



Long-term density fluctuations and microhabitat use of sympatric *Apodemus flavicollis* and *Myodes glareolus* in central Italy

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Abstract: The role and importance of interspecific competition for rodent communities have been much debated issues, with some early authors suggesting that these are important, and several recent articles suggesting the contrary. In this paper, we studied, for 14 years at a mountainous locality in central Italy, the coexistence dynamics of a two-species system (*Apodemus flavicollis*, *Myodes glareolus*) within a 1.44 ha trapping grid, by Capture-Mark-Recapture. Overall, we captured over 1000 rodents during the study period, with annual abundance ranging 2-7 individuals \times ha⁻¹. However, the density of the two species varied substantially across years and between sectors of the study plot. Thus, the distributions of the two species on the scale of the study grid were not related to one another. Density of a given species did not affect the percentage of lactating females in either *A. flavicollis* or *M. glareolus*. Individual traps differed in their rate of capture such that about 40% of traps were associated more with a particular species. Considering the spatial distribution of traps, we determined that three areas were associated with high probability of capture for only one of the two study species, two of these areas being associated to *A. flavicollis* and one to *M. glareolus*. Our analyses suggest that interspecific competition may be present at the local micro-scale, as explained by the fact that in the great majority of the cases in which a given trap was highly successful in capturing one species, it was also very unsuccessful in capturing the other species. However, manipulation experiments are needed to confirm that suggestion.

Abbreviation: CMR–Capture Mark Recapture.

Nomenclature for plants: Pignatti (2011).

Introduction

Recent meta-analyses revealed that competition is perhaps the prevalent force assembling whole guilds of particular taxonomic groups (e.g., Connell 1983, Gurevitch et al. 1992, Case and Taper 2000, Amarasekare 2003, Friggens and Brown 2005, Luiselli 2006, 2008). Grant (1972) was the first author highlighting the relevance of interspecific competition in rodents, and also Schoener (1983) confirmed that interspecific competition should occur among sympatric rodent species. However, other studies questioned whether interspecific competition does really matter in rodents (e.g., Galindo and Krebs 1985, Wolff and Dueser 1986, Scott and Dueser 1992). For instance, meta-analyses using null models revealed that there is little evidence for interspecific competition along West African small mammals (Amori and Luiselli 2011) as well as in rodents inhabiting tropical islands (Amori and Luiselli 2013).

Rodents can be expected to compete interspecifically when the available resources are limited (Morris 1984, 1987,

1996, 1999, 2000). Given the fast population growth of rodents, resource limitation may occur seasonally in appropriate habitats where rodent population density can increase near exponentially (Grant 1972, Jones et al. 2001, Eccard and Ylonen 2002, Amori and Luiselli 2013). Therefore, stronger interspecific competition should be expected among rodent assemblages living in seasonal habitats, where the resource availability is fluctuating and/or patchily distributed (e.g., Schmitt and Holbrook 1986). Theoretically, interspecific competition should be a relevant force for rodent assemblages inhabiting seasonally variable temperate regions, especially in wooded habitats where the seed productivity is well known to vary not only seasonally but also annually. When interspecific competition does occur because of the limited available resources, the succumbing species has been observed to limit the use of nesting sites, shelters and habitat types for foraging, even restricting their reproductive success (e.g., Schradin 2005). In addition, interspecific competition tended to increase with smaller body size differences between coexisting species and with the behavioral aggressiveness of the subordinate species (e.g., Schradin 2005).

European rodents of the genera *Myodes* and *Apodemus* are in general the predominant species in woodlands, agro-forest and forest habitats, where they tend to exhibit wide spatial overlap (e.g., see Montgomery 1979, 1980a, Canova 1993, Fasola and Canova 2000, Grüm and Bujalska 2000, Rico et al. 2007). Thus, they are good models for studies on the rodent coexistence dynamics (Amori et al. 2010). Indeed, several studies on this subject were published, using *Myodes glareolus* (Schreber) and *Apodemus sylvaticus* (L.) as study species (e.g., Kikkawa 1964, Flowerdew et al. 1985). However, there is comparatively less information on the coexistence of *M. glareolus* with *Apodemus flavicollis* (Amori et al. 1986, Gliwicz and Rajska-Jurgiel 1983, Gliwicz 1988, Grüm and Bujalska 2000, Rico et al. 2007). In this paper, we present a long-term (14-years-long) field dataset on the coexistence of *M. glareolus* and *A. flavicollis* at a forest zone in central Italy. We emphasize the spatial resource partitioning patterns between these rodent species. Our study area is particularly interesting because it is near to the southernmost border of the distribution range of these two species in Europe (Mitchell-Jones et al. 1999).

