SPATIAL DISTRIBUTION OF SMALL MAMMAL POPULATIONS IN DRAVA FLOODPLAIN FOREST

PROSTORNA DISTRIBUCIJA POPULACIJA SITNIH SISAVACA U POPLAVNOJ ŠUMI UZ DRAVU

Győző F. HORVÁTH[1], Dávid SCHÄFFER[1], Ákos POGÁNY[2], Dániel TÓTH[1]

Summary

In the present study we examined the spatial distribution of the small mammals of a floodplain forest by River Drava based on a three-year live trapping (capture-mark-recapture). We registered the presence of 5 shrew and 5 rodent species between 2001 and 2003. Of them *Apodemus agrarius*, *A. flavicollis*, *Myodes glareolus* and *Sorex araneus* were generally typical in the region. In our examination striped field mouse was the most frequently recorded species. The habitat use of the Apodemus species was equal, however the habitat use of bank vole was the opposite, preferring the area between the river and the dirt road. This indicates the spatial segregation of the bank vole and the two mouse species. Striped field mice travelled greater distances than bank voles did. Yellow-necked mouse individuals covered significantly greater movement distances than striped field mice. As suggested by our study, the dirt road as a dividing line of the trapped forests had no barrier effect on the movements of individuals of the three rodent populations.

KEY WORDS: floodplain forest, small mammals, capture-mark-recapture, spatial association

Introduction
Uvod

There are several environmental factors, which affect the spatial pattern of populations and influence the formation of unique motion patterns, for instance the availability of resources, the risk of predation and other abiotic environmental factors. These factors have mostly heterogeneous spatial distribution, therefore show mosaic-like pattern (Ims 1995). Understanding the temporal and spatial scales at which organisms perceive and respond to their environment is a central issue in ecology (Wiens 1989), although there has been a tendency by ecologists to study many phenomena within a narrow range of scales (Morris 1987a, 1987b, Bowman et al. 2000).

Floodplain and riparian areas are valuable ecosystems on every forest landscapes because of their high productivity and their inherent connection with the rest of the watershed. Riparian areas within forests are generally cooler, moister, and structurally more complex and more productive than the upland areas, so they afford home to distinct communities of plants and animals very often (McComb et al. 1993, Kelsey & West 1998). Small mammals play important roles in the riparian forest (Cockle & Richardson 2003), because they are the primary prey of many predators (Kelsey & West 1998, Hanski et al. 2001), some of them affect plant species composition and soil fertility through selective herbivory and seed dispersal (Sirotnak 2000) and finally because of their feeding and burrowing activities and their role in food webs (Wijnhoven et al. 2005, 2006). Small rodents are also an important factor in the regeneration of forest stands (Heroldová 2007, 2008, Suchomel 2008).

Periodic floods are important extrinsic environmental factors in riverine ecosystems. Flooding has a considerably negative impact on small mammal populations resulting in high mortality, and restricting their presence to refuges on elevated terrains after inundation (Pachinger & Haferkorn 1998, Andersen et al. 2000, Wijnhoven et al. 2005). Riverine landscapes are

[1]University of Pécs, Institute of Biology, Department of Animal Ecology, H-7624 Pécs, Ifjúság u. 6., Hungary, e-mail: hgypte@gamma.ttk.pte.hu
[2]Eötvös Lóránd University, Institute of Biology, Department of Ethology, H-1117 Budapest, Pázmány Péter sétány 1/C., Hungary

dynamic, biologically and spatially complex (Robinson et al. 2002). There are numerous factors in these ecosystems which determine the dispersal and spatial patterns of small mammals, such as the characteristics and connectivity of landscape elements, the presence and characteristics of barriers and the suitable habitat's spatial arrangement (Kozakiewicz 1993, Peles et al. 1999, Romanowski et al. 2008). The probability of local extinction and recolonization depends on the level of isolation of single patches in a heterogeneous landscape (Den Boer 1981, Fahrig & Merriam 1985). Therefore the distances which animals are able to cover and by that the level of their isolation are very important factors in the maintenance of the isolated population. The knowledge of animal motion probability and the covered distances contributes to understanding the stability of the whole ecological landscape (Adler 1987, Kozakiewicz 1993, Ims 1995).

There are still numerous semi-natural riparian and gallery forests along River Drava in South Hungary, which have mosaic-like pattern. The importance of River Drava from the aspect of Hungarian and European nature conservation is ensured by rare and threatened habitat types. River Drava is characterised with dynamic bank-destructing, bank-building and shoal-creating activity resulting in a diverse range of habitats. River Drava, as an ecological corridor and a continuous system of habitats is threatened by human disturbance (e.g. gravel mining, timber harvesting, clear-cutting), although the whole river is the part of Duna-Drava National Park and NATURA 2000 network (Závoczky 2005).

In the present study, we examined the small mammal population of a floodplain willow-poplar forest lying by the River Drava, laying emphasis on the spatial distribution of dominant species. The study investigates (*i*) how much the relative proportion of single species differs within the small mammal community in the examined years on the floodplain area and (*ii*) what kind of difference can be experience in the habitat use of the dominant species.

Materials and methods
Materijal i metode

Study area – Područje istraživanja

Trapping lines were traced out in a willow-poplar floodplain forest (*Salici-Populetum*) by River Drava, close to the village of Vízvár (46°5'N, 17°13'E). The mean width of the river basin is 150–400 m and the depth of the riverbed is 3–5 m with a maximum of 12 m. Higher water levels and floodings are typical in May–June and October–November, while low water levels can be seen in late summer and winter. Therefore, the changing in water level dynamics is an important limiting factor in the survival of coastal habitats and plays an admittedly important role in the survival of terrestrial species living here. As a second zone of the coastal zonation of rivers and streams, azonal high forests are found in the deeper parts of the low floodplains on young alluvial soils. The water turnover of these soils is relatively balanced, due to the degree of soil compactness.

The canopy layer of the willow grove is usually partially closed (50–70 %), sometimes reaching 25 m height. The grove is mostly formed by white willow (*Salix alba*) but there are some substances where crack willow (*S. fragilis*) forms the consociation. The lower canopy layer has 5–30 % coverage and its height is 10–15 m. Next to the juvenile individuals of the white- and crack willow, other tree species – e.g. European alder (*Alnus glutinosa*) or the European white elm (*Ulmus laevis*) occur only rarely. Their shrub layer is mostly absent and if present it is very thin. The herb layer shows great variety, it is well developed and has a coverage rate of 60–100 %. A specific facies of mostly marsh plants forms in this level, including slender tufted sedge (*Carex gracilis*), greater pond sedge and blister sedge (*Carex riparia, C. vesicaria*), common marsh bedstraw (*Galium palustre*), water forget-me-not (*Myosotis palustris*) and common reed (*Phragmites australis*).

