



## Smaller *Microtus* vole species competitively superior in the absence of predators

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Interspecific competition is assumed to generate negative effects on coexisting species, possibly including slower population growth and lower survival. The field vole (*Microtus agrestis*) and the sibling vole (*M. rossiaemeridionalis*) are sympatric close relatives which compete for similar resources. Previous non-experimental studies suggest that the smaller sibling vole is a superior competitor, yet more vulnerable to predation than the larger field vole. We studied the effects of coexistence on population densities, reproductive parameters, and survival in these two species by means of experimentation in large, predator-free outdoor enclosures. While populations of both species reached higher densities in the absence of the other, field voles appeared to suffer more from interspecific competition than sibling voles. The proportion of young individuals in the population was higher in the sibling vole than in the field vole at the end of the experiment. The presence of a coexisting species reduced the survival of field voles. Sibling voles, on the other hand, appeared to suffer more from intraspecific competition than interspecific competition. On a population level, the sibling vole seems to be a superior competitor in the absence of predators due to better survival and possibly a higher reproductive capacity. However, predation probably has a profound influence on the interspecific dynamics of these two species indicating that in natural surroundings apparent competition (i.e. competition via shared predators) is stronger than direct competition.

Competitive interactions between different species are one of the biological factors thought to have a strong impact on animal communities. In extreme cases, interspecific competition for limiting resources can make the co-occurrence of two species impossible leading thus to the local extinction of one species (the competitive exclusion principle, Gause 1934, Morris and Grant 1972, Koplin and Hoffmann 1986). Even when local coexistence is possible, interspecific competition may still produce negative effects on both competing species.

Interspecific competition has been studied widely in many animal groups including small mammals, and particularly rodents (reviewed by Grant 1972, Eccard and Ylönen 2003). In voles there are several examples where interspecific competition has been shown to have negative effects on population growth, survival or reproductive success of species. For example, in the absence of potential competitors, bank voles

(*Clethrionomys glareolus*) reached densities twice as high as during sympatry (Löfgren 1995). The survival of bank vole females was reduced under competition with field voles (*Microtus agrestis*) (Eccard and Ylönen 2002). On the other hand, there are also a number of cases where the presence of another closely related species seemed to have only minor or no obvious effect (Lin and Batzli 2001, Johannesen 2003).

Predators can alter interspecific competitive interactions substantially (reviewed by Sih et al. 1985, Gurevitch et al. 2000, Chase et al. 2002). For example, coexisting species may interact with each other indirectly via shared predators (i.e. apparent competition, Holt 1977). When predation pressure is high, the importance of direct competition can become reduced, and vice versa. Predators can also favour one species over the other and thus shape the composition of the prey community by selective hunting. If predators prefer a competitively dominant species over a

subordinate, intermediate levels of predation may promote the coexistence of the two species (Chase et al. 2002). Therefore, studies on interspecific competition carried out under high predation pressure may give results which underestimate the degree of potential direct competition.

Most studies on interspecific competition among boreal rodents have been carried out with species exhibiting a considerable difference in size or in their habitat or food niches (e.g. bank voles and field voles). In general, larger species emerge as superior competitors in a community (Grant 1972, Glazier and Eckert 2002, but see Persson 1985). However, while body size is not the only important feature affecting competitive outcomes, other possible mechanisms influencing interspecific competition may be considerably harder to identify. For example, very little is known about the competitive relationships between two similar-sized congeners, the common vole (*Microtus arvalis*) and the field vole in the wild (but see Dienske 1979, De Jonge 1983), although the field vole is the most common vole species in northern European grasslands. Also, only correlative data are currently available (Norrdahl and Korpimäki 1993) on the competitive interactions between the field vole and the sibling vole (*M. rossiaemeridionalis*). Both species use largely identical types of food (Myllymäki 1977a), but the mechanisms enabling their sympatric coexistence are not known.

