ACTA THERIOLOGICA
Vol. 23, 11: 213—238, 1978

Variations in Numbers and Social Factors in a Population of Field Voles [1]

Henryka CHEŁKOWSKA

Chełkowska H., 1978: Variations in numbers and social factors in a population of field voles. Acta theriol., 23, 11: 213—238 [With 4 Tables & 12 Figs.].

Examination was made of four populations of *Microtus arvalis* (Pallas, 1779) living in covered enclosures each measuring 150 m². Migration was reciprocally possible between three of the populations. Maximum population density was from 0.4 to 0.8 voles per m². An almost constant number of females (7—8) entered upon reproduction in the early spring, regardless of the number of females in the population. During the two-year study period the populations differed in respect of age structure and social relations. During the first year, after rapid disappearance of old adults, young animals with a high degree of reciprocal tolerance predominated in the populations. During the second year the density of old adults remained high and aggressive relations intensified. Survival of the different generations was in general greater during the first study year. The composition and persistence of winter groupings of voles were analyzed and different examples of association given for these animals. The number of migrating animals was three times greater during the second study year than during the first, and the lower the average population number subject to immigration, the greater the degree of settlement of immigrants. The author has shown that there are regulating mechanisms bringing about reduction in the rate of population growth in the study population of voles (by means of deterioration in social relations, an increase in migration, decrease in survival of young animals) or increase in numbers (through an increase in reciprocal tolerance, high survival rate of young animals, reproduction outside the normal breeding season).

[Inst. Ecol. Polish Acad. Sci., 05-150 Dziekanów Leśny].

1. INTRODUCTION

A number of authors have emphasized the role of social phenomena in the fates of populations and some of them consider that social organization may often be of decisive importance in control of the numbers of vertebrates living under natural conditions (Anderson, 1961; Wynne-Edwards, 1962, 1963 and others). Direct observations of contacts between individuals in rodent populations are rendered extremely difficult owing to the nocturnal activity of many of the

[1] Praca została wykonana w ramach problemu węzłowego nr 09.1.7.4 (grupa tematyczna „Prognozowanie masowych pojawów i kierowanie liczebnością wybranych gatunków ssaków")

species, their great mobility and, in the case of the field vole, also on account of their partially subterranean way of life and the difficulty in observating the animals amidst the compact vegetation of a cultivated field. Such observations are far easier in enclosed populations, but in this case many authors consider that the lack of opportunity to migrate is a disadvantage which quickly leads to overcrowding and deterioration in social relations (K r e b s *et al.*, 1969; L i d i c k e r, 1962).

The purpose of this study was to evaluate the formation of changes and the role of certain social phenomena such as: manifestations of aggressiveness, tolerant relations, association of individuals in relation to the course taken by variations in numbers, reproduction and mortality in four enclosed populations of the field vole *Microtus arvalis* (P a l l a s, 1779), when limited migration was possible between three of these populations.

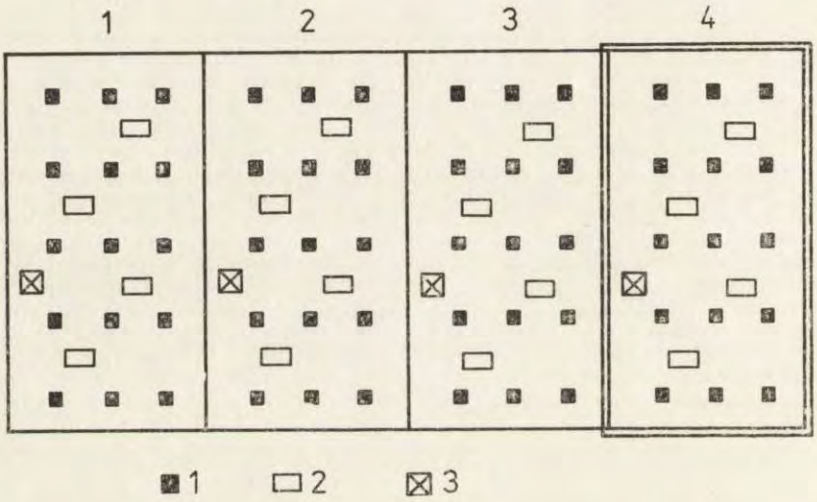

Fig. 1. Diagram of arrangement of four enclosures (1—4).
1 — trapping site, 2 — feeding box, 3 — nesting box. There were no opportunities of migration from enclosure 4.

2. METHODS AND MATERIAL

Studies were made on enclosed populations of the field vole in four enclosures surrounded by netting at the sides and covering the top, each of the enclosures measuring 150 m² (Fig. 1). The walls of the enclosure consisted of concrete up to a height of 80 cm, and the foundations extended to a depth of 60 cm into the soil. Reciprocal migration was possible between three of the populations, as parts of the foundation consisted of perforated bricks, while the fourth enclosure was completely impenetrable.

The surface of the soil in the enclosures was covered by grass with random admixture of various herbaceous plants.

In December 1970 the following numbers of field voles (*Microtus arvalis*) were released into successive enclosures: 10, 20, 30 and 40. The animals were obtained from captures made among populations living under natural conditions, sex ratio being 1:1.

In order to facilitate observations of the behaviour of the animals near food four feeding boxes, consisting of a metal frame (50×50×30) with glass side walls and a lid, were placed in each of the enclosures. A 40 W bulb was suspended from the lid and when lighted prevented the food from freezing in winter. Food was supplied *ad libitum*, giving carrot and dry rolls in winter and green lucerne from spring to late autumn. Water was also supplied during the summer period.

In order to ascertain when, under conditions of considerable overcrowding, field voles, which usually live below ground, occupy places above ground which are not typical of this species, one wooden nesting box was placed in each enclosure for the rodents and the number of voles occupying it was recorded twice a month.

A total of 15 trapping sites (Fig. 1) were set up in each of the enclosures, placing a wooden box containing three live-traps baited with oats on each site. Systematic trapping began at the beginning of February 1971 and continued until June 1973. The period from February to May 1971 was treated as a preliminary stage in order to establish correct study methods. Captures of the animals in traps were made twice a week, examining the traps three times daily (at 9^{00}, 13^{30} and 18^{00}). The *CMR* method was used, marking the voles by toe-clipping (Naumov, 1953). The captured animals were weighed, recording sex, place on which they were caught and individual number. A note was also made of the estimated sexual state of females, that is, the state of the vagina (open or closed), blood visible in the vagina, enlargement of teats in lactating females, visible pregnancy. Opening of the vagina was taken as proof of a female's ability to begin reproduction at the beginning of the mating season. Traces of biting by animals was also recorded according to a four-degree scale.

Observations of the voles' behaviour were made in the spring and autumn of 1972, recording the number of animals making use of the feeding box together and their behaviour for two hours daily (that is, for 30 minutes in each enclosure). Observations were made for a total number of 22 hours in spring and 22 in autumn.

The studies were ended in June 1973 with continuous trapping for several days, during which time the traps were kept constantly set for trapping, while the captured animals were collected and dissected. Average litter size was calculated on the basis of dissection of 21 gestating females caught during this final period and 36 gestating females which died in traps over the course of the two-year study period.

