects certain elements in its structure (e.g. decreased reproduction, increase in trappability, difference in spatial organization).

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1. INTRODUCTION

Populations of a large number of animal species may occur as islands, by their occupying suitable patches of biotope surrounded either by areas totally unsuitable for occupation or those only occupied periodically. The size of such local populations is limited to the size of the biotope occupied, while habitat barriers hindering dispersal of individuals may affect different elements of the structure and organization of such populations. Many authors draw attention to the important part played by dispersal in animal populations, since dispersal may affect the demographic properties of the population (e.g. age, sex, social structure etc.) and eventually may influence its stability (Gadgil, 1971; Van Valen, 1971; Lidicker, 1975; Bekoff, 1977 and others). In Tamarin's opinion (1980) dispersal is necessary to normal functioning of a population, and if inhibited may bring about a non-typical course of demographic phenomena. According to Christian (1970), the fact that individuals are unable

to emigrate from the population leads to increase in aggressive reactions between them and consequently to changes in the internal organization of the population. Chitty (1967) and after him Krebs (1978) have emphasized the strong connection between dispersal of individuals and numerous intrapopulation processes. Łomnicki (1978) maintains that in the mathematical model he described, complete stabilization of the population on a density level below the carrying capacity can be attained only if it is possible for individuals to emigrate.

Local populations (isolated by the habitat but not enclosed) would thus form a separate category differing from island populations (enclosed) and large open populations, since on the one hand the size and resources of a local biotope and also limitation of dispersal would set limits to the possibilities of population growth and would affect their organization, making it similar to the organization characteristic of enclosed populations. On the other hand the existence of the possibility for individuals to disperse from local populations might, in certain cases, constitute one of the ways of controlling numbers, as in the case of open populations.

Habitat islands and the populations occupying them have been examined by a large number of authors from the ecological aspect, but not from the aspect of the effect of habitat isolation on their organization (Culver, 1970; Vuilleumier, 1970; Brown, 1971; Brown & Kordic-Brown, 1977; Gottfried, 1979, 1982; Matthiae & Stearns 1981). The problem of populations inhabiting habitat islands on the mainland has also been discussed by MacArthur (1972) and Gliwicz (1980) without, however, stating precisely what role habitat isolation plays in formation of population structure and dynamics.

The purpose of the present paper was to attempt an ecological description of a local population of bank voles occupying an isolated patch of wooded land. By means of comparing it with an analogical population of bank voles in the open forest endeavour was made to estimate what effect habitat isolation exerts on formation of population structure and dynamics.

2. STUDY AREA, METHODS AND MATERIAL

The studies were carried out from 1977—1979 in the vicinity of Urwitak near Mikołajki (north Poland — N53°48' E21°34') simultaneously on two study areas separated from each other by a distance of about 3 km in a straight line.

The first area was 2.28 ha in extent and situated inside a large forest area of about 3000 ha, and included a part of open wooded land bordering the bank of a lake. The second area (2.43 ha in extent) consisted of a small patch of wooded land bounded on two sides by meadow, on the third side by a road running along

the shore of the lake and flooded when water level was high and on the fourth side by a sand dune with a scanty 5-year old growth of pine trees. The position off the part of wooded land examined, and also the distance of about 400 m in a straight line from the edge of the compact forest area, formed the habitat island character of the study area.

The pine wood on both study areas was similar in character from the phytosociological aspect and exhibited a considerable proportion of elements from the *Quercus-Fagetea* class. Only *Pinus silvestris* L. occurred in the tree layer, while the following species predominated in the bush layer: *Sambucus racemosa* L., *Prunus padus* L., *Sorbus aucuparia* L., *Quercus robur* L., and in the herb layer: *Dactylis glomerata* L., *Rubus idaeus* L., *Anthoxanthum odoratum* L., *Dryopteris spinulosa* Mull., *Geranium robertianum* L. and *Oxalis acetosella* L.

The animals were trapped three times each calendar year in 10-day trapping series: in spring (April), summer (July), and autumn (September-October). Trapping began in summer 1977 and ended in spring 1979 after obtaining data for two full years of study. Live-traps were used on both study areas, setting one trap on permanent sites which formed a grid 15×15 m. Oat grain was used as bait. Traps were inspected twice a day — morning and evening, while the CMR method was used for the studies.

