

SPATIAL ORGANIZATION AND HOME RANGE
OF APODEMUS FLAVICOLLIS AND A. AGRARIUS
ON MT. AVALA, SERBIA

VUKIĆEVIĆ-RADIĆ, O.¹, MATIĆ, R.¹, KATARANOVSKI, D.¹ and STAMENKOVIĆ, S.²

¹*Institute for Biological Research 'Siniša Stanković'*
Despota Stefana 142, 11000 Belgrade, Serbia and Montenegro
E-mail: olivera@ibiss.bg.ac.yu

²*Faculty of Biology, University of Belgrade*
Studentski trg 16, 11000 Belgrade, Serbia and Montenegro

Spatial organization and home range size of *Apodemus flavicollis* and *A. agrarius* were studied in a forest community (*Orno-Quercetum petraeae*) at Avala mountain (Serbia). From 1997–1999 a mark-recapture method on a 4 ha study plot was used to follow both species. Observed range length (ORL) and home range area (HR) were calculated for individuals recaptured 4–6 times. *A. flavicollis* had a smaller home range than *A. agrarius*, while males of both species had larger home ranges than females. The differences were significant for species but not for sexes. Both species had similar values of ORL and HR in periods of low density of both species, high density of both species and in periods of high density when the other species had low density. The magnitude of ORL and HR expansion in periods of low density was significantly smaller when the other species was in present in high density. This effect was more pronounced in *A. agrarius* than in *A. flavicollis*. We suggest that differential micro-habitat utilization within the study area by the two species was partly responsible for this phenomenon.

Key words: *Apodemus flavicollis*, *A. agrarius*, home range, spatial organization

INTRODUCTION

Understanding the spatial organization of animals is a general problem faced by ecologists, especially the determination of biological factors which affect spacing pattern. Spacing patterns, in turn, are frequently evaluated by estimating individual home range size and overlap. A home range is defined by BURT (1943) as "... the area traversed by individuals of a species in their normal activities of feeding, mating and caring for their young". Since "normal" activities are difficult to define, ANDERSON (1982) and BLUNDELL *et al.* (2001) define home range as the probability of locating an animal at a particular place by using a utilization distribution based on relative frequency of location. The utilization distribution represents space use, which is generally described by home range size and habitat composition. The home range may vary with sex, age, season, population density and it is in direct functional dependence of essential requirements for food, reproduction

and shelter (ADAMS & DAVIS 1967, HAMAR & SUTOVA-HAMAR 1969, BURGE & JORGENSEN 1973, FERNANDEZ *et al.* 1996).

The spatial distribution of small rodent species was analyzed by many authors (SZACKI & LIRO 1991, MONTGOMERY & DOWIE 1993, MARSH *et al.* 2001). However, it is not entirely clear how individual species occupy the habitat when they co-occur, and how they interact. A crucial resource in the social organization of mice is space. *Apodemus* females are territorial when breeding (WOLFF 1993) and maturation and reproduction in mice are regulated socially through the possession of a territory. Based on evaluation of density values, GLIWICZ (1981) indicated negative associations between *A. flavicollis* and *A. agrarius* and suggested significant overlap between the food resources as the cause for competition, but he also mentioned competition for hiding places as an alternative hypothesis. According to MAZEIKYTE (2002) *A. flavicollis* is being dominant over *A. agrarius* and likely compete by interference and aggression.

A rodent community of the yellow-necked mouse, *Apodemus flavicollis*, and the striped field mouse, *A. agrarius*, are typical for forest ecosystems on Avala mountain. These species coexist, and are the only rodent species, within an *Orno-Quercetum petraeae* community on Avala mountain. They are both residents of forest communities in Serbia, usually co-occurring with several other rodent species (*Clethrionomys glareolus*, *A. sylvaticus*, *Microtus arvalis*, and *Pitimys subterraneus*). During the 3-year study period only two specimens of *Microtus arvalis* and one of the doormouse, *Glis glis*, were registered. The yellow-necked mouse is characterized by greater mobility and is strongly dependent on the forest environment (MONTGOMERY 1985). The striped field mouse is a species typical for the agricultural field-forest habitat mosaic (KOZAKIEWICZ *et al.* 1999). While there are extensive data from Europe, there have been relatively few studies of these species in Serbia.

As part of a larger study (VUKICEVIC 2002) in this paper we investigated the home range of *A. flavicollis* and *A. agrarius*, in order to analyze their spatial organization. Specifically we reported data on the home range size of these species, and analysed possible inter- and intra-specific density-dependent effects. Further, bearing in mind the known similarity in bionomic characteristics of these species we analyzed their micro-habitat preferences in a heterogeneous forest environment and commented on their spatial structure related to differential micro-habitat utilization and overlap in habitat use.

MATERIALS AND METHODS

We carried out the study in an oak community (*Orno-Quercetum petraeae*) at Avala mountain (44°45'E, 18°10'N), located near Belgrade, Serbia. On the study area (4 ha), the over-storey height was 10–20 m with tree diameters ranging from 10–40 cm. Among the tree species, *Quercus petraea* predominates, accompanied by *Fraxinus ornus* and *Carpinus betulus*. The canopy cover was 70%. The middle-storey (0.5–5 m height) is well developed, covers 20–100% and composed mainly of *Acer campestre*, *Prunus avium* and *Tilia tomentosa*. The understorey and ground cover are variable, dominated by *Rubus hirtus* (10–100% cover), while *Dactylis glomerata*, *Lonicera caprifolium*, *Fragaria vesca*, *Galium aparine* are locally important. As the floristic composition varied in different parts of the grid, four micro-habitat patches were identified: A – Close canopy of mature *Quercus petraea*; B – Open canopy of mature *Quercus petraea*, *Fraxinus ornus* and *Carpinus betulus*; C – Very few mature trees, dense field layer of *Acer campestre*, *Prunus avium* and *Tilia tomentosa*; D – No mature trees, very dense *Rubus hirtus* (Fig. 6a).

