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Spatial avoidance between the bank vole *Clethrionomys glareolus* and the harvest mouse *Micromys minutus*: an experimental study

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The relationship between the harvest mouse *Micromys minutus* and the bank vole *Clethrionomys glareolus* was studied in two 0.5 ha enclosures differing in the distribution of food. In the enclosure with only one feeding point, harvest mice were excluded from the feeding point. Their survival was poor throughout the winter and the recovery of the breeding population was slow. The enclosure with evenly distributed food was divided between the two species. The harvest mouse population of the even habitat was also able to maintain the overwintering area after the onset of breeding and the population grew as rapidly as that of the voles. Female bank voles in particular avoided the area inhabited by the harvest mice. After the removal of the mice the voles rapidly took over the area. In laboratory experiments, bank voles preferred traps with vole odour. Harvest mice showed no significant preference between clean traps or traps with vole or mouse odour. I conclude that because of interspecific competition for limited food resources the two species exhibited exclusive spatial distribution during winter. At least when food was readily available the smaller species was able to maintain its range during the early part of the breeding season. The mechanisms of this maintenance possibly involve odour production by the mice. At the highest population densities late in the breeding season, the mice change to a three-dimensional way of life in the high vegetation and in this way minimize contacts with possible competitors in the ground layer.

1. Introduction

Interspecific competition among small rodents has been a subject of intense study (e.g. Grant 1969, 1972, Myllymäki 1977, Gliwicz 1981, Henttonen & Hansson 1984) and a good deal of critical discussion (e.g. Haila 1982, Simberloff 1982, Schoener 1983, Galindo & Krebs 1986). Most studies have been carried out in a two-dimensional habitat. The situation becomes more complicated for species, such as *Apodemus* sp., exhibiting a great deal of arboreal activity (Gliwicz 1981, Geuse 1985, Geuse & Bauchau 1985).

One species which has been little studied in this respect is the harvest mouse, *Micromys minutus*. During the summer the harvest mouse, which weighs about ten grams, prefers old fields and forest edges with high vegetation and lives to a great extent arboreally (Piechocki 1958, Böhme 1978, Trout 1978, Harris 1979, Dickman 1986). It shares its preferred breeding habitat with the much heavier field voles, *Microtus agrestis* and ocassionally also with bank voles, *Clethrionomys glareolus* (Ylönen, unpubl.). However, these latter species remain mainly on the ground.

It is generally assumed that due to their small size and arboreal habits harvest mice do not compete with other rodent species during the breeding season. *Micromys minutus* has not, however, been studied in this respect, although North-American studies with the *Reithrodontomys* species indicate that avoidance of larger sympatric rodents by the smaller harvest mice does occur (Cameron & Kincaid 1982, Heske et al. 1984, Heske & Repp 1986).

In autumn, harvest mice may leave the field habitats because of harvesting and ploughing and move into barns, if possible, or to forest edges and unharvested old fields. Little is known about the social organization of harvest mice or about their relationship to other species overwintering in the same habitat. The diet of *Micromys* — various seeds, berries, insects and their larvae (Böhme 1978, Dickman 1986) — suggests that the species could compete for limited winter food resources during high density years with mainly granivorous bank voles (Hansson 1985) overwintering in the same areas. Possible competition should be even more pronounced at this time as harvest mice are forced to change from a three-dimensional habitat to life in the same subnivean space as other small rodents overwintering in field habitats (see Piechocki 1958). Due to behavioural changes in the voles during maturation, one would expect exclusion of the harvest mice from the breeding habitats of the voles by the onset of breeding.

The aim of the present study was to clarify the competitive relationsip between *Micromys* and *Clethrionomys*. The study was carried out during the peak years of local vole populations and exceptionally dense *Micromys* populations. The main questions addressed were:

1) Is the spatial distribution of these species different in patchy vs. even wintering habitats?
2) Does one of the species exclude the other in an extremely patchy overwintering habitat, or are they able to coexist over the winter?
3) Does the larger bank vole exclude harvest mice from the available enclosed area during the higher densities of the breeding season?
4) What kind of adaptations enable harvest mice to survive in competitive situations during breeding and non-breeding seasons?