The date, species of animal caught, its individual number, sex, sexual activity, and co-ordinates of trapping site were noted for every capture. Males with visibly enlarged gonads were taken as sexually active, as were also females with vagina open, visible signs of gestation or post-copulation plug, or lactating. Individuals caught for the first time were marked with individual numbers by means of toe-clipping. In each study season the newly-marked animals were allocated to one group, and consequently young animals born since the preceding trapping series were included in this group, and also immigrants — possibly older animals.

The values of the turnover coefficient in the population were calculated by the method proposed by Petruszewicz (1966), using the equation: $Q_T = V_T / \bar{N}_T$, where:
 Q_T — turnover coefficient of individuals during T period,
 V_T — number of different animals registered in the population during period T ,
 \bar{N}_T — mean population numbers for period T .

On account of the unequal intervals of time between successive trapping series, the mean population numbers were calculated as a weight-average in accordance with the suggestion made by Petruszewicz & Macfadyen (1970). Knowing the turnover coefficient, calculation was made of the average length of stay of an individual in the study area.

When calculating home ranges the elliptical area model proposed and elaborated by Mazurkiewicz (1969, 1970) was used, defining home ranges for those animals caught more than three times. The degree of coverage of the area by home ranges was calculated by dividing the total area of all home ranges by the size of trapping sites (after previously establishing the random localization of centres of home ranges in the study areas). With analysis of the relation between population numbers and mean size of home range and degree of coverage of the area by home ranges, the value of the linear correlation coefficient (r) was calculated. After ascertaining that it was significant (with $p=0.05$) this relation was estimated from the straight-line regression equation ($Y=aX+b$).

The Student t — test was used to calculate the statistical significance of differences between mean values (equality of variances estimated by means of the Fisher F — test), and calculation was also made of the limits of confidence for

Table 1
Number of animals caught, segregated into species.

Species	Open population	Local population
<i>Clethrionomys glareolus</i> (Schreber, 1780)	334	225
<i>Sicista betulina</i> (Pallas, 1778)	1	0
<i>Apodemus flavicollis</i> (Melchior, 1834)	41	56
<i>Apodemus agrarius</i> (Pallas, 1771)	20	25
<i>Microtus arvalis</i> (Pallas, 1779)	27	5
<i>Microtus oeconomus</i> (Pallas, 1776)	2	4
<i>Microtus agrestis</i> (Linnaeus, 1761)	66	7
<i>Mus musculus</i> (Linnaeus, 1758)	3	3
Total	494	325

mean values, also examining the statistical significance of differences between proportions (in all cases with level of significance $p < 0.05$).

During the two study years a total of 819 different individuals were caught, belonging to 8 rodent species (Table 1), but only the bank vole population, *Clethrionomys glareolus* (Schreber, 1780), was analyzed in details, that is, the species dominating in both study areas and forming a local population in the isolated patch of wooded land.

3. RESULTS

3.1. Population Dynamics and Turnover of Individuals

Density in the both studied populations of bank voles increased from spring to autumn and was constantly greater in the open population (study area 1) than in the local population (study area 2); an exception

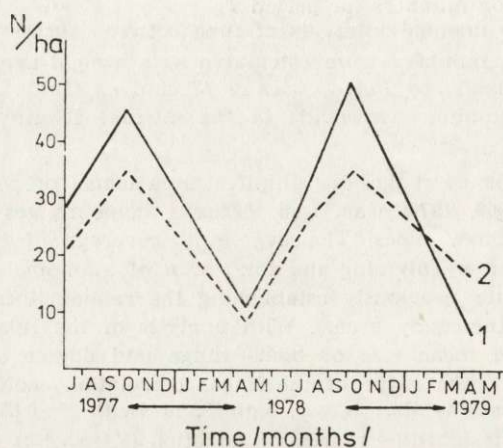


Fig. 1. Variations in numbers of bank vole populations. 1 — open population, 2 — local population

to this was the spring of 1979. Differences in density between the populations compared were greatest in autumn, but lesser in summer and spring (Fig. 1).