Small mammals were trapped during a three year period (1997–1999). A square trapping grid of 400 points (10 by 10 m) was used, with a Longworth trap at each point. Trapping was performed every month for 4 days and 3 nights. The study was conducted by the capture-mark-release (CMR) method. Each individual was marked by a combination of ear-punching and toe-clipping when trapped for the first time. Percentages of the trap station occupied were calculated for each trapping session, and the distribution of captures on the trap-grid was superimposed onto the microhabitat patches in order to assess possible differences in microhabitat use between species. The percentage of intra- and interspecific overlap ($Ov\%$) in trap use was calculated ($Ov(\%) = (Ns/T) \times 100$; Ns =number of traps shared by two or more individuals, T =total number of traps used, LÖFGRAN 1995) and used as an indicator of microhabitat selectivity. Population densities were estimated by the JOLLY–SEBER method (JOLLY 1965, SEBER 1965). From the observed densities we identified periods of high or low density for both species, leading to four possible density-species combinations for subsequent analyses (two levels per species).

Home range area (HR) was estimated by the inclusive boundary strip method (STICKEL 1954). As an index of home range, the maximum distance between traps where an individual was captured (observed range length = ORL) (MAZURKIEWICZ & RAJSKA-JURGIEL 1998) was calculated. Since preliminary analyses showed that ORL and HR were not normally distributed a $(\ln+1)$ -transformation and correction for bias related to number of trapping occasions was applied to the data. Subsequent test of normality by Shapiro-Wilk W test and Levene's test of homogeneity of variances showed non significant values for all the reported ANOVA breakdowns. Two-way factorial ANOVA designs using the Statistica 5.1. package (STATSOFT Inc., 1998, Statistica for Windows. Computer Program Manual. Tulsa, OK, USA), were performed on ORL and HR as follows: a) a sex by species analysis; b) a density by species analysis.

RESULTS

During the study period, we marked 2032 individuals, (1524 *A. flavicollis*, 508 *A. agrarius*). The ratio of males and females were 52.5:47.5% for *A. flavicollis* and 57.5:42.5% for *A. agrarius*. Trap success ranged from 7 to 45% for yellow-necked mouse and from 1 to 10% for striped field mouse. Abundance of both species varied markedly over the period of the study (Fig. 1a, b). Maximum popula-

tion densities of *A. flavicollis* peaked twice, once in June of 1997 (85 ind./ha), and once in June of 1998 (47 ind./ha). Lowest density was registered in January 1999 (3 ind./ha). *A. agrarius* populations peaked in April 1997 (21 ind./ha) and in Sep-

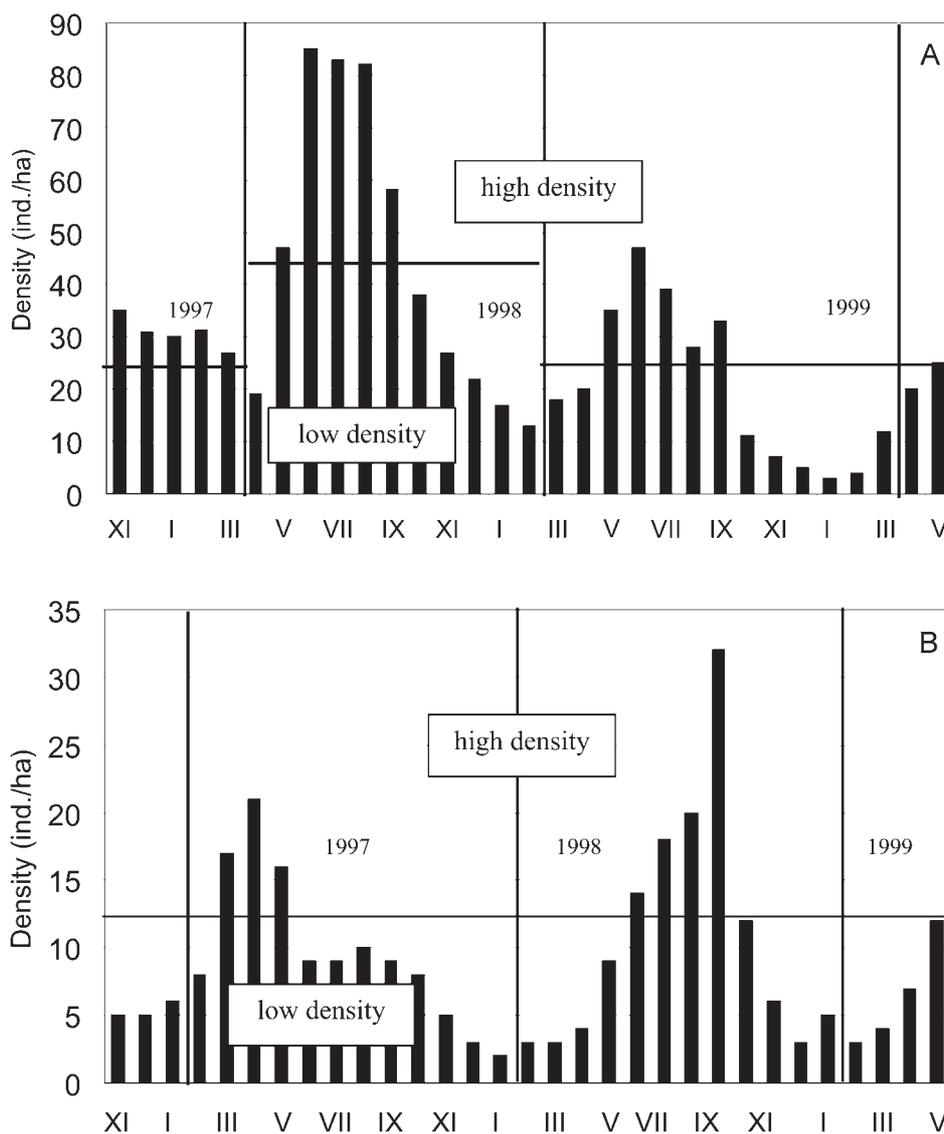


Fig. 1. Population densities of *A. flavicollis* (A) and *A. agrarius* (B) during the study period. The base line indicates arbitrarily defined periods of high versus low density