Trapping protocol – Protokol hvatanja klopkama

We captured the small mammals with live trapping through the examination and we used capture-mark-recapture (CMR) method with the same box-type live-traps (75x95x180 mm). Just like the traps themselves, the trapping technique was also alike in all sampling periods: bacon and cereals were mixed with aniseed extract and they were used with vegetable oil as bait. In line with the protocol we performed 5-night long trapping sessions, the traps were checked two times a day (7 am and 7 pm), and the traps were triggered during the day. For individual identification of the animals toe tattoo was used.

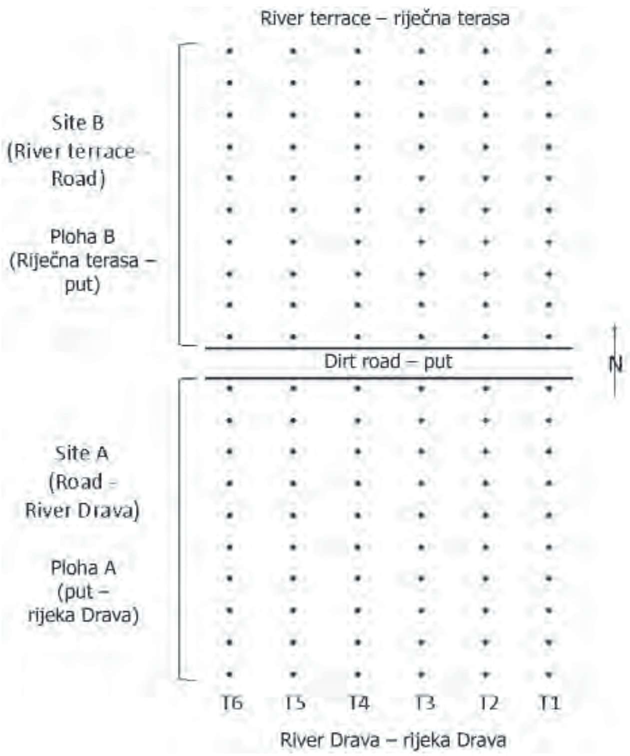

Figure 1 The location of the trap points and the transects as traced out near Vízvár

Slika 1. Mjesta i transekti postavljanja klopki kod sela Vízvár

We also recorded the sex, potential reproductive status (by females: gravidity or lactation too), approximate age and body mass. Approximate ages were determined based on body mass and overall appearance.

The monitoring of small mammals took place from June 2001 to October 2003, and lasted between two outstandingly high floods (November 2000–June 2004) in comparison with normal spring and autumn high-water periods. Due to the tall and dense undergrowth the use of line transects was appropriate and suitable instead of regular quadrates, moreover, moving away from River Drava the spatial distribution of the individuals of each population and the migration relationships arising from the rising water levels were easier to examine by this method (Fig. 1). In this research, we used the collected data of captures for the examination of the spatial distribution of populations.

Statistical methods – Statističke metode

The relative number and trapping proportions of small mammals from the trapping parameters (number of captures and number of individuals) was counted. We involved those 4 character species in the analysis which were present in the area in all the three sampling years, including *Sorex araneus* (Linnaeus, 1758) among the shrews. Among the rodents, the three highlighted species were the striped field mouse, *Apodemus agrarius* (Pallas, 1771), the yellow-necked mouse, *Apodemus flavicollis* (Melchior, 1834) and the bank vole, *Myodes glareolus* (Schreber, 1780) which appeared with the highest abundance values. For evaluating the capture data of small mammals we considered the water level data of River Drava which were obtained from the South-Transdanubian Environmental Protection and Water Management Directorate. Water levels were measured along upper Drava, near Őrtilos, west from the sampled floodplain.

We used capture data of transects for the statistical analysis separately and the separated captures of the two areas together. The distribution of the trapping data of transects were tested by chi-square (χ^2) test for independence. Based on the proportion of captures of the 4 examined species we compared the areas by variance analysis (ANOVA, LSD-test) (Zar 1996). We calculated the habitat preference of the species with Ivlev-index (Ivlev 1961): $P_x=(a–b)/(a+b)$, where "a" is the proportion of the caught animals in the given area, "b" is the proportion of the given area in relation to the whole. "P_x" is the preference ($-1 \leq P_x \leq 1$) or avoidance in each area (+1 is absolute preference, –1 is absolute avoidance). Counting only the Ivlev-indexes is not sufficient for demonstrating whether the preference values of the habitat types are significant or not. Testing significance can be done by the use of Bonferroni *z*-test.

Spatial association and movement distances of individuals were analyzed by the Biotas 2.0 program. Association was counted between the 4 species in pairs, for A, B and the whole sampling area. For the examination of the movements of the character species' individuals we gave the coordinates of the transect trap points. Based on these coordinates the Biotas program computed the individuals' movement distances and patterns, relying on recapture data. When evaluating the movement vectors we counted on the basis of three rodents only from among the 4 sampled species because we recorded only few recaptures in case of the common shrew, therefore had a limited amount of applicable movement vectors.

Results
Rezultati

Spatial and temporal distribution of capture parameters – Prostorna i vremenska distibucija čimbenika ulova

We registered the presence of 5 shrew (*Soricomorpha*) and 5 rodent (*Rodentia*) species between 2001 and 2003 in the sampled floodplain forest of River Drava. The species composition of small mammal community of floodplain forest and the abundance values of the species differed in the three sampling years (Table 1). As seen from the water level dynamics between 2000 and 2005 there was more than 250 cm water level rising in November of 2000 and July of 2004 above the sampled flooding forest which caused the flooding of the trapped area, therefore the start and end of the three-year long capture activity were marked by the two flooding periods. We identified 949 small mammal individuals through the three years and comparing the single sampling years, there was a statistical difference in the number of small mammals. We captured the most individuals in 2002 which significantly differed from both the 2001 and the 2003 summarized abundance values ($\chi^2 = 40.23–132.57$, $P < 0.001$). Comparing the two years with lower abundance (correlated with the results of 2002) we received significant difference as well ($\chi^2 = 29.25$, $P < 0.001$) which can be a result of the collapse of the small mammal populations in 2003.

Contrasting the capture values with water level data of the Drava suggests that the higher capture success of 2002 may result from the lower water level in January (38.06 a.s.l.) which was the greatest water level decline between the two floods. The second highest water level developed by 2002 December (211.64 a.s.l.) therefore small mammals could reach an expansive dispersal till the trapping months of 2002 which was not affected by the drastic change in water level values. Following the high water in December 2002, water levels followed a decreasing tendency in 2003, due to drier weather. In spite of this, small mammal capture numbers also declined in the summer and autumn of 2003, suggesting that the local density of species decreased even without the negative effect of high water levels, as a result of which the expected autumn density boom, typical of small mammals, did not set in (Fig. 2).