More specifically, our aims with this paper are to respond to the following key questions:

- Are the density fluctuations of the two species mutually influenced by each another or do they follow similar annual trends?
- Are the percentages of lactating females of a given species influenced by density variations in the potential competitor species (Watts and Holekamp 2008)?
- Do the study species coexist on a microhabitat scale?
- Is there any evidence that interspecific competition may shape the fine-scale ecological distribution of these species?

Materials and methods

Study area and trapping design

The study area was located in central Italy (Majella National Park, 42°08' N, 14°05' E, 1000 m a.s.l.), and is characterized by a thermophilous beech forest (*Fagus sylvatica*). The vegetation belongs to the association *Geranio-Fagion*.

We assessed the detailed vegetation and habitat at the study site by using Pirola's (1970) phytosociological method by analysing (i) the substratum characteristics both qualitatively and quantitatively, (ii) the total vegetation coverage (i.e., the percentage and height of the tree and bush layers), and (iii) the list of plant species with their relative abundance scored on the Braun-Blanquet (1928) scale. Based on Pirola's (1970) criteria, we subdivided the study area into six habitat types:

R1 – habitat characterized by presence of bushy *Fagus sylvatica* (30% of the area), with 70% of surface covered by grass, being this the only clearing found inside the grid.

R2 – habitat characterized by the presence of *Fagus sylvatica* only in its tree phase (90% of the area), with a few species

indicating a good conservation status of the area (*Acer platanoides*, *Cardamine enneaphyllos*, *Cephalanthera rubra*, *Polygonatum multiflorum*, *Tamus communis*; these latter species covering 10% of the area).

R3 – habitat characterized by the presence of *Fagus sylvatica* in both tree and bush phases (respectively covering 40 and 50% of the area), with a few species indicating a good conservation status of the area (*Acer platanoides*, *Cardamine enneaphyllos*, *Cephalanthera rubra*, *Polygonatum multiflorum*, *Tamus communis*; these latter species covering 10% of the area).

R4 – habitat characterized by the predominant presence of *Fagus sylvatica* in its tree phase (70% of the area), with grass cover of 20%, and with stony soil for about 10% of the area. Overall, this habitat type was particularly altered because of the presence of ruderal plant species.

R5 – habitat characterized by ferns (*Asplenium trichomanes*) and other plants (*Salvia glutinosa*, *Galium odoratum*, etc) in a relatively open area (100% of the area is grassy clearing habitat with no trees).

R6 – habitat characterized by the predominant presence of *Fagus sylvatica* in its tree phase (100% of the area).

We used live traps for performing the whole study. Live trapping was carried out with home-made PVC traps (7.5 × 7.5 × 23.5 cm³). Traps were provided with Plexiglas closures and with an automatic release mechanism made in ductile metal. Traps were placed in the same place of the grid every month during the 14 years study, thus, vegetation types for each trap were the same in all trapping sessions. Each trap was classified as being located inside one of the above-mentioned vegetation types. Data were obtained through Capture-Mark-Recapture (CMR; Gurnell and Flowerdew 1982) from spring to fall (i.e., monthly, from May to October) in 1988-1996 and 2000-2005. Trapping was suspended during the winter months (from November to April). Rodents were live-trapped in a 1.44 ha square grid, calculated including an outer boundary strip equal to half of the minimum distance between traps. Each trapping session was 3-nights-long, for a total of 1200-1500 trap nights per year. We arranged a square grid of 100 home-made live-traps (description in Fabbri 1989), and already used in Amori et al. 2000), spaced 12 m apart (see Amori et al. 2000 for more details). Traps were baited with chocolate cream, and seeds. The animals captured were tranquilized with ether, ear-tagged (Le Boulengé-Nguyen and Le Boulengé 1986), measured by a manual calliper (precision 0.02 mm) for body length, tail length, hind-foot length, and ear length. Rodents were also weighed by a Pesola precision scale (1 g). Rodents were released at the site of capture after having taken these measurements, and recorded their sex and sexual status (i.e., active/inactive) (see Amori et al. 2000).

Statistical analyses

Abundance estimates were generated by Minimum-Number-Alive (Krebs, 1999), on an annual basis. Density estimates were generated by Jolly-Seber index, calculated with MARK software (module POPAN; Table 1). Jolly-Seber

Table 1. Modelled density (individuals per ha) for each rodent species by season.