The rate of loss from the population of individuals in groups marked at different study seasons was slower in the local bank vole population than in the open population, and these differences applied to all the groups distinguished. In general it may be said that individuals in the summer group (that is, those which appeared in the population between April and July) remained longest in the population. This applies to both

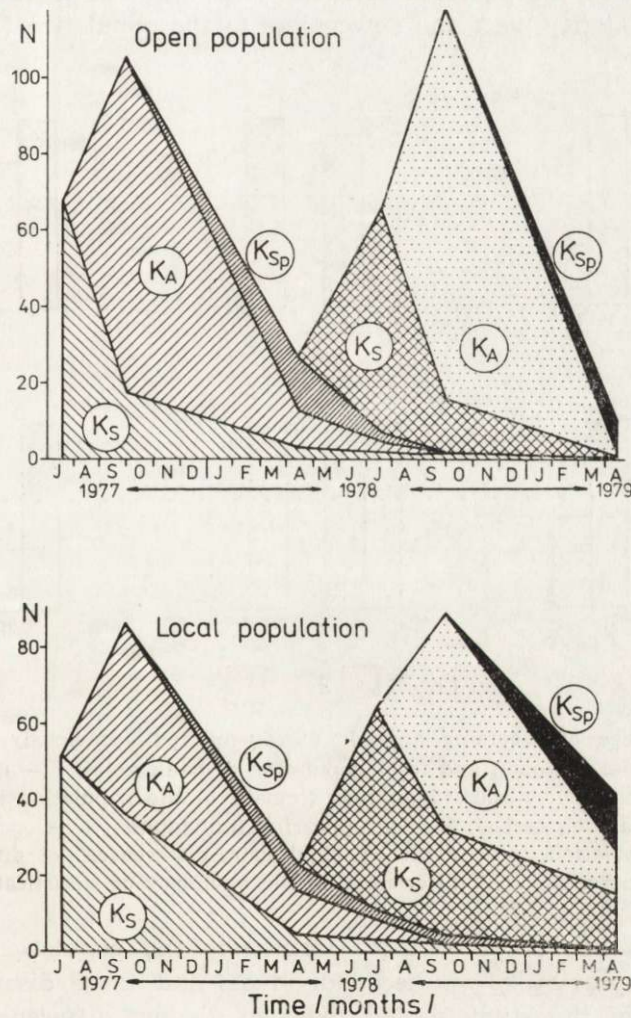


Fig. 2. Dynamics of groups of individuals marked at the same time in the open and local populations of bank voles. K_{Sp} — animals marked in spring, K_S — animals marked in summer, K_A — animals marked in autumn.

the compared populations (in both the summer group persisted for longer than the spring and autumn groups) although these differences are clearer in the local population (Fig. 2).

In different seasons the percentage of individuals belonging to different groups differed greatly in the two populations compared. In the local population the percentage of newly-marked individuals was far smaller in each season than in the open population. These differences were chiefly in respect of autumn. Similar differences also occurred in spring — in the local population the great majority consisted of individuals found in the previous calendar year, whereas in the open population the majority were the newcomers to the population (Fig. 2).

