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Relaxed competition during winter may explain the coexistence of two sympatric *Microtus* species

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Root voles (*Microtus oeconomus*) are competitively superior during summer and locally displace field voles (*M. agrestis*). Since the two species co-exist in many areas, competition may be relaxed or reversed during winter. To assess the competitive interaction during winter, we used PIT tags to study activity patterns and home range overlap of the two species in two enclosures with food-supplemented and non-supplemented plots during the winter of 2002–2003. Additionally, we established single species systems of root-vole and field-vole populations in the winter of 2004. Home-range size was smaller and activity lower in field voles than in root voles, and food supplementation caused an increase in activity in both species. Activity and home-range size in either species was not affected by the presence of the other. Despite the different activity patterns of the two species, home range overlap between field voles and root voles did not differ from random in the food-supplemented plots. In the non-supplemented plots daily overlap was higher than expected. As predicted, we were not able to detect any interference competition between field and root voles during winter. This supports our hypothesis that coexistence between the two may be caused by relaxed contest competition during winter.

Introduction

In northern habitats with distinct breeding and non-breeding seasons, seasonal variation in competitive intensity between species may be of importance. Studies of bank voles (*Myodes glareolus*, previously *Clethrionomys glareolus*) and field voles have shown that aggression levels in individual encounters are low during the non-breeding season both in mixed and single species communities (reviewed in Eccard & Ylönen 2003). The non-breeding season in the north is energetically demanding and may not allow maintenance of intensive competitive interactions. A prerequisite for competition between the two species is that there is a shortage of some resource that both depend upon. Korslund and Steen (2006) found that winter survival of root voles increased with increased food availability and we can therefore assume that there are food shortages during the winter. A study of grey-sided voles (*Myodes rufocanus*) supports this assumption since over-winter rate of population change was negatively affected by the size of the

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whole vole community and not just intra-specific density (Hansen *et al.* 1999). The winter is therefore a time of food shortage where we can expect intra- and inter-specific competition that may cause exploitation competition for a limited food source or interference competition by social exclusion (Schoener 1983). However, we do not know how food shortages affect social interactions between species. It is possible that relative competitive strength between species depends on whether they compete through interference or exploitation.

In Fennoscandia, root voles (*Microtus oeconomus*) and field voles (*Microtus agrestis*) often live in the same habitat in large parts of their distribution. Field voles are present at low densities when there are high numbers of root voles present, and they show high population densities when there are few root voles present. The inverse population dynamical trends of the two species suggest that the larger root vole is competitively superior to the smaller field vole (Tast 1968, Henttonen *et al.* 1977). Moreover, root voles force field voles into sub optimal habitats during the breeding season (Tast 1968, Henttonen *et al.* 1977). When root voles intrude into new habitats as population densities increase, field voles are forced into less profitable habitats. As root voles retreat from the same habitats, field voles again colonise these preferred areas. Despite root voles being competitively superior during summer, the two species coexist and can occur in the same localities simultaneously (Steven 1955). However, the mechanisms that allow coexistence, such as temporal and spatial variation in resource abundances or foraging efficiency and differences in the effect of competition between habitats, may differ between species and areas (Brown 1989, Ziv *et al.* 1993, Morris *et al.* 2000). Here we report an experimental study aimed at testing the hypothesis that contest competition (leading to social exclusion) between field voles and root voles is relaxed during winter.

Given that root voles and field voles coexist and compete through interference during the summer, we hypothesize that this type of competition between the two is relaxed during winter. Therefore, root voles should not exclude field voles from preferred areas, or inflict changes in activity and home range size of field voles. We tested this hypothesis in enclosures with homogenous habitat patches where we manipulated food availability and habitat quality. If the hypothesis is true, we predict that root-vole and field-vole habitat choice will be independent of the other species, but dependent on habitat quality. Specifically, inter-specific home range overlap will not differ from random, and activity will be unaffected by the presence of the other species. However, as for habitat choice, it may depend on habitat quality.

Material and methods

The experiments took place at Evenstad Research Station in southeastern Norway in December 2002, early March 2003, and early February 2004. The two enclosures (100 × 50 m each) used in the experiments consisted of two 851-m^2 large plots divided into two patches of habitat, 368-m^2 large, separated by five meters of uninhabitable matrix. The plots were five meters from the short edge of the enclosure and six meters from the long edges on each side of the enclosure, and separated from each other by 50 m of matrix (Fig. 1). Throughout the vegetative season prior to the experiments, we mowed the matrix area and treated it with herbicides. During the preceding summer and autumn, one patch in each plot was treated with herbicides (hereafter referred to as the treated patch) to reduce the standing biomass and thus the quality of the habitat. The patch not treated with herbicides functioned as a high quality control patch. In addition, one plot in each enclosure was subject to supplementary feeding during the experiment. Animals had ad lib availability of food (crushed oats) supplied through feeding automats that were distributed approximately along a 11 × 15-m grid in the food-supplemented plots. To keep track of the animal movements, we marked all individuals with passive integrated transponders (PIT tags, Trovan©) sub-cutaneously. In each habitat plot there were 24 trap stations (in a 7.5 × 8-m grid) protected by metal chimneys with open bases to allow vole access. In each trap station we placed antennas that were connected to LID665 PIT-tag decoders (EID-Aalten, NL) that recorded and stored an individual's ID number when a PIT-