2. Material and methods

2.1. Field experiments

The study was carried out in two enclosures, both 0.5 hectares in area at Konnevesi, Central Finland (62°N) in 1987–88. The enclosure fences were made of metre-high galvanized steel sheet, and extended to a height of 50 cm above the ground. The habitat in the enclosures was an abandoned field with some bushes. Each enclosure had 50 or 54 Ugglan Special multiple capture live traps, placed in a grid with ten metres between the trap stations. One of the enclosures, the patchy overwintering habitat (A), had one feeding station providing food. The feeding station consisted of four plastic feeding chambers, each with two entrance tubes that allowed only one individual to feed or pick up food at a time. This was to prevent too easy access to the food. The chambers were arranged in a square pattern 2 metres apart from each other. Oats were offered from October to April and sunflower seeds were added from January to April, in every chamber. In the other enclosure, i.e. the even habitat (B), there were 25 wooden feeding boxes distributed evenly (in every second trap row). The same food in about the same total amount as in enclosure A was offered during the study. Enclosure A also had 20 evenly distributed empty wooden boxes, in order to offer both populations the same chance of sheltering in boxes.

In October, 1987, experimental populations were established in both enclosures from voles

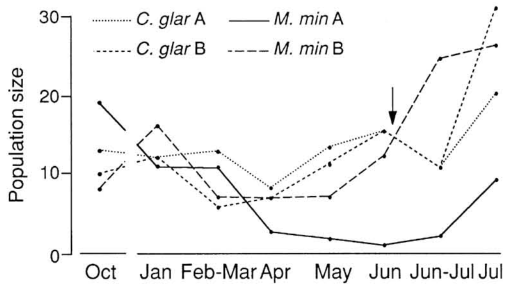

Fig. 1. Population densities (NA = number alive during trapping) of the bank vole and the harvest mouse in the two enclosures (A, B). The densities of *Micromys* were not manipulated. On 16 June (see the arrow) the vole densities were set to 10 individuals in each of the enclosures for other study purposes (see Ylönen et al. 1990).

and mice captured in the Konnevesi area. The initial populations during the first trapping at the end of October consisted of 19 harvest mice and 13 bank voles in enclosure A, and 8 harvest mice and 10 bank voles in enclosure B. The numbers stabilized up to January to about ten voles and mice per enclosure, except in enclosure B., where the number of harvest mice increased to 15 due to immigration (Fig. 1).

Trap chimneys of 50 cm height were used during the winter trappings (see Ylönen & Viitala 1985). Each trapping session, in October, January, February/March and April, normally lasted for seven days with approximately ten checks of the traps. During the breeding season, the enclosures were trapped intensively for a fortnight each month. The established populations were marked by toe-clipping.

To determine the effects of harvest mice on the spatial distribution of the breeding populations of the bank vole, harvest mice were removed from both enclosures in the last week of July. The study was unfortunately carried out without replicates due to difficult field work conditions during winter. Owing to the irregular occurrence of harvest mice it was impossible, as well, to repeat the experiment the next year as by then there were only a few harvest mice left in the Konnevesi area.

2.2. Data analysis

To describe space use (*SU*) by the two species I used the index

$$SU_i = 1/\Sigma p_{ih} ,$$

known as the inverse of the Simpson index in the ecological literature (e.g. Helle 1985), where p_{ih} is the frequency of the captures of the *i*-th species in the *h*-th trap. The index describes the relative width of the area of one species during each trapping period, weighting more the trap stations visited more frequently by the species. The use of this kind of index is possible, as the trapability of individual voles was about the same during the winter when all voles were immature (Ylönen & Viitala 1990). The overlap of the ranges used by the two species was measured using the relative similarity index (Renkonen 1938),

$$O_{ij} = \Sigma \min (p_{ih}, p_{jh}) ,$$

where p_{ih} and p_{jh} are the frequencies of the visits of the species *i* or *j* in the *h*-th trap.

2.3. Laboratory experiments

Laboratory studies were made during the late breeding season to test the preference for, or avoidance by, bank voles and harvest mice of traps bearing each other's odour. In a round arena of 60-cm diameter the rodents could choose from three Ugglan-traps:

1) a clean trap which was new and washed with distilled water,
2) a trap that had been occupied by a bank vole during the previous night,
3) a trap that had been occupied by a harvest mouse during the previous night.

Seven voles (four females and three males, all mature) and eight adult harvest mice (4 females and 4 males), were tested in a set of experiments extending over two days. Test subjects were placed in a tube in the middle of the arena and after 30 s the tube was removed and the rodents were free to enter one of the traps. The test was repeated three times to see if the information obtained from the first trap would influence the trap choice by the second/third time.

After the experiments on the first day the vole traps bearing vole odour were put in a cage with harvest mice overnight, and on the following day the trials were repeated using

1) clean traps,
2) new vole traps from the field and
3) previous vole traps inhabited by harvest mice for 24 hours.