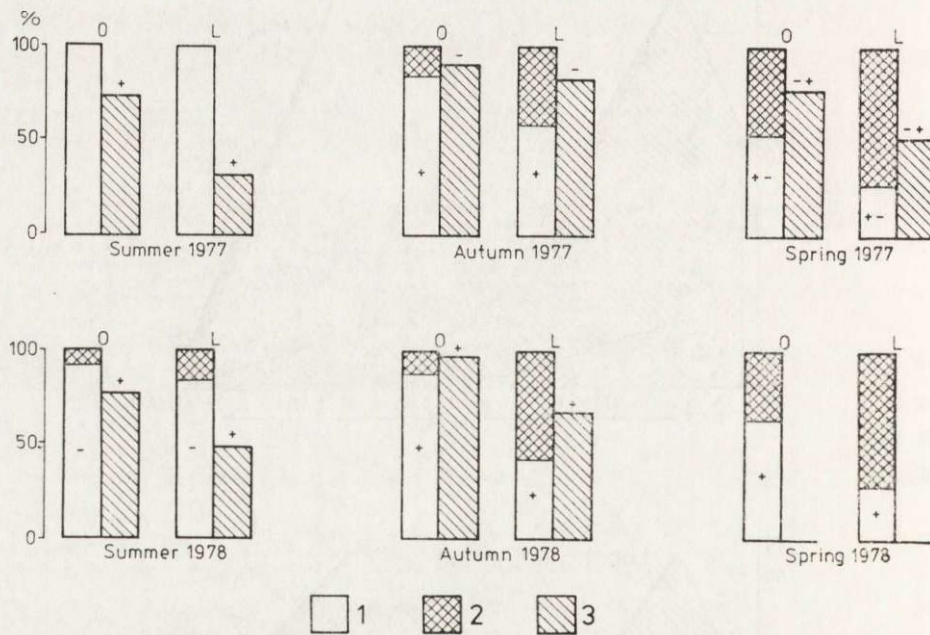


Fig. 3. Percentage of incoming animals (newly-marked), previously marked and disappearing from the open and local population of bank voles. 1 — newly-marked animals, 2 — previously-marked animals (remain in the population at least since the previous trapping series), 3 — disappearing individuals: O — open population, L — local population, + statistically significant differences, — differences not statistically significant, +- differences on the boundary of statistical significance.

Comparison of the percentages formed in the population of newly marked and previously marked individuals and those disappearing in each season of the study period revealed distinct differences between the open and local population (in the majority of cases they are statistically significant or close to significance). Both the percentage in the

population of newly-marked individual (entering the population), or those disappearing from it, is lower in the local than in the open population (Fig. 3).

Distinct differences also occurred in the winter survival of animals, particularly during the very hard winter of 1978/79. In the local population in the spring of 1979 individuals which had survived the winter formed about 75% of the population, but in the open population about 36% (statistically significant difference). Similarly in the autumn of 1978 the percentage of animals disappearing (that is, those which did not survive the winter of 1978/79) in the open population was as high as 96%, whereas the figure for the local populations was — 67% (difference statistically significant) (Fig. 3).

The values of the turnover coefficient for individuals also point to the different interchange rate of these animals. These values are decidedly higher for the open population than for the local population and consequently the mean period of stay of an individual in the open population is clearly shorter than in the local population, being respectively 135 days and 167 days.

3.2. Sex Ratio, Sexual Activity

The ratio of number of males to females was similar in both the populations compared, and was close to 1, with, however, a slight preponderance of males. Sex ratio in the two populations did not exhibit any distinct seasonal changes.

The percentage in the populations of sexually active animals was estimated only from the results of the summer trapping series. Spring trappings took place at the very beginning of the reproduction season when only old animals (sexually active overwintered) were found in the two study populations, while autumn trapping included the end period of the reproduction season, and thus all or almost all animals were sexually inactive.

The percentage of sexually active males was similar in both study years in the open population, while that of females was slightly greater and also similar in both study years. In the local population the percentage of sexually active animals, both males and females, was lower in both study years than in the open population. The percentage of sexually active females in the local population was, however, uniform in both study years (Fig. 4).

It is not the percentage of all animals capable of reproduction in a population which is directly responsible for intensity of reproduction, but the percentage of animals in fact reproducing. Thus for instance the

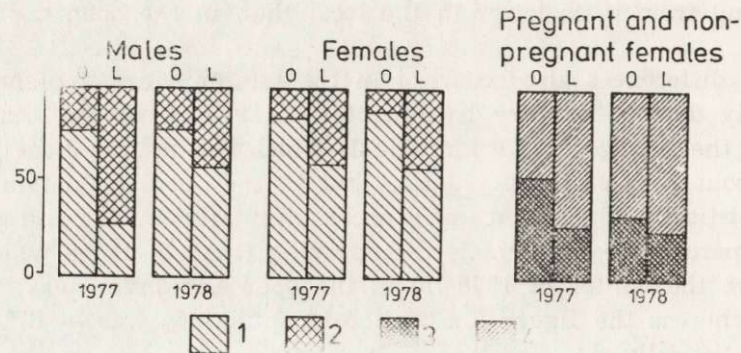


Fig. 4. Percentage of sexually active animals and percentage of gestating females in the group of females in open and local bank vole populations. 1 — sexually active, 2 — sexually inactive, 3 — gestating females, 4 — non-gestating females: O — open population, L — local population.

percentage of gestating females in the group of females varied in the two study years in the open population. In the local population the percentage of gestating individuals in the group of females was far lower than in the open population, and was uniform in both study years (Fig. 4).