tember 1998 (32 ind./ha). Minimal density was registered in January 1998 (2 ind./ha). From November 1996 to July 1998 the yellow-necked mice was dominant in this rodent community, accounting for 77.4–90.2% of the specimens, but both species occurred in almost equal proportions between September 1998 and January 1999. For home range analyses, two levels of density were distinguished for both species. In *A. flavicollis*, 24 ind./ha was taken as a base-line above which a high density level was recognized, corresponding to November 1996–March 1997 and May–September 1998. Since *A. flavicollis* from May to September 1997 showed a range of densities which were higher than the maxima observed in other periods, the base line was set at 45 ind./ha. All the other periods of the study, were designated as low density periods. The corresponding periods of high *A. agrarius* densities (base-line 12 ind./ha) were March–May 1997 and June–October 1998, with other months being assigned to low density periods.

We analyzed the capture data of 214 individuals that were recaptured 4–6 times (159 *A. flavicollis* and 55 *A. agrarius*) to estimate the size of their home range. ORL in different trapping sessions varied from 10 to 134 m for yellow-necked mice and from 10 to 137 m for striped field mice. The median ORL for *A. flavicollis* (AF) was 42.0 m for the males (N = 82) and 42.4 m for females (N = 77) of *A. flavicollis* (Fig. 2). The median ORL was 40.6 m for the males (N = 34) and 30.0 m for the females (N = 21) of *A. agrarius* (AG, Fig. 2). Two-way factorial ANOVA on the transformed and corrected ORL data testing for differ-

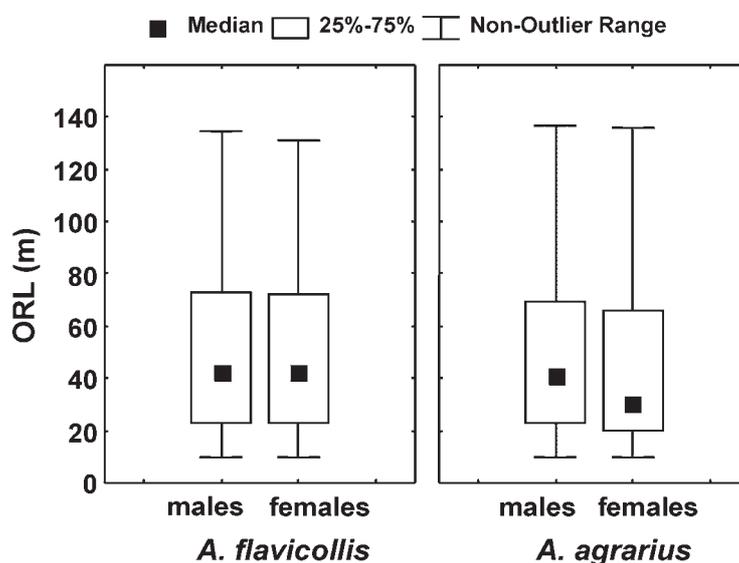


Fig. 2. Observed range length (ORL) values of *A. flavicollis* and *A. agrarius*

ences between sex and species showed non significant differences between sexes for both species [AF $F(1,157) = 0.12, p = 0.73$ and AG $F(1,54) = 1.27, p = 0.26$]. The differences in ORL were however highly significant between the species [$F(1,213) = 44.27, p < 0.001$].

The home range values obtained by the inclusive boundary strip method in case of *A. flavicollis* varied from 100 to 2300 m². The median value for males was 625 m² and 551 m² for females (Fig. 3). The home range values in *A. agrarius* varied from 100 to 2400 m². The median value for males was 716 m² and 585 m² for females. No significant difference between sexes was found for both analyzed species [$F(1,157) = 0.06, p = 0.79$ and $F(1,55) = 1.39, p = 0.24$]. The difference was highly significant between the species regarding home range [$F(1,213) = 40.62, p < 0.001$]. For both parameters of home range males had larger home ranges and greater variation in size than females for both species, while *A. flavicollis* had slightly larger values of ORL than *A. agrarius*, but slightly smaller values of HR than the other species.

A two-way factorial ANOVA design was used to test for intra- and inter-specific density-dependent effects on ORL and HR. The comparison was between periods of high and low density of both species (sexes were pooled) for four possible density combinations. As seen in Figure 4, the overall pattern of interactions between intra and interspecific density effects for both species were similar. For *A.*