The number of animals in a population was defined by means of the calendar of captures (Petrusewicz & Andrzejewski, 1962; Andrzejewski, 1969). New animals entering the populations over the course of one month were distinguished as separate cohorts. Cohorts were combined in the following generations; spring (animals born in February, March and April), summer (born in May, June and July), autumn (August, September, October) and winter (November, December, January) (Fig. 2). During the whole two-year study period a total of 1316 animals which were born and survived to the first capture in a trap were marked in all the populations, apart from the 100 individuals released as the initial stock in the enclosures, while the total number of captures was 27,196 (Table 1).

3. VARIATIONS IN NUMBERS

After trapping began in February 1971 it was found that nearly 100% of the individuals introduced into three of the enclosures in December

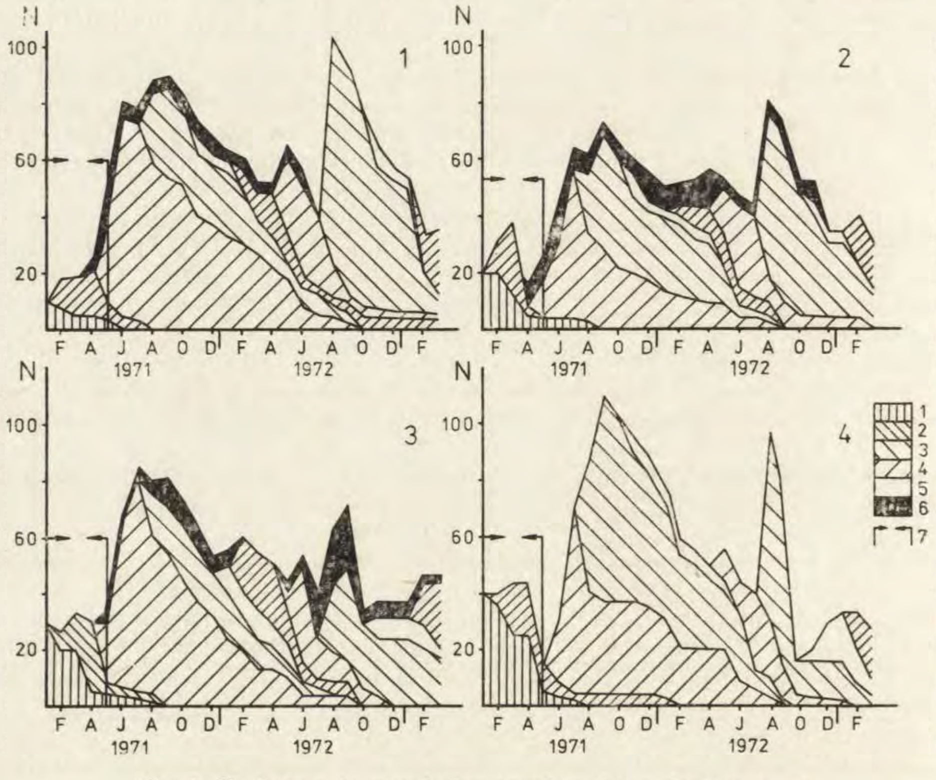

Fig. 2. Variations in population numbers in enclosures 1—4.

1 — voles introduced in December 1970, 2 — spring generation, 3 — summer generation, 4 — autumn generation, 5 — winter generation, 6 — immigrants (settled animals), 7 — preliminary period.

had survived, and in one enclosure 60% of the animals. New young individuals were caught in all the enclosures, which shows that reproduction began rapidly among the introduced voles. The numbers in each of the enclosures at the time the intensive studies proper began are illustrated in Table 1.

The oldest voles originating from introduction died during the first few months of 1971, and as from May the populations consisted almost entirely of young animals (Fig. 2). Peak population numbers were reached with a density from 0.3—0.7 individuals per m^2. After successful survival of the winter of 1971/72 there was fairly high density of the oldest animals, overwintered, and their numbers decreased far more slowly than they had done the previous year (Fig. 2). In some populations overwintered animals survived to August or even September. The age structure of the populations during the second study year was thus far older than in the preceding year.

In the spring of 1972 the first young voles begin to be caught in traps in February in three of the populations, but in the fourth enclosure, where density of overwintered individuals was greatest, this was not the case until May.

Table 1

Amount of material.

Enclosure	1	2	3	4	Total
1971					
No. of voles introduced in Dec. 1970	10	20	30	40	100
No. of voles at end of May 1971:					
overwintered	2	2	4	2	
young	33	17	27	5	
total	35	19	31	7	92
Extent of recruitment of young into populations	176	141	155	183	655
No. of captures	3,916	2,787	3,461	4,021	14,181
1972					
No. of overwintered at beginning of year	62	45	45	83	235
Extent of recruitment of young into populations	198	150	161	152	661
No. of captures	3,838	2,973	3.166	3,038	13,015

Two incidents temporarily reducing the numbers of animals took place in the populations during the second study year. About 15 animals escaped from enclosure no. 3 in the summer of 1972 and a weasel managed to get into enclosure no. 4. It is possible that this weasel also reduced density in the neighbouring enclosure (no. 3).

Density during peak numbers in the second study year was similar to that during the first year, varying from 0.4 to 0.8 animals per m^2.

4. NATALITY AND SURVIVAL OF GENERATIONS

The populations natality was estimated on the basis of analysis of physiological states of the various females and of variations in body weight (rapid increase in weight and then an abrupt drop indicating that birth had taken place). Analysis made of the number of females with open vaginas in February and March showed that initiation of the breeding season applies to only part of overwintered females present in the populations in spring. With the exception of the first population at the beginning of 1971, when there were five females and all of them participated in reproduction, in other populations and years an almost constant number of seven or eight females began reproduction, regardless of the number of females in the population (Fig. 3). This may

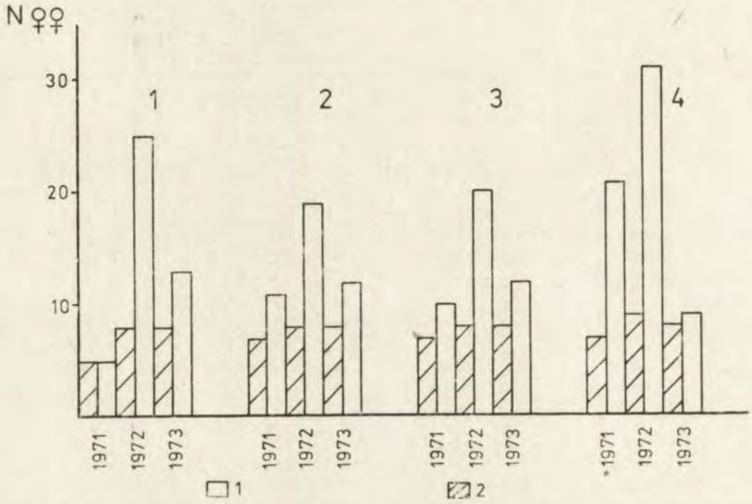

Fig. 3. Number of females beginning reproduction (in February—March) in relation to total number of females overwintered in four enclosures.

1 — total number of females, 2 — number of females beginning reproduction.

be evidence of the social differentiation of overwintered females, as the result of which the number of individuals beginning reproduction is adjusted to the space available to the population.

The number of females producing young over the whole year was fairly even in all the enclosures, varying from 16 to 19, 20 and 22, and in the second study year from 24 to 28.