Year	<i>Apodemus flavicollis</i>		<i>Myodes glareolus</i>	
	spring	autumn	spring	autumn
1988	7.03	6.11	1.1	0.08
1989	7.85	7.50	11.7	5
1990	6.23	1.08	11.37	6.63
1991	11.3	4.11	8.1	3.38
1992	5.8	4.9	8.23	3.77
1993	7.13	3.87	0.67	1.91
1994	21.3	12.11	49.26	39.13
1995	0.8	0.02	1.8	5.1
2000	7.25	4.33	11.2	6.23
2001	8.21	3.21	5.21	1.88
2002	5.01	4.07	6.13	2.77
2003	24.45	16.83	7.36	4.11
2004	17.34	11.6	12.03	3.88

index was calculated because assumption of equal catchability of all individuals was not satisfied. Nonetheless, age cohort, sex or reproductive status did not affect catchability as a whole (at least $P > 0.08$ in all cases). The density estimates (ind. \times ha⁻¹) were calculated independently for males and females, then they were divided by the grid size. For analysing the relationship between body mass and population density by year for the two study species, we considered only the adult males. This selection was due to avoid the biases caused by the presence of juveniles and by pregnant females. Comparisons between annual estimates, and seasonal estimates, of density in *Apodemus* vs. *Myodes* were performed by a Monte Carlo Analysis of Variance, with 30,000 random permutations by fixing the zero states in all the pseudo-matrices (Gotelli and Graves 1996). In these cases, the year was the grouping variable, and the annual or seasonal density estimates was the dependent variable. Monte Carlo ANOVAs were applied instead of one-way ANOVAs because of the non-normal data distribution of the annual estimates.

We explored whether spatial structure of the small rodent community is affected by population cohorts based on body length and mass. In order to do this, first we needed to identify a single parameter that may describe the population structure. We collected data on both body length and body mass. Yearly average body weight was ranging 21-24 g in *A. flavicollis* and 22-24 g in *M. glareolus*, with no interspecific statistical difference across years. Body length and body mass were regressed each against the other, and we found that they were highly positively correlated in both *A. flavicollis* ($r = 0.730$; $n = 544$; $P < 0.0001$) and *M. glareolus* ($r = 0.88$; $n = 516$; $P < 0.0001$). As these two variables were highly correlated, for further analyses we used the body length as an objective measure of population structure. Based on the fitting of the body length distribution to the normal curve, we distinguished three body length groups in *A. flavicollis* (class

I = up to 80 mm, class II = 81-110 mm, and class III = >111 mm) and in *M. glareolus* (class I = up to 80 mm, class II = 81-100 mm, and class III = >101 mm). Then, we repeated the same analyses presented above for the pairwise intersections among the different size classes of the two species. The effect of the magnitude of body-size-difference between species on the probability of getting a non-random spatial resource partitioning at the micro-habitat scale was investigated by Monte Carlo ANOVAs, with 30,000 random permutations.

Because of the reproductive pattern of the studied rodent populations (reproduction occurring all the year round; see Amori et al. 2000), which is clearly different from the type of cycles observed in conspecifics from northern Europe (e.g., Montgomery 1980a,b,c), our trapping regime was unable to catch the population cohorts born in late autumn (October-November). Therefore, we did not recapture any of the marked individuals inter-annually, despite over 1000 individual rodents examined. Accordingly, we believe that the counts made by trapping were quite independent from year to year, and thus temporal autocorrelation should not be a problem in our analyses. Nonrandom patterns of resource partitioning were explored by using C-score analysis, with traps capturing the two species during a same survey event being considered as '1 1' cells, the cases of traps capturing none of the two species as '0 0', and the cases of traps capturing either species as '1 0' and '0 1' cells (checkerboard units).

We used the software EcoSim software (Gotelli and Entsminger 2001) for creating Monte Carlo permutations, Mark software for density estimates (White and Burnham, 1999), and SPSS (version 14.0) software for all other statistics. We employed only two-tailed tests, with alpha set at 5%. Nonparametric tests were used when data were not normal neither normalized after appropriate transformation.