In the arena, the location of the traps was changed randomly after every trial and the trap which the vole or harvest mouse entered was replaced with another trap of the same category. The transitions between the first and the second, and the second and the third, choice were recorded. The transitions should give a better estimate than the plain frequencies as regards the olfactory information which the voles and harvest mice obtain from the trap and how they react to the information. The transitions observed in the trap preference were statistically analysed using the Markov process (Andersson 1980, Ripley 1981).

3. Results

3.1. Population turnover

In both enclosures the monthly survival (MS, see Table 1 for definition) of the founder individuals of the *Micromys* population was worse than that of *Clethrionomys* during late autumn and mid-winter (Table 1). The total population density of harvest mice in the enclosure with even food distribution (B) increased, however, due to immigration. This was impossible to avoid because the snow cover reached the height of the fence. Later in the winter, the MS of harvest mice in enclosure A decreased strongly. In enclosure B, it remained similar to that of the bank vole population. In *C. glareolus*, the difference between individuals present in April (enclosure A = 8, enclosure B = 7) vs. individuals emigrated or dead during mid-winter (A = 7, B = 8) was not significant (Fishers exact, P = 0.50). In *M. minutus* there was an indication that the disappearance from the "patchy enclosure" (3 present in April, 18 disappeared up to April) would have been greater than from the "even one" (6 present, 7 disappeared) (Fisher's exact, P = 0.057).

In both species, breeding began at the end of April in enclosure B. Bank voles also began breeding at this time in enclosure A. The harvest mouse population in enclosure A decreased up to June and then recovered slowly. The harvest mouse population in enclosure B grew as rapidly as that of *Clethrionomys* until the removal of the harvest mice during the last week of July. At the time of the removal, the *Micromys* population in enclosure B was three times larger than that in A (Fig. 1).

3.2. Spatial distribution

In enclosure A, the area inhabited by the bank voles decreased during the early winter months and remained fairly constant around the feeding station thereafter. In enclosure B, the area used by the bank voles decreased constantly until the beginning of the breeding season, then increased to the same level as that of the population in enclosure A (Fig. 2).

Table 1. Population turnover in the experimental populations of *C. glareolus* and *M. minutus* during the winter of 1987–88. The percentage change of the population shows the density of the population of each month compared with the founder populations in October 1987. This value includes the changes caused by immigration, emigration and the death of individuals. The monthly change expresses the percentage of individuals present from the population captured one month earlier.

	Change from			
	October 1987		previous month	
	C. gla.	*M. min.*	*C. gla.*	*M. min.*
A. Single food patch				
Oct	100	100	–	–
Jan	92	58	92	47
Feb-Mar	100	58	83	75
April	62	16	54	9
B. Even food distribution				
Oct	100	100	–	–
Jan	120	200	80	63
Feb-Mar	60	88	50	44
April	70	88	33	57

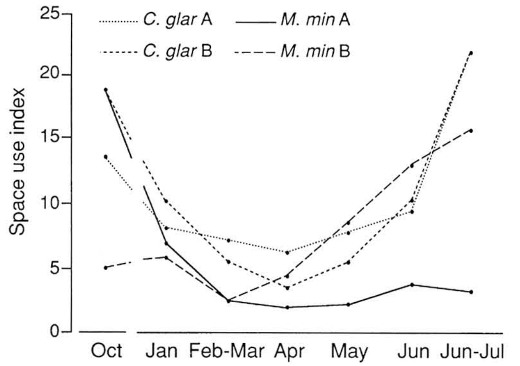

Fig. 2. Space use index for both species in the two enclosures during the winter and at the beginning of the breeding season.

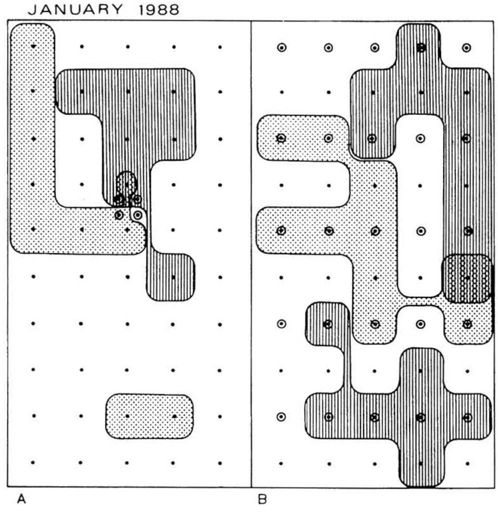

Fig. 3. Spatial distribution of *Micromys* and *Clethrionomys* in enclosures A and B during the trapping period in January 1988. The January trapping gives the best picture of the overwintering situation of immature individuals (10 harvest mice, 12 voles). The points of supplementary food are depicted with a circle around the trap point. The areas of the harvest mouse are dashed and those of the bank vole lined.

