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Spatial Interrelations between Bank Voles and Yellow-Necked Mice in Crabapple Island[1]

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Abstract—The investigations on spatial co-occurrence between *Myodes* (*Clethrionomys*) *glareolus* and *Apodemus flavicollis* conducted on Crabapple Island (NE Poland) in 1994 through 1999 reveal that: single mature females of both species often occur in the same places, whereas local groups of such females rarely cohabit the same place. Mature males of these species always avoid sites occupied by males of the other species. Immature males, however, seem to be mutually indifferent.

Key words: rodents, spatial interrelations, population, monitoring, habitat factors.

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Bank voles (*Myodes glareolus*) and yellow-necked mice (*Apodemus flavicollis*) often occupy the same habitat (Holišova, 1969; Pucek, 1983) and their populations exhibit correlated multiannual fluctuations (Kikkawa, 1964; Stubbe A. and Stubbe M., 1991; Geuse et al., 1985; Bujalska and Grüm, 2008). Sexually mature individuals of both species seem to be territorial (Bujalska, 1970; Bujalska and Grüm, 2005; Golikova, 1968; Wolton and Flowerdew, 1985). There are, however, important differences between them that may affect space use and population growth of the respective local populations of those species: territoriality of mature females and males of the bank vole inhibits maturation rate of the substantial part of the individuals of the respective sex (Bujalska and Grüm, 1989) whereas only mature males of the yellow-necked mouse seem to suppress maturation rate of the newly recruited males of the same species (Bujalska and Grüm, 2005). Females of the yellow-necked mouse do not show any sign of inhibition of their maturation rate in the breeding season, i.e., they all attain sexual maturity and the associated ability to breed (Bujalska and Grüm, 2005). However, actual breeding of the yellow-necked females (expressed in pregnant numbers) can be delayed in comparison to that of the bank vole females. Namely, the delay of the breeding in the peak years can be equal even to 40 days, whereas in the years of low population numbers there is no delay, that is the yellow-necked females and the bank vole females actually breed concurrently (Bujalska and Grüm, 2008).

The latter result suggests that locally high population densities of the species in question induce mutually competitive relations, whereas low densities provide some competitive relaxation. The present paper is aimed at testing such a hypothesis via analysis of spatial interrelations between females, as well as males, of the bank vole and the yellow-necked mouse.

MATERIAL AND METHODS

The study site was Crabapple Island on Beidany Lake (NE Poland) sampled in 1994 through 1999. The entire island area (4 ha) was covered by a regular net of 159 trap sites (mean distance between the sites was equal to 15 m, with 3 live traps per site). The traps were inspected twice daily (at 7 a.m. and 7 p.m.) during trapping session lasting 7 days. Each year four trapping sessions, covering the entire breeding season, were performed starting in the third decade of April and repeated in six weeks intervals, until the mid of September.

The Island habitat is broad leaved mixed forest with predominating *Tilio-Carpinetum* association (almost 80% of the area). The remaining part of the Island is covered by associations of *Salici-Franguletum* and *Alnetum*.

All individuals were individually marked when caught for the first time. At each capture they were sexed, weighed and their reproductive status was assessed (Bujalska, 1970). Among the females of both species sexually mature (perforate vaginal orifice) and immature (closed vaginal orifice) were distinguished.

[1] The article is published in the original.

Table 1. Regression of the number of bank voles in a trap site on various habitat factors