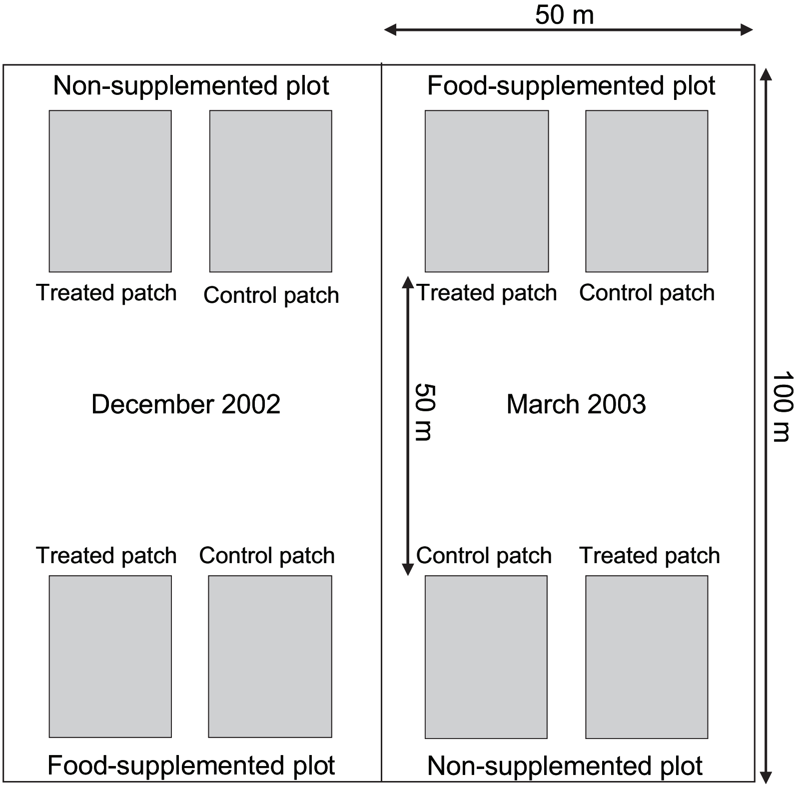

Fig. 1. Layout of the experimental enclosures used in this study. The grey squares represent the habitat plots in each enclosure, each divided into a treated patch and a control patch where the treated patch was sprayed with herbicides throughout the previous summer. The illustration also shows the arrangement of food supplementation in the plots, and the period each enclosure was used.

tagged individual passed through the antenna. The decoders were connected to a network supplied with electrical power through 12V batteries that were continuously recharged. During the first experiment (December 2002) we only had enough decoders to monitor one plot at a time. During the second experiment (March 2003) we had enough decoders to monitor two plots simultaneously. This restricted our experimental design to some degree. All animals used in the experiments originated from laboratory-bred populations kept at 8:16 LD regime and 5 °C to mimic winter conditions and were given food and water ad libitum while in captivity. All released animals were more than 60 days old and sexually mature. Mean weights of root voles and field voles were 25.2 g and 22.4 g in December 2002, 36.4 g and 35 g in March 2003, and 25.2 g and 31.5 g in February 2004, respectively. The higher mean weight of field voles as compared with that of root voles in the last release (February 2004) was a result of a higher mean age of field voles. This weight difference between species should not affect interspecific interactions as all voles in this release were introduced into one-species systems. The weight of individuals at release was within the range of body mass observed during winter at Evenstad (KSH pers. obs.). The PIT tags were injected approximately one week before release.