This study focuses on the effects of coexistence on demographic processes in two species of the genus *Microtus*, the sibling vole and the field vole. Previous non-experimental studies show that sibling voles are somewhat smaller in body size than field voles (Norrdahl and Korpimäki 2002). However, on a population level, sibling voles appear to be superior competitors (Norrdahl and Korpimäki 1993, but see Huitu et al. 2004), yet more vulnerable to patch-searching predators than field voles (Korpimäki 1992, Koivunen et al. 1996). Because the sibling vole has a more aggregated way of life than the field vole (Norrdahl and Korpimäki 1993), the population densities of the former can become locally high. Therefore, predators may be able to detect patches formed by sibling voles (so called "hot spots", Norrdahl and Korpimäki 1993) more easily than those of field voles (Korpimäki 1992, Koivunen et al. 1996). In addition, because both *Microtus* species are the main prey of avian and mammalian predators in western Finland and elsewhere in northern Europe (Korpimäki and Norrdahl 1991a, Korpimäki et al. 1991, Valkama et al. 2005), predation may play a greater role than interspecific competition in determining the relative and absolute abundances of these two species (Norrdahl and Korpimäki 1993, Huitu et al. 2004). We predicted that in the absence of predators, sibling voles would

perform better than field voles under coexistence of the two species.

## Methods

### Study species and study system

The study species, the sibling vole and the field vole, are the most common vole species in the grasslands of western Finland (Korpimäki and Norrdahl 1991b). The sibling vole has probably been unintentionally introduced from the Karelian isthmus, Russia, to western Finland in the 1940s (Sulkava and Sulkava 1967), and its recent distribution covers the agricultural areas near the western coast of the country. The two species are close relatives and occur naturally in the same areas, and use very similar kinds of habitats and food resources (Myllymäki 1977a). Although both species are folivorous they show some habitat and food niche division. For example, sibling voles are better adapted to shorter grass than field voles (Myllymäki 1977a, Norrdahl and Korpimäki 1993). Both species show synchronous high-amplitude cyclic population oscillations with a period of three years (Huitu et al. 2004, Korpimäki et al. 2005). The sibling vole is slightly smaller in size than the field vole. The average body mass (mean  $\pm$  SD) of an adult sibling vole female in the study area is  $24.6 \pm 6.1$  grams and that of an adult field vole female  $30.8 \pm 7.6$  g (Norrdahl and Korpimäki 1993). For the males the difference is even smaller: the mean body mass (mean  $\pm$  SD) of an adult sibling vole male is  $31.2 \pm 6.1$  g and that of an adult field vole male  $32.4 \pm 6.7$  g (Norrdahl and Korpimäki 1993).

We conducted the study in summer and autumn 2004 in Lapua, western Finland ( $63^\circ$  N,  $23^\circ$  E) in four separate study sites. The study sites were established in 1996 on old farmland and they are located 1.5–7 km apart and within an area of 12 km<sup>2</sup>. The sites are mostly dominated by graminoids such as canary grass (*Phalaris arundinacei*), and herbs, e.g. nettle (*Urtica dioica*), creeping thistle (*Cirsium arvense*) and fireweed (*Epilobium angustifolium*). A more detailed description of the study sites and vegetation is given in Norrdahl et al. (2002).

Each study site contained two 0.5-ha predator-proof enclosures. The enclosures were constructed using hardware cloth (mesh size 12.7 mm), which extends 0.5 m below and 1.3 m above ground. A metal sheet (40 cm) was fastened to the upper edge of the fence to prevent climbing by voles and mammalian predators. To prevent access by avian predators, the enclosures were covered with nylon net (mesh size 10 cm). In each enclosure, 48 traps (multiple capture Ugglan live-traps, Grahns, Sweden) were distributed evenly ca 10 m apart. The traps were placed individually in plastic

boxes ( $40 \times 30 \times 25$  cm) to provide protection from the weather. The grass of the central third of each enclosure was kept short (10–20 cm) by mowing for the purposes of another experiment. Natural vegetation in the enclosures reached a height of ca. 150–200 cm during the experiment.