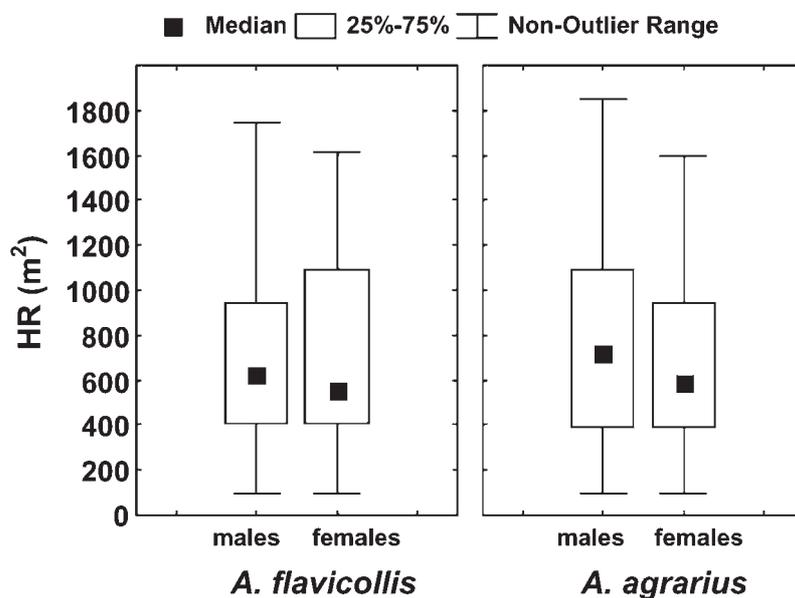


Fig. 3. Home range (HR) areas of *A. flavicollis* and *A. agrarius*

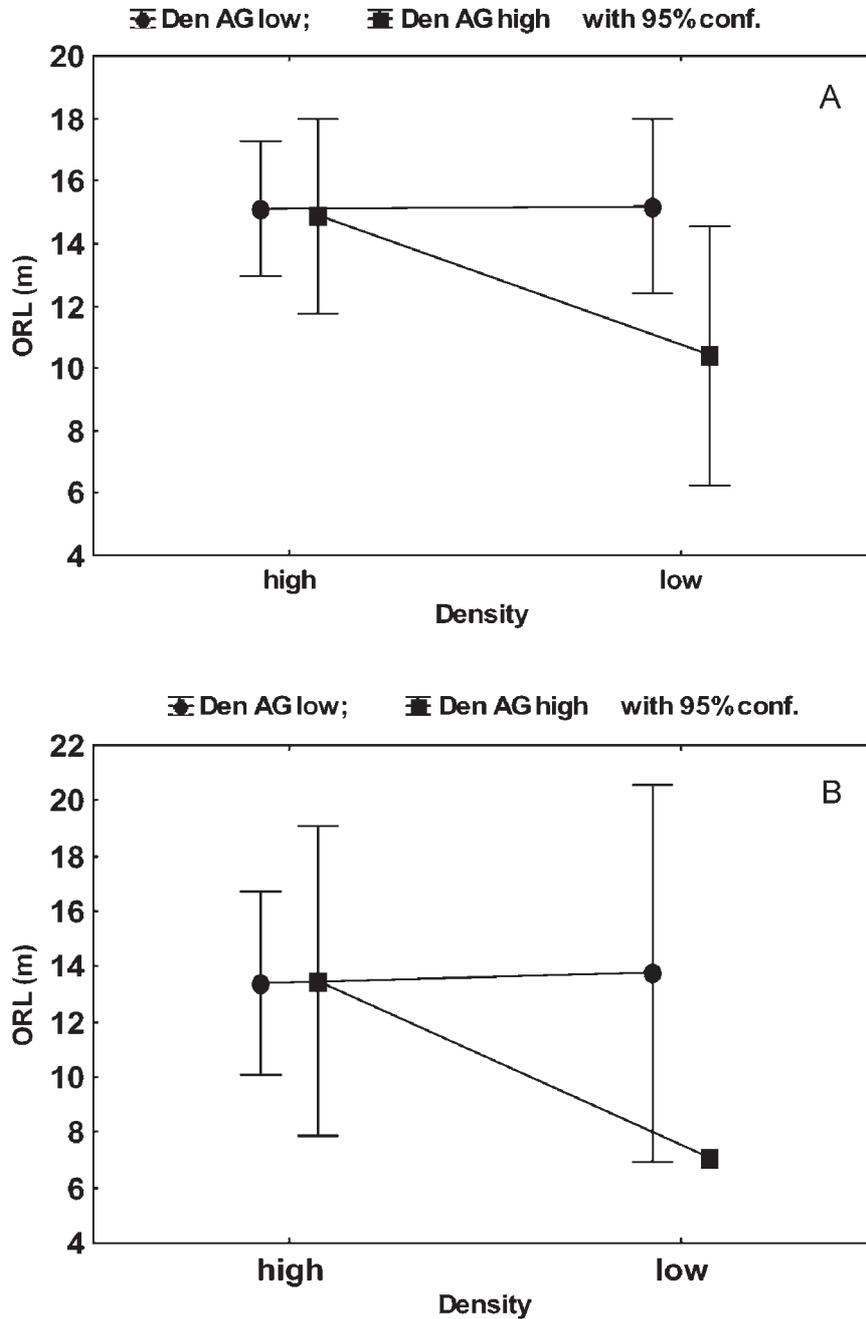


Fig. 4. Least-squared corrected means of observed range length (ORL) values (four possible density combination showing the interaction effects): A = *A. flavicollis*, B = *A. agrarius*

flavicollis the weighted means of ORL (Fig. 4a) had similar values in periods of low density of both species (15.2 m), high density of both species (14.9 m) and in periods of high density when the other species had low density (15.1 m). A significant reduction of ORL was observed in periods of low density of *A. flavicollis* (10.4 m) when *A. agrarius* had high density. For *A. agrarius* (Fig. 4b) the weighted means of ORL had smaller values by 10% (13.8, 13.5 and 13.4 m, respectively) than for *A. flavicollis*, while the reduction of ORL (7.1 m) was more pronounced in period of low density of *A. agrarius* when *A. flavicollis* had high density. This reduction accounted for 49% in comparison to the highest ORL observed in the period when both species had low density. The ANOVA's were highly significant at different combinations of densities for both species [AF $F(1,133) = 30.49$, $p < 0.001$], AG $F(1,35) = 8.28$, $p = 0.006$].

The same analysis performed on HR showed a generally similar pattern. In three of four possible combinations the weighted means of HR (Fig. 5) had similar values. For *A. flavicollis*, the weighted mean of HR was highest (245.6 m²) in periods of high density of *A. flavicollis*, and low density of *A. agrarius* (Fig. 5a). In the periods of high density of both species HR was slightly smaller (0.8%), while during low density periods of both species HR was smaller by only 3.1%. The smallest HR (188 m²) was observed in the period of low density of *A. flavicollis* and high density of *A. agrarius*. For *A. agrarius* the weighted mean of HR was highest (242 m²) in periods of high density of both species. (Fig. 5b). In the periods of low density of both species HR was smaller for 5.3%. The smallest HR was observed in the period of low density of both species (191.4 m²). Contrary to ORL, the observed reduction of HR was more pronounced in *A. flavicollis*, and was 23.5% lower than the highest observed HR. The ANOVA's as before were highly significant [AF $F(1,133) = 22.90$, $p < 0.001$, AG $F(1,35) = 4.61$, $p = 0.03$].

