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Population dynamics and spatial pattern of small mammals in protected forest and reforested area

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HORVÁTH, GY. MOLNÁR, D., & CSONKA, G.: *Population dynamics and spatial pattern of small mammals in protected forest and reforested area*

Abstract: Small mammal monitoring using live trapping was done along the upper section of river Drava in 2003-2004, using capture-mark-recapture. Our sample areas were located in a strictly protected alder gallery forest (Lankóci-erdő) and in a neighbouring plot under gradual reforestation which had been clear-cut in 2000. A total of 9 small mammal species were recorded in the two sites, each comprising a 1-hectare sampling grid. The small mammal community revealed here had three characteristic rodent species (*Apodemus flavicollis, A. agrarius, Clethrionomys glareolus*), and two frequent shrew species (*Sorex araneus, Crocidura leucodon*). With the populations assumed to be closed, population sizes of the three dominant rodents were estimated from daily capture data. The highest estimated values were obtained for the two *Apodemus* populations (*A. agrarius and A. flavicollis*). Population sizes of the bank vole could be estimated from the protected area only. A spatial analysis with the nearest neighbour method showed that individuals of the more frequent species aimed at an even distribution, both in 2003 when densities were lower, and in 2004 when densities were higher. The more detailed analysis of the spatial pattern in 2004 suggested that by the end of late autumn, the different species are already organised in a pattern of winter survival strategy. It was shown by spatial distribution data that in this period the area of the closed alder gallery forest was occupied by individuals of yellow-necked wood mouse and bank vole. In the inner, larger part of the 1 ha forest section, it was mostly yellow-necked wood mice that established their home ranges. Striped field mice occupied only the reforested areas. Using extensive areas, the reforested area was inhabited also by bank voles, which fact is a proof for population translocation between the two areas in this species.

Keywords: population dynamics, spatial pattern, nearest neighbour method, small mammal, *Apodemus, Clethrionomys*

Introduction

In animal ecological studies including small mammals, some of the authors have found it important in the recent 10-15 years that the analysis of species movements be done on a landscape ecological scale (MERRIAM 1990, 1991). As habitats are becoming increasingly fragmented, small mammal populations tend to occur in mosaical, heterogeneous habitat complexes that consist of patches of various size and character. Such habitat fragments can form also in an original forest, as a result of forestry activities (clear felling, regrowth, reforestation). In a heterogeneous environment, movement between various habitats has an important role, and it is also crucial how much the var-

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ious fragments are optimal or suboptimal for survival of the given population, and how the migration pattern between them influence the seasonal pattern of density. This relationship, however, works on the other way round too: density increase in a particular patch can force certain individuals of the population to migrate between habitats or microhabitats. Various population dynamic data and information on movements of small mammals in mosaic landscapes with variable vegetation are important for the understanding of casual interrelationships that determine the stability of landscapes in an ecological sense (SZACKI and LIRO 1991).

Focusing primarily on Europe, several publications have dealt with the study of structure and ecology of small mammal populations in various forest types (JENSEN 1975, SMAL and FAIRLEY 1982, JUCHIEWICZ et al. 1986; HESKE and STEEN 1990). Changes in the small mammal fauna were investigated in habitats of intact areas and in those under forestry management (HANSSON 1978). In several species, the number of captures as a function of plant cover was also analysed (JENSEN 1984, MAZURKIEWICZ 1994).

The live trapping study of small mammals in a strictly protected alder gallery forest (Lankóci-erdő) was launched in autumn 2000, in the upper Drava reach. In addition to the closed forest section, we also started trapping in plot that was clear-cut in 2000 and is now gradually regrowing beside the closed forest, thus in 2003-2004 the population- and community-level monitoring of small mammals was performed together in the two plots. One of our objectives has been to find out about the small mammal community and about the changes in its composition, in the alder bog-forest, a type of floodland forests. The 1-ha felled plot besides the strictly protected area is in a state of gradual spontaneous reforestation, thus our other objective has been to investigate the ecological question of how the two areas are used by small mammals, and whether there is migration between the old, closed alder gallery forest and the area which was felled some years ago but is now regrowing. The present study investigates (i) to what extent the composition of the communities in the two sample areas differ from each other, (ii) how dense the populations of characteristic species can grow in the different habitats, and (iii) what kind of spatial pattern these populations will have using the two different areas.

Material and method

Study area

The live-trapping monitoring of small mammals was done in two neighbouring habitats of Lankóci-forest in 2003-2004. One is a strictly protected lowland alder gallery forest (*Paridi quadrifoliae-Alnetum*), bordered by an edge zone abounding in shrubs. The other area is located beside the first one: it is an approximately 1 hectare forest section, in the state of gradual spontaneous reforestation following clear-felling. Since the area was clear-cut, plant cover has increased in the regrowing area, making the plot increasingly suitable for small mammals. In the studied alder forest, a highly variable plant association has formed, as a result of high levels of precipitation, with a number of larger, sedge-covered patches. Due to the wet period in late winter and spring, these patches turn into areas with stagnant water. In addition to the variable vegetation, the moss-covered stumps and fallen trunks provide excellent shelter for small mammals, and also serve as suitable trap stations. There is one forestry road north of the two selected forest sections and another one between the two, both of which, have played an important role in making the once continuous forest become fragmented.

Trapping protocol and monitoring

For population level monitoring the small mammals were captured using live-trapping, and the method of capture-mark-recapture was applied. One trapping session included five nights, this period being long enough, in case of sufficient number of captures and recaptures, for population sizes to be estimated using various models, as the shortness of the period allows the population to be considered to be closed. For capturing the animals, plastic box-type live traps were used in both areas, earlier tested by HORVÁTH et al. (1996) and HORVÁTH (1996). A trapping grid covering 1 hectare and consisting of 11 by 11 trap stations 10 m apart was used in both the protected alder gallery forest (Grid A) and the neighbouring regrowing plot (Grid B). Bacon and mixed grains with aniseed extract and vegetable oil added, were used as bait. Traps were checked twice each day, (at 7^{00} and at 19^{00}), thus each session yielded 9 checkings. In both years, monitoring was done in three trapping periods: in July, August and October in 2003, and in July, September and October in 2004. From the number of traps in the two grids and the number of sampling nights, our sampling covered 3630 trap-nights a year, that is a total of 7260 trap nights for the two years covered in the present study. Captured animals were marked individually according to BEGON (1979), and we also recorded the sex (in females: gravidity or lactation, too), age and body mass. Ages were determined based on body mass and overall appearance.

