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# Habitat selection of grey-sided voles and bank voles in two subalpine populations in southern Norway

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Bank voles and grey-sided voles occur in sympatry in large parts of boreal and subalpine Fennoscandia. The bank vole has been studied throughout its range, whereas the grey-sided vole has primarily been studied in northern Fennoscandia. We compared habitat selection of grey-sided and bank voles close to the southern edge of the grey-sided vole's range. Voles were live trapped in the summers of 1995 and 1996 in two plots located in boulder fields in birch forest. We used Principal Component Analysis based on six habitat variables to describe the habitat in the plots. In general, the grey-sided voles preferred areas with boulders and *Vaccinium* spp., whereas the bank voles avoided such areas, being found in association with herbs and grass. When the grey-side voles decreased and bank voles increased in abundance, bank voles used the habitat more according to the habitat availability within the plots, which suggests that competition affected habitat selection.

## 1. Introduction

Major evidence of interspecific competition is derived from cases where two sympatric species exhibit an inverse numerical or spatial relationship (Grant 1972). An inverse spatial relationship might come about by habitat selection, which is one of the principal mechanisms which permits species to exist in sympatry (e.g., Rosenzweig 1981, Hanski 1995). A shift in a species' habitat selection after a decrease or increase in density of its presumed competitor suggests an ongoing competition. Such observations may indicate which species compete and also what resources/habitat they compete for, even if the causal link between competition and the numerical and/or spatial relationship between the species can only be determined by experiments.

Here we present an observational study on sympatric populations of bank voles *Clethriono-*

*mys glareolus* and grey-sided voles *C. rufocanus* in southern Norway. The bank vole has a wide geographical distribution in Europe (Stenseth 1985) and accordingly, very flexible habitat and diet requirements (Hansson 1985a,1985b). The grey-sided vole has a more restricted and northern distribution extending northwards to the northern coast of Norway and NW-Russia (Henttonen & Viitala 1982, Stenseth 1985). The two species overlap in Fennoscandia in northern boreal coniferous forests (Henttonen *et al*. 1977, Hansson 1979, Hörnfeldt 1994, Løfgren 1995) as well as in alpine and subalpine habitats (Skar *et al*. 1971, Framstad *et al*. 1993, Heske *et al*. 1993, Heske and Steen 1993) from central to northern Fennoscandia (ca. 59°–67°N, Henttonen & Viitala 1982). In northern Fennoscandia, the grey-sided vole is found in wide variety of habitats (e.g. Tast 1968), but feeds preferentially on dwarf shrubs (*Vaccinium* spp.) especially in winter (e.g. Kalela, 1957, Viitala 1977, Oksanen & Oksanen 1981, Løfgren 1995, Hämbeck *et al*. 1998). However, from more southern parts of Fennoscandia, less is known about the grey-sided vole.

Interspecific dominance relationships in microtine rodents are believed to be based on body size (Grant 1972, Henttonen *et al*. 1977). Therefore, the bank vole is considered to be an inferior competitor to the larger grey-sided vole (e.g. Henttonen & Hansson 1984, Løfgren 1995, Hanski & Henttonen 1996). Accordingly, in boreal forest in northern Sweden, it has been shown that the bank vole changes in numbers as well as in habitat use according to the spatio-temporal distribution of the grey-sided vole (Løfgren 1995).

The present study was conducted in boulder fields in subalpine birch forest close to the southern limit of the range of grey-sided voles in southern Norway. The only rodents present were grey-sided voles and bank voles. The body weight (mean spring weights, males: 36 g, females: 35 g) of the grey-sided voles in this area during the two years of study was at least 10 g lower than in northern Fennoscandia (Bondrup-Nielsen & Ims 1990). However, at our study site grey-sided voles were still about 6–7 grams heavier than bank voles, which are of similar size to bank voles from northern Fennoscandia (Yoccoz & Mesnager 1998). The aim of the study was two-fold: first we examined which habitat types the two species selected within subalpine birch forest at the southern periphery of the grey-sided voles range in Fennoscandia. Then we examined whether or not bank voles, which we expect are subordinate to grey-sided voles, used a wider range of habitat types when the grey-sided voles declined in numbers.