Results

Overall analyses

Overall, we captured 960 individual rodents (491 *M. glareolus* and 469 *A. flavicollis*), with about 2000 recaptures. The annual number of captured and recaptured animals is given in Figure 1. The mean density of individuals per ha was 8.24 ± 5.95 individuals per ha (median = 6.23) for *A. flavicollis*, and 8.59 ± 11.82 (median = 5.56) for *M. glareolus*. The annual variations in the density are given in Figure 2. Density of *M. glareolus* was significantly higher in comparison to *A. flavicollis* in 1995 and 2001 (Monte-Carlo ANOVA after 30,000 iterations, pseudo-F = 33.66, $P < 0.001$), the density of *A. flavicollis* was significantly higher in comparison to *M. glareolus* in 2004 and 2005 (Monte-Carlo ANOVA after 30,000 iterations, pseudo-F = 21.43, $P < 0.001$). Thus, for 4 years the assemblage structure seems to be compatible with a competitive structure, whereas for 10 years it was not.

In both species there was a significant density fluctuation among seasons, with peaks occurring in spring versus autumn (*M. glareolus*: 10.32 ± 12.36 , versus 6.45 ± 9.98 , pseudo-F =

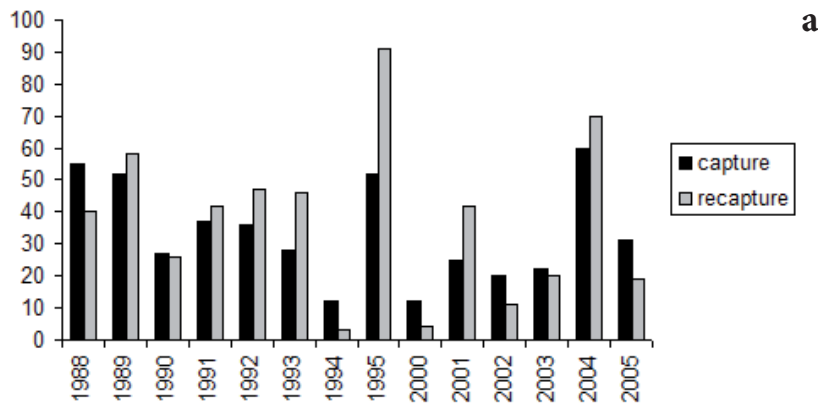
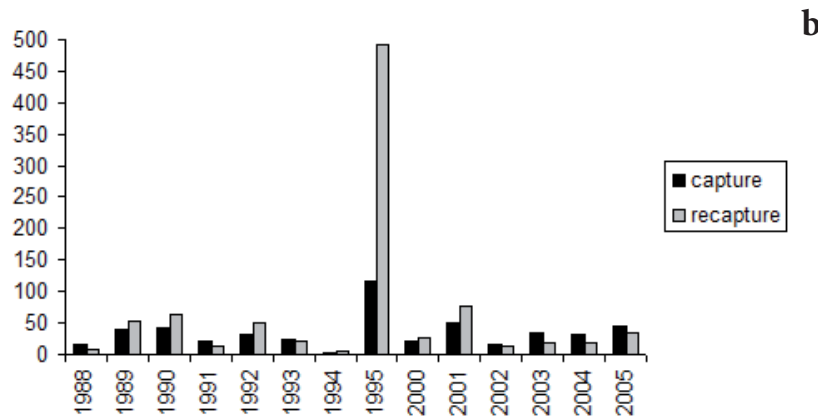


Figure 1. Annual number of captured and recaptured (a) *Apodemus flavicollis* and (b) *Myodes glareolus* in the study area.



b

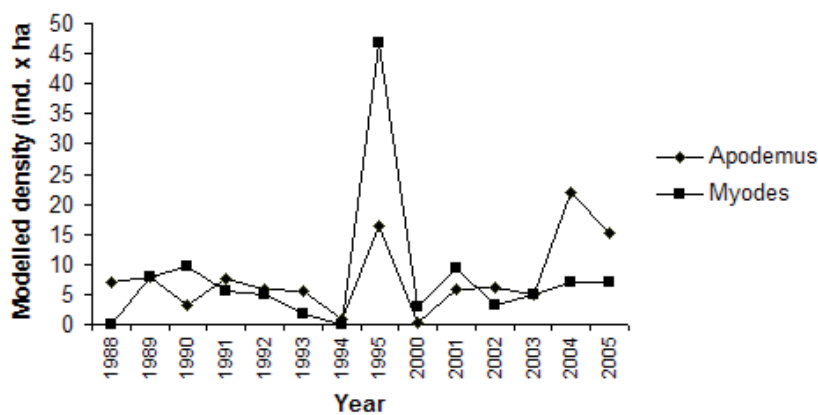


Figure 2. Mean modelled density (ind. × ha⁻¹) of the two rodent species, year-by-year, in the study area.

44.79, $P < 0.00001$; *A. flavicollis*: 9.98 ± 6.86 , versus 6.13 ± 4.75 , pseudo-F = 28.41, $P < 0.001$) (Table 1).