Period	CS	AU	TC	SC	LC	BC	MC	DB	DS
1994									
April	ns	ns	ns	**	ns	ns	**	ns	ns
June	ns	ns	ns	ns	ns	ns	ns	ns	*
July	**	ns	ns	ns	ns	**	ns	**	ns
Sept.	**	ns	ns	ns	*	ns	ns	**	ns
1995									
April	ns	**	ns	ns	ns	ns	ns	ns	ns
June	ns	ns	*	ns	ns	ns	ns	ns	ns
July	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sept.	ns	ns	*	ns	ns	ns	*	ns	ns
1996									
April	ns	ns	ns	ns	ns	ns	ns	ns	*
June	ns	ns	ns	ns	ns	ns	ns	ns	ns
July	ns	ns	ns	*	ns	ns	**	ns	ns
Sept.	ns	ns	ns	ns	ns	ns	ns	ns	ns
1997									
April	ns	ns	ns	ns	ns	**	ns	ns	ns
June	ns	ns	ns	ns	ns	ns	ns	*	ns
July	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sept.	ns	ns	ns	*	ns	ns	ns	ns	ns
1998									
April	ns	ns	ns	ns	ns	ns	ns	ns	ns
June	ns	ns	ns	ns	ns	ns	ns	ns	ns
July	ns	ns	ns	ns	ns	ns	ns	*	ns
Sept.	ns	ns	ns	ns	ns	ns	ns	ns	ns

Note: Explanation: ns – insignificant, * – $p < 0.05$, ** – $p < 0.01$, CS – bush cover (m^2), AU – undergrowth (pieces), TC – tree crown cover (m^2), SC – standing log cover (m^2), LC – laying log cover (m^2), BC – laying branch cover (m^2), MC – moss cover (m^2), DB – shortest distance to shore (m), DS – trap site distance to the closest shelter (m).

Table 2. Regression of the number of yellow-necked mice in a trap site on various habitat factors

Period	CS	AU	TC	SC	LC	BC	MC	DB	DS
1994									
April	ns	ns	ns	ns	ns	ns	ns	ns	ns
June	ns	ns	*	ns	ns	ns	ns	ns	ns
July	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sept.	ns	ns	ns	ns	ns	ns	ns	ns	ns
1995									
April	*	*	ns	ns	ns	**	ns	ns	ns
June	ns	ns	ns	ns	ns	ns	ns	ns	ns
July	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sept.	ns	ns	ns	ns	*	ns	ns	ns	ns
1996									
April	**	ns	ns	ns	ns	ns	ns	*	ns
June	ns	ns	ns	ns	ns	ns	ns	ns	ns
July	ns	ns	ns	**	ns	ns	*	ns	ns
Sept.	ns	ns	ns	ns	ns	ns	ns	ns	ns
1997									
April	*	ns	ns	ns	ns	ns	ns	ns	ns
June	ns	ns	ns	ns	ns	ns	ns	ns	ns
July	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sept.	ns	ns	ns	ns	ns	ns	*	ns	ns
1998									
April	ns	ns	ns	ns	ns	ns	ns	ns	ns
June	ns	ns	ns	ns	ns	ns	ns	ns	ns
July	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sept.	ns	ns	ns	ns	ns	ns	ns	ns	ns

Note: Explanation: ns – insignificant, * – $p < 0.05$, ** – $p < 0.01$, CS – bush cover (m^2), AU – undergrowth (pieces), TC – tree crown cover (m^2), SC – standing log cover (m^2), LC – laying log cover (m^2), BC – laying branch cover (m^2), MC – moss cover (m^2), DB – shortest distance to shore (m), DS – trap site distance to the closest shelter (m).

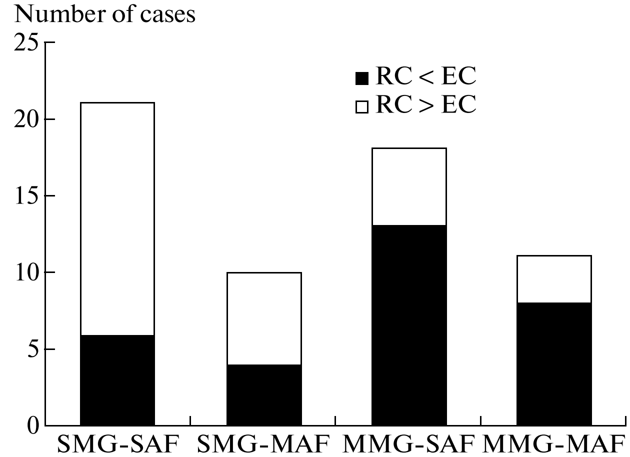

Fig. 1. Proportion of cases of positive and negative response among mature females of the bank vole and the yellow-necked mouse RC > EC – positive response, RC < EC – negative response, SMG-SAF – trap sites with single individual of each species, SMG-MAF – trap sites with single individual of the bank vole and at least two individuals of the yellow-necked mouse, MMG-SAF – trap sites with at least two individuals of the bank vole and single individual of the yellow-necked mouse, MMG-MAF – trap sites with at least two individuals of each species.