## 2. Methods

### 2.1. Study area and trapping

The study area was situated in Arabygdi, Telemark county, southern Norway, 59°44´N, 7°43´E. Trapping was conducted in two plots 1 km apart on the north-facing and south-facing slopes of a narrow valley ca. 700 m a.s.l. The habitats were similar in both plots: subalpine birch forest with ground covered with boulders of various sizes, as well as lichens, grasses, mosses, herbs and dwarf shrubs (*Vaccinium myrtillus* and *V. vitis-idaea*). There were also a few scattered stands of aspen and pine in the south-facing plot. The shrub layer was weakly developed and consisted of *Prunus padus* and *Juniperus communis* in both plots and a few *Salix* spp. in the north-facing plot. In general, the north-facing plot was moister and had later snow-melt in the spring than the south-facing plot.

We placed 84 Ugglan multiple-capture live-traps in the north-facing plot (1.4 ha) and 156 traps in the south-facing plot (3 ha). The traps were placed 15 m apart in both plots. The trapping grids were established in early summer 1995 (a post peak year) and live-trapped for three consecutive nights every two weeks until snowfall. The following year (1996), trapping was conducted the same way every three weeks. All caught animals were individually marked, weighted and their sexual condition was recorded. The traps were baited with oats, carrots, and apples.

### 2.2. Habitat variables

Six habitat variables were selected to represent characteristic structural and floristic habitat elements suspected to be important to the voles. Of these, five vegetation variables, lichens, grass, herbs, *Vaccinium myrtillus* and *V. vitis-idae* represented potential food, while the bare boulder variable represented potential protection against predators. All variables were recorded in a 4 $m^2$ square centred around each trap. The percentage coverage of bare boulder in the total square, and of the five vegetation variables in the part of the square not covered by bare boulder, were categorized into five classes (0, 1–25, 26–50, 51–75, 75–100).

Quantitatively, the habitat variables differed between the plots. Lichens, *V. myrtillus* and herbs were more common in the north-facing plot, while the three other variables (bare boulder, *V. vitis-idae* and grass) were more common in the south-facing plot. However, the correlation structure among the variables was similar between the plots, as the same variables occurred together in both plots (i.e., herbs tended to co-occur with grasses, *V. myrtillus* with *V. vitis-idae*, and bare boulder with lichen). As the habitat variables were correlated, we used a Principal Component Analysis (PCA) to create new, uncorrelated habitat variables (i.e., Principal Components).

The two first PC axes had eigenvalues > 1, and accounted for 49% of the variation in the habitat variables, while the third axis had eigenvalue < 1, and was thus not considered. The first PC (PC1) axis was negatively correlated with lichens and bare boulder, and positively correlated with herbs and grass, and to a lesser extent with *V. myrtillus* (Fig. 1). The second PC axis (PC2) was negatively correlated with both *Vaccinium* spp. and positively correlated with the other variables (Fig. 1). The PC scores were normalized within plots so that the mean score of both axes within both plots was zero.

### 2.3. Habitat selection analysis

Habitat selection was estimated as the mean PC1 and PC2 scores for the species (*see* e.g. Scott & Dueser 1992). We applied repeated measurement ANOVA, entering each individual as the subject factor and the PC score of the trap of each capture of an individual as the within-subject measurement. We used PROC Mixed in the software package SAS to select the autocorrelation function fitting the repeated measurements in time (Littell *et al.* 1996).

## 3. Results

Generally, the densities of grey-sided voles decreased from 1995 to 1996 (most in the south-facing plot), while the densities of the bank voles increased from 1995 to 1996 (most in the north-facing plot). The grey-sided voles dominated in numbers only in one year and in one plot (the north facing plot in 1995) (Fig. 2 and Table 1).

According to the repeated measurement analysis, there was an overall differentiation in habitat selection between species on both axes (PC1: $F_{(1,592)} = 101.8, p < 0.0001$, PC2: $F_{(1,592)} = 34.3, p < 0.0001$). The bank voles were trapped in traps with positive PC1 and PC2 scores (mean score PC1: 0.47, mean score PC2: 0.25), whereas the grey-sided vole were trapped in traps with negative scores on both axes (PC1: –0.26, PC2: –0.09). This means that the bank voles were positively associated with herbs and grass (both axes), whereas the grey-sided voles with boulders and lichen (the first PC axis) and *Vaccinium* spp. (the second PC axis) (Fig. 1 and Fig. 3). This was also supported by the univariate analysis on the same data based on the separate habitat variables (E. Johannesen unpubl.).