A further analysis of spatial distribution of *A. flavicollis* and *A. agrarius*, was performed to assess micro-habitat preference and selectivity based on available data. Yellow-necked mice were caught at every quadrat of the grid during the study period. On the other hand, individuals of the striped field mouse were not caught at 168 quadrates of the grid. With micro-habitat variation as encountered on the study area, it could be expected that mice occupy some parts of the grid preferentially over others. For the study period, we compared the distribution frequency of captures per grid with micro-habitat units A-D designated on the basis of vegetation cover (see above). The distribution of habitat patches A–D and capture frequency per grid cell for both species are illustrated in Fig. 6. The frequency of capture on the grid was compared with expected random distributions for both species under the hypothesis that they occurred in the study area irrespective of micro-habitat proportion (Table 1). Statistically significant difference in distribution of

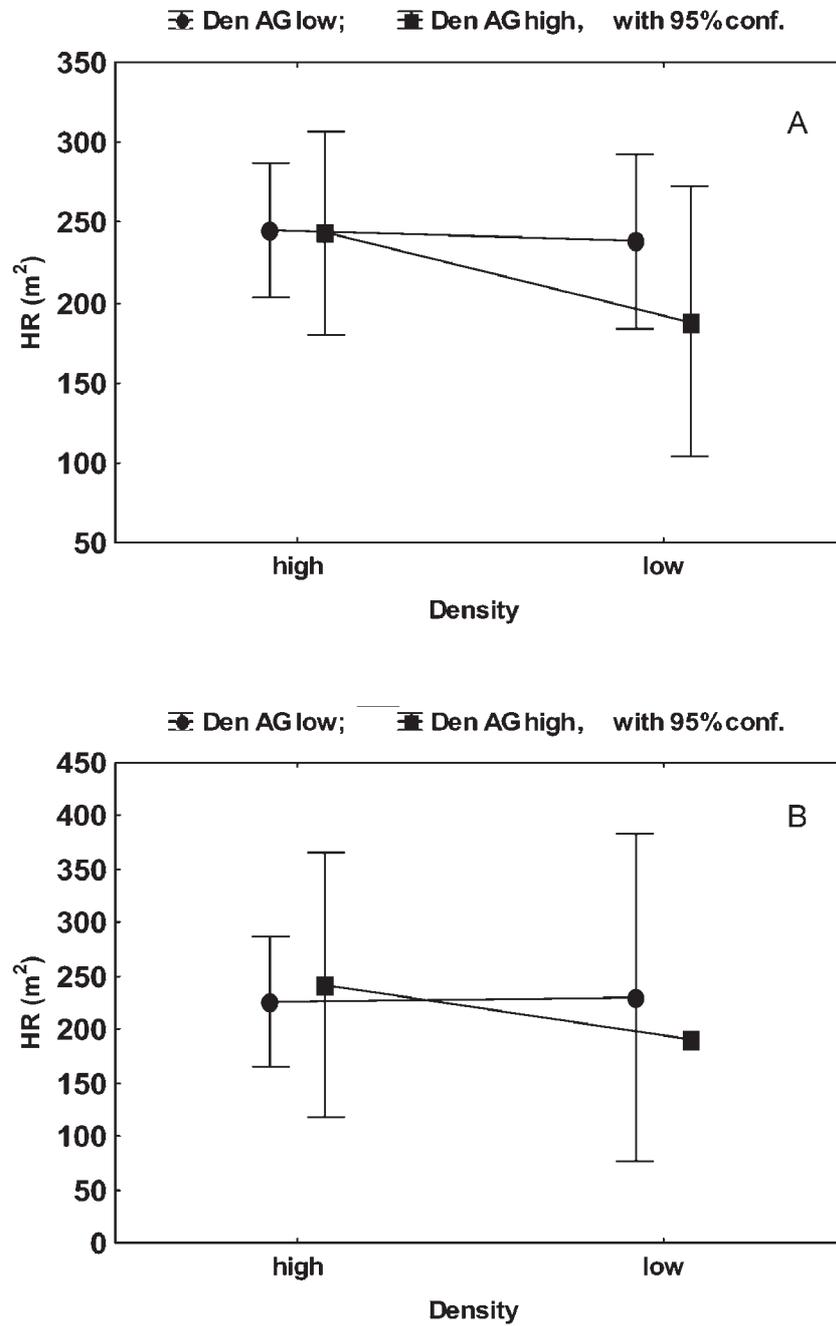


Fig. 5. Least-squared corrected means of home range (HR) area (four possible density combination showing the interaction effects): A = *A. flavicollis*, B = *A. agrarius*

Table 1. Chi-square values for frequency distribution of *A. flavicollis* and *A. agrarius* in the different habitat subunits (***) $p < 0.001$, ** $p < 0.01$), A – Close canopy of mature *Quercus petraea*; B – Open canopy of mature *Quercus petraea*, *Fraxinus ornus* and *Carpinus betulus*; C – Very few mature trees, dense field layer of *Acer campestre*, *Prunus avium* and *Tilia tomentosa*; D – No mature trees, very dense *Rubus hirtus*

	<i>A. flavicollis</i>	<i>A. agrarius</i>
A	96.8***	10.7
B	44.8**	13.7
C	5.2	57.3**
D	47.5	158.2***

A. flavicollis was found for subunits A and B which are areas of developed tree-cover (closed or open canopies) of *Quercus petraea*, *Fraxinus ornus* and *Carpinus betulus*. The distribution of *A. agrarius* is significantly non-random for habitat subunits with a dense shrub layer and very dense *Rubus hirtus* undergrowth with low or absent tree-canopy covers (units C and D). This pattern suggests that the species show a degree of habitat preference for the respective units. The percentage of inter- and intra-specific overlap in trap use among individuals of two studied species is presented on Table 2 to provide additional information on microhabitat selectivity in the absence of other data. The overlap in trap use was generally low. The highest values were observed (1.7–2%) in July and during the winter (November–January). Intraspecific overlap for *A. flavicollis* reached maximums in July