We examined the relative abundance values of the species throughout the given years. Only the species recorded in all 3 years were analysed. Common shrew showed significant differences between the years ($\chi^2 = 8.00$, $P < 0.05$) which was due to the large increase of the proportion of this species in 2003. For the abundance of bank vole we received significant differences as well ($\chi^2 = 13.43$, $P < 0.01$) comparing the years, which

Table 1. Number of individuals and relative abundance values of small mammals in the sampling years
Tablica 1. Broj primjeraka i relativna brojnost sitnih sisavaca u godini uzorkovanja

Number of individuals (n_i) and relative abundance (p_i) / Sampling years	2001		2002		2003	
Species – Vrsta	n_i	p_i (%)	n_i	p_i (%)	n_i	p_i (%)
Sorex araneus (Linnaeus, 1758)	14	4.71	29	6.13	28	15.64
Sorex minutus (Linnaeus, 1758)	–	–	–	–	3	1.67
Neomys fodiens (Pennant, 1771)	6	2.02	–	–	–	–
Crocidura suaveolens (Pallas, 1811)	–	–	1	0.21	–	–
Crocidura leucodon (Hermann, 1780)	6	2.02	2	0.42	–	–
Myodes glareolus (Schreber, 1780)	34	11.45	176	37.21	53	29.61
Apodemus agrarius (Pallas, 1771)	199	67.00	236	49.90	85	47.49
Apodemus flavicollis (Melchior, 1834)	38	12.80	29	6.13	8	4.47
Apodemus sylvaticus (Linnaeus, 1758)	–	–	–	–	1	0.56
Mus spicilegus (Petényi, 1882)	–	–	–	–	1	0.56
Total – Ukupno	297	100	473	100	179	100

resulted from the low values of 2001. There were no significant differences in the abundance values of the striped field mouse and the yellow-necked mouse between the years (C^2 = 4.13–4.98, n.s.), the proportion of these species were balanced in every sampled year.

The mean capture proportions were analysed by comparing the species and sampling years (Fig. 3). The proportion of striped field mouse was the highest in every year. Common shrew got the smallest capture proportion in 2001, and the relative abundance values of yellow-necked mouse and bank vole were approximately equal, however the proportion of striped field mouse was 7 times greater than the latter two typically forest-living rodents. The proportion of bank vole increased till 2002 while yellow-necked mouse and common shrew occurred with the same low frequency. The distribution of the capture frequencies of the three rodents was similar in 2003 compared to the value of the previous year, however, the proportion of common shrew increased in comparison with the registered frequency values of the previous two years. Therefore, based on Kruskal-Wallis test there was a significant difference between the frequency values of the capture of the species in all 3 years (2001: $H = 30.479$, $P < 0.001$, 2002: $H = 38.642$, $P < 0.001$, 2003: $H = 33.625$, $P < 0.001$). The Kruskal-Wallis test did not give a significant result in case of the yellow-necked mouse when the sampled years were compared ($H = 4.981$, n.s.), the capture data of this species remaining balanced through the years. However, regarding the capture frequencies of the other three species, there was significant difference between the years (*A. agrarius*: $H = 11.864$, $P < 0.05$, *M. glareolus*: $H = 19.039$, $P < 0.01$, *S. araneus*: $H = 8.335$, $P < 0.05$).

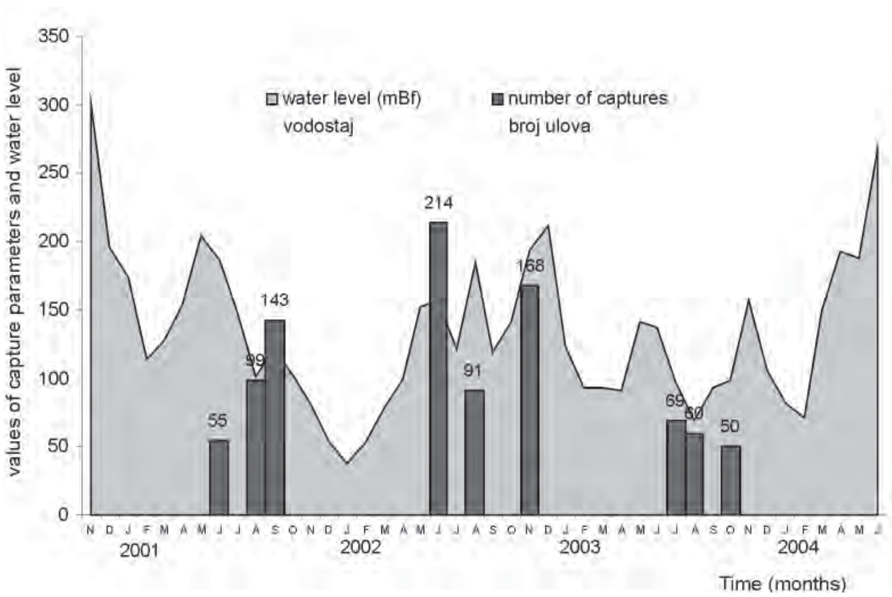

Figure 2 Water levels of River Drava and small mammal capture numbers during the three-year long monitoring period
Slika 2. Vodostaj rijeke Drave i broj ulova sitnih sisavaca tijekom trogodišnjeg monitoringa

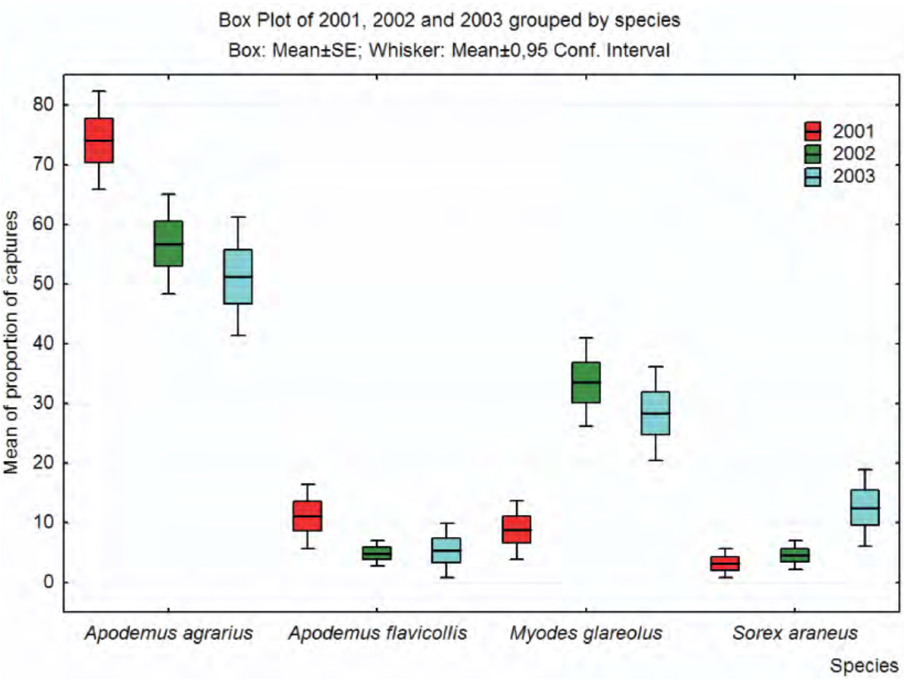

Figure 3 Distribution of mean capture proportion values of the four examined small mammal species