3.3. Mean Number of Captures

The mean number of captures for one individual was higher in the local than in open population. The differences observed were statistically significant in all study seasons except for the summer of 1977 (Fig. 5).

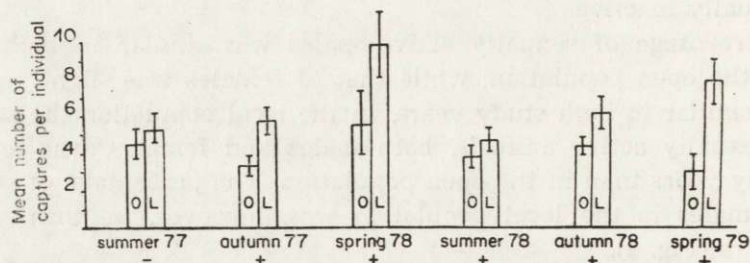


Fig. 5. Comparison of the mean number of captures per one animal in the open and local population of bank voles. O — open population, L — local population, + statistically significant differences, — differences statistically not significant.

3.4. Spatial Organization of the Populations

The mean sizes of the voles' home ranges in the two study populations exhibited considerable variation, depending and both on season on sex, sexual activity and length of stay of individuals in a population. In both the populations compared the mean sizes of males' home ranges are greater than those of females in the majority of seasons. Gestating and lactating females have larger home ranges than the other females. In both populations animals remaining longer in the population have larger home ranges than those of newly-marked individuals (Table 2).

Table 2

Average sizes of home ranges (m²) for different categories of animals in the open and local bank vole populations.

Category of individuals	Su, 1977	Au, 1977	Sp, 1978	Su, 1978	Au, 1978	Sp, 1979
Local population						
All voles	1467	1475	1662	2124	968	4490
Males	2089	1324	2288	3472	956	5385
Females	1027	1670	910	910	990	1561
Pregnant and lactating females	977	1999	1275	1017	917	
Other females	1190	1569	666	483	999	1561
New marked	1467	1519	1297	1506	933	3429
Previously marked		1376	1698	3461	1144	5021
Open population						
All voles	2224	992	2009	1782	1147	2456
Males	2887	870	2712	2500	1112	4291
Females	1260	1130	804	542	1188	1132
Pregnant and lactating females	1680	1361	871	589	2288	990
Other females	524	1093	639	416	1088	1309
New marked	2224	1082	1486	779	1028	1613
Previously marked		918	2149	3788	1241	2659

In the open population the degree of coverage of the area by home ranges, calculated as the ratio of total area of all home ranges to the size of the study area, was lowest in spring in both study years (lowest population density) and highest in autumn (maximum density). The degree of coverage of the area by home ranges exhibited a statistically significant, positive correlation with population numbers. It was also found that there was no statistically significant correlation between the mean size of home range and population numbers (Fig. 6). This means that in the open population with increase in numbers certain individuals failed to reduce the size of their home ranges and increase in reciprocal overlapping of home ranges took place.

In the local population the degree of coverage of the area by home ranges varied very little depending on the season. No significant difference was found between population numbers and degree of coverage of the area by home ranges. The mean size of home range exhibited a distinct statistically significant negative correlation with population numbers (Fig. 6). In the local population the size of home ranges decreases with increase in population numbers, which limited increase in their overlapping.