Table 2. Percentage of intra- and interspecific overlap in trap use among *A. flavicollis* and *A. agrarius*

month	Interspecific overlap	Intraspecific overlap for	
		<i>A. flavicollis</i>	<i>A. agrarius</i>
I	1.7±0.92	1.3±0.72	0.3±0.20
II	0.3±0.17	1.2±0.85	0
III	0.3±0.26	0.5±0.26	0
IV	0	1.3±0.56	0.3±0.17
V	1.3±0.61	1.5±0.87	0
VI	1.0±0.40	3.3±1.05	0
VII	2.0±0.66	4.5±1.95	0.5±0.30
VIII	1.1±0.46	3.3±1.49	0.3±0.26
IX	1.0±0.36	3.3±0.96	0
X	0.3±0.20	1.4±0.60	0
XI	1.7±0.26	0.3±0.26	0
XII	1.8±0.78	1.8±0.85	0

(4.5%) and was at a minimum in November (0.3%), the highest percentages were observed in the summer months (3–4.5%). During the studied period, intraspecific overlap in the trap use for *A. agrarius* was smaller by an order of magnitude (<1%). If we compare inter- and intra-specific overlap, we can note that *A. flavicollis* overlap measures are larger for intra-specific trap use, while the reverse is true for *A. agrarius*, suggesting that it tends to overlap within the grid more with the other species than with itself. We see this as an indication that the yellow-necked mouse has lower micro-habitat selectivity within its preference than the striped field mouse.

DISCUSSION

Many authors assessed spatial relationships among the most abundant small rodent species by estimating their home range size (RANDOLPH 1977, WOLTON & FLOWERDEW 1985, KOZAKIEWICZ *et al.* 1993). There are no studies where the yellow-necked and striped field mice are the single members of the rodent community. Typically, *A. flavicollis* and *Clethrionomys glareolus*, as the dominant generalist species in European deciduous forest areas, were the objects of the home range investigations (BERGSTEDT 1966, ANDRZEJEWSKI & MAZURKIEWICZ 1976, KARLSSON & AS 1987). The mature deciduous forests are the favoured habitat of *A. flavicollis*, and it is restricted to areas where sufficient plant diversity ensures an adequate food supply each year (MONTGOMERY 1985). Striped field mice, how-

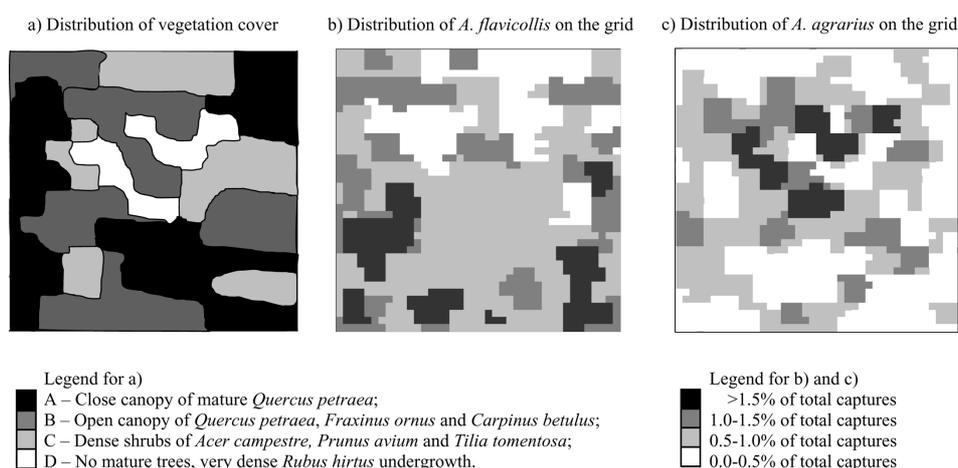


Fig. 6. Correspondence of vegetation cover (a) and capture frequency of both species (b, c) on the grid as an indicator of their habitat preferences

ever, are commonly found in grassy fields, cultivated areas, and woodlands in that order (CHELKOWSKA *et al.* 1985). The trophic niches of both studied species are similar. Both are granivorous, with seed and fruits of trees being their predominant food resource. The yellow-necked mouse is more of a seed specialist and supplements its diet with up to 20% of invertebrate food, while the striped field mouse has more varied diet with up to 40% invertebrate supplement (HOLISOVA 1967, OBRTTEL & HOLISOVA 1974). GLIWICZ (1981) pointed out that *A. agrarius* holds an inferior position in the community and that other rodents strongly influence its population processes. HORVÁTH and WAGNER (2003) investigated patterns of co-existence of all these three species in riverine forest habitats of Southern Hungary. They found that *C. glareolus* and *A. agrarius* have constraining effects on the density and spatial distribution of *A. flavicollis*. They suggested that significant overlap in food resource utilization and competition for hiding places were alternative hypotheses which explained the observed negative interactions. They also stressed that the relations between these species was highly influenced by the qualitative characteristics of their habitat as reported by KOZAKIEWICZ *et al.* (1993). KOZAKIEWICZ and BONIECKI (1994) showed that intolerant behaviour (aggression) is likely to evolve between *C. glareolus* and *A. agrarius*. In contrast to other reported studies, in this case *A. flavicollis* and *A. agrarius* coexist as the only rodent species, within a typical *Orno-Quercetum petraeae* community for Serbia.