Spatial micro-distribution of the two species

Yearly variation in the percentage of lactating females

The percentage of lactating females fluctuated substantially across years (Figure 3). However, the (arc-sine) density of the potential competitor did not affect the (arc-sine) percentage of lactating females in either *A. flavicollis* ($r = -0.390$, $r^2 = 0.152$, $P = 0.188$) or *M. glareolus* ($r = -0.213$, $r^2 = 0.046$, $P = 0.484$).

The frequency of capture of the two rodent species varied across traps, thus showing a non-uniform and specifically different micro-distribution of the two species at the local scale. In particular, 20 traps were particularly favourable for capturing *M. glareolus*, 20 for capturing *A. flavicollis*, 35 for capturing either species, and 23 for capturing neither species (Table 2). Considering the spatial distribution of traps, we may determine three areas which were associated with high probability of capture for only one of the two study species,

Table 2. Spatial arrangement of the trap-grid, including different symbols for the vegetation types (a) and for the likelihood of capturing each of the two interacting species (b). * = high likelihood of capturing MG but not AF, ** = high likelihood of capturing AF but not MG. Black cell = high likelihood of capturing both AF and MG, White cell = low likelihood of capturing both AF and MG, The symbols ‘AF’ and ‘MG’ denotes a multi-trap area where one of the two species is respectively dominant (AF for *A. flavicollis*, and MG for *M. glareolus*).

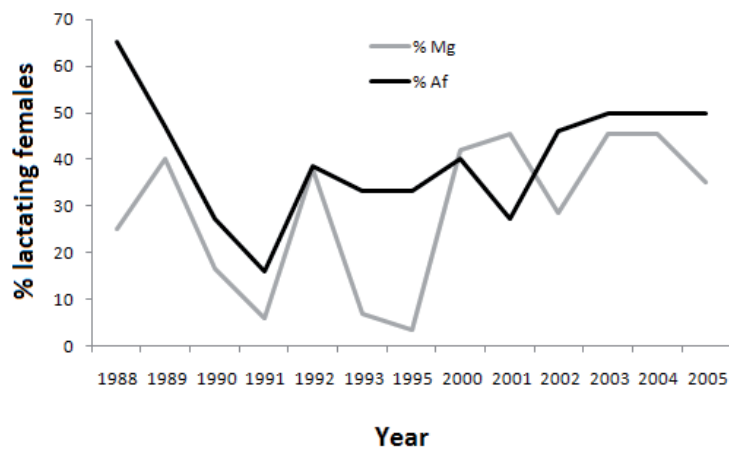
a

	1x	2x	3x	4x	5x	6x	7x	8x	9x	10x
1y	R2	R5	R5	R5	R5	R4	R4	R4	R4	R4
2y	R2	R2	R6	R6	R6	R1	R4	R4	R4	R4
3y	R2	R2	R2	R5	R5	R5	R1	R4	R4	R4
4y	R2	R2	R2	R5	R5	R5	R5	R5	R6	R6
5y	R2	R2	R2	R2	R5	R5	R5	R5	R6	R6
6y	R2	R2	R2	R2	R3	R5	R5	R5	R5	R5
7y	R2	R2	R2	R2	R2	R3	R3	R5	R5	R3
8y	R2	R2	R2	R2	R2	R3	R3	R3	R3	R3
9y	R2	R2	R2	R2	R2	R3	R3	R3	R3	R3
10y	R2	R2	R2	R2	R2	R3	R3	R3	R3	R3

b

	1x	2x	3x	4x	5x	6x	7x	8x	9x	10x
1y	*									
2y				**AF	**AF	**AF	*			*
3y		*	**AF	**AF						
4y						*		*		
5y									*MG	*MG
6y	*	*	**		**	**	*MG	*MG	**	*MG
7y		**		**AF		*	*MG	*MG		
8y			**AF	**AF	**AF	**AF	*MG	*MG	*	*
9y	**			**AF	**AF		**	**		
10y					**AF				*	

Figure 3. Yearly variation in the percentage of lactating females in the two study species. Mg = *Myodes glareolus*; Af = *Apodemus flavicollis*.



one of these areas being associated to *A. flavicollis*, one to *M. glareolus*, and one to both species together (Table 2). The areas where the two species occurred corresponded to vegetation types R2 and R3. Indeed, our logistic regression model showed that the presence of *A. flavicollis* was positively influenced by habitat R2 (logistic regression: $P < 0.01$) and *M. glareolus* with R3 ($P < 0.02$).