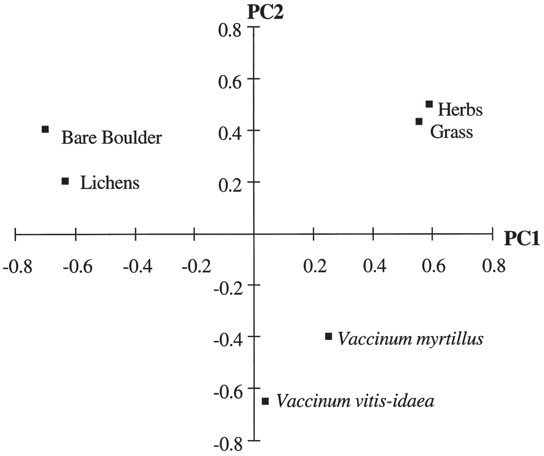

**Fig. 1.** The score of the habitat variables plotted against the two first PCA axes.

We used date as a continous variable in evaluation of the effect of season on habitat selection. All populations (i.e. the two species in the two plots) selected habitat with more lichens and boulders (lower PC1 scores) from spring until autumn, this being significant for all populations ($p < 0.003$) except bank voles in the south-facing plot ($p = 0.07$). The bank voles on the south-facing plot had a significant seasonal change in its preference towards more *Vaccinium* spp. (lower PC2 scores) over the season ($p = 0.03$). No other population changed significantly according to PC2 over season (all $p > 0.27$).

The changes in habitat selection from 1995 to 1996 for all four populations are shown in Table 1 and in Fig. 3. The grey-sided voles had a weaker association with bare boulder and lichen (higher PC1 score) and a stronger association with *Vaccinium* spp. (lower PC2 score) in 1996 than in 1995. This was tendency was consistent, but not significant on both of the two plots (PC1: south-facing plot: $F_{(1,72)} = 1.7, p = 0.20$, north-facing plot: $F_{(1,138)} = 1.6, p = 0.21$, PC2: south-facing plot: $F_{(1,72)} = 1.7, p = 0.20$, north-facing plot: $F_{(1,139)} = 1.1, p = 0.29$).