The percentage of females producing young out of the total number of females of a given generation (Fig. 4) was calculated. The highest percentage of females taking part in repreduction in 1971 was found for overwintered animals and in two of the enclosures, the spring generation. In the second enclosure the number of females from the spring generation was very small, the animals lived only a short time and none of them produced young. Participation in reproduction of females of the summer generation is fairly balanced in all the enclosures. In 1972 overwintered females represented the highest percentage

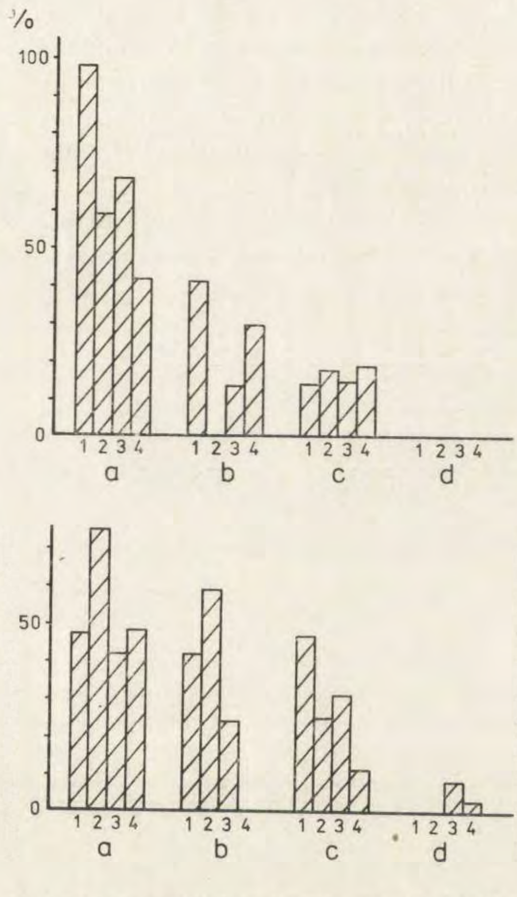

Fig. 4. Percentage of females producing young out of total number of females of the given generation.

Generations: a — overwinterd, b — spring, c — summer, d — autumn, enclosures 1—4.

in reproduction, similarly to the preceding year. In that year also females from the spring generation participated to a great extent in reproduction. In the fourth enclosure not a single individual of the spring generation survived to the time of the first trapping in live traps and therefore that generation did not take part in reproduction.

The participation of females of the summer generation is far greater than in the previous year.

In many of the rodent species females of the autumn generation do not mature sexually before the winter and therefore do not participate in reproduction during the year of their birth (Sadleir, 1969). The present study showed that this is not the rule in the case of the field vole. In 1972 after a considerable drop in the numbers of animals in enclosure three and four in autumn, several females of the autumn generation attained sexual maturity and produced young during the late autumn and winter. This points to the existence in the population of a mechanism making it possible for reproduction to be set in motion also by means of accelerating maturation of females, even after the reproductive season proper.

After dissection of 47 females, the average litter size, was calculated which was 7.0 ± 0.5. This high value for average litter size may have

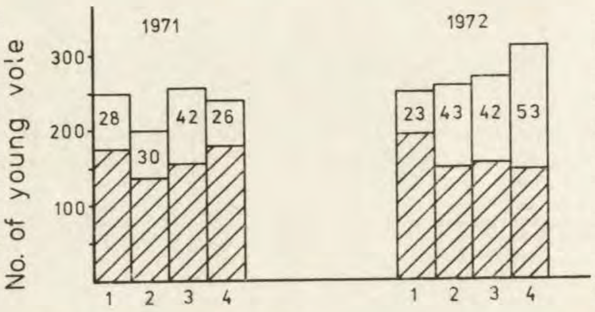

Fig. 5. Estimate of postnatal mortality rate among young voles (unshaded parts of columns). Numbers indicate percentage of young dying before first capture in traps. Shaded parts of columns indicate number of marked young animals.

been due to the fact that the material used for dissection was obtained almost entirely from the summer, when litters age largest in many species of rodents (Sadleir, 1969). This value may have been smaller in spring and autumn.

In order to estimate the degree of mortality among young voles from birth to the time they begin to be caught in traps, the number of births was assessed in different populations and multiplied by average litter size, thus obtaining the number of young born in the enclosures for both study years. The difference between the calculated number of newborn animals and number of young marked in the populations constitutes the degree of postnatal mortality among young voles up to the time of their first capture (Fig. 5). This mortality, expressed by the percentage of young animals dying before their first capture out of the total number born, fluctuated from 26 to 42% in 1971 and from 23% to 53% in 1972 in different populations.

Survival was illustrated by the percentage of individuals surviving through successive months out of the total number of animals of the given generation caught for the first time. For 1971, on account of the small number of individuals from spring, survival of males and females was estimated only for the summer and autumn generations for the four enclosures together. For 1972 the survival of the spring, summer and autumn generations was calculated (Fig. 6). As only a small part of the animals from the summer and autumn generations survived in 1972 up to the end of the studies, the curves of survival do not descend to zero.

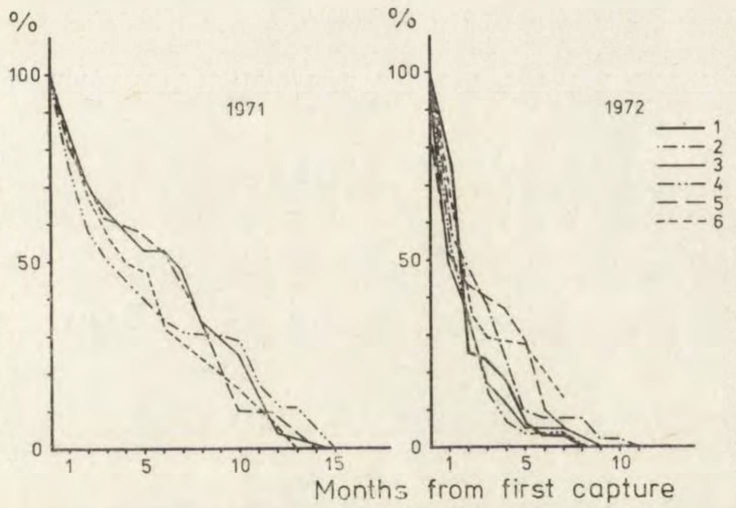

Fig. 6. Survival of generations (average for 4 populations).
Legend: spring generation 1-♂, 2-♀, summer generation 3-♂, 4-♀, autumn generation 5-♂, 6-♀.

In order to evaluate differences in survival of the different generations of the same year, and also between the first and second study year, calculation was made of the mortality coefficient separately for the two sexes of all the generations mentioned above. The coefficient was calculated for the first and second, and jointly for the third, fourth and fifth, month of the individuals' lives in populations counting from the first capture. The following equation was accepted for estimating mortality coefficient

$$m_1 = d_i / n_i$$

where d_i — number of individuals dying during a given period for generation i
n_i — number of animals living in the population at the beginning of this period for generation i

Values m_i obtained for different generations, allowing for sex and study year, were compared by means of the statistics χ^2.

Comparison of mortality coefficients calculated for 1971 ($P > 0.05$) showed that there are no significant differences in survival between the sexes or between generations in any of the periods of the population's life examined.

Table 2

Comparison of survival in the summer and autumn generations for the two study years. χ^2 values have been given only for differences statistically significant ($P < 0.05$).