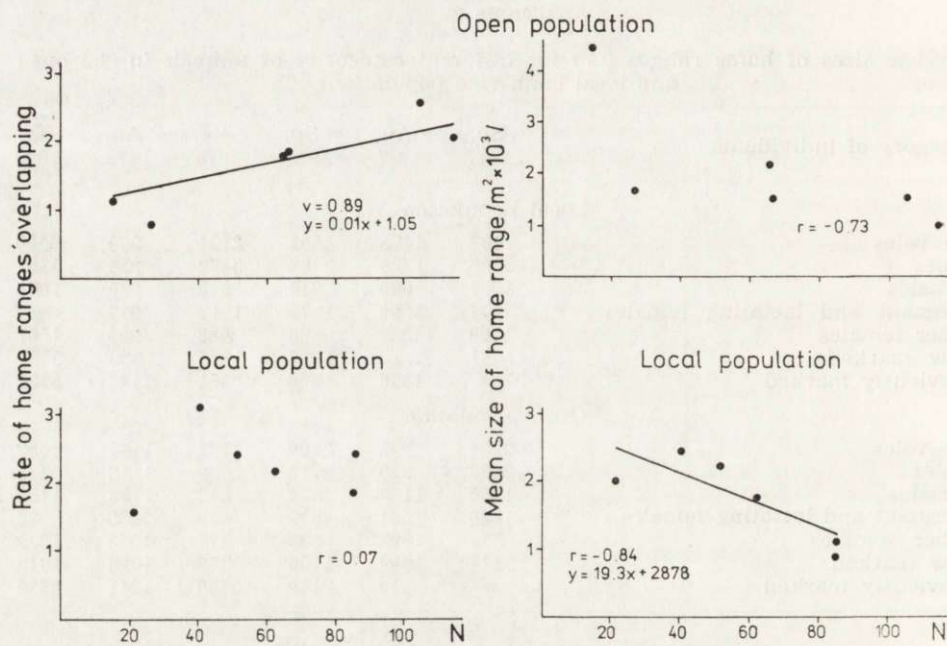


Fig. 6. Relation between population numbers and degrees of overlapping of home ranges and average size of home range in the open and local population of bank voles.

Calculation was made for animals which remained in the study area longer than one season of the mean values of shift in geometric centres of home ranges from season to season for each pair of two successive trapping series. Mean values for shift in geometric centres of home ranges were greater in all cases in the open than in the local population. These differences were caused chiefly by males (Table 3).

4. DISCUSSION

The persisting (except for the spring of 1979) greater density of voles in the open than in the local population (Fig. 1) would appear to be contradictory to the so-called Krebs' rule (MacArthur, 1972), also called Petruszewicz's rule (Gliwicz, 1980). This rule, supported by numerous examples also applying to small rodents, states that in small enclosed populations density reaches a far higher level than in open population under analogical habitat conditions. In the opinion of Krebs *et al.* (1969) the reason for the high density level in island populations the lack of opportunity for individuals to emigrate. According to Petruszewicz (1963, 1978) the reason for differences in the density of open and enclosed populations could also be differences in quantity and quality of contacts between individuals and variations in mortality due to this.

Table 3

Average shifts in centres of home ranges (m) in the open and local bank vole populations.

Season	Open population	Local population
Summer 1977 — Autumn 1977	15.3	12.9
Autumn 1977 — Spring 1978	35.1	20.1
Spring 1978 — Summer 1978	86.7	33.8
Summer 1978 — Autumn 1978	37.3	33.0
Autumn 1978 — Spring 1979	37.3	22.9
Average	34.5	23.4
Avg. males	50.3	32.2
Avg. females	14.8	13.5

In accordance with Krebs' rule it should be expected that the density of voles in the local population would be higher than in the open population. The disagreement observed between the results of these studies and this rule would, however, seem to be apparent only since the local population, despite small size and "island" character, is not enclosed. It is possible for the animals to emigrate at any time from this population and thus possible to control its numbers in this way. It may, however, be assumed that there is very little probability of immigration of animals into the population, since immigrants would have to overcome the alien habitats surrounding the local population which are not inhabited by the given species, and find their way exactly to the occupied island habitat.

In long-term studies of a bank vole population inhabiting an island in a lake Gliwicz *et al.* (1968) did not find even a single individual origina-

ting from the mainland, although occasional cases were found of emigration (by swimming) of animals from the island to the mainland situated about 120 m away.

Lower density in a population living in an habitat island than in a control open population was also found by Gottfried (1979, 1882) in the case of *Peromyscus leucopus*, and density decreased with an increasing degree of isolation of such habitat islands.

It may therefore be assumed that in local populations of animals emigration may greatly exceed immigration, and in consequence cause reduction in their density. On the other hand it is generally accepted that in open populations the number of emigrants is equal to the number of immigrants (in an average place in the population). It is only the resident part of the population which could have been controlled by means of migration in this case, the total number decreasing by only so much as they alter by the higher mortality of migrants as compared with that of resident animals.