In December 2002, we released ten root voles and ten field voles (117.5 ind. ha^{-1} of each species) in each habitat plot in one enclosure. Activity recordings of individuals using the PIT-tag antennas and decoders lasted for ten continuous days starting one week after release in the non-supplemented plot and for seven continuous days starting two weeks after release in the food-supplemented plot. At the time of recording ten (117.5 ind. ha^{-1}) root voles and five (59 ind. ha^{-1}) field voles were present in the non-supplemented plot, and nine root voles (106 ind. ha^{-1}) and nine (106 ind. ha^{-1}) field voles in the food-supplemented plot with an approximately even sex ratio (*see* Table 1 for a summary of the design). In March 2003, we released five root voles and five field voles (59 ind. ha^{-1} of each species) in the food-supplemented plot, and five (59 ind. ha^{-1}) root voles and three (35 ind. ha^{-1}) field voles in the non-supplemented plot. Both plots were monitored at the same time. We let the animals settle for only two days before a six-day long continuous recording of PIT-tag passes was initiated. The time from release to the initiation of recording in this experiment was reduced as compared with that in the first experiment to maximize the number of animals present. Data from the previous experiment showed that activity distributions were comparable from release to when recordings ended, and the reduced time from introduction to activity and home range recording should be comparable. At the time of recording, six (70.5 ind. ha^{-1}) root voles and three (35 ind. ha^{-1}) field voles were alive in the food-supplemented habitat plot, and one (12 ind. ha^{-1}) root voles and three (35 ind. ha^{-1}) field voles were alive in the non-supplemented plot (Table 1). The higher number of observed as compared with released root voles in the food-supplemented plot was caused by one individual moving from the non-supplemented plot to the food-supplemented plot. The introduced root voles had an even sex ratio, while there were twice as many female as male field voles present.

The single species study was conducted in February 2004 when six (70.5 ind. ha^{-1}) root voles were released in one habitat plot, and six (70.5 ind. ha^{-1}) field voles in another. Because of logistic restrictions of the technical equipment, we used the non-supplemented plot from the December 2002 experiment and the food-supplemented plot from the March 2003 experiment by dividing the previous enclosures in two by setting up a temporary vole proof fence in the middle of each enclosure. Starting on day five after release we recorded movements using the PIT-tag readers for eight days in both plots. At this time, four (47 ind. ha^{-1}) field voles and three (35 ind. ha^{-1}) root voles were alive (Table 1). Release densities in all patches were chosen based on information available from previous winter trappings at Evenstad (G. Gundersen pers. comm.).

Analyses

For each individual, we measured the level of activity as the mean number of recorded passes through the antennas per day. Individual home range sizes were calculated by Kernel estimation, using ArcView 3.2 with Animal Movement (Hooge & Eichenlaub 2000). We chose to use 50% Kernel home range estimates in the analyses instead of 95% estimates because most of the individual 95% home ranges in the experiments during the winter 2002/2003 covered most of the available habitat area. Activity and home range size were log-transformed before performing a mixed-effects modelling procedure (lme) using the "nlme" package of R 2.1.1 (http://www.R-project.org) as described by Pinheiro and Bates (2000). We analysed differences in activity and home range size between one-species and

Table 1. Overview of the different experiments, the time they were conducted, the type of experiment and plots used, and the number of individuals of each species alive. The numbers of individuals released are shown in parentheses. In two-species systems, both field voles and root voles were released in the same plots, in the one-species system, only one species was released in each plot.

	Time	Type of data and plots	Number of individuals	
			Root voles	Field voles
Experiment 1	December 2002	Two-species systems		
		Food-supplemented plot	9 (10)	9 (10)
		Non-supplemented plot	10 (10)	5 (10)
Experiment 2	March 2003	Two-species systems		
		Food-supplemented plot	6 (5)	3 (5)
		Non-supplemented plot	1 (5)	3 (3)
Experiment 3	February 2004	One-species systems		
		Non-supplemented plots	3 (6)	4 (6)

two-species systems using data from non-supplemented plots only, as one-species systems only appeared in non-supplemented enclosures. We fitted activity and home range size to a variable discriminating one-species and two-species systems and a factor with species (and their interaction) as fixed factors. Species was included in the model to see if there was an interactive effect between treatment system and species, and will not be presented in the results unless significant. Plot ID was included in the models as a random factor to control for the pseudo-replication in the dataset. Differences in activity and home range size between individuals from food supplemented and non-supplemented patches were tested using data from two-species systems only. Models were chosen by a forward selection procedure and the fixed effects considered in the models were period (December 2002, March 2003, and February 2004), food-supplemented versus non-supplemented plots, species, and sex. Plot ID was included in the models as a random factor. To see if the activity of root voles and field voles was affected by the quality of habitat patches, we calculated habitat occupancy as the proportion of encounters in the herbicide treated patch as compared with that in the control patch. The variable was arcsine-transformed before performing a mixed-effects analysis as described above, choosing among the same variables except the factor one-species versus two-species systems. The latter factor was excluded because in the one-species systems both root voles and field voles were mostly observed in the patch where they were released and all visits to the neighbouring patch was at the edge. To avoid spurious results caused by the experimental procedure, we excluded these measurements from the dataset.