Age, months	1972		Summer, 1971		Autumn, 1971	
			M	F	M	F
1	Summer	M	19.708			
		F		9.933		
	Autumn	M			15.380	
		F				7.306
2	Summer	M	4.676			
		F		15.235		
	Autumn	M			4.610	
		F				8.555
3—5	Summer	M	32.046			
		F		27.682		
	Autumn	M				
		F				

In 1972 during the first month of life (counting from the first capture) survival for males of the summer generation was significantly lower ($P < 0.05$) than that of males of the spring generation, but as early as the second month of life survival of spring generation males was significantly lower than that of males and females of other generations, and of females of the same generation. During the 3—5 month of life survival of males and females of the autumn generation was significantly higher ($P < 0.05$) than in the preceding generations. The remaining differences were not statistically significant.

Comparison of mortality coefficients for the summer and autumn generations for 1971 and 1972 (Table 2) showed that survival of males and females was higher ($P < 0.05$) during the first study year than in the second, particularly during the first two months of life in the population. It is only in autumn that this difference is not statistically significant for animals from 3—5 months old, and this may be connected with the different age structure of the populations in the two study years. During the first year the populations were very young (no overwintered animals present), whereas in the second year the oldest animals overwintered predominated for the first months, which might affect the survival of young entering the vole populations (Chitty, 1952; Healey, 1967; Sadleir, 1965).

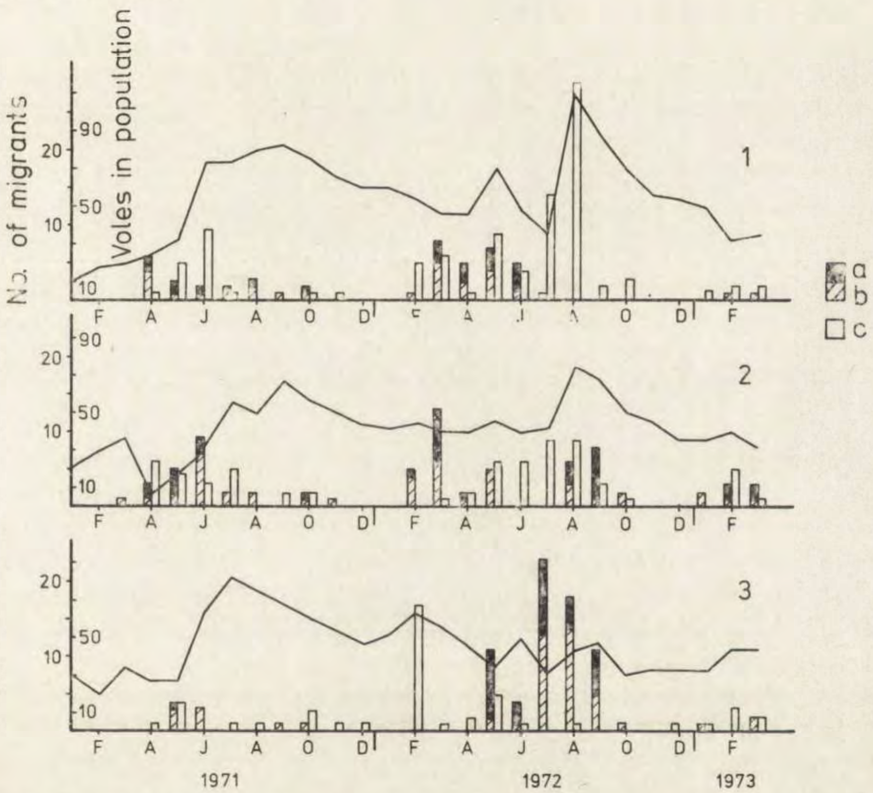

Fig. 7. Extent of migration in relation to variations in numbers in three populations (1—3).
Legend: a — staying short time, b — resident, a+b immigration, c — emigration.

5. MIGRATIONS

An animal caught in a different population from that in which it had been marked with an individual number was held to be a migrant. Despite internal migrations (between the three enclosures) the populations retained their separate character. There were almost no animals common to the enclosures, that is, caught during the same period of time in two or three enclosures (eight animals in 1971 and only two in 1972). Emigration was a distinct departure from the given population, in 97% of the cases departure without return. The number of returns from emigration was very small (six cases out of 189 migrating animals).

Analysis was made of the extent of emigration and immigration and settlement of immigrants in three populations (in the fourth, as already stated, there was no opportunity of migration — Fig. 7). The start of early spring migrations occurred in both study years in February and March (similarly to the cases given by other authors for populations living under natural conditions — Wilusz, 1956; Bashenina, 1962). During this period it was chiefly overwintered males which emigrated, and even so they were males with smaller body weight than those which remained in the population. During the period from February to May the average body weight of emigrating males was 29.9 ± 2.6 grams whereas that of non-emigrating males was 29.9 ± 2.1 g (difference significant $0.1 < P < 0.02$). In summer it was primarily the young animals of both sexes which emigrated. As from September the number of migrants decreased and was smallest from October to January inclusive, as it was in the case of populations living under natural conditions (Fig. 7).

An animal was considered as a settled immigrant if it had remained in its new population for at least three weeks. The percentage of settling immigrants, depending on numbers in the population into which settlement took place was calculated. Average numbers were calculated for the lowest, medium and greatest densities encountered in populations in different months of the two study years and correspondingly, the number of immigrants settling there with the given density. With average numbers of:

34	individuals	60% of the immigrants settled
50	,,	41% ,, ,, ,, ,,
75	,,	30% ,, ,, ,, ,,

The difference in the percentage of settling immigrants is statistically significant with the lowest and highest numbers ($0.02 < P < 0.001$). Thus the lower the average populations numbers, the higher the percentage of immigrants which settle in the population.

6. RELATIONS BETWEEN INDIVIDUALS

As the size of an enclosure was smaller than the size of the smallest individual home range given in literature (Reichstein, 1960) and taking into account the compulsory nature of the distribution of individuals under conditions of the enclosures, no effort was made to determine the size of individual home ranges by the methods used for populations living under natural conditions, but instead an attempt was made at estimating seasonal variations revealed during trapping on individual home ranges, the number and kind of individuals possessing group ranges in common etc.

The trapping sites on which an animal was caught over the course of a month (not however less than six times) were held to constitute the home range of an individual and captures were compared with it the following month. Capture on a site belonging to this range was indicated by h, while newly revealed sites were given the symbol m. In order to estimate spatial relations in the populations, particularly the degree to which home ranges vary, the index of the relation of h to m was used (P e t r u s e w i c z & A n d r z e j e w s k i, 1962). The

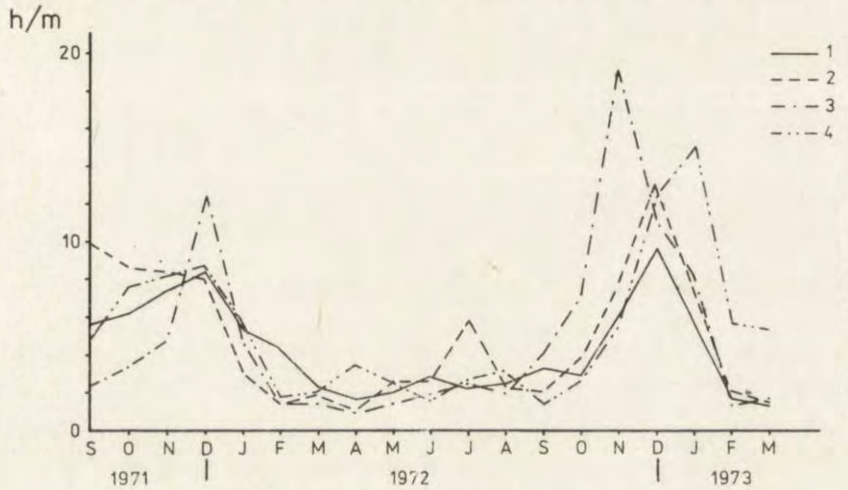

Fig. 8. Index of variation in home ranges (h/m).

higher the value of this relation, the greater the degree to which the animals had a stabilized home range (Fig. 8). In none of the cases was a zero value obtained by m, which eliminated the possibility of calculating this index.