Slika 3. Distribucija srednjih vrijednosti udjela ulovljenih četiriju vrsta sitnih sisavaca

We evaluated the capture results of the four typical small mammal species in respect of the two areas separated by the dirt road as well. The mean capture numbers of the two separated forest sites showed that the four examined species used the two sites equally therefore the variance analysis gave no significant result in the comparison of the capture proportions of the two areas separated by a dirt road (Kruskal-Wallis ANOVA: H = 0.362–1.881, n.s.). Furthermore, using Ivlev's habitat preference calculation we examined the habitat usage of the two forest sites compared to the whole forest area covered by the six transects. In case of the two *Apodemus* species we revealed the same habitat preference (Fig. 4): in 2001 the woodland between River Drava and the dirt road (Site A) was preferred both species, while the two mice avoided this woodland in 2002. In case of the bank vole we observed contrary habitat use with the two *Apodemus* species in 2001 and 2002. The result of area preference calculation from the two years capture data suggested a strategy leading towards the spatial segregation of the bank vole and the two mice species. The common shrew, with the increase of its area occupation rate in 2002–2003, preferred significantly the area lying close to the river which justified the shrew's presence associated with wet areas (Fig. 4).

Spatial association and movement distance – Prostorna povezanost i udaljenost kretanja

We analysed the habitat use and the overlap of the four examined species with reference to the grid defined by the trap stations of the transects. All significant spatial association values were positive in all cases (Table 2) which referred to a considerable spatial overlap and common habitat usage. There was significant positive association between yellow-necked mouse and bank vole on the dirt road-river terrace area in 2001. The same positive association appeared in 2002 between the two species as well, also between dirt road and the river terrace, however we could not show any significant association between these species in 2003. In case of the striped filed mouse and the bank vole, there was significant association between dirt road and the river terrace or rather the road and Drava, but considering the whole area we did not receive a significant value. In 2003 it was a significant positive association between the species in case of the area lying between the dirt road and Drava. Between yellow-necked mouse and common shrew we received significant positive spatial association for the whole area in 2002, however, when examining the two areas separately we could prove a significant positive association only between the road and the river terrace. There was a significant positive association between the striped field mouse and the common shrew in the area between the dirt road and River Drava (A) in 2003 (Table 2).

Regarding the analysis of the association, it is important to look back at the results of the preference of the two forest-sites separated by a dirt road. Although the bank vole used the two forest areas with opposite preference in 2001 and 2002 which suggested that the species avoids the sites used by the two competing mice, but concerning the interspecific spatial association, its spatial segregation was successful only against the striped field mouse in 2001; in 2002 the vole's significant spatial overlap was observed with both Apodemus species, which fact was reflected for this year by the significant association values as well.

We evaluated the movement distances of the three frequent rodents in the analysis of spatial distribution of the fragmented floodplain forest. Based on the three sampling years the movement distances of striped field mouse had the greatest standard deviation, the average movement distance of the species showing an increasing tendency between 2001 and 2003. The most balanced and largest average movement distances were recorded for the yellow-necked mouse while the smallest move-

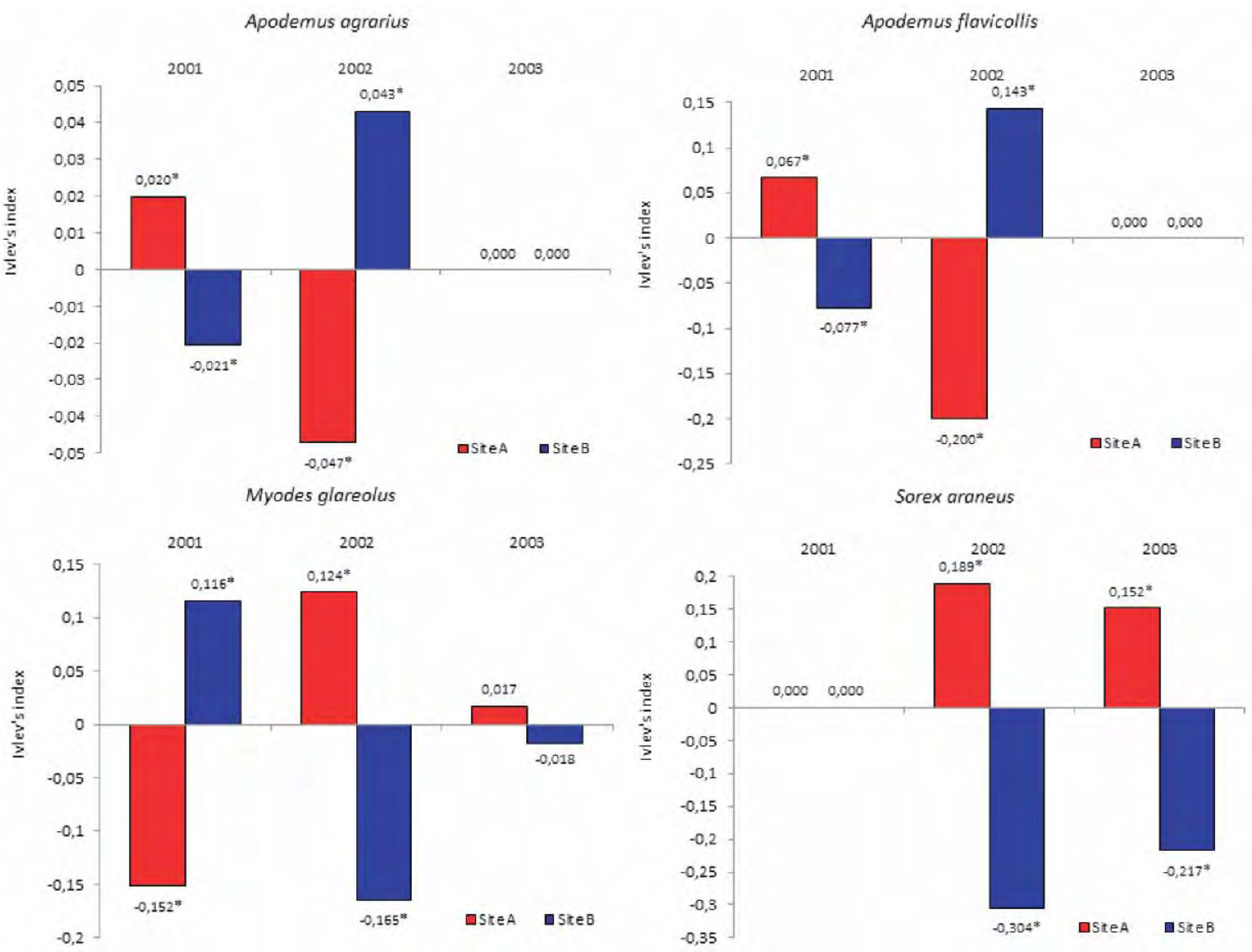

Figure 4. Values of habitat preference based on Ivlev's index of the four species (*: significant)
Slika 4. Vrijednosti preferencije staništa na temelju Ivlev-ovog indeksa za četiri vrste (*: signifikantna razlika)

ment distance was typical for the bank vole (Fig. 5). Bank vole could be characterised by approximately average movement distances in 2001 and 2002, but the mean of its movement distances decreased in 2003. Based on the statistics of movement distance values, the yellow-necked mouse covered significantly greater distances than the bank vole (ANOVA: $F = 20.97$, $P < 0.01$; LSD test: $P = 0.0013$) and the striped field mouse, the latter characterised by rapid, expansive dispersal (ANOVA: $F = 20.97$, $P < 0.01$; LSD test: $P = 0.0063$). It was the bank vole that covered the smallest average distances in the comparison of the three examined rodents.