The finding of the greatest differences in density of the open and local population in autumn would appear to provide evidence of the possibility of controlling the numbers of the local population by means of individual animals emigrating (with simultaneous limited immigration). Several authors (e.g. Lidicker, 1962; Kozakiewicz, 1976 and others) have drawn attention to the phenomena, density dependent, migration in populations of small rodents. Intensification of migratory processes in autumn (connected with increase in population density) would thus cause a considerable increase in the number of emigrants in the local population of bank voles with only a slight increase in the number of immigrants. In effect this may lead to increase in the difference in density between the local and open population in favour of the latter.

The second (in addition to limited immigration) cause of lower density in the local population in comparison with the open population may be the distinct limitation of reproduction found in the local population (Fig. 4).

Natality is one of the main factors controlling population density. In the case of isolated populations density may be controlled only by changes in natality and mortality in the population (Gliwicz, 1980). In isolated populations reproduction is usually found to be lower than in open population — this is one of the characteristic properties of such populations (Gliwicz, 1980). Bujalska (1970, 1973) showed that in an island population of bank voles the number of adult females is constant in successive years and does not depend on the current population density. The author considers this as due to the limited area of the island capable of "accommodating" a certain defined number of home

ranges of adult females exhibiting a strong sense of territorialism.

Limitation of reproduction in island populations is thus connected with the population's isolation and is the consequent result of the specific social and spatial organization of the population. It would seem that in the local population limitation of its range may cause similar reduction in reproduction.

The assumed limitation of the bank voles' immigration and reduced reproduction in the local population might have caused the far slower exchange rate of individuals in comparison with the open population (Fig. 3). The reason for differences in exchange rate between individuals could also have been differences in mortality among voles in the two populations, but there are, however, no data on mortality of the animals in the study populations: it is only possible to draw conclusions indirectly by analyzing the disappearance of animals from the populations. Such disappearance was decidedly slower in rate in the local than in the open population, particularly during the severe winter of 1978/79. These differences would appear to point to better survival of animals in the local population. It would seem that the far better survival through the winter of voles from the local population might have been the cause of its greater density observed only in the spring of 1978, as compared with the open population (Fig. 1).

The slower exchange rate of individuals in the local population would appear to have an important influence on formation of its organization. Gliwicz (1980) gives more intensive interaction between different individuals as one of the characteristics of island populations of small rodents. The considerable intensity of contacts between individuals in enclosed populations is caused by the limited area of the island and high population density, bringing about in effect a different spatial and social structure and daily activity of individuals in isolated population, as is "strongly expressed" in the organization of such populations. It would seem that similar effects may occur in the case of local populations.

According to Naumov (1977) different individuals in a population leave signals in it by their presence in the habitat (in the form of e.g. smell, burrows, paths, excrements etc.) forming a kind of information for other individuals in the population. Such "information centres" and direct contacts between individuals form the basis for creation of a given population organization. In Andrzejewski's opinion (1977) "internal arrangement" of a population — establishment of the normal character of contacts between individuals, distribution of individuals in space etc. is greater where there is the most constant possible, repeatable information reaching its individual members. It would seem that such pos-

sibilities are created when the same animals live together for a considerable time in a local population.

The differences found between the study populations in respect of the average number of captures per individual (Fig. 5) and spatial organization would appear to point to the relative permanence of population structures and the "strongly expressed" organization in the local population.

Trappability of animals in a population depends on a large number of factors, including social and spatial organization of the population and the age of individuals (e.g. Kikkawa, 1964; Gliwicz, 1970). Greater trappability is found in the case of old, settled animals occupying a high position in the social hierarchy of the population. Juvenile individuals, with a low social position, having small home ranges or none at all, are characterized by low trappability. Low trappability is also characteristic of newcomer animals to the population, e.g. introduced animals, immigrants (Petrusewicz & Andrzejewski, 1962; Andrzejewski, 1963). The higher average number of captures per individual in a local population than in the open population might therefore have been due to two causes: (1) small number of immigrants — individuals with low trappability, (2) establishment of a more stable social and spatial structure which, by reducing direct competition for a trap, created greater chances of the respective animals being trapped.