It was found that it is possible to distinguish a period of considerable stabilization of animals in winter — usually from September to February, and low stabilization from spring to autumn.

Analysis was made of the places in which the various voles were caught during the winter period of maximum stabilization of these animals. On the diagram giving the enclosures with the trapping sites entered on them, the areas including sites on which single animals were caught during the winter months were indicated by closed lines. In this way groups of voles caught in this same range throughout the whole of the winter were distinguished. Distribution of group ranges within the first enclosure during the winter of 1971/1972 has been presented as an example of spatial picture obtained of winter aggregations of voles (Fig. 9). The number of groups and their sex composition in other enclosures and in relation to population numbers are shown in Table 3. In general the number of groups in one population over two winter seasons was from two to four and the number of animals in a group from five to thirty-two individuals. Groups occurred in which

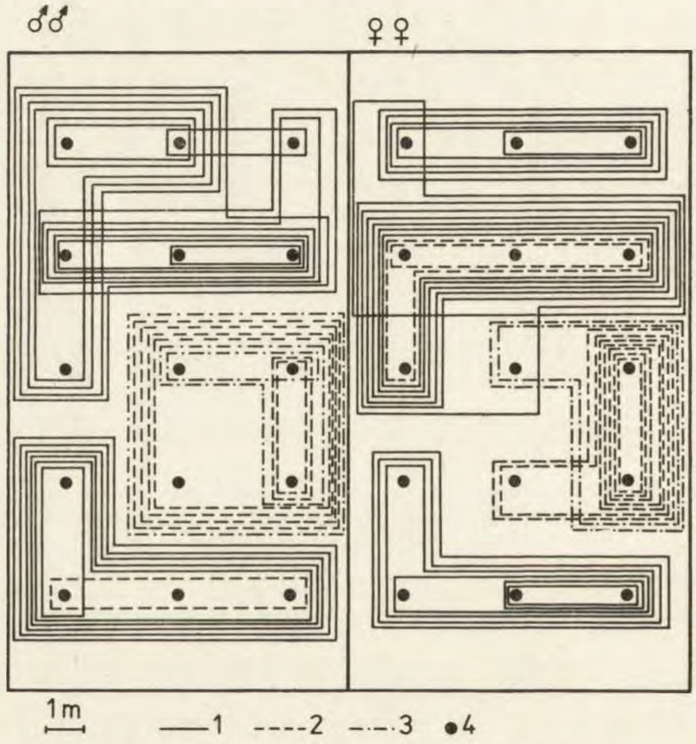

Fig. 9. Diagram of winter home ranges (September 1971—February 1972) of males and females in enclosure 1. Each line defines the home range of one individual. Legend: 1 — May-June cohorts, 2 — July-August cohorts, 3 — September-November cohorts.

there was marked preponderance of one sex (*e.g.* 2 females and 13 males in the first enclosure in 1972/1973 — Table 3). It was found that individuals forming a group which overwintered together were often of similar age, since they originated from the same generation, although sometimes young voles remained for the winter in the family range among the older animals. It was possible to observe differentiation in respect of the number of trapping sites visited within the group range within the group itself. Some of the individuals appeared on all the trapping sites of this range and others on only part of the sites. Changes in the places in which an individual was caught usually applied to the same group range, whereas cases of an individual being caught in the range of another group were rare. This points to the isolation of the various groups.

In spring and summer variation in time of captures on trapping sites of individuals is sufficiently great to make it usually impossible to draw up diagrams of ranges in the same way as was done for the winter. During this time, however, aggregations of different kinds were observed in the populations. In the summer of 1971 and 1972 small family groups composed of a female with her young, caught on the same places for a certain time (4—8 weeks) were observed twelve times, and in four cases the family jointly changed its home range. Sometimes a female together with several young was caught in one trap, while several (maximum eight) young animals (3—5 weeks of age) were very frequently found in one trap which shows that they visit the trapping sites as a group.

Another interesting case of aggregations within a population was that of young animals in July 1971 in the third enclosure. The group consisted of 14 to 33 males and 1—2 females which fed together, occupied a common range and together moved to another range. The animals in this group kept together for a long time — until February 1972, after which almost all the males from this group emigrated to other enclosures.

A further example of aggregations within populations was supplied by animals isolated in the nesting box in the fourth enclosure in 1971 when population density was high. The group numbered 35 animals in all, 22 males and 13 females. When inspections of the nesting box were the animals could be found huddled together and lying one on top of each other. They were sometimes caught in the two nearest trapping sites. This group was observed during inspections of the box up to the end of December. With the onset of severer frosts the whole group probably moved underground and various individuals continued to be caught on these same two sites. Only 38% of the animals survived the winter in the group of 35 animals, as compared with the 63% surviving from the 85 animals constituting the remaining part of the population.

Groups of young animals, usually of very similar age (originating from the same cohort) were observed in all populations during the course of trapping, but their separate character or isolation was not as sharply defined as in the examples given above.

Table 3

Winter associations in the populations. *A* — intergroup.

Enclosure	1971/72 No. of individuals in the population	1971/72 No. of group	1971/72 No. of trapping sites occupied	1971/72 No. of individuals in a group ♂♂	1971/72 No. of individuals in a group ♀♀	1971/72 No. of individuals in a group Total	1972/73 No. of individuals in the population	1972/73 No. of group	1972/73 No of trapping sites occupied	1972/73 No. of individuals in a group ♂♂	1972/73 No. of individuals in a group ♀♀	1972/73 No. of individuals in a group Total
1	62	1	4	11	9	20	49	1	5	6	9	15
		2	7	14	15	29		2	6	13	2	15
		3	4	7	6	13		3	4	15	4	19
2	49	1	4	7	5	12	34	1	8	10	8	18
		2	4	5	5	10		2	7	7	9	16
		3	4	9	6	15						
		4	3	6	6	12						
3	66	1	3	2	10	12	38	1	4	2	9	11
		2	3	19	12	31		2	7	12	4	16
		3	6	3	9	12		3	2	3	3	6
		4	3	4	7	11		4	4	2	3	5
4	99	1	2	7	3	10	24	1	5	5	5	10
		2	5	15	10	25		2	5	2	3	5
		3	5	12	20	32		3	6	4	3	7
		4	5	15	17	32		*A*		1	1	2

During the first study year and spring of 1973 no fights or traces of biting were observed on the animals in the populations, and the few cases of individuals having been bitten occurred only with migrants. In the spring of 1972, however, with very high density of overwintered animals in the populations, an increase was observed in the aggressiveness of animals engaged in fights and the number of bitten individuals was greater (males only).