Table 2. Spatial association between the species pairs at the two sampling sites and for the whole area (A: Road-Drava, B: River terrace-Road)
Tablica 2. Prostorna povezanost između parova vrsta sa dva mjesta uzorkovanja i cijelog područja (A: Put-Drava, B: Riječna terasa-Put)

Year Godina	Species pair	Site	Type of association	Yates Chi-square	*P*
2001	*A. flavicollis* + *M. glareolus*	River terrace-Road (B)	+	5.086	< 0.05
	A. agrarius + *M. glareolus*	Road-Drava (A)	+	20.089	< 0.001
	A. agrarius + *M. glareolus*	River terrace-Road (B)	+	10.500	< 0.001
2002	*A. flavicollis* + *M. glareolus*	River terrace-Road (B)	+	4.856	< 0.05
	A. flavicollis + *S. araneus*	Total area (Ukupno)	+	3.957	< 0.05
	A. flavicollis + *S. araneus*	River terrace-Road (B)	+	4.720	< 0.05
2003	*A. agrarius* + *M. glareolus*	Road-Drava (A)	+	7.424	< 0.01
	A. agrarius + *S. araneus*	Road-Drava (A)	+	5.239	< 0.05

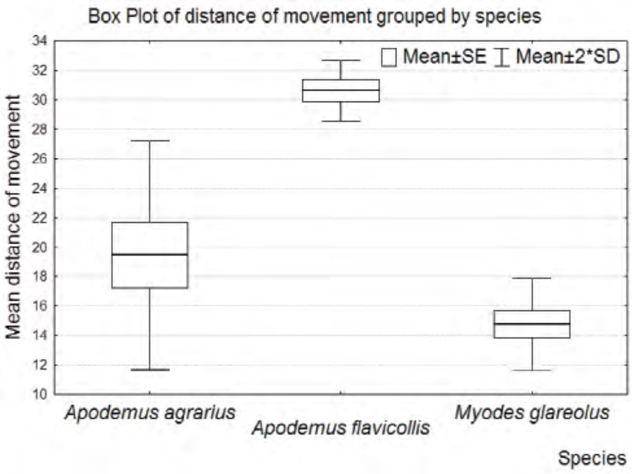

Figure 5. Mean distance of the movements of the three rodent species
Slika 5. Prosječne vrijednosti udaljenosti kretanja triju vrsta sitnih glodavaca

Discussion
Rasprava

In the present study we examined the spatial distribution of the small mammals of a willow-poplar floodplain forest by the upper River Drava located along the south-western boarder of Hungary, based on a three-year long live trapping (summer and autumn). Only fragments have remained along the Drava of the studied floodplain forest type, a hygrophilous azonic forest in the coastal zonation. In terms of the survival of the species, it is forest interventions (e.g. clear-cutting), dynamic changes in water level and thus the flooding of the forest areas that are the most important constraint variables. The effects of dynamic changes of environment as an ecological constraint are particularly important in case of terrestrial species on the floodplain areas. The heterogeneous landscape may change the spatial dynamics of species at the regional scale and consequently their local scale distribution and abundance (Ricklefs 2008). Small mammals represent an important component of these floodplain forest ecosystems. Therefore several researchers have studied the spatial-temporal patterns of terrestrial small mammals and took into consideration the effects (e.g. periodic floods) and processes (colonisation, recolonisation) in the former floodplain forests (Andersen et al. 2000, Wijnhoven et al. 2005, 2006).

In our examination, we captured the striped field mouse in the largest quantity which is a species capable for expansive dispersal. Haferkorn (1994) detected six small mammal species in the floodplain forest among River Elbe. Similar to our investigation the bank vole, the yellow-necked mouse and the common shrew were typical among the Elbe, but there the bank vole was the most common species. In the floodplain forest among Drava, bank vole was the second species of the dominance ranking. Mazurkiewicz (1994) pointed out that bank vole is numerically dominant in small mammal communities in temperate forests. Based on our studies among the upper section of Drava, bank vole was an absolutely dominant species in a lowland alder gallery forest (*Paridi quadrifoliae-Alnetum*) lying close to River Drava (Horváth et al. 2005). However, in our present study the dominance of bank vole was much smaller than the dominance of the striped field mouse in the examined floodplain forest (*Salici-Populetum*). Comparing our data from Drava's floodplain with data of Haferkorn (1994), there were greater differences in the appearance of rare species. By the Elbe banks e.g. the pygmy shrew (*S. minutus*) and the harvest mouse (*M. minutus*) were rare species, among which the harvest mouse did not appear in the floodplain forest along Drava, however depending on the water supply some shrew species appeared as rare species. *Crocidura* spp. (Lesser white-toothed shrew, bicoloured white-toothed shrew) indicated the drier periods while the water shrew (*N. fodiens*) indicated the wetter ones. In the Netherlands Wijnhoven et al. (2005) researchers trapped seven small mammal species from which five proved to be common. Common vole and bank vole occurred with the greatest density in that area. During the investigation they found major difference in the recolonisation of different small mammal species between two consecutive floods, which correlated with the quality and range of available habitat patches.

In our studies the sampling transects were arranged perpendicular to the Drava and followed the water gradient between the river and the river terrace. Our result showed that the success of acceptability of observed species does not depend on the spatial arrangement of transects. However, when analysing the annual data we obtained differences in the area preference of the various species. The habitat use of the two mice (*A. flavicollis*, *A. agrarius*) were the same, while the habitat use of bank vole was contrary; the vole mostly preferred the area between Drava and the dirt road, which suggested the spatial segregation of the bank vole and the two *Apodemus* species. These results confirmed the earlier studies of interspecies competition and spatial patterns (Gliwicz 1981, 1984; Mazurkiewicz & Rajska-Jurgiel 1998). Studies of the habitat selection of bank vole showed a preference towards older forest stands with dense ground cover in the form of undergrowth and dead woody material, providing food and coverage (Mazurkiewicz 1994, Miklos & Ziak 2002). Previous studies dealing with the population density and the spatial patterns showed that the density of yellow-necked mouse was always higher than the density of bank vole in smaller isolated forest patches (Rajska-Jurgiel & Mazurkiewicz 1988, Rajska-Jurgiel 1992), although the bank vole reached much higher densities in extended forests (Mazurkiewicz & Rajska-Jurgiel 1987). The bank vole is considered as an immovable species (Mazurkiewicz 1971, Löfgren 1995), while the yellow-necked mouse is more mobile (Bergstedt 1966, Mazurkiewicz & Rajska-Jurgiel 1987, see also Andrzejewski & Babińska-Werka 1986, Kozakiewicz & Szacki 1995, Liro & Szacki 1994). The mice are specialist from the perspective of habitats and live in alder texture forests (Montgomery 1980; Gurnell 1985).