Statistical methods

Our capture data were recorded based ion a Manly-Parr diary of captures. Three capture parameters were specified: total number of captures, total number of recaptures, number of known individuals). Small mammal species percentages were calculated for the different sampling plots and for the sampling periods. Capture data of the strictly protected area and the regrowing plot were compared using homogeneity G-tests (ZAR 1996). As trapping sessions lasted for 5 nights, the populations can be considered to be closed, without any births, deaths emigration or immigration. For the estimation of population size we applied the MARK (COOCH and WHITE 1998) software used primarily for testing and modelling survival and capture probabilities, and the program also includes the CAPTURE application that was designed earlier for estimating sizes and densities of closed populations, here operating as a submenu. The various estimators for closed populations running within that consider the constancy or temporal dependence of capture probability, the reaction of individuals to being trapped, and also the possible change of capture probability due to individual characteristics of the animal. Based on the 5-day periods, we could perform population size estimations for the 2004 data only.

For the analysis of spatial distribution of individuals and populations we recorded the coordinates of trap stations and captures, based on which it was possible to analyse the spatial distribution of the various species both statistically and graphically, using the new Biotas 2.0 program. For analysing the distribution of individuals within the population, the nearest neighbour method, and the evaluation of spatial relationship between the populations was done by calculating the degree of association (Yates-correction χ^2-value). Changes in the space use of the frequent species were evaluated using the higher amount of capture data from 2004, by charting together the monthly capture values in the two areas, emphasising the spatial arrangement occurring after the autumn peak density.

Results

In the two year period (2003-2004) within the monitoring in Lankóci-forest, analysed in the present paper, a total of 9 small mammal species were found to occur in the trapping grid set up in the protected alder gallery forest and in the neighbouring regrowing area (both the scientific names of species, and their abbreviation used in our database are indicated):

MAMMALIA
Insectivora:
Soricidae:
1. *Sorex araneus* (Linnaeus, 1758) [SAR]
2. *Crocidura suaveolens* (Pallas, 1811) [CSU]
3. *Crocidura leucodon* (Hermann, 1780) [CLE]

Rodentia:
Muridae:
Arvicolinae:
4. *Clethrionomys glareolus* (Schreber, 1780) [CGL]
5. *Microtus arvalis* (Pallas, 1779) [MAR]
6. *Microtus subterraneus* (de Sélys Longchamps, 1836) [MSU]

***Murinae*:**
7. *Apodemus agrarius* (Pallas, 1771) [AAG]
8. *Apodemus flavicollis* (Melchior, 1834) [AFL]
9. *Apodemus sylvaticus* (Linnaeus, 1758) [ASY]

In 2003 a much lower number of animals were captured in Lankóci forest than the average of earlier monitoring years, which was even more pronounced in the number of recaptures. Therefore, it was not possible to make seasonal population size estimations, not even with closed population models. Among earlier years, the number of captured species was 8 in 2000-2001, which dropped to 6 in 2002. In 2003, despite the fact that there were two sampling grids that year (which doubled the number of trap stations), there were 7 species in the closed forest section (Grid A), and 5 species in the regrowing plot (Grid B). Although 2004 was a more favourable year in terms of weather (lush vegetation, sufficient amount of available food), only 5 species were found to occur in the closed forest. Two protected shrew species (*S. araneus, C. leucodon*) reappeared in the area, thus the number of shrew species was the same as in the previous year, and together with earlier years (2000-2002), we found 5 protected native shrew species in the study area. As to rodents, 5 species were captured in 2003: besides the three wood mouse species, a colouring element of the community, i.e. the pine vole, (*M. subterraneus*) was also captured, as well as the bank vole (*C. glareolus*) that had strikingly high density values in former years. In 2004, however, the common wood mouse (*A. sylvaticus*) was not revealed, and only one vole species, i.e. the bank vole was found to be present. Although the latter species started to stabilise again, it was still not abundant enough to be able to become the dominant species. The yellow-necked wood mouse (*A. flavicollis*) continued to be the leader one in the ranking of dominance in 2004, in both of the small mammal communities sampled (Tables 1-2.).

The relative frequencies of the three common rodent species (*A. agrarius, A. flavicollis, C. glareolus*) and of the two common shrews (*S. araneus, C. leucodon*) in the studied months differed in both years between the closed alder gallery forest and the regrowing area. In 2003 the proportion of A. agrarius in the protected forest was highest in August, this species showing up in the closed forest in the autumn as well, although with lower frequency. In the regrowing plot this animal appeared in the two summer months

Table 1. Capture parameters of species trapped in Lankóci forest in 2003

Species	Number of captures			Number of recaptures			Number of individuals		
Months	06.	08.	10.	06.	08.	10.	06.	08.	10.
Grid A									
Sorex araneus	10	10	2	1	1	-	9	10	2
Crocidura leucodon	2	3	2	-	-	-	2	3	2
Clethrionomys glareolus	17	3	-	6	-	-	13	3	-
Microtus subterraneus	1	-	-	-	-	-	1	-	-
Apodemus agrarius	3	13	6	1	7	4	2	9	3
Apodemus flavicollis	41	12	4	8	6	0	35	10	4
Apodemus sylvaticus	-	1	-	-	-	-	-	1	-
Grid B									
Sorex araneus	3	14	9	-	-	2	3	14	8
Crocidura leucodon	-	10	6	-	1	1	-	9	6
Clethrionomys glareolus	-	-	2	-	-	1	-	-	1
Apodemus agrarius	3	3	-	1	3	-	2	2	-
Apodemus flavicollis	9	5	3	1	-	2	8	5	2