Analysis of aggressive relations between voles was based on the number of traces of bites on the bodies of males. A four-degree scale was used for this purpose: 0 — no traces of biting, 1 — slightly bitten, 2 — medium degree of bites, 3 — badly bitten. Calculation was made for overwintered male young voles born in a given population and immigrant males, of the percentage of animals in each degree of the

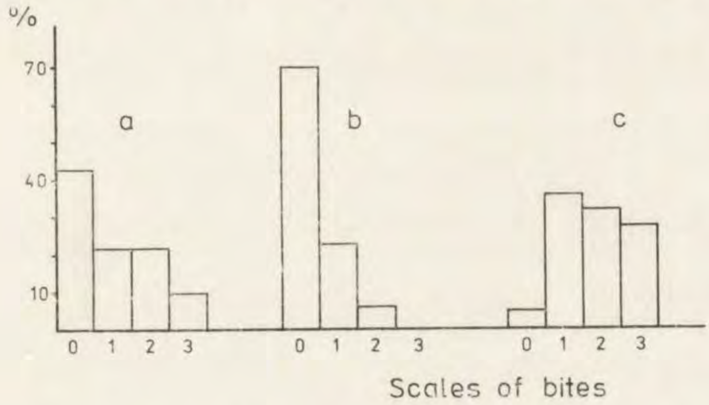

Fig. 10. Percentage of animals bitten.
a — overwintered, b — young, c — immigrants.

above scale, together for the four enclosures (Fig. 10). The largest number of animals bitten was found among immigrants — 95%. Also about 50% of the overwintered males had traces of bites on their bodies, although only about 10% of them were badly bitten. It was unfortunately impossible to establish to what degree traces of bites were left as the results of fights with immigrants and to what degree between members of the populations. The small percentages of animals bitten among young males — in all 30%, and in no case badly bitten, is remarkable. It may be assumed that only a few individuals in this age class take part in the fights in the populations.

Results of observations of the behaviour of animals on feeding sites made both in spring and autumn of 1972 provide evidence of increase in the degree of aggressiveness together with the onset of the reproduction season and a decrease in this degree after the season. A record was kept of the number of animals making use of the feeding box together and of their behaviour towards each other (Table 4). During the 22 hours of observations from March to May inclusive, out of a total number of 123 animals in all the enclosures, in 116 cases these were single animals and only in 8 cases two individuals together. Voles were often observed to look into the feeding box and, on finding another individual already in it, to run away or to wait not far from the box until the other animal had come out from it. This may point to a considerable degree of reciprocal intolerance among voles during this period. Identical observations made in autumn after the reproduction season gave a completely different result. Several animals were relatively frequently observed simultaneously to make use of the feeding boxes (Table 4), which is evidence of the increase in reciprocal tolerance. This was not due to increase in average numbers, as numbers were similar in spring and autumn (Table 4).

Table 4

Encounters between voles in feeding boxes.

Observation period	III—V					IX—XI				
Number of individuals in feeding-boxes	1	2	3	4	5	1	2	3	4	5
Number of cases observed	116	8	—	—	—	94	31	23	6	1
Average number of animals in the enclosures			48.6					54.2		

7. INDIVIDUALS GROWTH AND POPULATION RELATIONS

In the present studies analysis was made of the increase in average weight of males from different cohorts during the eight weeks following their first capture (females were excluded from this analysis on account of error due to gestation). An estimate of the course taken by curves jointly for four enclosures shows that in 1971, with a small number of overwintered animals and absence of manifestation of aggressiveness between the animals, voles of the spring generation grew the best (Fig. 11). The later the generation, the more slowly the animals grew. In 1972, with a large number of overwintered animals and intensified aggressiveness, voles of the spring generation grew far more slowly than those from the analogical generation in 1971, and at a rate very similar to that of males of the summer generation. Individuals of the autumn generation grew far more slowly, as had been the case in 1971.

An exact analysis of the curves of average body weight for individuals in the different enclosures permits of drawing attention to three interesting cases (Fig. 12). In 1971 males of the spring cohorts (March, April) in the fourth enclosure, where the density of old adults was greatest, grew more slowly than in the other three enclosures (Fig. 12a), whereas the May cohort in this enclosure, entering the population after a considerable drop in the density of old adults (Fig. 2), grew very rapidly, more quickly than in the other enclosures (Fig. 12b). In 1972 the quicker increase in average body weight of males of the first spring cohorts in the third enclosure is remarkable (Fig. 12c). This may be connected with the sex ratio existing during this time in the population among the overwintered animals: 5 males and 20 females.

The data presented here on differentiation in individual growth permit of assuming that the growth of young voles may be affected by the

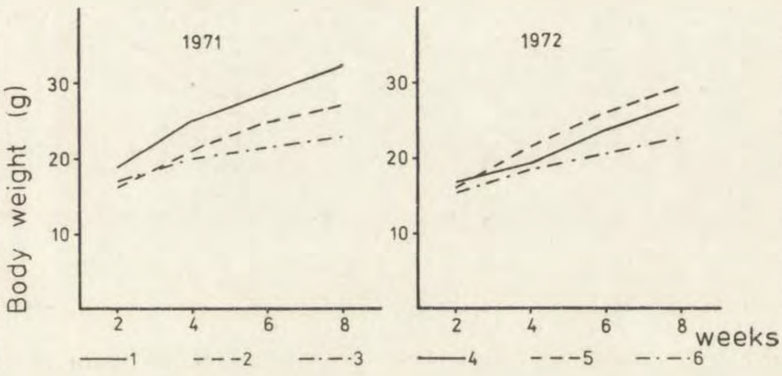

Fig. 11. Curves of average body weight of males.

1971: 1 — March-April cohorts, 2 — May-June cohorts, 3 — July-September cohorts.
1972: 4 — March-May cohorts, 5 — June-July cohorts, 6 — August-September cohorts.

population situation encountered by the incoming cohort, namely: density, age structure (particularly the number of overwintered animals), sex structure and the relations between individuals due to this situation.

8. DISCUSSION

On the strength of data obtained both by means of direct observations of social relations in the study populations and analysis of the course taken by population processes, it was found that there is a close connection between variations in numbers and the parameters defining them, and relations between individuals. Social relations in the study populations were manifested in a variety of ways, from open aggression in the form of fights between males, through avoidance of reciprocal contacts, mutual tolerance up to formation of small family groups or different individuals in a group associating for a considerable time. Thus reciprocal social relations in populations of field voles are similar to those shown for other rodent populations (Calhoun, 1952, 1956; Petrusewicz, 1958, 1966; Anderson, 1961; Sadleir, 1965; Terman, 1965; and others).

In the study populations of voles various mechanisms regulating numbers and preventing overcrowding, and also supplementing over-rapid losses, were found to operate. During the time when dynamics

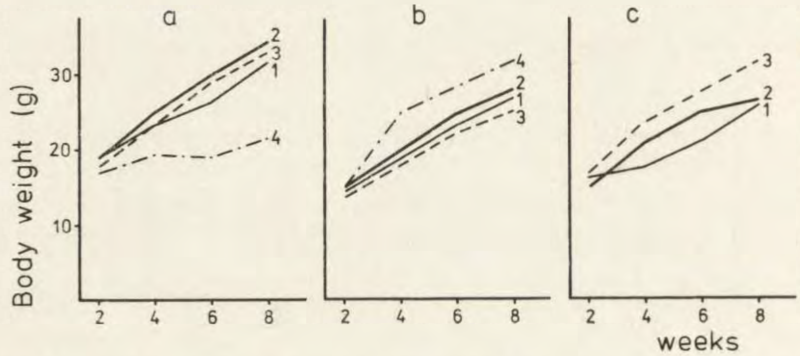

Fig. 12. Differences in body weight of male voles from different cohorts in different population situations.