The movement distance of striped field mouse had the highest standard deviation but despite of this, yellow-necked mouse covered significantly greater distances than the specimens of striped field mouse, a species that can have much higher dispersal movements (Liro & Szacki 1994). Yellow-necked mice travel significantly greater distances than the bank vole, a species characterised with the smallest movements in the comparison of the three rodent species. The movement distance of species is determined greatly by the species' typical seasonal dispersal pattern which occurs mostly in two different periods (spring and autumn) according to earlier studies in population of the yellow-necked mouse and the bank vole. The bimodal pattern of dispersal suggests that the two waves of dispersers move because of different reasons and those characteristics of dispersing individuals differ in the two periods of the year (Gliwicz 1988, 1992). According to our examinations the dirt road which divides the trapped forest into two parts has no barrier effect in case of the specimens of the three rodent populations. According to the study of Bakowski & Kozakiewicz (1988) a road which goes through a forest limits the movement of bank vole but has no effect on the movement of yellow-necked mouse. When studying the long-term movement of striped field mouse there was no significant difference in the sex, weight and the reproductive condition of the individuals that travelled long distances. Studies in a fragmented forest of Southeast Asia have also confirmed that the striped field mouse is less sensitive to the presence of roads then the related species (*Apodemus peninsule*). These studies showed that the roads have different effects on different small mammal species which affects their habitat selection (Rhim et al. 2003). Our results performed along River Drava showed that the striped field mouse used the two forest areas with of the same intensity and dispersed in the whole study area which contributed to an absolute dominance in the small mammal community. Because the intensity of the dispersal can increase together with the density of the population (Kozakiewicz 1976), the periods of seasonal dispersal patterns determine the number of movements across the road. The lower population density results in lower number of movements across the road. Bakowski & Kozakiewicz (1988) trapped in August which is a high-density period of the bank vole, thus the results justified even more the philopatry of bank vole which is also described by other studies (Mazurkiewicz 1994).

Long-term botanical studies of willow stand fragments in floodplains of River Drava have pointed out, that the coenological characteristics of the plant community changed from year to year. The analysis of data from the surveys together with field observations has clearly shown that these changes were closely related with changes in the water supply of the studied habitat (Juhász & Dénes 2005). Small mammals respond rapidly to such changes, thus they are good indicator objects in the study of natural and anthropogenic disturbance factors to the vegetation structure of forests. The spatial and temporal pattern of small mammals in floodplain forests is determined at the greatest degree by the fluctuation of water levels, the frequency of floods, and the duration of periods between high flood waves. Changing water levels as an ecological constraint factor can mean temporary habitat loss for small mammals and the shrinkage of dispersal possibilities. When flooding recedes and the negative constraint disappears, small mammals use different recolonisation strategies to spread in the floodplain area once again, in which various characteristics of the landscape play an important role (Wijnhoven et al. 2006).

Spatial behaviour may reflect population dynamics (Wiens et al. 1993), thus the relative habitat use and the spatial association of coexistent small mammals have been important research areas since long time ago. These contribute to understanding the environmental needs of different species and the intra- and interspecies relationships of these small mammals.

Conclusions
Zaključci

In the examined floodplain willow-poplar grove forest next to River Drava, the following conclusions were drawn from the CMR-trapping monitoring performed during the period between two substantial floods:

The species composition and species abundance values of the small mammal community in the floodplain forest were different in the three sampling years. The species number of the small mammal assemblage varied between 6 and 10, suggesting that species abundance can change in the short term as well, depending on environmental factors.

The dirt road had no barrier effect in the movement of individuals of the studied populations. Although the calculated area preference values showed variation among the years, our results suggested that a spatial segregation strategy was present in the relationship between bank vole and the two wood mouse species. These results confirmed the findings revealed by former investigations looking at competition and spatial relationships. As the space occupation of the water shrew increased, a significantly positive preference for areas along the Drava was found, confirming the association of this species with wet areas.

Our results obtained along the River Drava for the habitat generalist striped field mouse, a species often used as a model in movement pattern research, show that this species used both sides of the forest areas divided by the dirt road with the same intensity, dispersing in the entire studied forest, this behaviour leading to absolute dominance by this species within the small mammal community.

During the period between the two major floods, differences between yearly spatial relations among the dominant small mammals suggested fine differences in their strategies, expressed in interspecies relations, which allow the lasting coexistence of various small mammals in the rapidly changing, heterogeneous environment of floodplain forests.

Acknowledgement
Zahvala

Monitoring activities were supported by Dunav-Drava National Park Directorate. We are grateful to Jenő Purger for the Croatian translation.