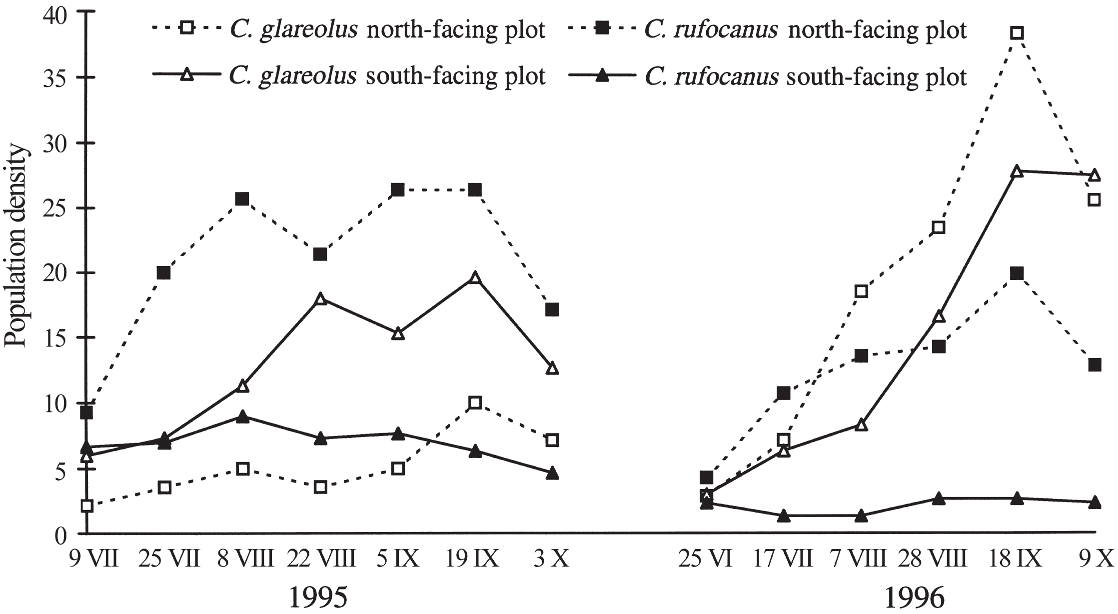

**Fig. 2.** Density measured as the number of trapped animals per hectare.

The bank voles on the north-facing plot had a significantly weaker association with herbs and grasses (lower PC1 score) and showed less avoidance of *Vaccinium* spp. (lower PC2 score) from 1995 to 1996 (PC1: $F_{(1,129)} = 5.2$, $p = 0.02$), PC2: $F_{(1,129)} = 21.1$, $p < 0.01$). On the south-facing plot, bank voles changed non-significantly towards being less restricted to herbs and grasses (lower PC1 score) while the association with *Vaccinium* spp. did not change from 1995 to 1996 (PC1: $F_{(1,251)} = 2.4$, $p = 0.13$, PC2: $F_{(1,251)} = 0.0$, $p = 0.86$).

The species were more differentiated along the PC1 axis than along the PC2 axis, that is, more differentiated according to grasses and herbs *versus* lichen and boulders, than according to *Vaccinium* spp. This can be judged from (1) size of the *F*-ratio of the overall test of species difference (*see* above), (2) the difference in the year specific estimates for the two sepcies (Fig. 3 and Table 1), and (3) because the estimates of PC1 differed from random (i.e. from 0) for both species on both plots except for grey-sided voles in 1996 (Table 1). In contrast, the PC2 estimates of the grey-sided voles, although consistently negative, never differed from random (Table 1). This means that the PC1 score of a trap (i.e., boulder and lichen *versus* the vegetation variables grass and herbs), was a better predictor for where to find the two species than the PC2 score of a trap (i.e., *Vaccinium* spp. versus the other variables).

## 4. Discussion

Our results show that the two species occurring in sympatry were trapped in different habitats. In the following discussion, we assume that the habitat around the trap where a vole was trapped, was representative of the habitat within the vole's home-range, i.e., that a vole doesn't select one type of habitat to live and breed in, and one type of habitat to be trapped in. Assuming this, bank voles preferred habitat with herbs and grass (both PC axes) and grey-sided voles preferred habitat with lichen and boulders (PC1) and *Vaccinium* spp. (PC2).

That grey-side voles showed preference for *Vaccinum* spp., is in accordance with what is known about this species further north in Fennoscandia (e.g., Kalela 1957, Viitala 1977, Løfgren 1995, Hämbeck *et al.* 1998). However, none of these studies on grey-sided voles from northern Fennoscandia have noted that this species was positively associated with boulder- and lichen rich habitat and negatively with grasses and herbs as we found at our study area in southern Norway.

**Table 1.** Sample sizes and estimates of PC scores for each species on the two plots during the two years of study. The estimates are given from models including season in addition to year, species and plot. To compare the estimates with what would be obtained if the voles selected habitat randomly according to PC scores, the upper and lower 2.5 percentile of a random distribution of habitat scores was derived from the 25 highest and 25 lowest mean values of 1 000 resamples of the PC scores in the specific plot. The sample size of the resamples is equal to the year-specific number of captures of each species in each plot.