Numbers near curves indicate numbers of enclosures a — March-April cohorts 1971, b — May-June cohorts 1971, c — February-April cohorts 1972.

of numbers started from a low level during the first study year (May 1971), with an age structure strongly tending towards young animals, relatively considerable reciprocal tolerance favoured rapid increase in numbers, rapid growth and maturation of the young animals and good survival of the cohorts. In the second year, when initial numbers were high, with a preponderance of older animals — overwintered — an increase in density was restricted by continuing deterioration in social relations until fights took place, increased migration and low level of survival of young animals from the first cohorts. After the drop in density of overwintered animals and reduction in agressiveness, there was considerable recruitment into the populations of young voles from the late cohorts, and in populations with a sudden and considerable decrease in density, numbers were supplemented by means of females from the autumn cohorts maturing and starting reproduction. The period of greater reciprocal tolerance begins in many species of animals with the end of the breeding season and usually lasts for the whole of the winter. It was found in the present studies that during this time the animals often make use of the feeding boxes together and that they form fairly sharply defined separate groups which overwinter together. Groups of this kind were also observed in *Microtus arvalis* by Frank (1954) and Bashenina (1962), but they did not analyze either their composition or stability. The winter groups in the populations discussed here had a very stable home range and contacts between groups were few in number. Thus tolerance during this period did not consist in contacts each of each individuals. The period of reciprocal tolerance in winter is not the rule, as is shown by Clark's studies (1955), since he observed fresh wounds on the body of males and females during the post-breeding period in populations of *Microtus agrestis* kept in enclosures.

During the breeding period tolerant relations were observed in the different aggregations in the study populations. The groups observed were not strictly isolated, but examples of joint changes of home range provide evidence of the strength of the links connecting individuals in groups. Similar groups of animals associating together were observed by Petrusewicz (1966) in populations of white mice. In Wijngarden's studies (1960) on populations of field voles kept in enclosures, large aggregations of animals (about 50 individuals) formed, with very high densities of over 7 individuals per m^2. Aggregation of individuals in overcrowded populations of the migrant rat were also observed by Calhoun (1962), who considered this as a pathological symptom. Other authors are of the opinion that isolation of an excessive number of young within the population constitutes a reserve in the event of it becoming necessary to increase recruitment into the population (Wynne-Edwards, 1963, 1965; Healey, 1967). It is however difficult to ascertain what it is that causes some of the animals to combine in groups and remain in a population, and others to emigrate from the population.

As has been shown, the degree of aggressiveness in the field vole does not depend solely on density. It would seem that it is primarily age structure (percentage of overwintered animals) in the population, and the social relations connected with it, which are important, as intensification of aggressiveness took place when the density of overwintered animals was high, but did not occur with similar density of young animals. Many authors attribute an important role in regulation of numbers to aggressiveness (Calhoun, 1949; Clark, 1956; Krebs, 1970, 1971). Mykytowicz (1959, 1960, 1961, 1964) considers that aggressiveness in adult animals contributes to losses in litters in socially subordinated young females. In the present studies far greater survival of young animals was found during the first study year (when there were no overwintered animals) than in the second year. The first spring litters entering the populations during a period of conflicting social relations exhibited the poorest survival rate. In the enclosure with the greatest density of overwintered animals, the effect of aggressive relations was so strong that not a single individual from the first cohorts survived to the age of being caught for the first time in a trap, up to May, that is, up to the time when the aggressiveness of the old adults declined.

In the present studies, unlike many other studies on enclosed populations of rodents, there were limited opportunities for migration (to adjacent enclosures). This fact brought the living conditions in the populations slightly closer to natural conditions and possibly led to setting regulating mechanisms based on migration in motion. In the second study year the number of migrants was almost three times greater than in the first year (despite the lesser average density). This may have been due to the period of markedly poorer social relations manifested in biting. Krebs *et al.* (1969) consider that biting among males isolates their excess numbers from taking part in reproduction and also controls populations numbers by stimulating migration. In isolated populations the lack of opportunities for migration usually results in deterioration of social relations. Krebs *et al.* (1969) conside that dispersal is an essential factor for normal regulation of numbers in many species of voles, while enclosed populations deprived of such opportunities exhibit disturbance of their capacity for self-regulation and easily reach a state of overcrowding. In addition to the direct effect, by means of reducing density through emigration or increasing it by accepting immigrants into the population, it is possible that migrants remaining in a population for a short time only many also affect population numbers, if we accept that the phenomenon of blocking gestation in the presence of even the smell of a stranger male takes place in natural populations (Parkes & Bruce (1962). Although the population without opportunities of migration (No. 4) during the first study year reached the highest level of numbers and its numbers were still high during the second year, manifestations of regulation of numbers both in plus and in minus occurred in both years. During the first year, when density was high, this took place in the form of isolating a large group of young animals and in the second year by females from the autumn cohort maturing and beginning reproduction following a marked drop in populations numbers. Also, in none of the study population did such very great overcrowding occur (up to over 7 individuals per m^2) as that in the studies made by W i j n g a a r d e n (1960) or F r a n k (1954).

On the basis of the data presented it was found that the study populations of field voles possessed a variety of mechanisms for regulating numbers. The question then arises as to why mass irruptions of the field vole occur every so often under natural conditions, if this species possesses such effective internal mechanisms for regulating population numbers. It may be assumed that natural population mechanisms regulating numbers are disturbed by human activities — chiefly agrotechnical operations. This hypothesis has been put forward by a large number of authors, in particular by W y n n e - E d w a r d s (1965).

Acknowledgements: My thanks are due to Dr. R. A n d r z e j e w s k i for his guidance during the course of these studies and preparation of the paper, to Professor K. P e t r u s e w i c z for his comments on the text of this paper, the Section of Statistics and Models of the Institute of Ecology, Polish Academy of Sciences for making calculation for analysis of survival and to Dr. T. W i e r z b o w s k a for mathematical consultations.

REFERENCES

1. A n d r z e j e w s k i R., 1969: Analiza wyników połowów drobnych ssaków metodą „kalendarza złowień". PAN, Instytut Ekologii, Zeszyty Naukowe, *2*: 1—104. Warszawa.
2. A n d e r s o n P. K., 1961: Density, social structure and non-social environment in house-mouse populations and implications for regulation of numbers. Trans. N. Y. Acad. Sci. *23*: 1447—1451.
3. B a s h e n i n a N. V., 1962: Ekologia obyknovennoj polevki. Izd. Mosk. Univ.: 1—307. Moskva.
4. C a l h o u n J. B., 1952: The social aspects of population dynamics. J. Mammal., *24*: 138—159.
5. C a l h o u n J. B., 1956: A comparative study of social behaviour of two inbred strains of house mice. Ecol. Monogr., *26*: 81—103.
6. C a l h o u n J. B., 1962: Population density and social pathology. Scientific American, *206*: 139—148.
7. C h i t t y D., 1952: Mortality among voles (*Microtus agrestis*) at Lacke Vyrnwy, Montgomeryshire in 1936—1939. Phil. Trans. R. Soc. B., *236*: 505—552.
8. C l a r k e J. R., 1955: Influence of numbers on reproduction and survival in two experimental vole populations. Proc. R. Sci., B *144*: 68—85.
9. C l a r k e J. R., 1956: The aggressive behaviour of vole. Behaviour, *9*: 1—23.
10. F r a n k F. 1954: Beitrage zur Biologie der Feldmaus *Microtus arvalis*. I. Gehegeversuche. Zool. Jahrb. *3*, 82: 354—404.