with nearly identical frequency values, but instead of the expected density growth, no individuals of this species were captured in the autumn sampling month. The unfavourable environmental conditions encountered in 2003 are best expressed by the monthly distribution of *A. flavicollis* relative frequency. In both areas this species was most frequent in June, then decreased gradually by autumn when the population was rather found in the regrowing forest area. The distribution revealed for *C. glareolus* can be evaluated if the very low numbers are regarded. The strong preference of this species for closed forests is shown mainly by the values obtained in June. This year, with its densities much lower than the average, only few individuals were found in the regrowing plot. The proportion of common shrew in June was higher in the closed alder forest than in the regrowing area, and in August it was present in the two areas with more or less similar frequencies, but its proportion at the October sampling was higher in the regrowing area. The relative frequencies of *C. leucodon* during the months was quite even in the closed forest section, suggesting that in the strictly protected area this species is also continuously represented at lower numbers besides common shrew. *C. leucodon* was a more characteristic species in the regrowing area (Table 1.), appearing mostly in the drier August and October, clearly shown by relative frequency values (Fig. 1.).

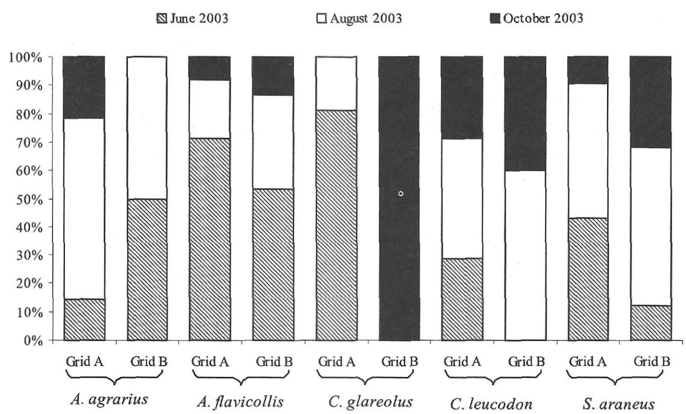

Fig. 1.: Distribution of the relative frequency values of characteristic small mammal species in the sampling months in 2003

Table 2: Capture parameters of species trapped in Lankóci-forest in 2004

Species	Number of captures			Number of recaptures			Number of individuals		
Months	08.	09.	10.	08.	09.	10.	08.	09.	10.
Grid A									
Sorex araneus	-	5	1	-	-	-	-	5	1
Crocidura leucodon	-	1	2	-	-	-	-	1	2
Clethrionomys glareolus	38	34	35	9	14	24	29	27	20
Apodemus agrarius	18	12	-	8	6	-	12	8	-
Apodemus flavicollis	46	37	55	13	27	48	33	23	23
Grid B									
Sorex araneus	-	1	-	-	-	-	-	1	-
Crocidura leucodon	3	1	14	1	-	4	3	1	10
Crocidura suaveolens	-	-	2	-	-	-	-	-	2
Clethrionomys glareolus	9	5	31	1	-	16	8	5	21
Microtus arvalis	2	-	-	-	-	-	2	-	-
Apodemus agrarius	36	25	29	22	16	19	17	15	14
Apodemus flavicollis	29	4	-	13	2	-	19	4	-
Apodemus sylvaticus	4	1	1	2	-	1	2	1	1

Capture numbers of the same small mammals were higher the following year, and because environmental parameters were also different in 2004 (the dry year was followed by one with more precipitation), species distributions in the various sampling months were also different, even if it is considered that sampling was done from August to October. *A. agrarius* was present in the regrowing area with almost identical proportions as in the forest plot, which fact - with capture parameters (Table 2.) also regarded - indicates that this species preferred this type of habitat to the closed alder gallery forest. In the case of A. flavicollis the results were the other way round, with an even distribution of its relative frequencies during the months being characteristic for Grid A. In the regrowing area its proportion was remarkable in August, then in autumn individuals of the population began to use this habitat less. The bank vole was found to be more stabile in 2004 both in capture parameters and in the distribution of relative frequencies during the months. Even the seasonal distribution of its relative frequency suggested that this species used not only the closed forest this year, but by autumn a considerable proportion of its population also occupied the regrowing plot. Among the two shrews, common shrew tended to use the closed forest, whereas *C. leucodon* was found in the regrowing area, but both species were captured only from August on (Table 2.) (Fig. 2.).

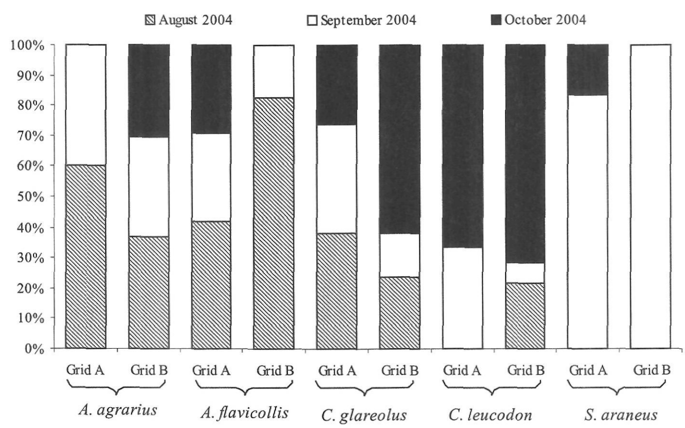

Fig. 2.: Distribution of the relative frequency values of characteristic small mammal species in the sampling months in 2004

Table 3: Results of the homogeneity test (G-test) between the two sample areas

Speies	Grid A		Grid B		G-values
	N_i	p_i	N_i	p_i	
S. araneus	21	19.26	25	41.66	8.43**
C. leucodon	7	6.42	15	25	1.27
C. glareolus	16	14.67	1	1.67	11.89***
M. subterraneus	1	0.91	0	0	11.73***
A. agrarius	14	12.84	4	6.67	1.98
A. flavicollis	49	44.95	15	25	5.77*
A. sylvaticus	1	0.91	0	0	1.27