Temporal overlap between the species was estimated as the mean number of days in which an individual's home range overlapped with individual home ranges among the other species for each of the December 2002 and March 2003 plots separately. In these analyses, we excluded the data from the non-supplemented plot in March 2003 because of the extremely low number of individuals present. To obtain reliable standard errors and confidence intervals for expected overlap, we performed a bootstrap procedure to re-sample estimates of mean number of days with overlap between root voles and field voles. The estimated expected overlap was based on 10 000 iterations where we re-sampled (with replacement) from the pool of true home range shapes of each individual, but with random location and orientation. For each of the random iterations, we sampled as many random locations as there were individuals present in the original data. Observed overlap values that were outside the bootstrapped 95% confidence interval of the expected overlap were considered significantly different from expected.

In order to test if different photoperiods between experiments had any effect on activity, we estimated diurnal and crepuscular activity on cumulative data for each 24-hour period. We counted the cumulative number of recordings during each hour for the whole experimental period for each individual. To estimate diurnal and crepuscular activity, we used the equations suggested by Halle (1995). Diurnality refers to the allocation of activity between night and day, and is described by:

$$I_{\mathrm{D}} = \left(\frac{\dfrac{\sum c_{\mathrm{L}}}{h_{\mathrm{L}}}}{\dfrac{\sum c_{\mathrm{L}}}{h_{\mathrm{L}}} + \dfrac{\sum c_{\mathrm{D}}}{h_{\mathrm{D}}}} \right) \times 2 - 1$$

where Σc_{L} is the number of recordings during daytime for the experimental period, Σc_{D} is the number of recordings during night time, and h_{L} and h_{D} are the length of day and night in hours, respectively. Thus, the formula takes into account the variation in photoperiod, and is insensitive to its variation (Halle 1995). The diurnality index (I_{D}) is positive if the animals are active mainly during the day and negative if night activity prevails. The crepuscularity index (I_{C}) describes how much of the 24-hour activity occurs at sunset and sunrise, and it is described by:

$$I_{\mathrm{C}} = \log \left(\frac{\dfrac{\sum c_{\mathrm{SR}} + \sum c_{\mathrm{SS}}}{\sum c_{24}}}{\dfrac{4}{24}} \right)$$

where Σc_{SR} and Σc_{SS} are the number of recordings during the one-hour time interval surrounding sunrise and sunset, respectively. Σc_{24} is the total number of recordings during the experiment. The index is positive when individuals are more active at sunrise and sunset compared to the overall 24-hour period, and negative if they are less active (Halle 1995). To test if there were differences in diurnality and crepuscularity between species and experiments, we performed a forward selection procedure using mixed-effects models. For both diurnality and crepuscularity, plot ID was included as a random effect. As fixed effects for models explaining diurnality, we used species, sex, and period (December 20002, March 2003, and February 2004). Since crepuscularity could not be defined for most of the field voles, as most individuals never were active during dusk and dawn, we tested only root vole crepuscular activity by fitting models with sex and period as fixed effects.

Results

The analyses are based on 5152 recordings of individuals passing through the antennas. For field voles, we recorded 754 encounters in the two-species systems and 190 in the one-species system. The corresponding numbers for root voles are 4063 encounters in the two-species systems and 146 encounters in the one-species system. Climatic conditions varied slightly between periods. Similar for all experimental periods was a constant snow cover from early December to late March. During the December 2002 experiment, mean ambient temperature was –17.9 ± 1.3 °C (mean ± SE) and the snow depth was 56 cm. The equivalent values of temperature and snow depth in the March 2003 experiment were –0.2 ± 1.3 °C and 88.5 cm, respectively, and in the February 2004 experiment –6.1 ± 1.7 °C and 84.4 cm, respectively. Despite the variable surface temperatures, the snow pack creates a subnivean space with temperatures close to 0 °C (Marchand 1996).

There was no difference in activity ($F_{1,19} = 2.43$, $p = 0.14$) or home-range size ($F_{1,19} = 0.43$, $p = 0.52$) between one-species and two-species systems (treatment system, Table 2), neither was there a significant interaction between treatment system and species (activity: $F_{1,19} = 0.001$, $p = 0.97$; home range size: $F_{1,19} = 1.32$, $p = 0.26$). Thus neither field vole activity nor home-range size was affected by the presence of root voles.