## Experiment procedures

Before the beginning of the experiment we emptied the enclosures of rodents using both live-capture and snap traps. In early July we released four pairs of field voles and four pairs of sibling voles into two randomly selected enclosures each (single-species populations) and a combination of two pairs of field voles and two pairs of sibling voles into four enclosures each (two-species populations). Thereby, all replicates were founded with an equal density of 16 voles  $\text{ha}^{-1}$ . The voles were originally caught from the wild in Lapua and surroundings and kept in single-species populations for a month in two 0.5-ha predator-proof enclosures to reproduce. Vole individuals were allocated randomly to different treatments and areas for the experiment. Only sexually mature individuals were used, as judged by a perforate vagina in females or scrotal testes in males.

Vole population growth was monitored by live-trapping on seven occasions from the end of July to the beginning of November, using standard capture–mark–recapture techniques. The time period between trappings was on average two weeks, being shortest at the beginning of the experiment and longer towards the end of the experiment. Each trapping period lasted six days. Two sites were trapped first for three days and then the other two sites for a further three days. Traps were baited with Rat/Mouse Breeding Diet pellets (Altromin GmbH, Germany) and checked three times per day, in the morning (at 6:00), in the afternoon (14:00) and in the evening (21:00). Voles were marked individually, weighed, sexed and their current reproductive status (males: mature/submature/postmature, females: submature/mature/gravid/lactating/postmature) noted. A vole is classified postmature, if it has reproduced during summer, but ceased breeding due to the onset of winter. All other rodents (bank voles, harvest mice *Micromys minutus* and house mice *Mus musculus*) occasionally caught in the traps were removed from the enclosures.

For the estimation of reproductive parameters, voles were classified as young or adult by weight. Individuals weighing 15 grams or less were defined as young and all above that as adults (Myllymäki 1977b, Innes and Millar 1994). The reproductive status of adult voles was classified as either active (mature/gravid/lactating) or inactive (submature/postmature).

## Statistical analyses

Population density estimates were calculated from the trapping data using the jackknife estimator for model  $M_h$  in the program CAPTURE (Otis et al. 1978). Estimates were calculated for the different enclosures and for both species separately. Population densities of single-species populations were divided by two so they would correspond to the species-specific densities of the mixed-species populations. This is justified, as populations were still increasing in size during the experiment and had therefore not reached their carrying capacity; based on previous studies conducted in the enclosures (Klemola et al. 2000, Huitu et al. 2003) it takes two summers for the populations to reach maximum densities. Statistical analyses were conducted with PROC MIXED in the SAS statistical software with random coefficients regression models (Littell et al. 1996), defining population density as a dependent factor and species, coexistence and time as fixed explanatory factors and intercept and time as random factors.

Statistical analyses on reproductive parameters were conducted with generalized linear models in the GLIMMIX macro for SAS statistical software using species, competition and time as fixed explanatory factors and intercept and time as random factors. Dependent factors were: proportion of reproductively active voles out of all individuals, sex ratio of all individuals, proportion of young animals among all individuals, proportion of reproductively active adult females of all adult females, proportion of gravid females of all adult females, proportion of reproductively active young females of all young females and sex ratio of all young individuals. Estimates were calculated for the different enclosures and for both species separately, and enclosure was used as a statistical replicate. All analyses of proportional data were done applying a binary error distribution and a logit link function to relate the dependent variables linearly to the explanatory variables.

Analyses of survival rates were run using the program MARK (White and Burnham 1999). To avoid overfitting the models (Ginzburg and Jensen 2004), we conducted the analyses of survival rate ( $\Phi$ ) and recapture rate ( $p$ ) separately for both species, with group (competition vs no competition) as a treatment factor. All possible model combinations of the aforementioned terms were explored and ranked according to AICc (corrected Akaike's information criterion) values. All models which had AICc values differing from the best model by  $<2$  were deemed equally representative of the data (Burnham and Anderson 2002). Figures were drawn from the estimates of the best model.