*: $p < 0.05$; **: $p < 0.01$; $p < 0.001$

Table 4: Results of the homogeneity test (G-test) between the two sample areas (August)

Speies	Grid A vs. Grid B		G-values
	A%	B%	
Sorex araneus	0	0	-
Crocidura leucodon	0	3.89	5.40*
Clethrionomys glareolus	37.25	11.68	14.04***
Apodemus agrarius	17.64	46.75	13.64***
Apodemus flavicollis	45.09	37.66	0.66

*: $p < 0.5$,**: $p < 0.01$, ***: $p < 0.001$

For a detailed statistical analysis of differences between the two study plots, capture data from 2003 proved to be insufficient. The assumed differences between the areas were thus evaluated based on the cumulated data of 3 months only. From the results of G-tests performed for each species it appears that in most species inhomogeneity was found to exist between the two areas. The two, typically forest-dwelling species that had been more abundant before 2003 (*A. flavicollis, C. glareolus*) were now found to be characteristic for the closed forest, whereas for the distribution of A. agrarius no significant difference was found between habitat types. Apparently, this generalist species was found with similar proportions in the two areas, with individuals of the population moving about in the boundary area between the two plots, i.e. in the edge zones. The significant difference found for the distribution of *S. araneus* is a consequence of merging its data, as it could be seen above from relative frequencies during the months that this species changed location, moving mostly to the regrowing area in August and October. However, the significant result of the G-test cannot clearly prove whether it is the closed alder gallery forest or the regrowing forest area that is the more suitable habitat for this species (Table 3.).

The higher number of captures in 2004 made it possible to analyse the assumable difference between the two plots month by month (Tables 4-6.). From G-tests for the various species it appears that there was inhomogeneity for most of the species in all three months between the two plots. For August, the significant G-test results obtained for the striped field mouse and for the bank vole must be noted. The striped field mouse which is capable of fast dispersal, was found to be occurring at significantly higher frequencies in the regrowing area than the 1:1 distribution hypothesised by the G-test., whereas the bank vole was more abundant in the closed forest. Another important phenomenon in the comparison of the two areas in the same month is the homogenous distribution of the yellow-necked wood mouse, showing that the reforested area is also a suitable habitat for this species, and that individuals of the population establish their home ranges here, too (Table 4.).

Table 5: Results of the homogeneity test (G-test) between the two sample areas September)

	Grid A vs. Grid B		G-values
Speies	**A%**	**B%**	
Sorex araneus	**5.61**	2.77	0.98
Crocidura leucodon	**1.12**	2.77	0.72
Clethrionomys glareolus	**38.20**	13.88	11.80***
Apodemus agrarius	**13.48**	**69.44**	41.33***
Apodemus flavicollis	41.57	11.11	18.75***

*: $p < 0.5$, **: $p < 0.01$, ***: $p < 0.001$

Table 6: Results of the homogeneity test (G-test) between the two sample areas (November)

	Grid A vs. Grid B		G-values
Speies	**A%**	**B%**	
Sorex araneus	1.07	0	1.17
Crocidura leucodon	2.15	18.91	15.31***
Clethrionomys glareolus	**37.63**	41.89	0.22
Apodemus agrarius	**0**	39.18	54.32***
Apodemus flavicollis	59.13	0	883.15***

*: $p < 0.5$, **: $p < 0.01$, ***: $p < 0.001$

Results of homogeneity tests for September showed that the distribution of striped field mouse was again inhomogenous, in preference for Grid B. Similar inhomogeneity was received for the bank vole too, but this species remained to be present in higher numbers in the closed alder gallery forest. The former homogenous distribution of the yellow-necked wood mouse now changed: individuals of the population rather occupied the closed forest, thus the G-test for the distribution of relative frequencies revealed significant difference. For shrews, the statistical analysis indicated homogenous distribution in the two areas (Table 5.).

The unexpected results described earlier for November capture data were confirmed by the G-tests too. Striped field mice were present only in the regrowing plot by then, clearly indicated by significant inhomogeneity. The same result was obtained for the yellow-necked wood mouse, its individuals captured in November in the closed forest only. Finally, the most striking piece of result was that the distribution of the bank vole turned the other way round: higher percentages were found in the regrowing plot than in the closed forest (Table 6.). Significant difference was found for the distribution of the white-toothed shrew, found in greater numbers in the regrowing forest, thus it is assumed that it prefers the vegetation structure found there.

In the monitoring years before 2003 when trapping was done only in the strictly protected forest, it was primarily the common shrew whose population size could be estimated a from capture-recapture data. In the sample area of the closed alder gallery forest shrew density decreased considerably in 2003, therefore insufficient capture-recapture data were obtained, so it was not possible to apply estimation methods (MARK/CAPTURE). However, from data collected in 2004, we could perform population size estimations of the three dominant species (*A. agrarius, A. flavicollis, C. glareolus*). From capture or life history matrix on Grid A, estimations were made for all three populations. Although the bank vole was present in higher numbers in Grid B in November 2004, it was still not possible to perform population estimation for this area. The success of estimations is greatly influenced by recapture rates, i.e. the success of capture-mark-recapture, thus there were of course months in the two other species too

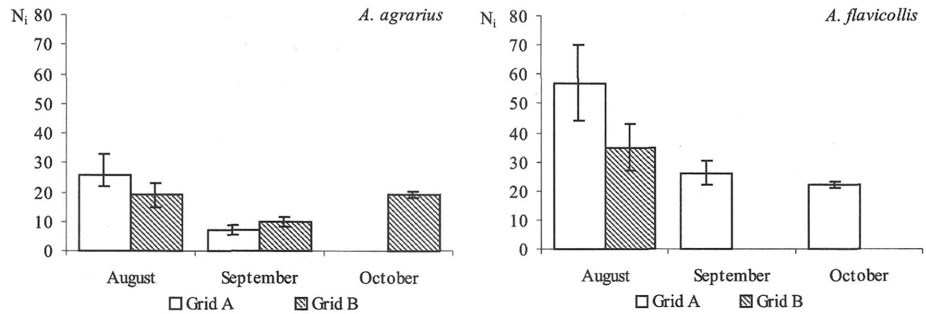

Fig. 3.: Estimated abundance values of striped field mouse (*A. agrarius*) and yellow-necked wood mouse (*A. flavicollis*) populations in Grids A and B of the sample area of Lankóci-forest in 2004

when data in the life history matrix proved to be insufficient for an estimation. The most estimations were obtained for the two *Apodemus* (*A. agrarius* and *A. flavicollis*) populations. Estimated population sizes were charted for each species, with data for Grids A and B shown in the same graph, the standard error of the estimation also indicated (Fig. 3.).