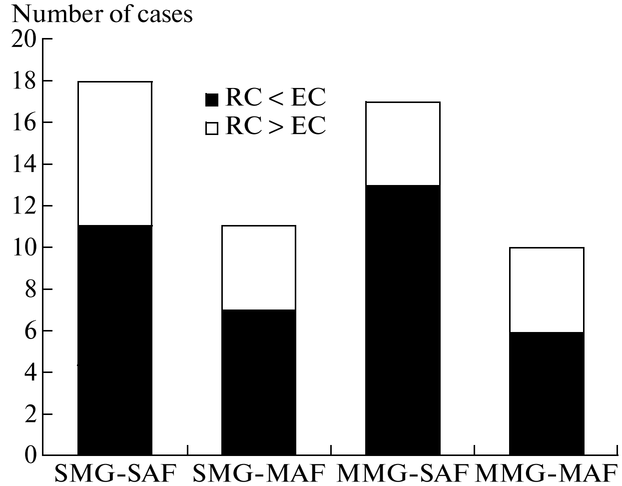

Fig. 2. Proportion of cases of positive and negative response among mature males of the bank vole and the yellow-necked mouse. For abbreviations see Fig. 1.

The position of testes was used to distinguish between mature (scrotal) and immature (abdominal) males.

To evaluate the importance of habitat factors on spatial distribution of the investigated rodent species the number of individuals (irrespectively of the number of recaptures) of a species in a trap site was correlated (using 159 trap sites) with the estimate of a habitat factor. The following habitat factors surrounding trap site (of 225 m^2 in area) were considered: shrub density indexed as shrub cover (m^2), undergrowth density expressed as number of trees per site area, shadowness expressed as crown cover (m^2), standing dead trees in m^2 within the site area, laying dead trees in m^2 within the site area, laying tree branches in m^2, and moss cover (m^2). Apart from that, the shortest distance between the site and the island shore (m), and the shortest distance between the traps and the potential closest shelter (m) were calculated. That procedure was repeated four times a year in 1994 through 1998. Linear correlation coefficients (least square method) were considered significant when $p < 0.05$.

A simple model of random co-occurrence of individuals of the studied species, based on the assumption that the number of sites occupied jointly by bank voles and yellow-necked mice should be proportional to the number of the sites occupied by each of them, was applied:

$$EC = (A/159)(B/159)159 = (AB)/159,$$

where EC – expected number of the sites occupied jointly by both species, A – number of trap sites occupied by individuals (irrespectively of the number of recaptures) of species a, B – number of trap sites occupied by individuals (irrespectively of the number of recaptures) of species b, 159 – total number of trap sites.

Comparing the empirically found number of trap sites occupied jointly by both species (RC) versus the expected number (EC) we concluded: if RC > EC then the examined species show mutually positive response, however, if RC < EC then there is negative response.

All cases when EC was less than one (EC < 1) were rejected from calculation of the ratio RC/EC. The response values were calculated separately for mature females, mature males and immature males. Because of low abundance of immature females of yellow-necked mice the EC values for their co-occurrence with immature females of the bank vole were not calculated.

Within each of the three groups of individuals (mature females, mature males and immature males) the following four variants were distinguished:

trap sites occupied by single individuals of bank voles and single individuals of yellow-necked mice (abbreviated SMG-SAF);

trap sites occupied by single individuals of bank voles and two or more individuals of yellow-necked mice (SMG-MAF);

trap sites occupied by two or more individuals of bank voles and single individuals of yellow-necked mice (MMG-SAF);

trap sites occupied by two or more individuals of each species in question (MMG-MAF).