References
Literatura

- Adler G.H., 1987: Influence of habitat structure on demography of two rodent species in eastern Massachusetts. Canadian Journal of Zoology, 65: 903–912.
- Andersen D.C., K.R. Wilson, M.S. Miller, M. Falck, 2000: Movement patterns of riparian small mammals during predictable floodplain inundation. Journal of Mammalogy, 81: 1087–1099.
- Andrzejewski R., J. Babińska-Werka, 1986: Bank vole populations: are their densities really high and individual home ranges small? Acta Theriologica, 31: 407–420.
- Bakowski C., M. Kozakiewicz, 1988: The effect of forest road on bank vole and yellow-necked mouse populations. Acta Theriologica, 33: 345–353.
- Bergstedt B., 1966: Home range and movements of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linne) in southern Sweden. Oikos, 17: 150–157.
- Bowman J., G. Forbes, T. Dilworth, 2000: The spatial scale of variability in small-mammal populations. Ecography, 23: 328–334.
- Cockle K.L., J.S. Richardson, 2003: Do riparian buffer strips mitigate the impacts of clearcutting on small mammals? Biological conservation, 113: 133–140.
- Den Boer P.J., 1981: On the survival of populations in a heterogeneous and variable environment. Oecologia, 50: 39–53.
- Fahrig L., G. Merriam, 1985: Habitat patch connectivity and population survival. Ecology, 66: 1762–1768.
- Gliwicz J., 1981: Competitive interactions within a forest rodent community in central Poland. Oikos, 37: 353–362.
- Gliwicz J., 1984: Competition among forest rodents: effects of *Apodemus flavicollis* and *Clethrionomys glareolus* on *A. agrarius*. Acta Zoologica Fennica, 172: 57–60.
- Gliwicz J., 1988: Seasonal dispersal in non-cyclic populations of *Clethrionomys glareolus* and *Apodemus flavicollis*. Acta Theriologica, 33: 263–272.
- Gliwicz J., 1992: Patterns of dispersal in non-cyclic populations of small rodents. In: Stenseth N.C., Jr W.Z. Lidicker (eds.): Animal dispersal: Small mammals as a model. Chapman & Hall, London: 147–159.
- Gurnell J., 1985: Woodland rodents communities. Symposia of London, 55: 377–411.
- Haferkorn J., 1994: Population ecology of small mammals in a floodplain forest in the central part of the Elbe river. Polish Ecological Studies, 20(3–4): 187–191.
- Hanski I., H. Henttonen, E. Korpim, L. Oksanen, P. Turchin, 2001: Small-rodent dynamics and predation. Ecology, 82: 1505–1520.
- Heroldová M., J. Suchomel, L. Purchart, M. Homolka, J. Kamler, 2007: Small forest rodents – an important factor in the regeneration of forest stands. Beskydy, 20: 217–220.
- Heroldová M., J. Suchomel, L. Purchart, M. Homolka, 2008: The role of granivorous forest rodents in beech regeneration in the Beskidy Mts. (Czech Republic). Beskydy, 1: 131–134.
- Horváth Gy., D. Molnár, G. Csonka, 2005: Population dynamics and spatial pattern of small mammals in protected forest and reforested area. Natura Somogyiensis, 7: 191–207.
- Ims R.A., 1995: Movement patterns related to spatial structures. In: Hansson L., L. Fahrig, G. Merriam (eds.): Mosaic Landscapes and Ecological Process. Chapman & Hall, London: 85–109.
- Ivlev V.S., 1961: Experimental ecology of the feeding of fishes. Yale University Press, New Haven Conn: 302
- Juhász M., A. Dénes, 2005: Biomonitoring of alluvial willow forests. Natura Somogyiensis, 7: 11–18.
- Kelsey K.A., S.D. West, 1998: Riparian Wildlife. In: Naiman R.J., R.E. Bilby (eds.): River Ecology and Management: Lessons from the Pacific Coastal Ecoregion. Springer-Verlag, New York: 235–258.
- Kozakiewicz M., 1976: Migratory tendencies in population of bank voles and description of migrants. Acta Theriologica, 21: 321–338.
- Kozakiewicz M., 1993: Habitat isolation and ecological barriers – the effect on small mammal populations and communities. Acta Theriologica, 38: 1–30.
- Kozakiewicz M., J. Szacki, 1995: Movements of small mammals in a landscape: Patch restriction or nomadism? In: Lidicker Jr W.Z. (ed.): Landscape approaches in mammalian ecology and conservation. University of Minnesota Press, Minneapolis: 78–94.
- Liro A., J. Szacki, 1994: Movements of small mammals along two ecological corridors in suburban Warsaw. Polish Ecological Studies, 20(3–4): 227–231.
- Löfgren O., 1995: Niche expansion and increased maturation rate of *Clethrionomys glareolus* in the absence of competitors. Journal of Mammalogy, 76(4): 1100–1112.
- Mazurkiewicz M., 1971: Shape, size and distribution of home ranges of *Clethrionomys glareolus* (Schreber, 1780). Acta Theriologica, 16: 23–60.
- Mazurkiewicz M., 1994: Factors influencing the distribution of the bank vole in forest habitats. Acta Theriologica, 39(2): 113–126
- Mazurkiewicz M., E. Rajska-Jurgiel, 1987: Numbers, species composition and residency of a rodent community in forest and field-forest ecotones. Acta Theriologica, 32: 413–432.
- Mazurkiewicz M., E. Rajska-Jurgiel, 1998: Spatial behavior and population dynamics of woodland rodents. Acta Theriologica, 43: 137–161.
- McComb W.C., K. McGarigal, R.G. Anthony, 1993: Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, western Oregon. Northwest Science, 67: 7–15.
- Miklos P., D. Ziak, 2002: Microhabitat selection by three small mammal species in oak-elm forest. Folia Zoologica, 51: 275–288.
- Montgomery W.I., 1980: Population structure and dynamic of sympatric *Apodemus* species (Rodentia: Muridae). Journal Zoology of London, 192: 351–377.
- Morris D.W., 1987a: Ecological scale and habitat use. Ecology, 68: 362–369.
- Morris D.W., 1987b: Spatial scale and the cost of density-dependent habitat selection. Evolutionary Ecology, 1: 379–388.
- Pachinger K., J. Haferkorn, 1998: Comparison of the small mammal communities in floodplain forests at the Danube and Elbe rivers. Ekológia (Bratislava), 17: 11–19.
- Peles J.D., D.R. Bowne, G.W. Barrett, 1999: Influence of landscape structure on movement patterns of small mammals. In: Barrett G.W., J.D. Peles (eds.): Landscape Ecology of Small Mammals. Springer Verlag, New York: 41–62.
- Rajska-Jurgiel E., 1992: Demography of woodland rodents in fragmented habitat. Acta Theriologica, 37: 73–90.
- Rajska-Jurgiel E., M. Mazurkiewicz, 1988: The effect of spatial structure of environment on density of rodents in suburban zone. Polish Ecological Studies, 14: 145–169.

- Rhim S.J., C.B. Lee, W.H. Hur, Y.S. Park, S.Y. Choi, R. Piao, W.S. Lee, 2003: Influence of roads on small rodents population in fragmented forest areas, South Korea. Journal of Forestry Research, 14(2): 155–158.
- Ricklefs R.E., 2008: Desintegration of the ecological community. The American Naturalist, 172: 741–750.
- Robinson C.T., K. Tockner, J.V. Ward, 2002: The fauna of dynamic riverine landscapes. Freshwater Biology, 47: 661–677.
- Romanowski J., D. Dudek, K. Kowalczyk. 2008: The role of islands in maintaining the connectivity of habitat for mammals in middle Vistula river valley. Ecohydrology & Hidrobiology, 8: 411–418.
- Sirotnak J.M., 2000: Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. Ecology, 81: 78–87.
- Suchomel J., 2008: A contribution towards the knowledge of the effect of small mammals on the regeneration of forest trees in selected stands of the Keleč Upland (Czech Republic). Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis, LVI: 267–270.
- Wiens J.A., 1989: Spatial scaling in ecology. Functional Ecology 3: 385–397.
- Wiens J.A., N.C. Stenseth, B. Van Horne, R.A. Ims, 1993: Ecological mechanism and landscape ecology. Oikos, 66: 369–380.
- Wijnhoven S., G. van der Velde, R.S.E.W. Leuven, A.J.M. Smits, 2005: Flooding ecology of voles, mice and shrews: the importance of geomorphological and vegetational heterogeneity in river floodplains. Acta Theriologica, 50: 453–473.
- Wijnhoven S., G. van der Velde, R.S.E.W. Leuven, A.J.M. Smits, 2006: Modelling recolonisation of heterogenous river floodplains by small mammals. Hydrobiologia, 565: 135–152.
- Zar J. H., 1996: Biostatistical analysis. Prentice-Hall International, Inc: 662
- Závoczky Sz., 2005: Hydroelectricity or national park? Natura Somogyiensis, 7: 5–9.