Reduction in the size of home ranges together with increase in density in the local population was the reason for maintenance of a constant degree of overlapping of home ranges independent on population density (Fig. 6). It may be concluded that in the local population, just way as in island population, more intensive antagonistic interactions take place between individuals. Such interactions may result in low mutual tolerance of individuals in the overlapping parts of their home ranges. Under such circumstances, with increase in population density and simultaneous limited space, decrease in the size of home ranges must take place, with consequent maintenance of their low degree of overlapping, permitting of limiting direct contacts between individuals.

Similar reduction in size of home ranges together with increase in density was observed in the island population of bank voles, the average number of individuals per trapping site not differing significantly in years of high and low population numbers (Mazurkiewicz, 1981). It would appear that this is the natural consequence of the reverse relation between size of home range and population numbers.

In the local population examined this may have been the cause of the animals' high degree of trappability.

The fact that only slight shifts in the centres of home ranges belong

to animals remaining longer than one study season in the population may form evidence of the "strongly expressed" organization of the local population consisting, *inter alia*, in "... arrangement of individuals in space..." (Andrzejewski, 1977) (Table 3).

In the open population of bank voles increase in the degree to which home ranges overlap was observed together with increase in density (the size of the home range in this case was independent on density) (Fig. 6), and also far greater than in the local population shifts in the centres of home ranges in the case of animals remaining in the population for longer than one study season (Table 3). These results would appear to form evidence for the "more weakly expressed" organization of this population and in effect — for its lesser stability in comparison with the local population.

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ROLA IZOLACJI SIEDLISKA W KSZTAŁTOWANIU STRUKTURY
I DYNAMIKI POPULACJI NORNICY RUDEJ

Streszczenie

Prowadzono połowy nornic rudych, *Clethrionomys glareolus* (Schreber, 1780) w żywołówki metodą CMR jednocześnie na dwóch niezależnych od siebie powierzchniach badawczych. Powierzchnia 1 (kontrolna) położona była wewnątrz dużego kompleksu leśnego i obejmowała niewielki jego fragment; powierzchnię 2 stanowił mały, izolowany płat lasu o charakterze wyspy środowiskowej. Zwierzęta łowiono trzykrotnie w ciągu każdego roku kalendarzowego w 10-dniowych seriach połowów: kwiecień, lipiec, wrzesień—październik. Połowy rozpoczęto w lipcu 1977, zakończono w kwietniu 1979. Ogółem złowiono 819 zwierząt należących do 8 gatunków gryzoni, w tym 559 nornic (Tabela 1). Dokonano charakterystyki lokalnej populacji nornicy zasiedlającej izolowany płat lasu i porównano ją z kontrolną populacją otwartą.

Populacja lokalna nornicy rudej charakteryzowała się niższymi zagęszczeniami w porównaniu z otwartą (Ryc. 1), co prawdopodobnie spowodowane było ograniczeniem imigracji oraz obserwowanymi ograniczeniami w rozrodczości populacji lokalnej. Wykazano wolniejsze tempo wymiany osobników w populacji lokalnej w porównaniu z otwartą (Ryc. 2, 3) — średnia długość przebywania osobnika w populacji wynosiła odpowiednio 167 i 135 dni. W populacji lokalnej stwierdzono też niższy udział osobników aktywnych płciowo oraz wyższą łowność zwierząt (Ryc. 4, 5). W populacji otwartej stwierdzono wzrost stopnia pokrywania się arealów osobniczych wraz ze wzrostem liczebności, przy jednoczesnym braku zależności wielkości arealu od liczebności populacji (Ryc. 6). W populacji lokalnej (podobnie jak w opisywanych w literaturze populacjach wyspowych) średnia wielkość arealu osobniczego zmniejszała się wraz ze wzrostem liczebności populacji (Ryc. 6). Powodowało to zachowanie stałego stopnia pokrywania się arealów nawet przy wysokiej liczebności populacji i „zmieszczenie” większej liczby arealów na ograniczonej przestrzeni.

Zasugerowano, że niewielkie tempo wymiany osobników powodujące dłuższe przebywanie ze sobą w populacji tych samych zwierząt może wpływać na wzrost trwałości struktur populacyjnych i „silniej” wyrażoną organizację populacji lokalnej. Znajduje to między innymi wyraz w obserwowanej wysokiej łowności zwierząt, organizacji socjalnej i przestrzennej populacji, regulowaniu liczby samic uczestniczących w rozrodzie.