The analyses of the effect of food supplementation showed that only species affected home-range size ($F_{1,40} = 6.48$, $p = 0.02$). Home ranges of root voles were larger than those of field voles (Table 2). The mean level of activity (Table 2), measured as the number of recordings observed per individual per day, was affected by species ($F_{1,39} = 4.88$, $p = 0.03$) and sex ($F_{1,39} = 6.44$, $p = 0.02$), and tended to be higher in food-supplemented plots than in non-supplemented plots ($F_{1,2} = 14.49$, $p = 0.06$). Activity was 60% lower in field voles than root voles and males were more

Table 2. Mean and standard error of the 50% Kernel home-range estimate, activity (mean number of encounters per day), percentage of encounters in the control habitat patch, diurnality (I_D), and crepuscularity (I_C) for field voles and root voles in the food-supplemented and non-supplemented habitat plots. The non-supplemented plots are further divided into one-species systems (February 2004) and two-species systems (December 2002 and March 2003). The crepuscularity values of field voles were not calculated since most field voles were not active in the hours around sunrise and sunset.

	Food-supplemented		Non-supplemented			
	Field vole	Root vole	Field vole		Root vole	
			One-species	Two-species	One-species	Two-species
50% home range	14.12 ± 4.43	29.06 ± 9.59	23.84 ± 15.95	23.70 ± 9.39	78.46 ± 26.25	45.13 ± 11.59
Mean activity	8.47 ± 3.29	35.96 ± 13.51	6.21 ± 3.16	2.26 ± 0.63	6.27 ± 1.46	4.19 ± 1.10
% control patch	0.28 ± 0.11	0.51 ± 0.09	0.25 ± 0.25	0.58 ± 0.16	0.14 ± 0.03	0.73 ± 0.09
I_D	0.48 ± 0.10	0.25 ± 0.07	0.33 ± 0.22	–0.02 ± 0.24	0.35 ± 0.05	0.20 ± 0.14
I_C	–	0.24 ± 0.06	–	–	0.12 ± 0.14	0.27 ± 0.06

active than females in both species and across all plots (male root voles: 27.48 ± 13.28; female root voles: 18.26 ± 10.75; male field voles: 9.86 ± 4.93; female field voles: 3.50 ± 0.78, mean ± SE calculated from all plots combined).

The model describing activity distribution between the herbicide treated and control patches showed that species was important for the distribution ($F_{1,39} = 6.02$, $p = 0.02$), as well as an interaction between species and experimental period ($F_{1,39} = 9.42$, $p = 0.004$). Period was not significant on its own ($F_{1,2} = 4.46$, $p = 0.17$). In December 2002, root voles used mostly the control patch (63% ± 0.09%, mean ± SE) and field voles mostly the herbicide treated patch (19% ± 0.09% of the activity observed in the control patch), irrespective of the level of food supplementation. In March 2003, field voles used mostly the control patch (83% ± 0.06%), while root voles were equally active in the control and treated patches (51% ± 0.08%).

The observed overlap between field voles and root voles was 3.44 ± 0.67 and 1.67 ± 0.33 days (mean ± SE) in the food-supplemented plots, in December 2002 and March 2003 respectively. These observations were well within the 95% confidence intervals of the bootstrap frequency distributions (December CI: 1.33–4.22 days, March 2003 CI: 1.00–4.33 days, Fig. 2a and b), suggesting that the number of days with overlap between the two species did not differ from random. In the non-supplemented plot in December 2002, field voles and root voles overlapped 1.60 ± 0.68 days, which was higher than the estimated confidence interval that ranged from 0.20 to 1.20 days with overlap (Fig. 2c).

Root and field voles did not differ in the diurnal activity patterns ($F_{1,40} = 1.45$, $p = 0.24$). Both species were more active during day than night (Table 2). There was no difference in diurnal activity patterns between the different experiments ($F_{2,40} = 1.73$, $p = 0.19$), suggesting that time of year did not affect diurnal activity patterns significantly. The different sexes within each species did not differ in activity either ($F_{1,40} = 0.006$, $p = 0.94$). Additionally, root voles did not differ in the amount of crepuscular activity between experimental periods ($F_{2,21} = 0.55$, $p = 0.58$), nor between sexes ($F_{1,21} = 0.22$, $p = 0.65$). However, they were more active during dusk and dawn than the rest of the 24-hour cycle (Table 2). The data on field voles did not allow for a similar analysis of crepuscular activity because most individuals were never encountered during dusk and dawn. The crepuscularity index was therefore indefinable.