The *Micromys* population still ranged fairly widely in enclosure A in October, but the area used by it decreased quite drastically up to January. During the January trapping, the harvest mice had access to only one feeding chamber at the feeding station and the area inhabited by the mice was separated from that of the bank voles (Fig. 3). Several multiple captures of up to five harvest mice in one trap were observed during the January and February trappings. Competition for food is suggested by the vigorous dispersal of *Micromys* before the snow melt; 72% of the March population was captured in April in one or other of the two neighbouring enclosures, used for another winter experiment (Ylönen & Viitala 1990).

In enclosure B the area was divided between the species from the very beginning of the study (Fig. 3). This division also lasted after the onset of breeding in both species. The overlap of the ranges between the two species was greater in the enclosure with only one food patch during the winter months (Table 2). Even at the beginning of July the ranges of *Micromys* and *Clethrionomys* were almost exclusive in enclosure B (Fig. 4, Table 2). In particular the breeding bank vole females established their home ranges outside the harvest mouse area. The few visits of the voles to this mouse area (Fig. 4B) were exclusively made by males moving between the distinct areas of the mature females. During the next two weeks, after the removal of the harvest mice, bank voles occu-

Table 2. The space use overlap between *C. glareolus* and *M. minutus* in both enclosures. The overlap is calculated according to Renkonen (1938). Supplemental feeding was stopped at the end of April. The overlap between the species seemed to be higher during the winter months in enclosure A, apparently due to competition on access to food. The result was not significant, however (Wilcoxon's signed rank test, one tailed $P = 0.06$). After April the *Micromys* population declined strongly in A.

	Oct	Jan	Feb–Mar	Apr	May	June	July
A. A single food patch	0.12	0.11	0.05	0.16	0	0.02	0
B. Even food distribution	0	0.06	0	0.07	0	0	0.13

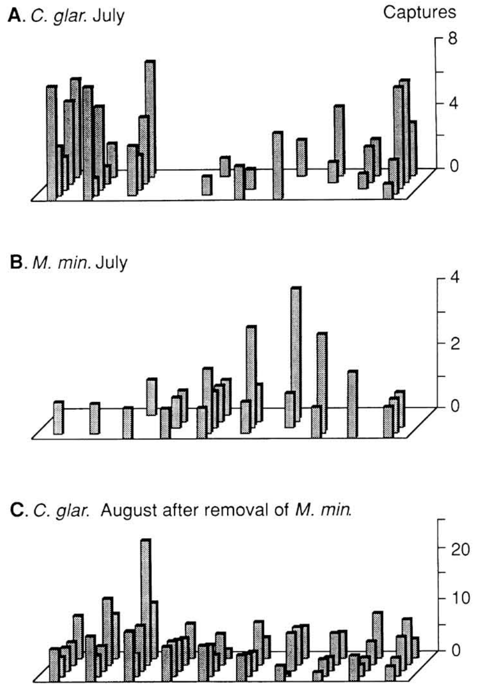

Fig. 4. The number of captures of bank voles (A) and harvest mice (B) in each trap of enclosure B (a grid of 10 × 5 traps) during the trapping period in late June — early July (14 checks) and the number of captures of bank voles (C) two weeks after the removal of harvest mice from the enclosure (15 checks).

pied the previously exclusive harvest mouse areas (Fig. 4C).

3.3. Trap-choice experiments

During the first set of laboratory experiments *C. glareolus* preferred traps previously visited by bank voles (Fig. 5). In the Markov process analysis the probabilities of transitions from one trap to another were in equilibrium ($\chi^2 = 1.53$, $df = 2$, $P = 0.465$) and the preference for the vole traps was significantly different from the null hypothesis of equal distribution of the visits ($\chi^2 = 9.183$, $df = 2$, $P = 0.010$). In the second set of trials one day later, the traps preferred during the first day were chosen less than the "fresh" vole traps (Fig. 5), but the difference was not significant ($\chi^2 = 0.58$, $df = 2$, $P = 0.748$).

The harvest mice did not show a preference for any particular kind of trap ($\chi^2 = 2.39$, $df = 2$, $P = 0.303$) during the first day's trials. For this reason I carried out only this one set of trials.