## Results

The presence of a coexisting species lowered population densities in both species ( $F_{1,82.8}^{\text{coexistence}} = 5.85$ ,  $p = 0.018$ ) (Fig. 1). Population densities of field voles were lower than those of sibling voles ( $F_{1,82.8}^{\text{species}} = 7.32$ ,  $p = 0.008$ ) (Fig. 1). Population densities grew over time in both species ( $F_{1,68.6}^{\text{time}} = 80.05$ ,  $p < 0.0001$ ), but to a lesser extent in field voles ( $F_{1,85.4}^{\text{time} \times \text{species}} = 8.66$ ,  $p = 0.004$ ). Population growth was slower in both species when under coexistence ( $F_{1,68.6}^{\text{time} \times \text{coexistence}} = 8.73$ ,  $p = 0.004$ ), but the effect did not differ quantitatively between the two species ( $F_{1,82.8}^{\text{species} \times \text{coexistence}} = 0.72$ ,  $p = 0.40$ ,  $F_{1,85.4}^{\text{time} \times \text{species} \times \text{coexistence}} = 0.80$ ,  $p = 0.37$ ).

Coexistence lowered the proportion of gravid females in both species ( $F_{1,69}^{\text{coexistence}} = 5.07$ ,  $p = 0.028$ ), but the effect was clear only in the beginning of the experiment. The proportion of gravid females and the proportion of reproductively active voles decreased during the experiment ( $F_{1,6}^{\text{time}} = 10.68$ ,  $p = 0.012$ ,  $F_{1,6}^{\text{time}} = 48.48$ ,  $p < 0.005$ , respectively). The proportion of reproductively active voles tended to be higher in sibling voles than in field voles during the whole experiment ( $F_{1,76}^{\text{species}} = 3.74$ ,  $p = 0.057$ ). In the autumn this proportion and the proportion of young was higher in sibling voles than in field voles ( $F_{1,76}^{\text{time} \times \text{species}} = 4.28$ ,  $p = 0.042$ ,  $F_{1,76}^{\text{time} \times \text{species}} = 4.41$ ,  $p = 0.039$ , respectively) (Fig. 2). No other obvious effects on reproductive parameters were found (all  $p$ -values  $> 0.08$ ).

The survival of field voles was lower than that of sibling voles and decreased during the experiment (Fig. 3). Field vole survival was higher in single-species populations than in the presence of the coexisting species (Fig. 3b), while the opposite was true for sibling

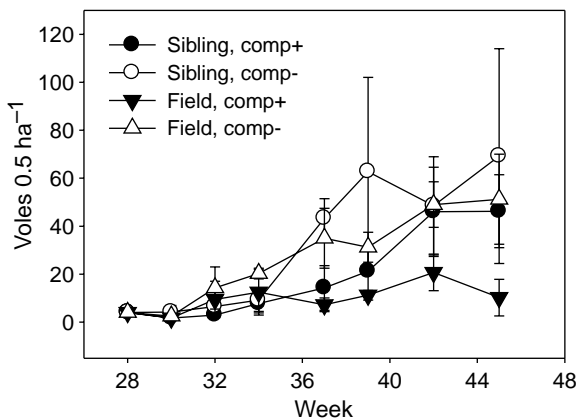


Fig. 1. Mean ( $\pm$ SE) population density estimates of sibling voles (circles) and field voles (triangles) in the presence (black symbols) and absence (white symbols) of the other species during the experiment. Population densities of single-species populations have been divided by two. Week refers to calendar weeks of the year.