The problem of choosing adequate methods for home range evaluation is linked, especially for very mobile small mammal species, to the problem of results interpretation (GURNELL & GIPPS 1989, ROGERS & GORMAN 1995). As seen from our results *A. flavicollis* had a larger range length than *A. agrarius*, and their females had larger ORL than males, while this relation was opposite regarding to *A. agrarius*. Concerning ORL and home range size no significant differences were found during the studied period regarding sex. We see that observed variances of these parameters were higher in males than in females for both studied species. The differences in ORL were higher for females (ORL was smaller for 29.2% in *A. agrarius*) than for males (ORL was smaller for 3.3%). With respect to the other parameter, home range area, *A. flavicollis* had a smaller home range than *A. agrarius* (HR of males was smaller for 12.7%, and for females for 5.8%), while males of both species had larger home ranges than females. The differences were significant for species but not for sexes. Although our reported differences are statistically verifiable, even by casual inspection of Figures 2 and 3, we see that the magnitudes of variation observed in our data were very large – in fact much larger than the magnitude of differences. We can further see that the magnitude of species' differences is significant largely because of the large sample sizes in the analysis. Our estimates of ORL and HR are comparable with the results reported in several other

studies (TODOROVIC *et al.* 1968, ZEJDA & PELIKAN 1969, MAZURKIEWICZ & RAJSKA-JURGIEL 1998).

Changes in home range size with variation in the density of forest rodent were observed by many authors (WOLFF 1985, BUJALSKA & GRÜM 1989, MAZURKIEWICZ & RAJSKA-JURGIEL 1998) and are considered to be inversely related to both resource abundance and species density. Further, resource limitation and higher selectivity (or lower efficiency) in resource use are seen as leading to stronger density-dependent effects. The usual mechanism invoked is the strengthening of intra- and/or inter-specific competition intensity resulting in a density-dependent reduction in home range. Competition intensity is further seen as coupled with interference mechanisms, leading to aggressive behaviour patterns, stronger territoriality and age or socially dependent dispersal (ODUM & BARRET 2005, KREBS 2001, PIANKA 2000). Densities of *A. flavicollis* and *A. agrarius* varied considerably over the study period and we expected that this variation should influence home range. Our results show that both species hold larger home ranges in periods of low density and slightly smaller in periods of high density, but the magnitude of ORL and HR expansion in periods of low density was significantly smaller when the other species was present in high density. This effect was more pronounced in the subdominant *A. agrarius* than in *A. flavicollis*, the differences being more pronounced for ORL than HR. Generally, the results were as expected, although we cannot identify the particular mechanism of density dependence from our data.

The analysis of spatial relationships was performed in order to discover whether or not both species inhabited the same patches of habitat. Spatial distribution of many species depends on the distribution of necessary resources – food and abundance of shelter. Even in ecologically similar species, selective use of micro-habitats can be a mechanism to promote coexistence and reduce possible negative interactions. Our results indicate differential space exploitation within habitats by the two species. The habitat patches preferred by *A. flavicollis* were those with a dense and closed tree canopy dominated by *Quercus petraea*. Individuals of *A. agrarius* inhabited patches with dense shrub covers or dense *Rubus hirtus* undergrowth with low canopy cover or treeless. Both correspond to their bionomic affiliations – the yellow-necked mouse as a typical forest dweller occupying forest-like patches, while the striped field mouse is seen as being less selective for forest habitats and occurring in more open field-like patches. Again, as for the other analyses reported in this study, although differential habitat preferences are statistically verifiable, the distribution of the species on the study plot overlapped highly (as did the overlap in trap use) and prevented detailed explorations of possible mechanisms.

In summary, our results showed that both species have home range sizes comparable to other reported data. The heterogeneous habitat of the study area promoted coexistence of both species by offering possibilities for differential micro-habitat utilization based on bionomic preferences. *A. agrarius* was seen as being more selective in habitat use than the dominant *A. flavicollis*. Density dependent reduction of home ranges was less pronounced in periods of high density both intra- and inter-specifically. Reductions in home range were markedly larger when inter-specific differences in density were large. We surmise that when both species have low or high density, they are more confined to their preferred habitat patches, while competition-induced spill-over occurs between patches when differences in density are large, leading to the observed reduction in home range size.

*

Acknowledgments – This study was supported by the Ministry of Science and Environmental Protection of the Republic of Serbia (grant 143038).

REFERENCES

- ADAMS, L. & DAVIS, D. S. (1967) The internal anatomy of home range. *J. Mammal.* **48**: 529–536.
- ANDERSON, D. J. (1982) The home range, a new non-parametric estimation technique. *Ecology* **63**: 103–112.
- ANDRZEJEWSKI, R. & MAZURKIEWICZ, M. (1976) Abundance of food supply and the size of the bank vole's home range. *Acta Ther.* **21**: 237–253.
- BERGSTEDT, B. (1966) Home range and movements of rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linne) in southern Sweden. *Oikos* **17**: 150–157.
- BLUNDELL, G. M., MAIER, J. A. K. & DEBEVEC, E. M. (2001) Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecol. Monographs* **71**: 469–489.
- BUJALSKA, G. & GRÜM, L. (1989) Social organization of the bank vole (*Clethrionomys glareolus* Schreber 1780) and its consequences: a model. *Oecologia* **80**: 70–81.
- BURGE, J. R. & JORGENSEN, C. D. (1973) Home range of small mammals: A Reliable Estimate. *J. Mammal.* **54**: 483–487.
- BURT, W. H. (1943) Territory and home range concepts as applied to mammals. *J. Mammal.* **24**: 346–352.
- CHELKOWSKA, H., WALKOWA, W. & ADAMCZYK, K. (1985) Spatial relationship in sympatric population of the rodents: *Clethrionomys glareolus*, *Microtus agrestis* and *Apodemus agrarius*. *Acta Ther.* **30**: 51–78.
- FERNANDEZ, F. A. S., EVANS, P. R. & DUSTONE, N. (1996) Population dynamics of the wood mouse *Apodemus sylvaticus* (Rodentia: Muridae) in a Sitka spruce successional mosaic. *J. Zool.* **239**: 717–730.
- GLIWICZ, J. (1981) Competitive interactions within a forest rodent community in central Poland. *Oikos* **37**: 353–362.