Non-parametric statistics (Chi-square and Mann-Whitney) were used to estimate differences between the results obtained for the considered variants.

Table 3. Comparison of proportion of positive (RC > EC) to negative (RC < EC) responses between the four distinguished variants among mature females of *M. glareolus* and *A. flavicollis*. The X^2 test with Yates correction is used. Variant explanation: SMG-SAF – trap sites with single females of both species, SMG-MAF – trap sites with single female of *M. glareolus* and at least 2 females of *A. flavicollis*, MMG-SAF – trap sites with at least 2 females of *M. glareolus* and single female of *A. flavicollis*, MMG-MAF – trap sites with at least 2 females of each of the species

Compared variants	SMG-SAF	SMG-MAF	MMG-SAF	MMG-MAF
SMG-SAF	–	$X^2 = 0.05$, $p > 0.05$	$X^2 = 5.74$, $p < 0.025$	$X^2 = 4.06$, $p < 0.05$
SMG-MAF	$X^2 = 0.05$, $p > 0.05$	–	$X^2 = 1.61$, $p > 0.05$	$X^2 = 1.15$, $p > 0.05$
MMG-SAF	$X^2 = 5.74$, $p < 0.025$	$X^2 = 1.61$, $p > 0.05$	–	$X^2 = 0.16$, $p > 0.05$
MMG-MAF	$X^2 = 4.06$, $p < 0.05$	$X^2 = 1.15$, $p > 0.05$	$X^2 = 0.16$, $p > 0.05$	–

RESULTS AND DISCUSSION

It appears that the considered single habitat factors do not exert important effects on the spatial distribution of number of individuals of the studied species: generally they rarely correlate with the species spatial distribution. Out of 20 repeated correlation estimates the most persistent effect on the numbers of bank voles was exerted by the distance between the trap site to the island shore: four correlation coefficients were significant (Table 1). The same factor only once correlated with the numbers of yellow-necked mice (Table 2). The numbers of yellow-necked mice were most persistently correlated with another factor, that is bush cover: 3 correlation coefficients were significant (Table 2). That factor two times correlated also with the numbers of bank voles (Table 1).

Irrespectively of the reasons of the rare correlations between the estimated habitat factors and the respective population distribution in space (improper choice of habitat factors, their low diversification or predominant impact of mutual interrelations between the studied species), such a result indicates to reliability of conclusions on mutual impact of population factors on spatial distribution numbers of the studied species under the conditions of Crabapple Island.

The analysis of spatial co-occurrence of mature females of bank voles and yellow-necked mice reveals that:

single mature females of both species frequently exhibit mutually positive response (RC > EC). The negative response (RC < EC) is less frequent (Fig. 1);

single mature females of the bank vole more often show positive than negative response to two or more mature females of the yellow-necked mouse (Fig. 1);

positive response of two or more bank vole females encountering single female of the yellow-necked mouse was seen in less numerous cases (Fig. 1), and finally;

positive response in the case of 2 or more mature females of both species occupying the same trap sites was again less frequent than the negative response (Fig. 1).

The above presented description of spatial relations between mature females of the species in question is supported by statistical verification using two-sided Chi-square test with Yates correction (Table 3). Also the mean estimate of the ratio of RC/EC brings about the same results (applying two-sided Mann-Whitney test) when comparing the differences between each of the four variants (Table 4).

The analysis of spatial co-occurrence between mature males of bank voles and yellow-necked mice reveals that in each of the four variants the ratio of positive responses (RC > EC) to negative ones (RC < EC) did not differ (Fig. 2). This was confirmed when comparing the mean RC/EC ratio in each variant (Table 5). The positive vs. negative responses ratio in all variants with mature males (19 to 37) shows that positive responses are less frequent than negative ones: $X^2 = 5.78$, $p < 0.05$.