Population size of the bank vole, thus, could be estimated for Grid A only. Quite similar results were obtained for August and September (August: 41 individuals/ha, September: 46 individuals/ha). In August it was the most fitting M_{th}-estimator, (Mth: recapture probability is time-dependent and also depends on individual variability within the population), and in September the M_0-estimator (M_0: recapture probability is constant in time) that proved to be suitable for population estimation. In November the estimated population size (11 individuals/ha) indicated well that individuals emigrate from the area, resulting in a population decline in the closed forest. When estimations were made from August and September data, high standard errors were obtained, thus variation coefficients produced percentages that were higher than acceptable (August: cv = 27.12 %, September: cv = 27.99 %), based on which the estimated values for these two months can not be regarded statictically acceptable. In November higher capture success produced acceptable estimation for this species, too (cv = 10.14 %) (Fig. 4.).

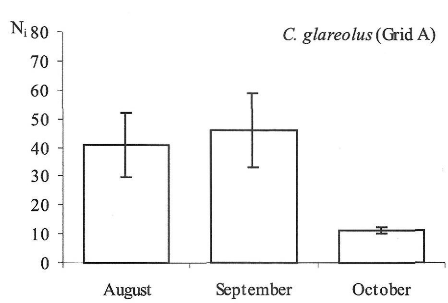

Fig. 4.: Estimated abundance values of the bank vole (*Clethrionomys glareolus*) population in Grid A of the sample area of Lankóci forest

Both the homogeneity tests of capture data in the two study plots and the population dynamics of the frequent rodent species indicated that the spatial arrangement of individuals of the various populations is an important factor in creating and changing the spatial and temporal pattern of small mammals moving between the strictly protected closed forest and the regrowing area. By evaluating capture point coordinates in the Biotas program we first analysed the space use and distribution of individuals in the populations of the three frequent rodents. Because of the low capture rates in 2003, in this analysis we used yearly cumulated data in both years (2003, 2004) for performing the graphical analysis of space use and the distribution investigations applying the nearest neighbour method. The use of the closed forest and the regrowing area in the three studied species was different among the two years. The striped field mouse, a generalist species in habitat use, occupied the edge area between Grids A and B in 2003. In 2004, the greater density of its population resulted in an increased space use, thus the striped field mouse populated the regrowing plot as well as the edge areas. Difference in the space use of the yellow-necked wood mouse between the two years was smaller. This species clearly preferred to use the closed alder gallery forest, although even in 2003 it did occur in a certain patch of the regrowing plot that was covered by larger trees and dense vegetation. In the following year, individuals of the population dispersed more intensely in the regrowing forest area. In the comparison of the two years, the most striking difference in space use was found for the bank vole. When it had low densities in 2003, it used mostly the closed forest, with only few individuals captured in the edge zone of the regrowing plot. In the following year it was found that as density grew, individuals started to use the regrowing plot more intensely (Fig. 5.).

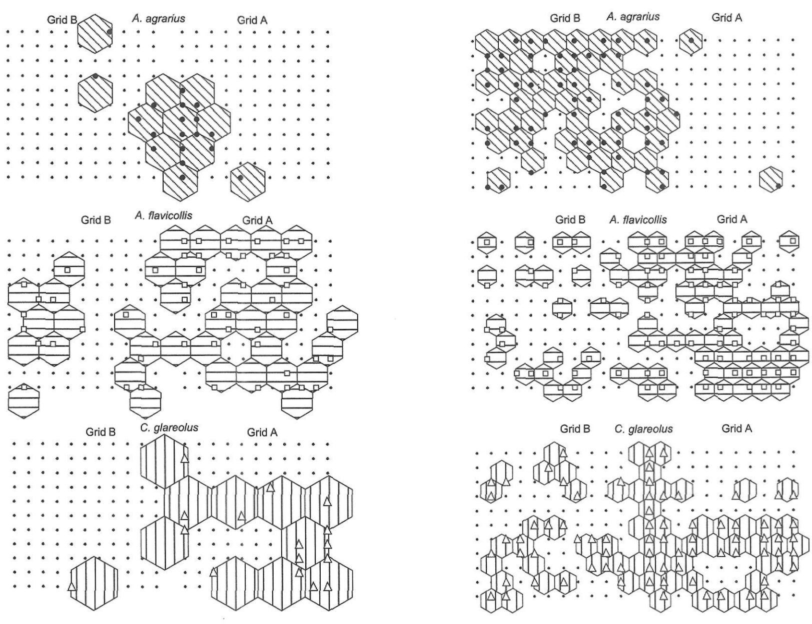

Fig. 5.: Space use by the three characteristic species in the regrowing forest area (B) and the closed alder gallery forest (A) in 2003 (left) and in 2004 (right)

Table 7. Nearest neighbour distances within populations of the three frequent rodent species. with stadard deviation values. in 2003-2004

Statistical values	2003		2004	
Species	**Mean distance (m)**	**± SD**	**Mean distance (m)**	**± SD**
A. agrarius	14.98	0.75	13.36	0.23
A. flavicollis	15.97	0.37	15.33	0.15
C. glareolus	47.25	0.83	12.46	0.19

However, the analysis of the distribution of individuals within the populations showed that although densities were different in the two years, individuals in all three species aimed at reaching an even spatial distribution. According to the null-hypothesis of the nearest neighbour method individuals are randomly distributed. Yet, results of the two years showed in all three species that this hypothesis should be rejected, the distribution of individuals being even. In terms of the average distance of nearest neighbours, the bank vole had significant difference between the two years, indicating that individual territories were further apart in 2003 when densities were low. The two Apodemus species are known to have larger home ranges and are capable of covering considerable distances, yet the average distance from the nearest neighbour was almost the same in the two years, for both species (Table 7.).