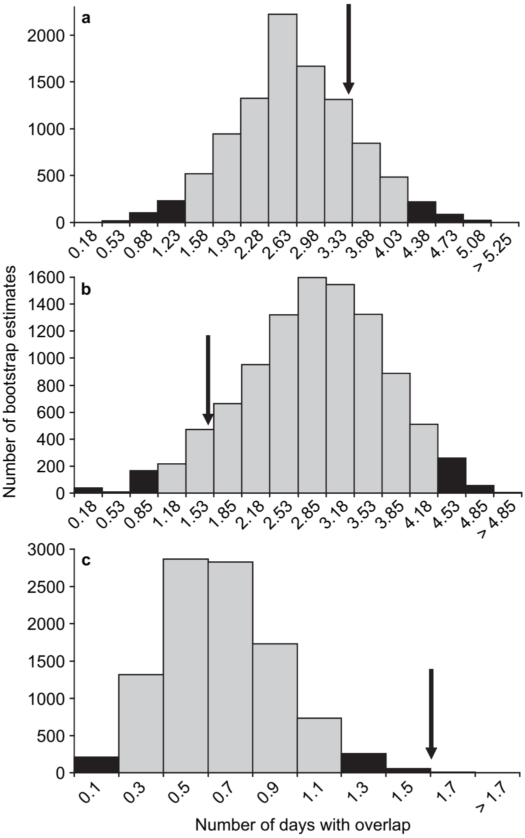

Fig. 2. The observed number of days with overlap between field voles and root voles is compared with the bootstrap estimates of expected overlap in the food-supplemented plots from the (**a**) December 2002 and (**b**) March 2003 experiments, and in the non-supplemented plot from (**c**) December 2002. The non-supplemented plot from the March 2003 experiment is excluded because of the low number of individuals present. Dark areas show the 95% confidence intervals. Grey bars correspond to the estimated number of days with overlap within the 95% confidence intervals. The observed number of days with overlap between root voles and field voles were 3.44 in **a**, 1.67 in **b**, and 1.60 in **c** and are illustrated by arrows.

Discussion

In this study we have documented differences in the activity level and home-range size between field voles and root voles independent of whether species were together or not. Despite the interspecific differences in home-range size and activity, home-range overlap between root and field voles did not differ from what would be expected from random. These results suggest that root voles and field voles do not compete through interference during winter. Our results correspond with observations of field voles and root voles from winter habitats in northern Finland (Tast 1966), where field voles could be found in the root vole habitat despite the strong competitive exclusion experienced during summer. Similar results also exist for meadow voles (*Microtus pennsylvanicus*) and red-backed voles (*Myodes gapperi*) in North America, where red-backed voles where observed in grassland habitats in winter despite being excluded during the breeding season (Iverson & Turner 1972). In December 2002, the distribution in activity between high- and low-quality patches of root voles and field voles could suggest that root voles force field voles into low quality habitats. However, the opposite pattern found in March 2003 shows that this is not the case. Seasonal variation in aggression can explain why there is no interference competition between root voles and field voles in this study. Research on meadow voles in North America has shown that males are more aggressive in the breeding season than the non-breeding season (Turner & Iverson 1973, Madison & McShea 1987), and that reduced aggression during the non-breeding season allows competing species to settle in habitats predominated by meadow voles (Iverson & Turner 1972). Aggression levels are also reduced in the non-breeding season in mixed and single species populations of bank voles and field voles in Fennoscandia (reviewed in Eccard & Ylönen 2003).

The home ranges of root voles and field voles in food-supplemented areas did not overlap more or less than it would be expected in case from random overlap. However, in the non-supplemented area the two species overlapped more with each other than expected from random localization of each individual's home range. It is possible that food supplementation caused individuals to stay closer to trap stations. In the non-supplemented plots movements were not restricted because of the distribution of reliable food resources. Given no competitive interactions, space-use overlap will naturally be higher. The lack of spatial aggregation between the two species in the food-supplemented areas can be explained in two ways: (1) root voles and field voles have no concern about individuals of the other species during winter because inter-specific competition in itself is not beneficial, or (2) the very setup of the feeding stations, uniformly distributed throughout the habitat areas, makes it difficult to monopolize food resources and interference is of low value for acquiring food. In this situation, exploitation competition is more important for describing interspecific relationships between the two species. Our short-term experiments have shown that competition through interference between root voles and field voles is not important during winter. Additionally, competition for food may not be the only source of exploitation competition. Individuals may also compete for other resources, such as nest material or available space. However, we do not have data to determine to what extent exploitation competition is involved and which resources are involved, so further experimentation is needed to resolve this question.

One problem with our design is that the different experiments were conducted in different years and seasons. We argue however, that this is not a major problem for several reasons. Firstly, we did not find any difference in activity, home-range size, or distribution of activity between experiments. Secondly, there was no difference in diurnal or crepuscular activity either, despite different photoperiodic regimes between periods. We also released naïve individuals under the snow, giving them no opportunity to prepare nests and open runways for the winter which may have resulted in odd behaviours. However, the voles did not change their behaviour over time judged from the overlap data which were calculated for separate plots and thus at different times from release. Since the voles did not change behaviour in the latter parts of the study as compared with that in the earlier parts they must have resumed normal activity quite soon after release. We will therefore argue that our results reflect those of voles living in natural environments.