The analysis of spatial co-occurrence of immature males of the bank vole and the yellow-necked mice brings a picture about similar to that for mature males. There was no significant difference between the ratio

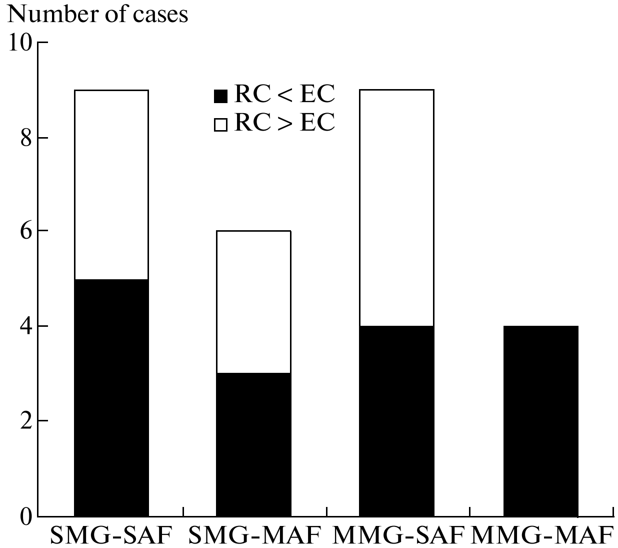

Fig. 3. Proportion of cases of positive and negative response among immature males of the bank vole and the yellow-necked mouse. For abbreviations see Fig. 1.

of positive to negative responses found in the four variants (Fig. 3), as it appeared from the comparison of the mean RC/EC ratio in each of the variants (Table 6). The only difference between the mature and immature males was that the latter showed equally frequent positive and negative responses jointly in all variants (12 to 16): $X^2 = 0.57$, $p > 0.05$.

Comparison of differences between three distinguished categories of individuals (mature females, mature males and immature males) showed that:

only single mature females of the studied species co-occur much more frequently than expected following the model of random co-occurrence (Fig. 1);

in all males, both mature and immature, no significant deviation from the model of random co-occurrence was found (Figs. 2, 3);

in mature females, as well as immature males, the total number of positive responses (co-occurrence more frequent than expected) did not differ from negative ones (29/31, $X^2 = 0.07$, $p > 0.05$ in mature females, and 12/16, $X^2 = 0.57$, $p > 0.05$ in immature males);

in mature males the total number of positive responses was significantly smaller than that of negative ones: 19/37, $X^2 = 5.78$, $p < 0.05$.

The results obtained on spatial co-occurrence between mature females of bank voles and yellow-necked mice seem to be consistent with those describing time-distribution of pregnancies, as reported by Bujalska and Grüm (2008). Namely, spatial co-occurrence between single females in most cases is more frequent than expected following the random co-occurrence model (Fig. 1). This corresponds to almost concurrent timing of pregnancies found in the years with low population densities of both species, when trap sites with single females seem to predominate. Contrary to that, local patches of two or more females coexist less frequently than might be expected by the random co-occurrence model (Fig. 1). Such a picture presumably exists mostly in the years of peak densities, that in those with time separation of the pregnancy periods (Bujalska and Grüm, 2008). The above described interactions between mature females may explain why the two species of potential competitors (Andrzejewski and Olszewski, 1963; Bergstedt, 1965; Greenwood, 1978) often coexist: strong competition that occurs in the peak years seems to be separated by periods of relaxation lasting for a few years of lower population abundances. This supports the idea of

Table 4. Spatial co-occurrence of mature females as seen from the obtained ratios of empirically found to the expected values (RC/EC) for the considered variants. See Table 3 for variant abbreviations. Mann-Whitney test (two-sided) shows significant differences ($p < 0.05$) of the mean values between the following variant pairs: SMG-SAF vs. MMG-SAF, SMG-SAF vs. MMG-MAF, SMG-MAF vs. MMG-SAF, and MMG-SAF vs. MMG-MAF