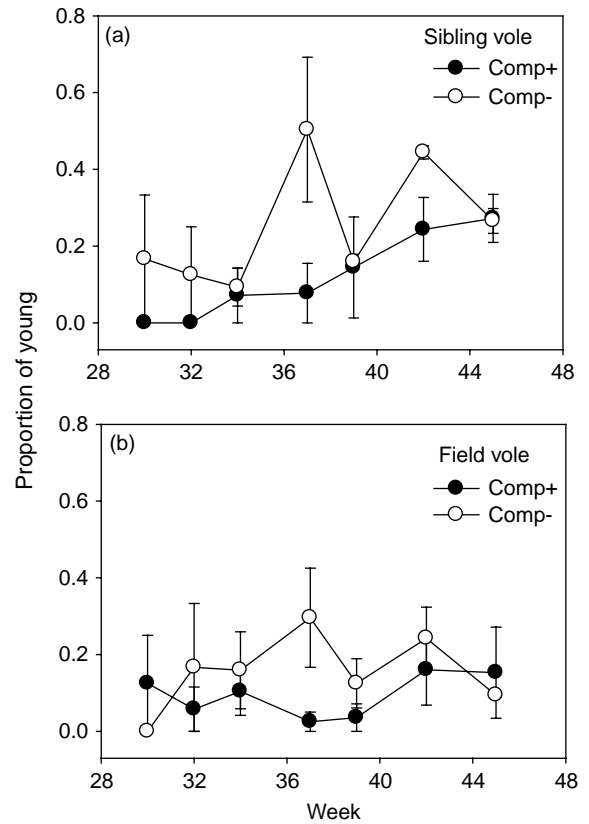


Fig. 2. The proportion (mean  $\pm$  SE) of young (weight 15 grams or less) voles in populations of (a) sibling voles and (b) field voles in the presence (black symbols) and absence (white symbols) of the other species. Week refers to calendar weeks of the year.

voles (Fig. 3a). For both species, all models differing in AICc values from the most parsimonious model by  $< 2$  contained both the group factor (g; competition/no competition) and time (t) as additive components (sum of model weights across all models containing survival  $\Phi(g+t)$ : sibling vole 0.92, field vole 0.81).

## Discussion

Population densities of both *Microtus* species were lower in the presence of the other species (Fig. 1), so coexistence was apparently deleterious to both species. Although the statistical power of our analyses was not sufficient to discern quantitative differences between the species in their response to interspecific competition, the qualitative differences emerging from the observed population dynamics (Fig. 1) strongly suggest that field voles suffer more from the presence of coexisting species than sibling voles. On a population level, sibling voles seem to be superior competitors in the absence of

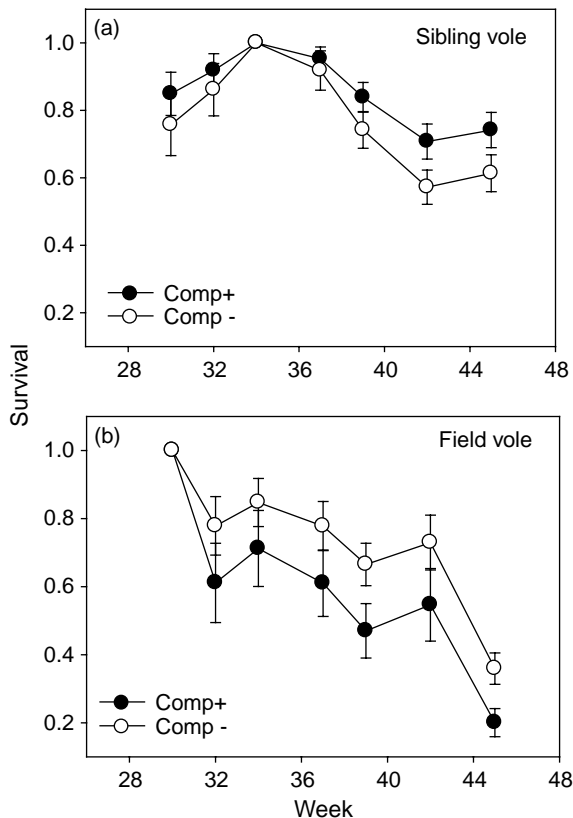


Fig. 3. Survival (mean  $\pm$  SE) of (a) sibling voles and (b) field voles in the presence (black symbols) and absence (white symbols) of the other species. Week refers to calendar weeks of the year.

predators, due to better survival and reproductive capability.