Sažetak:

Sitni sisavci igraju značajnu ulogu u poplavnoj šumi (Cockle & Richardson 2003), s obzirom da su primarni plijen mnogim grabežljivcima (Kelsey & West 1998, Hanski et al. 2001), preko selektivne herbivorije i rasprostiranja sjemena neki od njih utječu na sastav biljnih zajednica, pa čak i na plodnost tla (Sirotnak 2000), a preko ishrane i kopanja podzemnih tunela imaju ulogu u mreži ishrane (Wijnhoven et al. 2005, 2006). Sitni sisavci važni su čimbenici u obnovi šuma (Heroldová 2007, 2008, Suchomel 2008). Isto tako važan vanjski čimbenik okoliša u ekosustavu poplavne šume su periodične poplave, koje negativno djeluju na populacije sitnih sisavaca, s obzirom da rezultiraju velikom smrtnošću, a prisutnost sitnih sisavaca ograničavaju na uzdignutije terene (Pachinger & Haferkorn 1998, Andersen et al. 2000, Wijnhoven et al. 2005). U ovome radu prikazani su rezultati trogodišnjih istraživanja prostorne distribucije sitnih sisavaca u poplavnoj šumi uz rijeku Dravu. Rijeka Drava, kao ekološki koridor i kontinuirani sustav staništa, ugrožena je utjecajima čovjeka (npr. iskapanje šljunka i pijeska, gospodarenje šumama kao što su sječa i krčenje šuma), unatoč tomu što je rijeka cijelom dužinom dio Nacionalnog Parka Dunav-Drava i pripada mreži Natura 2000.

Sitni sisavci lovljeni su klopkama-živolovkama, a korištena je metoda ulov-markiranje-ponovni ulov (capture-mark-recapture – CMR) s intervalima lovljenja od pet noći. Uzorkovanje je provedeno u blizini sela Vízvár, uz Dravu u poplavnoj mekoj lišćarskoj šumi vrbe i topole (*Salici-Populetum*) (46°5'N, 17°13'E). Na prostoru između rijeke Drave i riječne terase, u poplavnoj šumi koju presjeca šumski put, postavljeno je šest linijskih transekata sa po10 klopki. Transekti su bili udaljeni jedan od drugog 10 m, a pružali su se s jedne strane u smijeru paralelno s Dravom, okomito na šumski put, a s druge strane puta u smijeru riječne terase (Slika 1). Monitoring je obavljan u razdoblju između dva iznimno visoka vodostaja (studeni 2000 i lipanj 2004), u usporedbi s proljetnim i jesenjim srednjim vodnim valom, karakterističnim za Dravu.

U statističku analizu uvrstili smo 4 karakteristične vrste koje su bile prisutne u sve tri godine istaživanja. Šumska rovka Sorex araneus (Linnaeus, 1758) bila je stalno prisutna i s relativno većom abundancijom bili su prisutni primjerci triju vrsta glodavaca: prugasti poljski miš Apodemus agrarius (Pallas, 1771), žutogrli šumski miš Apodemus flavicollis (Melchior, 1834) i riđa voluharica Myodes glareolus (Schreber, 1780). Istraživali smo vezanost ovih četiriju dominantnih vrsta za prostor u šumi sa dvije strane šumskog puta, povezanost vrsta u prostoru, kao i udaljenost kretanja jedinki koje pripadaju populacijama ovih vrsta.

U razdoblju od 2001. do 2003. godine zabilježili smo prisutnost 5 vrsta rovki i 5 vrsta glodavaca. Zajednica sitnih sisavaca u poplavnoj šumi, kao i vrijednosti abundancije pojedinih vrsta razlikovala se u trima godinama istraživanja (Tablica 1). Tijekom tri godine determinirano je 949 jedinki sitnih sisavaca, a broj jedinki ulovljenih u različitim godinama statistički se razlikovao. Usporedba vrijednosti ulova s visinom vodostaja, ukazuje na mogućnost da je na iznimno velik broj ulovljenih primjeraka tijekom 2002. godine utjecao ekstremno nizak vodostaj rijeke Drave u siječnju (38.06 mBf), što je bio najveći pad vodostaja u razdoblju između dviju poplava (Slika 2). Pomoću Kruskal-Wallis testa pokazane su u svakoj godini značajne razlike između vrijednosti učestalosti četiriju istraživanih vrsta. Uspoređujući podatke

o ukupnom broju godišnje uhvaćenih primjeraka, ustanovili smo da je u razdoblju od tri godine broj ulovljenih primjeraka žutogrlih šumskih miševa (*Apodemus flavicollis*) bio približno sličan, dok se broj ulovljenih jedinki ostalih triju vrsta značajno razlikovao među godinama (Slika 3). Dvije *Apodemus* vrste na sličan su način koristile prostor, tijekom 2002. godine jedinke obiju vrsta izbjegavale su prostor između rijeke Drave i šumskog puta, dok su pokazivale signifikantnu pozitivnu preferenciju u korištenju prostora između puta i terase (Slika 4).

Korištenje prostora četiriju vrsta i njihovo preklapanje određivali smo prema mreži koju smo dobili projektiranjem pojedinih klopki u prostor. Signifikantne vrijednosti prostornih asocijacija u svim slučajevima bile su pozitivne (Tablica 2), što ukazuje na veliko preklapanje, te na zajedničko korištenje prostora. Na temelju trogodišnjih uzoraka najveće razlike u udaljenosti kretanja ustanovili smo kod prugastih poljskih miševa (*A. agrarius*), a srednje vrijednosti udaljenosti kretanja bile su u porastu iz godine u godinu. Najujednačenije i ujedno najveće srednje distance kretanja ustanovili smo za žutogrle šumske miševe (*A. flavicollis*), dok su se riđe voluharice (*M. glareolus*) kretale na mnogo manjim udaljenostima (Slika 5). Na temelju vrijednosti dobivenih metodom ulov-markiranje-ponovni ulov, ustanovili smo da su se žutogrli šumski miševi (*A. flavicollis*) kretali signifikantno dalje nego li jedinke prugastih poljskih miševa (*A. agrarius*) i riđih voluharica (*M. glareolus*).

Dugogodišnja botanička istraživanja na poplavnom području uz rijeku Dravu u različitim sastojinama vrbe pokazala su da se fitocenološke karakteristike biljnih zajednica mijenjaju iz godine u godine (Juhász & Dénes 2005). Sitni sisavci brzo reagiraju na ove promjene, te se mogu koristiti u istraživanjima kao indikatori promjena u strukturi šumskih zajednicama koje su izazvane prirodnim ili antropogenim utjecajima.

KLJUČNE RIJEČI: poplavna šuma, sitni sisavci, ulov-markiranje-ponovni ulov, prostorna povezanost