Coexistence analyses on the population parameters

Spatial partitioning between species increased with the increases in body size differences between potential competitors (Appendix 1): indeed, there was a statistically significant decreasing exponential curve between body-size-differences between species groups and probability of non-random spatial resource partitioning (Figure 4). The effect of the magni-

Table 3. Relative probability of occurrence of a non-random spatial partitioning of the captures of the two rodent species along the trap-grid by sex and by year. Symbols: A = *Apodemus*, M = *Myodes*. Statistically significant values are in bold.

<i>Apodemus</i> - <i>Myodes</i>	1988	1991	1993	1994	1995	2001	2003	Overall
Male _A -Male _M	0.0800	0.0400	0.0200	0.0600	0.0500	0.2310	0.0900	0.093
Male _A - Female _M	0.0010	0.0500	0.0100	0.0400	0.0001	0.0200	0.0300	0.00001
Female _A - Male _M	0.3320	0.2630	0.1180	0.1960	0.0900	0.6310	0.3930	0.06
Female _A - Female _M	0.0700	0.0100	0.1110	0.1320	0.0010	0.0900	0.0900	0.339

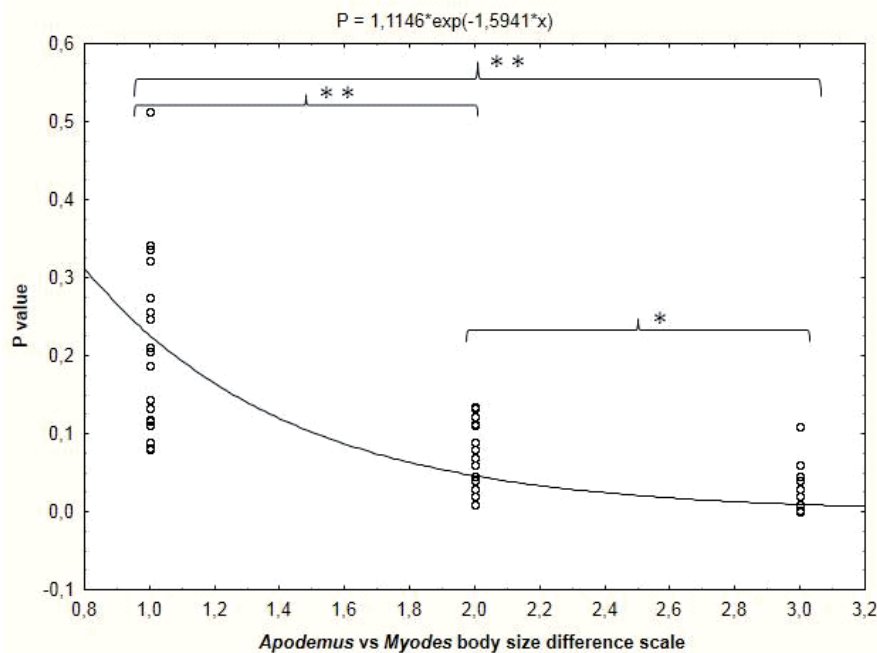


Figure 4. Exponential relationships between the body-size difference between *A. flavicollis* and *M. glareolus* and probability of non-random spatial partitioning. ** = $P < 0.05$; * = $P > 0.05$. For more details, see the text.

tude of body-size-difference between species was significant on the probability of getting a non-random spatial resource partitioning ($F_{2,42}=27.854, P < 0.0001$). It was evident that the smaller individuals of each species avoided the larger individuals of the other species in a non-random matter; this was more evident for *M. glareolus* (Appendix 1).

When conducting the same analyses as for sex (see data in Table 3), it resulted that the spatial partitioning between species was significantly non-random between male *A. flavicollis* and female *M. glareolus*, and between females of the two species, and between males of both species at least for three years (1991,1993 and 1995) (Table 3). However, there was considerable variation across-years in the magnitude of statistical significance of these paired comparisons (Table 3). Overall, it was evident that the male *A. flavicollis* significantly avoided female *M. glareolus* or vice-versa (either overall or year-by-year), whereas the other paired relationships were less strong. This trend was clearly confirmed by the significantly higher interactions of male *Apodemus* and female *Myodes* versus female *Apodemus* and male *Myodes* (Table 3).

There was no significant correlation between (log) male body mass and (log) population density in both *A. flavicollis* ($r = 0.276, n = 14, P = 0.339$) and *M. glareolus* ($r = - 0.154, n = 13, P = 0.615$). But, it should be noted that year 2004 was not included for *M. glareolus* in the analysis due to the small sample size.