In the food-supplemented plots, the addition of regularly distributed food gave the individuals known, inexhaustible food resources. This might both have made it possible for individuals to have a higher activity level, and restrict the area needed in order to get hold of enough food for survival. In the non-supplemented plots, individuals move over larger areas, probably in order to obtain enough food, but retain a rather low activity level. The reduced home-range sizes and increased activity when artificially fed during the non-breeding season in winter is also observed during summer (Ims 1987, Jonsson *et al.* 2002, Nie & Liu 2005). This suggests that these behaviours are independent of reproductive status, and dependent on food alone.

The individual activity levels were lower in field voles than in root voles in the food-supplemented and non-supplemented plots. Both species were more active when fed, and root voles were more active than field voles. Home-range size of field voles was smaller than that of root voles as well, but did not differ between food-supplemented and non-supplemented plots. These patterns in activity and home-range size may relate either to exploitation competition or general characteristics of the two species. In a rodent community with similar restrictions in food availability as in our experiments, enrichment of food resources resulted in stronger interference competition against the subordinate species, followed by a decline in the number of subordinate individuals present in the supplemented areas (Banks & Dickman 2000). Despite the similarities with our experimental system, the root voles did not seem to out-compete the field voles, supporting the conclusion that interference probably is not an important factor in winter. Root voles are larger than field voles (Tast 1968, Henttonen *et al.* 1977) and given that home-range size scale positively with body size (e.g. Harestad & Bunnell 1979, Schmidt *et al.* 2002, Borowski 2003) our observations are to be expected. The lack of difference in activity and home range size between one-species and two-species systems support the hypothesis that differences in activity and home-range size are species-specific (Makarieva *et al.* 2005), suggesting that field and root voles have different strategies to cope with the winter season, especially when food resources are high.

Home-range size is larger in males than in females in many promiscuous and polygynous microtine species (Erlinge *et al.* 1990, Gliwicz 1997, Slade *et al.* 1997). Most of these data come from studies on breeding animals, and the observed difference in home-range size is hypothesized to be caused by males maximizing the number of females and copulations. During winter, breeding is highly variable in microtine species (Hansson 1984), and completely absent in our study populations. Males therefore do not need to get access to breeding females, thus large home ranges are unnecessary. It is more adaptive to restrict home range size as much as possible to save energy and increase survival prospects. Male and female home ranges should therefore be equal in size during winter, as observed in this study and in several other studies of wintering small mammals (Bergallo & Magnusson 2004, Getz *et al.* 2005).

Grant (1972) claims that competitive interactions between small rodents are present in the form of interference competition rather than exploitation competition. Given differences in body size, large species should exclude smaller species. However, the distribution of closely related species indicates that mechanisms exists that allow for coexistence in many situations (Brown 1989, Ziv *et al.* 1993, Morris *et al.* 2000). For the vole communities in Fennoscandia, fluctuations of populations have been suggested as such a mechanism (Henttonen & Hansson 1984). Our study, however, presents an alternative explanation that works just as well in non-fluctuating populations. During winter, when food resources are scarce, interference competition may be too costly to maintain and competitive strength through exploitation may not follow the same pattern as through interference. If the dominant species loose the competitive edge during winter because interference is too costly to maintain, it might be possible for other species to survive in these areas.

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References

Banks, P. B. & Dickman, C. R. 2000: Effects of winter food supplementation on reproduction, body mass, and numbers of small mammals in montane Australia. — *Canadian Journal of Zoology* 78: 1775–1783.

Bergallo, H. G. & Magnusson, W. E. 2004: Factors affecting the use of space by two rodent species in Brazilian Atlantic forest. — *Mammalia* 68: 121–132.

Borowski, Z. 2003: Habitat selection and home range size of field voles *Microtus agrestis* in Słowinski National Park, Poland. — *Acta Theriologica* 48: 325–333.

Brown, J. S. 1989: Desert rodent community structure: a test of four mechanisms of coexistence. — *Ecological Monographs* 59: 1–20.

Eccard, J. A. & Ylönen, H. 2003: Interspecific competition in small rodents: from populations to individuals. — *Evolutionary Ecology* 17: 423–440.

Erlinge, S., Hoogenboom, I., Agrell, J., Nelson, J. & Sandell, M. 1990: Density-related home-range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. — *Journal of Mammalogy* 71: 597–603.

Getz, L. L., Oli, M. K., Hofmann, J. E., McGuire, B. & Ozgul, A. 2005: Factors influencing movement distances of two species of sympatric voles. — *Journal of Mammalogy* 86: 647–654.