It must be emphasised for Fig. 5 above that it is created from cumulated data, and besides the fact that spatial distribution is density dependent, it is also important to find out how space use and spatial patterns transform as population sizes change throughout the year. For such analyses monthly data should have contained higher capture values, thus the seasonal changes of spatial distribution were analysed from our 2004 data only.

For the closed alder gallery forest and the regrowing forest area it was assumed that due to the difference in resource distribution and interspecific competition, the two habitats are used by the various species taking turns, therefore considerable migration and partial population translocation can be measured among the two areas. For the analysis of the assumed population translocation between the closed forest and the regrowing plot, i.e. between two areas with dissimilar physiognomic structure, the daily capture data of the three populations in the two plots were charted on a graph so that the daily and monthly changes in population dynamics can demonstratively indicate changes in space use (Fig. 6.). In the case of yellow-necked wood mouse, even the August data were remarkable, as capture maxima in the two areas appeared distinctly even within the five-day trapping session. In the closed forest, the capture peak occurred in the first few days, whereas in the regrowing plot it commenced in the second half of the period. From data of the two autumn months it clearly appears that individuals of the population tended to leave the regrowing area and occupied the closed forest where the spatial arrangement of the population then stabilised. For the striped field mouse, capture maximum clearly occurred in August in the regrowing plot, with its abundance decreasing gradually in the closed alder gallery forest, to disappear completely from this area by November. In the more open habitat its spatial structure stabilised, its abundance not reaching the August maximum. The population of bank voles in August-September had higher abundance in the closed forest, then in November it had higher capture rates in the regrowing plot (Fig. 6.). Looking at the trend of population sizes throughout the months, the most striking shift between the use of the two habitats was observed in the case of the yellow-necked wood mouse and the striped field mouse. As to the bank vole, its appearance in the regrowing plot is a result of dispersal, shown by the fact that a part of the population, with similar size to that migrating to the open area, stayed in the closed forest. Emigration from the closed alder gallery forest can be assumed, even if capture coordi-

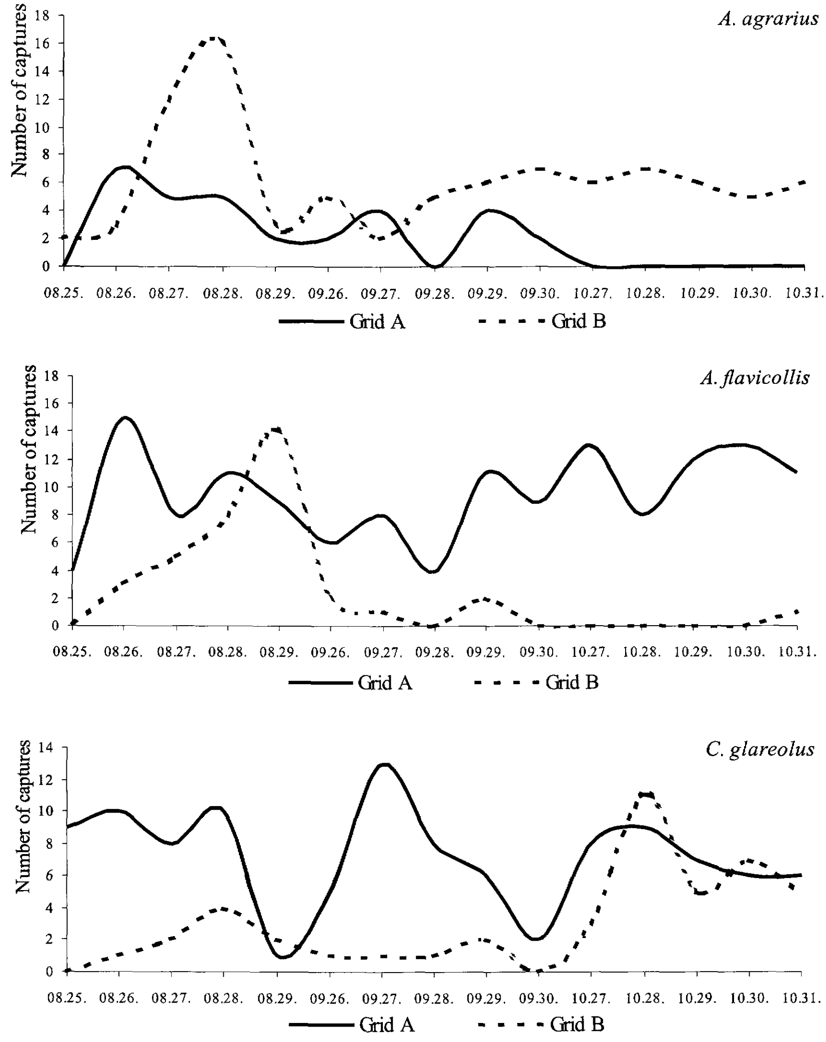

Fig. 6.: Daily capture numbers of the three characteristic species during the three sample months in Grids A and B of the sample area of Lankóci forest in 2004

nates of individuals caught at least twice did non confirm i.e. it was not possible to show individuals that proved this migration direction.