Discussion

Are the density fluctuations of A. flavicollis and M. glareolus synchronized?

Our study revealed several patterns that appeared quite consistent across-years. To begin with, we observed an average density (ind. \times ha⁻¹) that was grossly similar between species, what means that, at the level of the grid scale, there was no clear dominance of one species versus the other, with population sizes changing in parallel year-by-year in the two species. The same phenomenon was similar to patterns observed for the same taxa, for instance, in German wood-

lands over a period of four years (Döhle et al. 1984), and to general conclusions provided by Gurnell (1985) for English populations. Our data also agree with findings of non-related density values between sympatric *Apodemus* and *Myodes* in both Italy (Canova 1993) and Belgium (Geuse 1985, Geuse and Bauchau 1985). This density is relatively similar to that observed in mature woodlands of northern Italy for *M. glareolus* (Canova and Fasola 1991). However, in Canova and Fasola's (1991) study *M. glareolus* was sympatric with *A. sylvaticus*, that had a much higher density than *A. flavicollis* at our study site (i.e., 31.6 ind. \times ha⁻¹). Parallel density fluctuations between European sympatric rodents were also detected in Poland (Pucek et al. 1993). Obviously, these density estimates should be considered as the averages of the annual counts, given that both species showed clear density fluctuations over seasons. Also in this case, however, the two species were apparently consistent with each other, with peak densities occurring always in spring versus autumn. This pattern is consistent with data provided by Amori et al. (2000) for *M. glareolus* in Italy, whereas no other study detailing the annual activity patterns of *A. flavicollis* in Italy is available.

Overall, we conclude that in our study system there was no competition between species at the landscape scale, since both species attained similar densities at the same time (no temporal exclusion). Instead, interspecific competition should be more intense at the micro-habitat scale (see below). However, it should be mentioned that, although our data are consistent with the hypothesis that there is no interaction between these species at a landscape level, we have merely survey data, with no experimental manipulation, and also from only a single location rather than multiple independent points across a landscape. Thus, our conclusions should be confirmed by further experimental studies.

Are the percentages of lactating females of a given species influenced by density variations in the potential competitor species?

Contrary to other cases available in the literature (for instance, in the case of the macro-carnivores hyenas and lions; see Watts and Holekamp 2008), we did not find any effect of the density of a given species on the percentage of lactating females (= reproductive success) of the other species. Watts and Holekamp (2008) considered that, in their study case, competition between hyenas with lions operated primarily via food competition, rather than direct killing, to generate the fitness differences. In our study case, there is clearly no such evidence.

Is there any coexistence between species at the microhabitat spatial scale?

We observed a non-random separation of the two species' spatial niches based on the different trappability (= affinity) in some traps by the two species. Indeed, the different trappability observed by species and by single traps revealed that micro-habitat played a crucial role in separating the ecological niche of these two rodent species, with *A. flavicollis* being

especially linked to micro-habitat type R2 and *M. glareolus* to R3. Both habitats were the most intact at the study site, although the relative coverage of *Fagus sylvatica* was much higher in R2 than in R3. However, *M. glareolus* tended to prefer an habitat type with a vegetation component of rich underbrush, that was on the other hand not important for *A. flavicollis*. Given that no previous study has explored the microhabitat preferences of *A. flavicollis* in Italy, it is obviously difficult to compare our results with bibliographic data. So, we are forced to compare our data with literature available from other European countries (e.g., Grüm and Bujalska 2000). The affinity of *M. glareolus* for low bush cover and *A. flavicollis* for more open mature forest is established in northern communities, for instance for *Apodemus* by Bergstedt (1965, 1966, in Sweden), and by Montgomery (1980a,b,c, in England). *Apodemus flavicollis* and *A. sylvaticus* are not equivalents with regards to spatial ecology and behaviour. Indeed, *A. sylvaticus* is subordinate to *A. flavicollis* but like *M. glareolus* it favours denser ground cover. Polish work by Bobek (1969) on populations of *A. flavicollis* and *M. glareolus* might also be useful in relation to co-fluctuation of population dynamics.