11. Healey M. C., 1967: Aggression and self-regulation of population size in deermice. Ecology, *48*: 377—392.
12. Krebs C. J., Keller B. L. & Tamarin R. H., 1969: *Microtus* population biology: Demografic changes in fluctuating populations of *Microtus pensylvanicus* and *Microtus ochrogaster* in southern Indiana. Ecology, *50*: 587—607.
13. Krebs C. J., 1970: *Microtus* population biology: Behavioral changes associated with the population cycle in *Microtus ochrogaster* and *Microtus pensylvanicus*. Ecology, *51*: 34—52.
14. Krebs C. J., 1971: Genetic behavioral studies on fluctuating vole populations. [In: »Dynamics of populations«, Centre for Agricultured Publishing and Documentation]. Wageningen: 243—257.
15. Lidicker W. Z., 1962: Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Amer. Naturalist, *96*: 29—33.
16. Mykytowicz R., 1959: Social behaviour of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). II. First breeding season. C.S.I.R.O. Wildl. Res., *4*: 1—13.
17. Mykytowicz R., 1960: Social behaviour of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.), III. Second breeding season. C.S.I.R.O Wildl. Res., *5*: 1—20.
18. Mykytowicz R., 1960: Social behaviour of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). IV. Third breeding season and starvation. C.S.I.R.O. Wildl. Res., *6*: 142—155.
19. Naumov N. P., 1954: Tipy poselenij gryzunov i ich ekologičeskoe značenie. Zool. Ž., *33*: 268—289.
20. Parkes A. S. & Bruce H. M., 1962: Pregnancy-block in female mice placed in boxes soiled by males. J. Reprod. Fertility, *4*: 303—308.
21. Petrusewicz K. 1957: Investigation of experimentally induced population growth. Ekol. pol. A, *5*: 281—309.
22. Petrusewicz K., 1966: Dynamics, organization and ecological structure of population. Ekol. pol. A, *14*: 413—436.
23. Petrusewicz K. & Andrzejewski R., 1962: Natural history of free-living population of house mice (*Mus musculus* L.) with particular reference to grouping within the population. Ekol. pol. A, *10*: 85—122.
24. Reichstein R., 1960: Untersuchungen zum Actionsraum und zum Revierverhalten der Feldmaus (*Microtus arvalis* Pall.) -Markierungversuche. Z. Saügetierk., *25*: 150—169.
25. Sadleir R. M., 1965: The relationship between agonistic behaviour and population changes in the deermouse (*Peromyscus maniculatus* Wagner). J. Anim. Ecol., *34*: 331—352.
26. Sadleir R. M., 1969: The ecology of reproduction in wild and domestic mammals. Methuen: 1—321. London.
27. Terman C. R., 1965: A study of population growth and control exhibited in the laboratory by praire deermice. Ecology, *46*: 890—895.
28. Wijngaarden A. V., 1960: The population dynamic of four confined populations of the continental vole *Microtus arvalis* (Pall) R.I.V.O.N. Mededeling, *84*: 1—28.
29. Wilusz Z., 1956: Z badań nad migracją *Microtus arvalis* Pall. Ekol. pol. A., *4*: 333—348.

30. Wynne-Edwards V. C., 1962: Animal dispersion in relation to social behaviour. Oliver and Boyd.: 1—653. Edinburg.
31. Wynne-Edwards V. C., 1963: Intergroup selection in the evolution of social systems. Nature, *200*: 623—626.
32. Wynne-Edwards V. C., 1965: Self regulating systems in populations of animals. Science, *147*: 1543—1548.

Accepted, August 22, 1977.

Henryka CHEŁKOWSKA

DYNAMIKA LICZEBNOŚCI A CZYNNIKI SOCJALNE W POPULACJI NORNIKA POLNEGO

Streszczenie

Przez dwa lata (1971—1972) prowadzono badania nad czterema populacjami *Microtus arvalis* (Pallas, 1779) żyjącymi w wolierach o powierzchni 150 m² każda (Ryc. 1). Ocenę liczebności, wskaźników demograficznych oraz niektórych elementów zjawisk socjalnych oparto na metodzie łowienia, znakowania i wypuszczania zwierząt. Norniki łowiono dwa razy w tygodniu w pułapki umieszczone po trzy w piętnastu punktach połowu w każdej wolierze. Złowione zwierzęta ważono, notowano płeć, miejsce złowienia, numer indywidualny oraz oceniano kondycję płciową samic (otwarta lub zamknięta pochwa, widoczna ciąża). Zapisywano także w skali czterostopniowej ślady pogryzienia zwierząt jako wskaźnik agresywnych stosunków w populacjach. Liczbę zwierząt określano na podstawie metody kalendarza złowień.

Między trzema wolierami możliwa była wzajemna migracja co nie powodowało jednak pełnego mieszania się populacji. Maksymalne zagęszczenie populacji w obu latach badań wynosiło od 0,4 do 0,8 norników na m². Wczesną wiosną do rozrodu przystępowała prawie stała liczba samic (7—8) bez względu na liczbę samic w populacji (Ryc. 3). W obu latach badań populacje różniły się strukturą wiekową i stosunkami socjalnymi. W pierwszym roku, po bardzo szybkim spadku liczebności zwierząt najstarszych (przezimków) dominowały w populacji zwierzęta młode o dużej wzajemnej tolerancji (Ryc. 2). W drugim roku wiosną było duże zagęszczenie przezimków i liczba ich zmniejszała się wolno (Ryc. 2). Notowano też nasilenie stosunków agresywnych. Przeżywalność pokoleń była na ogół wyższa w pierwszym roku badań (Ryc. 6, Tabela 2). Zaobserwowano związek agresywnych stosunków w populacjach z liczbą przezimków oraz wpływ tych stosunków na tempo wzrostu i przeżywalność młodych zwierząt (Ryc. 11, 12).

Zanalizowano skład i trwałość zimowych zgrupowań norników (Ryc. 8, 9, Tabela 3) oraz inne przykłady stowarzyszania się tych zwierząt. Liczba zwierząt migrujących była trzy razy większa w drugim roku badań niż w pierwszym, a osiedlanie się imigrantów tym większe im niższa średnia liczebność populacji podlegającej imigracji (Ryc. 7).

Wykazano istnienie w populacji norników mechanizmów regulacyjnych, prowadzących do zmniejszenia tempa wzrostu populacji (drogą zaostrzenia sto-

sunków socjalnych, zwiększenia migracji, spadku przeżywalności młodych zwierząt) lub do zwiększenia liczebności (przez wzrost wzajemnej tolerancji, dobrą przeżywalność młodzieży, uruchomienie rozrodu poza normalnym sezonem rozrodczym).