The program Biotas, compatible with GIS softwares, is capable of displaying the spatial arrangement of several populations together, based on which it is possible to calculate spatial association between two particular populations. Similarly to the evaluation of populations one by one, we calculated spatial association between species pairs on a monthly basis, regarding the entire study area (Grids A and B together). Yates correction χ^2-values obtained for the August data were low in all three species pairs (*A. agrarius vs. A. flavicollis, A. agrarius vs. C. glareolus, A. flavicollis* vs. *C. glareolus*), thus significant spatial association - i.e. statistically confirmed common space use - could not be proved in either of the pairings ($\chi^2 = 0.008 - 0.506$, NS). For September 2004 there was no significant spatial association for the pairs *A. agrarius* vs. *A. flavicollis* and *A. agrarius* vs. *C. glareolus* ($\chi^2 = 0.4 - 0.68$, NS), sugesting that the two typical forest dwelling species (*A. flavicollis, C. glareolus*) are spatially separated from the population of the striped field mouse preferring more open areas yet having wide tolerance in terms of habitat. However, in the pairing of *A. flavicollis* vs. *C. glareolus* significant spatial association was observed ($\chi^2 = 6.95$, $p < 0.05$). In September, the yellow-necked wood mouse completely moved into the closed forest, and also the bank vole population increased in the area near the closed alder gallery forest. Consequently, the two populations had to share habitats in the protected forest section at a greater degree, the significant spatial association thus being the result of higher spatial overlap in September. For the November capture data, low, non-significant levels of association were obtained again in all three pairings ($\chi^2 = 1.18 - 1.84$, NS). This result, too, suggests that this month individuals of the various populations were arranged in a way that spatial overlap is minimal, the three populations trying to occupy suitable habitat patches in segregation from each other. The detailed seasonal analysis of population dynamics and spatial organisation of species suggests that by November, after density peaks, the species are already arranged according to their winter survival strategies. Because unexpected results were produced in that month - especially in terms of the spatial distribution of the bank vole - we therefore charted the November capture and location data of the three frequent species together. In that graph capture locations of individuals of the three species, and hexagonal grids corresponding to space coverage. That way, graphics show the areas that are separated with no overlap between populations, as well as those with spatial overlap between two or three populations (Fig. 7.).

Based on spatial distributions observed by early November, the area of the closed alder gallery forest was occupied by individuals of the yellow-necked wood mouse and the bank vole populations. In the larger, central part of the 1 hectare forest section only yellow-necked wood mice had their home ranges. In the inner, marginal rows of the grid where higher bank vole capture densities occurred in August and September, the habitat use of the two populations overlapped in November. There were yet another two patches in the closed forest with the space use of the two typically forest-dwelling species overlapping in November, both areas touching the border zone towards Grid B. Based on our November data, the most striking result in Grid B was that bank voles, a species with higher capture frequency, gained space. Thus, it was mostly the striped field mouse and the bank vole that shared among themselves the more open, regrowing forest area. Bank voles were present in higher numbers in the section of Grid B closer to the forestry road, whereas the striped field mouse tended to use the more centrally located areas where in small patches it had habitat overlap with bank voles that had much lower capture frequencies (Fig. 7.).

Conclusions

Research done both in nearctic and palearctic temperate regions has proved that small mammals are important indicator objects, signifying degradation processes of the areas, as well as the harmful effects of forestry interventions that decrease biological diversity (e.g. MAZURKIEWICZ 1984, STEPHENSON 1993, LINZEY and KESNER 1997, SAITOH and NAKATSU 1997, STEVENS and HUSBAND 1998). Long-term studies have also revealed how drastic changes to ecological background parameters (e.g. droughts that can influence

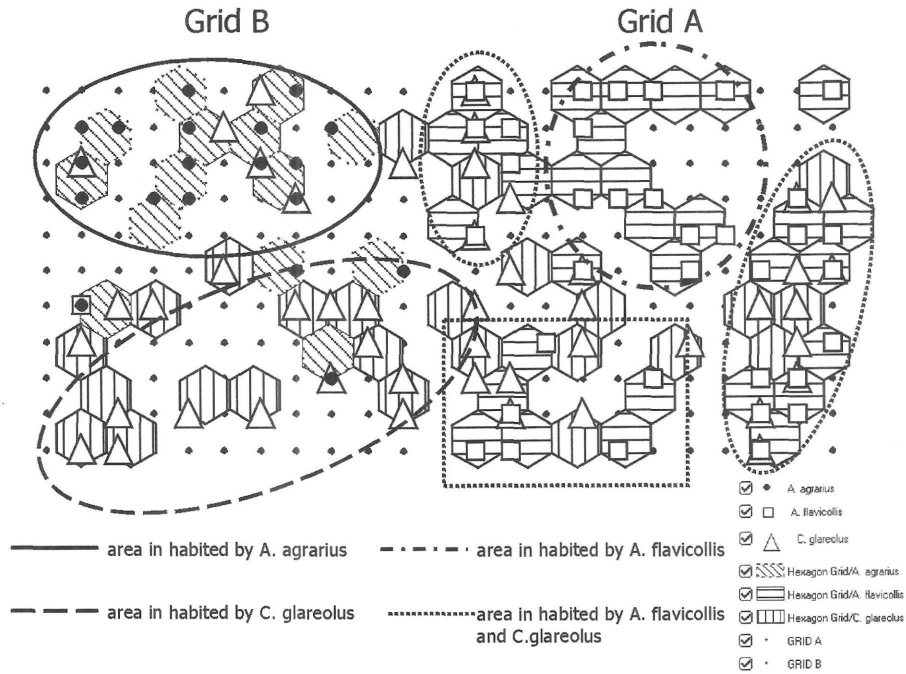

Fig. 7.: Space use and spatial overlap by the three frequent species after the density peak in 2004 in the alder gallery forest and in the regrowing forest

structural factors of floodland forests, or considerable water cover) acting as environmental disturbance can transform quantitative characteristics of small mammal populations and their spatial patterns. In the case of small mammals acting as indicator species, positive or negative changes in the quality of habitats are signified by transformations in the structure of their populations and communities.