Previous studies on the coexistence of *A. flavicollis* and *M. glareolus* (Bobek 1969, 1973, Pucek et al. 1993) indirectly showed that these two species tend to coexist with moderate competition, although *A. flavicollis* being more aggressive than *M. glareolus* (Gurnell 1985, Grüm and Bujalska 2000), and although a mutually exclusive daily activity rhythm seems to be present (Wojcik and Wolk 1985). In this regard, our study provided evidence that these two species clearly divided their microhabitat niche, with vegetation aspects being important for niche separation at the spatial micro-scale. Kikkawa (1964) suggested that the spatial distribution of *M. glareolus* is influenced by the presence of bushy ground cover, unlike that of *A. sylvaticus*. The same pattern was also observed by Healing et al. (1983) in Skommer Island, Dyfed, but also in this case on *A. sylvaticus*. Thus, our study suggested that the type of microhabitat separation between *M. glareolus* and *A. flavicollis* in central Italy is very similar to that observed in northern Europe between *M. glareolus* and *A. sylvaticus*, and that, overall, mice and voles do consistently select different microhabitat types inside the forested landscape (see also Kozakiewicz et al. 1999).

Is there any evidence that interspecific competition may shape the fine-scale ecological distribution of these species?

Our analysis suggests, on the whole, that interspecific competition should indeed be present at the local micro-scale, as explained by the fact that in the great majority of the cases in which a given trap was highly successful in capturing one species, it was also very unsuccessful in capturing the other species. This was not merely an outcome of the different microhabitat selection by these rodents (although, as already explained, this factor undoubtedly had some relevance), as evidenced by the fact that several traps in a same microhabitat type had different power in capturing one species versus the other. On the other hand, this pattern seemed more likely

explained by the direct avoidance of one species by the other (e.g., see Wojcik and Wolk 1985), also when the microhabitat type was still suitable for it (in this regard, it should be noted that all six microhabitat types had at least a few captures of both species). Thus, it is possible that behavioural interactions between the two species may play a role in explaining the fine-scale (apparently competitive pattern) evidenced by our study.

In this regard, however, we could not ignore the fact that also a relatively large number of traps (35) had captures of both species. Moreover, the presence of spatial segregation between species is not, per se, indicative of demonstrated competition, as pointed out by several other studies on different systems (e.g., Wojcik and Wolk 1985, Connor and Bowers 1987). In this regard, body-size dependent dispersal may also be an important factor for explaining the above-mentioned observed patterns (see the case of *Microtus townsendii*, see Beacham 1979).

What are the demographic parameters that are under pressure of competition?

From the literature, it is well known that interspecific competition may act on several, independent demographic parameters (e.g., Douglass 1976, Walter et al. 1996, Chesson 2000). For instance, growth rates, age at maturity, and reproductive output may be inhibited by competition (e.g., Griffiths et al. 1991). In our study, however, we analysed the effects of competition on spatial partitioning mediated by both body size differences between species and sex. We found that both parameters exercised a significant influence on non-random space utilization by species, that is an evidence of a mediation effect of both body size and sex (and presumably the interaction between the two) on resource partitioning and minimization of competition strength. The main patterns were an avoidance of the larger individuals (class I) by the smaller individuals (class III) in both species, and an avoidance of the male *Apodemus* by the female *Myodes* and/or vice versa. These patterns should be interpreted ecologically. On the one hand, it seems likely that small rodents tends to avoid large competitors to avoid being preyed, i.e., to reduce the potential for interference competition. These data agree fully with findings of interference competition in northern Italian rodents (Fasola and Canova 2000), in small mammal communities from Nevada (Lemen and Freeman 1986), Colorado (Stapp 1997), in Israeli gerbils (Yom-Tov and Dayan 1996), in Finland voles (Eccard and Ylonen 2002), as well as in many other animal groups (e.g., see Yoshimoto et al. 2007).

Concerning the rodent assemblages inhabiting the temperate forests, it is well known that their population dynamics are strongly affected by seeds production of trees (e.g., Pucek et al. 1993) and, more importantly, that fluctuating food resources will affect degree of competition between species. In 1995, when the populations of the two species increased substantially, it is likely that an unprecedented food supply had sustained this substantial population growth. Thus, it is likely that in our study system the intensity of interspecific

competition should have shifted considerably from the high-productivity to the low-productivity years.

Overall, we suggest that the interspecific competition should indeed be present at the local micro-scale, as explained by the fact that in the great majority of the cases in which a given trap was highly successful in capturing one species, it was also very unsuccessful in capturing the other species. In addition, our study was suspended during the winter season, which is in theory the most disfavoring period for these species in the study area because of food resource limitation. Thus, the overall interspecific competition between these species could be even greater than observed in our study.

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Electronic supplement

Appendix 1. Relative probability of occurrence of a non-random spatial partitioning of the captures of the two rodent species along the trap-grid by size class and by year.

The file may be downloaded from www.akademai.com