4. Discussion

In the northern parts of its range the harvest mouse has a very hard time because of harsh weather and human agricultural activities. During the autumn harvest mice may migrate (Koskela & Viro 1976) to suitable overwintering habitats or barns in the agricultural areas. Permanent snow cover for over half the year forces the harvest mice overwintering in old fields and forest edges to live in the same subnivean space as possible rodent competitors, field voles and bank voles. In the present study, *Micromys* made very few visits to the snow surface to seek food in dry plants standing above the snow as suggested by Kaikusalo (1983). The reason for this could be the availability of supplemental food under the snow with no need to search for food elsewhere. However, in a situation of intense competition arboreal feeding could be of advantage for the survival of the mice over the winter.

During the whole study, avoidance between the two species was strong in both enclosures. This almost led to the exclusion of the harvest mouse during late winter in the enclosure with one food patch. This is also the time of the most severe food situations for overwintering rodents. It is worth pointing out that in January the harvest mice sometimes "occupied" one of the four feeding chambers at the feeding point in enclosure A (Fig. 3). After such a visit, the chamber was not visited by the voles. The avoidance of a *Micromys* feeding chamber by the bank voles could be due to odours left by the mice in the chamber. However, the basic reason for the avoidance could be the feeding behaviour of the harvest mice: their food usage seems to be very extensive (see Piechocki 1958) and the food in feeding chambers was exploited very quickly compared with the food usage in the chambers visited by the voles. The result of this quick feeding was a mixture of half-eaten seeds, white starch crumbs and mouse ex-

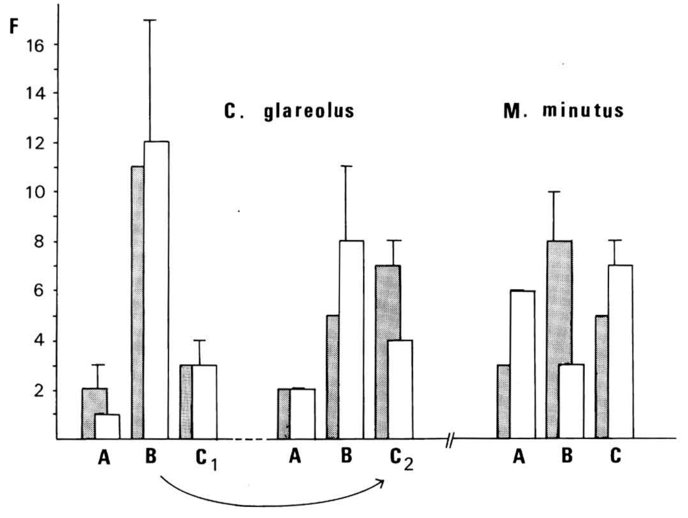

Fig. 5. Number of transitions between the traps for *C. glareolus* and *M. minutus* in the laboratory experiments. A = clean traps, B = vole traps from the field, C_1 = harvest mouse traps from the field, C_2 = vole traps from the first set of trials which were inhabited by harvest mice 24 h after that and used as harvest mouse traps in the second set of trials. Black bars show the transitions from the first to the second trap and white bars the transition between the second and the third choice. Total frequencies for the chosen traps are shown with a thin bar. For the single set of experiments with harvest mice trap category C is the same as C_1 for bank voles.

crement. This kind of feeding could lead to strong interference competition between harvest mice and co-overwintering species. It has been observed in caged animals (A. Kaikusalo, pers. comm., H. Ylönen, unpubl.). No observations under natural conditions on this subject exist, however.

Because of the rich food supply and the fact that the animals were immature during the winter I observed almost no aggressive behaviour between the species (no interspecific multiple captures, exclusive ranges). The poor survival of harvest mice during the spring in enclosure A could be due to the onset of breeding in the voles, however. The maturation of voles could cause increasing agressiveness, not only intraspecifically (Ylönen & Viitala 1990) but also towards harvest mice still visiting the only feeding place in the enclosure.

The preference by bank voles for traps containing the odour of their own species and the total lack of interspecific multiple captures during the field experiment suggest the importance of interspecific odour communication (see Stoddart 1982, 1986). Social odours have not been studied in *Micromys* at all (see Brown 1985). The present study indicates that the larger species as well might avoid interference competition with a smaller one. The ultimate reason for this avoidance could be the better exploitation of winter resources by the harvest mice combined with social odours and behavioural characteristics of immature voles. In the late breeding season with high densities and dispersal rates in voles, the harvest mouse must make use of another adaptation in order to survive: a change to an arboreal way of life as far as the height of the vegetation allows it.

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