In the first three years (2000-2002) of small mammal monitoring in Lankóci-forest in the upper Hungarian reach of river Drava we had samplings only in the strictly protected closed alder gallery forest where 8 small mammal species (5 rodents and 3 shrews) were recorded. The results of that trapping period have already been compared in our other papers with data from a long-term monitoring in a lowland oak-hornbeam forest (Bükkhát-forest, Baranya county) where the 10-year investigation yielded occurrence data of a total of 10 small mammal species (HORVÁTH et al. 2004). These 8 and 10 species, respectively, that were shown in our investigations can be regarded as good results: both the drier lowland oak forest and the alder bog forest studied in the upper Drava reach are quite diverse if compared with surveys of small mammal communities of other European temperate forests. As part of the IBP programme, JENSEN (1975) made surveys in beech forests and recorded 8 species (2 shrews and 6 rodents). HAFERKORN (1994) recorded 6 species in ash-elm gallery forest, but due to the insufficiency of data, for several years he could track the dynamics of three populations only. JUCHIEWICZ et al. (1986) performed small mammal community investigations in beechwoods and pine forests in the Carpathians, revealing 6 species in both habitat types, but with no considerable difference in diversities (although data were not analysed statistically). In two out of three study years, the small mammal community turned out to be more diverse in the pine forest.

During the studies in 2003-2004 analysed in the present paper, the number of species recorded decreased because of the unfavourable survival conditions in 2003, despite that the regrowing forest area neighbouring the strictly protected forest section was also introduced to the investigations. Changes in environmental conditions had the greatest influence on the bank vole population which had twice or three times higher densities in earlier years than had the *Apodemus* species that were characteristic species in the present study period as well. Due to more favourable survival conditions, capture parameters improved in 2004, based on which it was possible to analyse the space use and spatial overlap of the three most frequent species, as well as we could determine any spatial association between their populations. We clearly showed a shift in area and habitat use by the two *Apodemus* populations in autumn, and the higher bank vole capture frequency in the regrowing area around November was explained by emigration starting from the closed forest as abundance grew. However, due to the low rate of recaptured individuals we could not directly confirm the assumed directions of migration. In the case of striped field mouse, the preference of the edge zone of forest habitats could be demonstrated here in Lankóci forest too, as well as the fact that in this habitat individuals of the population dispersed in the regrowing area instead of the closed forest. Looking at the edge zone - closed forest gradient, it was the A. agrarius population that was present with higher abundance in the edge zones than in the central and inner patches of the studied forest section. This phenomenon has been noted earlier for this species in papers produced at our department (HORVÁTH et al. 1996, HORVÁTH et al. 2001). The considerable degree of dispersion by *A. agrarius* in the regrowing area of Lankóci forest is primarily the result of habitat selection, and is caused also by competition between populations of the the three dominant species (*A. agrarius, A. flavicollis, C. glareolus*) (ZEJDA 1967, GLIWICZ 1984, CHELKOWSKA et al. 1985). In the case of the bank vole, the pure faunal evaluation of capture data, the statistical analysis of relative proportions, and results from the investigation of space use by the population all suggest that it was a pronounced surge of emigration that caused the observed spatial pattern between the closed alder gallery forest and the regrowing area, possibly enhanced by competition with the yellow-necked wood mouse showing similar densities (GLIWICZ 1981, 1984). Of course this cannot be proved during a single trapping period, but the distribution of individuals does follow the arrangement of resources (shelter, food), which is probably entirely different in respect of the two areas in November than in the summer months.

With a view to the results having gained we believe that continuing monitoring is important; the synchronous monitoring of the two habitats with different vegetation structure has yielded many information about small mammal ecology, despite the fact that the year 2003 had low density values. Based on longer term studies it will be possible to seek answer to such actual questions about the upper Drava reach like how drastic changes in the water regimes of floodland forests influence the spatial patterns and demographic fluctuations of settling and dispersing small mammals.

Acknowledgement

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Kisemlősök populációdinamikája és térbeli mintázata védett erdei és újraerdősödő területen

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A Dráva felső szakasza mentén 2003-2004-ben a kisemlősök elevenfogó csapdázásos monitorozását végeztük fogás-jelölés-visszafogás módszerrel. Mintaterületünk egy fokozottan védett égerligetben (Lankóci-erdő) és az ezzel szomszédos, 2000-ben tarra vágott, majd fokozatosan újraerdősödő területen volt. A két évében összesen 9 kisemlős fajt mutattunk ki a két területen működtetett, egyenként 1 ha-os mintavételi kvadráttal. Az itt található kisemlős közösségnek három karakter rágcsáló faja (*Apodemus flavicollis, A. agrarius, Clethrionomys glareolus*), valamint gyakoribb két cickányfaj (*Sorex araneus, Crocidura leucodon*) volt. A napi fogási adatokból a populációkat zártnak feltételezve becsültük a három karakter rágcsáló populáció méretét. A legtöbb becsült értéket a két *Apodemus* (*A. agrarius* és *A. flavicollis*) populációnál kaptuk. Az erdei pocok populáció méretét csak a zárt védett erdő adataiból tudtuk becsülni. A legközelebbi szomszéd módszerrel végzett térbeli elemzés azt mutatta, hogy a gyakori populációk egyedei az egyenletes eloszlásra törekedtek, ami mind a kisebb sűrűségű 2003-as, valamin a nagyobb denzitású 2004-es évben is jellemző volt. A két *Apodemus* (*A. agrarius, A. flavicollis*) populációnál az őszi időszakban egyértelműen kimutattuk a terület-, illetve élőhely-váltást, míg az erdei pocoknál a népesség növekedésével a zárt erdőből kiinduló emigráció eredményeként értelmeztük az újraerdősödő területen novemberre megjelenő nagyobb fogási gyakoriságot. A kevés többször visszafogott egyed azonban nem tudta konkrétan igazolni a feltételezett migrációs útvonalakat. A térbeli mintázat 2004-es részletesebb elemzése azt sugallta, hogy ősz végén a fajok már a téli túlélési stratégiának megfelelően rendeződtek. Ebben az időszakban a térbeli eloszlások alapján a zárt égerliget területét a sárganyakú erdeiegér és az erdei pocok populáció egyedei foglalták el. A kijelölt 1 ha-os erdőtag belső, nagyobb részében inkább a sárganyakú erdeiegér egyedek jelölték ki mozgáskörzeteiket. A pirók erdeiegér kizárólag az újraerdősödő területet foglalta el. Jelentős területet használva, az újraerdősödő területen az erdei pocok jelent meg mellette, amely eredmény ennél a fajnál a két terület közötti jelentős populáció transzlokáció tényét bizonyította.