Population densities in all treatments increased during the experiment, but to a greater extent in sibling voles than in field voles (Fig. 1). The main difference between these two very similar species lies in their sociality: sibling voles tend to live at higher densities than field voles (Norrdahl and Korpimäki 1993). The common vole, which is a close relative of the sibling vole, and which coexists with the field vole in central and western Europe (Dienske 1979), is known to reproduce in family groups (Boyce and Boyce 1988a, b, c), but it is not known whether the sibling vole has a similar reproductive system. Because of its better tolerance of conspecifics, the sibling vole may be better able to utilize habitats and exclude potential interspecific competitors than field voles (Norrdahl and Korpimäki 1993). Since space, and therefore also food, are limited in the enclosures (Klemola et al. 2000, Huitu et al. 2003), competition is bound to increase at high densities. Persson (1985) suggests, contrary to the usual expectation, that in some

situations (e.g. when food is scarce), smaller species can actually have a competitive advantage over larger ones, because of their lower food requirements. Nevertheless, on an individual level, sibling voles are probably not able to exclude field voles from preferred areas due to their smaller size. Thus their competitive superiority is most likely based on their more aggregated way of life, which gives them an advantage through numbers, but also makes them more vulnerable to predation (Norrdahl and Korpimäki 1993). Since competition for food is probably fiercer in winter than in summer, the sociality of sibling voles may be even more pronounced during winter.

There was no obvious difference between the proportions of gravid females in the two species; however, the proportion of young individuals in autumn was higher in sibling voles than in field voles. The number of offspring born and the proportion of them surviving to weaning age are not known in our study system, since young voles enter the traps only when they are old enough to move outside the nest. Based on Norrdahl and Korpimäki (1993), natality in sibling voles is higher than in field voles only at very high densities. Since killing of young individuals by adults is common in rodents (Agrell et al. 1998), infanticide, intra- or interspecific, can affect the survival of offspring (Andreassen and Gundersen 2006). Whereas infanticide is known to occur in field voles (Agrell 1995), there are no studies to document the same with sibling voles. However, given that the overall survival of field voles was lower throughout the experiment, it is also plausible to consider that both adult and offspring survival are influenced by common factors.

Sibling voles experienced higher rates of survival than field voles during the course of the experiment. The survival of field voles decreased towards winter both with and without the coexisting species. Because the reproductive season of field voles ends sooner than that of sibling voles (Norrdahl and Korpimäki 1993), there might be some mutual factor affecting both reproduction and survival. These may include, e.g. changes in the vegetation (species composition or plant quality), which can be disadvantageous to the performance of field voles ("midsummer crisis", Myllymäki 1977b). In addition, the summer density decline often observed in vole populations (Korpimäki and Norrdahl 1998) would be the result of the combined effects of predation and its disruptive effect on the reproductive system of voles, primarily through infanticide caused by immigrant males (Andreassen and Gundersen 2006). Although plausible in natural settings, our experimental treatment excludes any possible effects of predation, direct or indirect. Contrary to field voles, the survival of sibling voles was even higher in the presence of congeners than when alone. This can be due to stronger

intraspecific than interspecific competition in this species for space and food. However, if survival is density dependent, this finding may partly reflect the greater densities of the single-species sibling vole populations as compared to those competing with field voles.

Although sibling voles appear to be superior competitors in the absence of predators, field voles are primarily more numerous in nature in our study area (Huitu et al. 2004). This indicates that predation most likely has a profound influence on the interspecific dynamics of these two species in natural surroundings (Norrdahl and Korpimäki 1993), i.e. apparent competition is stronger than direct competition. However, since sibling voles were unable to extirpate field voles in any of the enclosures during the experiment, we do not expect sibling voles to be able to entirely outcompete field voles even in predator-free natural surroundings. The limited and relatively insular distribution of the sibling vole in western Finland can be due to its incompetence to occupy new areas because of apparent competition or, alternatively, because of dispersal barriers.

There are still a number of questions that need to be answered to fully understand the relationship between the sibling vole and the field vole. For example, different kinds of predators (avian/mammalian) may have distinct effects on the interspecific dynamics of these two species. Patch-searching avian predators seem to prefer sibling voles over field voles as prey in our study area (Korpimäki 1992, Koivunen et al. 1996), but the possible prey preference of small mustelid predators (least weasels and stoats) is more poorly known. Also, the outcome of competitive interactions on an individual level may be different from that on a population level.

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