SMG-SAF	SMG-MAF	MMG-SAF	MMG-MAF
0.69	1.85	0.34	0.70
1.23	0.76	0.78	0.78
1.34	1.13	0.85	1.04
2.06	0.90	0.39	1.01
1.18	1.21	1.13	0.90
0.57	1.15	0.92	0.88
0.91	2.59	0.85	0.55
0.99	1.26	0.00	0.00
1.01	0.88	1.15	0.23
1.28	0.80	0.52	0.79
1.97		1.01	1.31
1.15		0.95	
0.86		1.58	
1.05		0.72	
0.75		0.83	
1.06		0.78	
1.07		1.13	
1.11		0.83	
1.55			
1.04			
1.07			
Mean = 1.16	Mean = 1.25	Mean = 0.82	Mean = 0.75

Table 5. Spatial co-occurrence of mature males as seen from the obtained ratios of empirically found to the expected values (RC/EC) for the considered variants. For variant abbreviations see Table 3. Mann-Whitney test shows no difference ($p > 0.05$, two-sided) between the mean values of any variant pair

SMG-SAF	SMG-MAF	MMG-SAF	MMG-MAF
0.98	2.65	1.24	0.86
0.42	1.35	0.94	1.36
0.57	0.45	2.31	0.00
0.91	0.79	0.96	0.86
1.65	0.80	1.11	1.22
0.23	0.37	1.04	0.55
1.08	1.73	0.38	1.10
0.79	0.60	0.69	0.00
0.83	1.66	0.57	0.00
1.34	0.46	0.97	1.45
0.98	0.00	0.86	
0.92		0.00	
0.42		0.99	
0.56		0.91	
1.24		0.85	
1.61		0.45	
1.84		0.78	
1.26			
Mean = 0.98	Mean = 1.01	Mean = 0.89	Mean = 0.74

Table 6. Spatial co-occurrence of immature males as seen from the obtained ratios of empirically found to the expected values (RC/EC) for the considered variants. For variant abbreviations see Table 3. Mann-Whitney test shows no difference ($p > 0.05$, two-sided) between the mean values of any variant pair

SMG-SAF	SMG-MAF	MMG-SAF	MMG-MAF
0.92	0.88	1.30	0.82
1.27	0.67	0.99	0.90
0.80	1.24	1.47	0.86
1.55	1.52	0.76	0.88
1.21	0.83	1.02	
0.39	1.63	0.93	
0.72		1.17	
1.34		0.00	
0.59		1.99	
Mean = 0.98	Mean = 1.13	Mean = 1.07	Mean = 0.87

occasional competition between bank voles and the mice, expressed by Gurnell (1985) who sought it in microhabitat separation.

On the other hand, the interactions between mature males present an entirely different case: irrespectively of the number of individuals per trap site, the cases of more frequent vs. expected co-occurrence were less numerous than those of less frequent than expected following the model (Fig. 2). This is to evidence constant mutual avoidance (or repulsion) between the mature males of the studied species, regardless of their population densities.

The spatial co-occurrence between immature males of the bank vole and the yellow-necked mouse presents still different picture: regardless of the numbers of individuals per trap site the mutual response is the same, namely similar numbers of positive and negative responses. This can be described as mutual indifference (Fig. 3).

Evaluations of population dynamics of rodents usually apply the density-dependent approach, based on the assumption that all individuals in the population are exact equivalents (e.g. Stenseth et al., 2002). On the other hand, just several years earlier, population dynamics was considered to be influenced by population structure (e.g. Petrusewicz, 1966). The density-dependent approach can be seen in considerations on competition between rodent species (e.g. Stapp, 1997), however, there were also approaches to discriminate between males and females (Fasola and Canova, 2000), as sexual differences could possibly play distinct role in interspecific competition.

The behavioral differences between mature females, mature males and immature males in spatial interactions between bank voles and yellow-necked mice provide evidence that there is no only one and persistent sort of interspecific interactions.

CONCLUSIONS

1. Single mature females of the bank vole and the yellow-necked mouse co-occur more often than expected, and this seems to result from their mutual tolerance, whereas local groups of mature females and all mature males of these species rarely co-occur, what can be the sign of mutual competitive repulsion.

2. Interspecific competition between all individuals of coexisting populations seems to be a simplification, and should be replaced by more insightful study, indicating for a category of individuals and/or circumstances that induce real interspecific competition.

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