- GURNELL, J. & GIPPS, J. H. W. (1989) Inter-trap movement and estimating rodent densities. *J. Zool.* **217**: 241–254.
- HAMAR, M. & SUTOVA-HAMAR, M. (1969) Estimation of rodent home ranges in different agro systems. Pp. 99–109. *In*: PETRUSEWICZ K. & RYSZKOWSKI L. (eds): *Energy flow through small mammal population*. Proceedings of IBP Meeting on Secondary Productivity in Small Mammal Populations. Oxford, England, July 29th August 2nd.
- HOLISOVA, V. (1967) The food of *Apodemus agrarius* (Pall.). *Zool. Listy* **16**: 1–14.
- HORVÁTH, G. & WAGNER, Z. (2003) Effects of densities of two coexistent small mammal populations on the survival of *Apodemus flavicollis* in a forest habitat. *Tiscia* **34**: 41–46.
- JOLLY, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52**: 225–247.
- KARLSSON, A. F. & AS, S. (1987) The use of winter home ranges in a low density *Clethrionomys glareolus* population. *Oikos* **50**: 213–217.
- KOZAKIEWICZ, M., KOZAKIEWICZ, A., LUKOWSKI, A. & GORTAT, T. (1993) Use of space by bank voles (*Clethrionomys glareolus*) in a Polish farm landscape. *Landscape Ecol.* **8**: 19–24.
- KOZAKIEWICZ, A., & BONIECKI, P. (1994) Intra- and interspecific behaviours in bank vole and striped-field mouse under enclosure conditions. *Acta Ther.* **39**: 29–36.
- KOZAKIEWICZ, M., GORTAT, T., KOZAKIEWICZ, A. & BARKOWSKA, M. (1999) Effects of habitat fragmentation on four rodent species in Polish farm landscape. *Landscape Ecol.* **14**: 391–400.
- KREBS, C. J. (2001) *Ecology*. Addison/Wesley/Longman Inc., San Francisco, pp. 695.
- LÖFGREN, O. (1995) Spatial organization of cyclic *Clethrionomys* females: occupancy of all available space at peak densities? *Oikos* **72**: 29–35.
- MARSH, A. C., POULTON, S. & HARRIS, S. (2001) The Yellow-necked Mouse *Apodemus flavicollis* in Britain: status and analysis of factors affecting distribution. *Mammal Rev.* **31**: 203–227.
- MAYEIKYTE, R. (2002) Small mammals in the mosaic landscape of Eastern Lithuania: species composition, distribution and abundance. *Acta Zool. Lituanica* **12**: 381–391.
- MAZURKIEWICZ, M. & RAJSKA-JURGIEL, E. (1998) Spatial behavior and population dynamics of woodland rodents. *Acta Ther.* **43**: 137–161.
- MONTGOMERY, W. I. (1985) The behaviour of *Apodemus*. *Symp. Zool. Soc. Lond.* **55**: 89–115.
- MONTGOMERY, W. I. & DOWIE, M. (1993) The distribution and population regulation of the wood mouse *Apodemus sylvaticus* on field boundaries of pastoral farmland. *J. App. Ecol.* **30**: 783–791.
- OBRTEL, R. & HOLISOVA, V. (1974) Trophic niches of *Apodemus flavicollis* and *Clethrionomys glareolus* in low-land forest. *Acta Sc. Nat. Brno* **8**: 1–37.
- ODUM, E. P. & BARRET, G. (2005) *Fundamentals of Ecology*. 5th ed. Thompson/Brook/Cole Inc., New York, 624 pp.
- PIANKA, E. R. (2000) *Evolutionary ecology*. 6th ed., Addison/Wesley/Longman Inc., San Francisco, pp. 512.
- RANDOLPH, S. . (1977) Changing spatial relationships in a population of *Apodemus sylvaticus* with the onset of breeding. *J. Anim. Ecol.* **46**: 653–676.
- ROGERS, L. M. & GORMAN, M. L. (1995) The home-range of wood mice *Apodemus sylvaticus* living in set-aside and surrounding semi-natural and crop land. *J. Zool.* **237**: 675–678.
- SEBER, G. A. F. (1965) A note on the multiple-recapture census. *Biometrika* **52**: 249–259.
- STICKEL, L. F. (1954) A comparison of certain methods of measuring range of small mammals. *J. Mammal.* **35**: 1–15.
- SZACKI, J. & LIRO, A. (1991) Movements of small mammals in the heterogeneous landscape. *Landscape Ecol.* **5**: 219–224.

- TODOROVIĆ, M., MIKES, M. & SAVIĆ, I. (1968) Untersuchungen zum Aktionsraum der Gelbhalsmaus, *Apodemus flavicollis* (Melchior, 1834). *Z. f. Säugetierkunde* **33**: 100–106.
- VUKIĆEVIĆ, O. (2002) Population ecology of *Apodemus flavicollis* and *A. agrarius* (Rodentia, Mammalia) in Orno-Quercetum petraeae community (Bor. 1955) Mistic, 1972 at Avala mountain [Populaciona ekologija vrsta *Apodemus flavicollis* and *A. agrarius* (Rodentia, Mammalia) u zajednici Orno-Quercetum petraeae (Bor. 1955) Mistic, 1972 na Avali]. PhD Thesis, Faculty of Biology, University of Belgrade.
- WOLTON, R. J. & FLOWERDEW, J. R. (1985) Spatial distribution and movements of wood mice, yellow-necked mice and bank voles. *Symp. zool. Soc., Lond.* **55**: 249–275.
- WOLFF, J. O. (1985) The effects of density, food and interspecific interference on home range size in *P. leucopis* and *P. maniculatus*. *Canadian J. Zool.* **63**: 2657–2662.
- WOLFF, J. O. (1993) Why are female small mammals territorial? *Oikos* **68**: 364–370.
- ZEJDA, J. & PELIKAN, J. (1969) Movements and home ranges of some rodents in Lowlands forests. *Zool. listy* **18**: 143–162.

Revised version received August 22, 2004, accepted October 24, 2005, published April 10, 2006