Gliwicz, J. 1997: Space use in the root vole: basic patterns and variability. — *Ecography* 20: 383–389.

Grant, P. R. 1972: Interspecific competition among rodents. — *Annual Review of Ecology and Systematics* 3: 79–107.

Halle, S. 1995: Effect of extrinsic factors on activity of root voles, *Microtus oeconomus*. — *Journal of Mammalogy* 76: 88–99.

Hansen, T. F., Stenseth, N. C., Henttonen, H. & Tast, J. 1999: Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. — *Proceedings of the National Academy of Sciences of the United States of America* 96: 986–991.

Hansson, L. 1984: Winter reproduction of small mammals in relation to food conditions and population dynamics. — In: Merritt, J. F. (ed.), *Winter ecology of small mammals*: 225–234. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Harestad, A. S. & Bunnell, F. L. 1979: Home range and body weight — a reevaluation. — *Ecology* 60: 389–402.

Henttonen, H. & Hansson, L. 1984: Interspecific relations between small rodents in European boreal and subarctic environments. — *Acta Zoologica Fennica* 172: 61–65.

Henttonen, H., Kaikusalo, A., Tast, J. & Viitala, J. 1977: Interspecific competition between small rodents in subarctic and boreal ecosystems. — *Oikos* 29: 581–590.

Hooge P. N. & Eichenlaub B. 2000: *Animal movement extension to ArcView*, 2.0 ed. — Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.

Ims, R. A. 1987: Responses in spatial organization and behavior to manipulations of the food resource in the vole *Clethrionomys rufocanus*. — *Journal of Animal Ecology* 56: 585–596.

Iverson, S. L. & Turner, B. N. 1972: Winter coexistence of *Clethrionomys gapperi* and *Microtus pennsylvanicus* in a grassland habitat. — *American Midland Naturalist* 88: 440–445.

Jonsson, P., Hartikainen, T., Koskela, E. & Mappes, T. 2002: Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. — *Evolutionary Ecology* 16: 455–467.

Korslund, L. & Steen, H. 2006: Small rodent winter survival: snow conditions limit access to food resources. — *Journal of Animal Ecology* 75: 156–166.

Makarieva, A. M., Gorshkov, V. G. & Li, B. L. 2005: Why do population density and inverse home range scale differently with body size? Implications for ecosystem stability. — *Ecological Complexity* 2: 259–271.

Madison, D. M. & McShea, W. J. 1987: Seasonal changes in reproductive tolerance, spacing, and social organization in meadow voles: a microtine model. — *American Zoologist* 27: 899–908.

Marchand, P. J. 1996: *Life in the cold*. — University Press of New England, Hanover.

Morris, D. W., Fox, B. J., Luo, J. & Monamy, V. 2000: Habitat-dependent competition and the coexistence of Australian heathland rodents. — *Oikos* 91: 294–306.

Nie, H. & Liu, J. 2005: Regulation of root vole population dynamics by food supply and predation: a two-factor experiment. — *Oikos* 109: 387–395.

Pinheiro, J. C. & Bates, D. M. 2000: *Mixed-effects models in S and S-plus*. — Springer-Verlag, New York.

Schmidt, N. M., Berg, T. B. & Jensen, T. S. 2002: The influence of body mass on daily movement patterns and home ranges of the collared lemming (*Dicrostonyx groenlandicus*). — *Canadian Journal of Zoology* 80: 64–69.

Schoener, T. W. 1983: Field experiments on interspecific competition. — *American Naturalist* 122: 240–285.

Slade, N. A., Russell, L. A. & Doonan, T. J. 1997: The impact of supplemental food on movements of prairie voles (*Microtus ochrogaster*). — *Journal of Mammalogy* 78: 1149–1155.

Steven, D. M. 1955: Small mammal communities of the north scandinavian birch forest. — *Journal of Animal Ecology* 24: 403–411.

Tast, J. 1966: The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. — *Annales Zoologici Fennici* 3: 127–171.

Tast, J. 1968: Influence of the root vole, *Microtus oeconomus* (Pallas), upon the habitat selection of the field vole, *Microtus agrestis* (L.), in northern Finland. — *Annales Academiae Scientiarum Fennicae* (A IV) 136: 1–23.

Turner, B. N. & Iverson, S. L. 1973: Annual cycle of aggression in male *Microtus pennsylvanicus*, and its relation to population parameters. — *Ecology* 54: 967–981.

Ziv, Y., Abramsky, Z., Kotler, B. P. & Subach, A. 1993: Interference competition and temporal and habitat partitioning in two gerbil species. — *Oikos* 66: 237–246.