| Vole species | Plot | Year | No. of ind. | No. of capt. | PC1 | | | PC2 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Year specific Estimate (± SE) | Upper and lower percentile of random distribution | 2.5 Estimate different from random? | Year specific Estimate (± SE) | Upper and lower percentile of random distribution | 2.5 Estimate different from random? |
| Bank | North-facing | 1995 | 26 | 87 | 0.79 (± 0.16) | –0.26; 0.26 | yes | 0.70 (± 0.12) | –0.24; 0.22 | yes |
| | | 1996 | 106 | 322 | 0.50 (± 0.07) | –0.13; 0.14 | yes | –0.02 (± 0.10) | –0.12; 0.12 | no |
| Grey-sided | North-facing | 1995 | 87 | 418 | –0.17 (± 0.09) | –0.14; 0.14 | yes | –0.02 (± 0.05) | –0.12; 0.11 | no |
| | | 1996 | 55 | 259 | 0.00 (± 0.10) | –0.29; 0.26 | no | –0.11 (± 0.08) | –0.14; 0.12 | no |
| Bank | South-facing | 1995 | 54 | 320 | 0.37 (± 0.07) | –0.11; 0.10 | yes | 0.15 (± 0.07) | –0.09; 0.10 | yes |
| | | 1996 | 116 | 532 | 0.20 (± 0.07) | –0.11; 0.09 | yes | 0.17 (± 0.07) | –0.08; 0.09 | yes |
| Grey-sided | South-facing | 1995 | 136 | 619 | –0.55 (± 0.11) | –0.13; 0.13 | yes | –0.05 (± 0.08) | –0.12; 0.12 | no |
| | | 1996 | 21 | 83 | –0.35 (± 0.10) | –0.15; 0.15 | yes | –0.21 (± 0.09) | –0.24; 0.23 | no |

On the contrary, Ims (1987) found that grey-sided voles had the highest reproductive output in a moist habitat in Finnmark, northern Norway, and Tast (1968) found grey-sided voles in all habitat types including what he called mesic meadow forest in northern Finland (*see* also Kalela 1957, 1971, Oksanen & Oksanen 1981).

However, anecdotal observations from further south in Fennoscandia (Hansson 1974, Heske *et al.* 1993, Strøm-Johansen & Lie 1996, R. A. Ims pers. comm.) and southern Finnish Lapland (Henttonen & Viitala 1982) have indicated that grey-sided voles may be restricted to boulder fields. It is possible that boulder has the same function as shrub cover in areas where shrub cover is less developed. Shrub cover (*Salix* spp. and *Betula nana*) can protect against predation and ensure sites with good micro-climatic conditions during winter, and was more important than coverage of *Vaccinium* spp. when grey-sided voles selected their overwintering sites in Finmark, northern Norway (Hämbeck *et al.* 1998). We observed a change towards stronger association with boulders throughout the season, which may indicate that boulders became more important towards winter. We found, however, no effect of boulders on winter survival ($F_{(1,227)} = 1.9$, $p = 0.17$, both species pooled, using the average PC1 score of the traps that an animal was trapped in during the last trapping period in October in both years as a measure of the amount of boulders in its winter habitat. Note that the amount of data is small as few animals survive the winter and that the animals might have moved after the last trapping occasion in October).

The bank vole is less folivorous than the grey-sided vole, and often prefers high quality food such as seeds. However, it also shows a gradient towards more folivorous diet from south to north in Fennoscandia (Hansson 1985a/1985b), where *Vaccinium* spp. constitutes a considerable part of its diet (Hansson 1971, 1979, 1988). Thus the avoidance of *Vaccinium* spp. that we found was not consistent with other studies on bank voles in Fennoscandia. The avoidance of boulders found in our study is also inconsistent with the studies of Hansson (1993, 1997) and Karlsson (1988) in South-Central Sweden. These authors showed that bank voles prefer boulder fields, especially towards winter, where such sites give them a higher

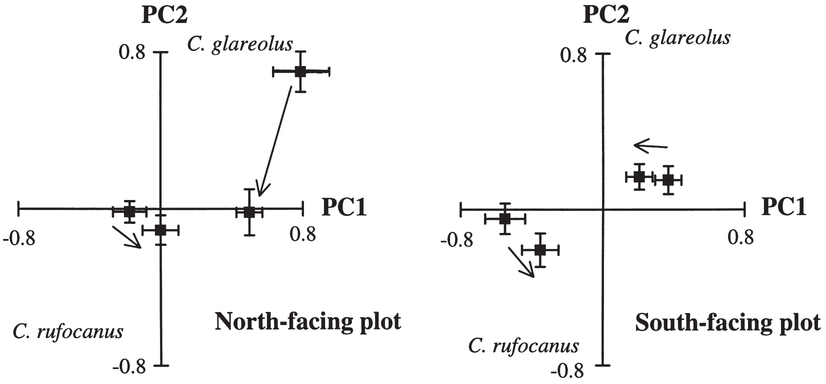

**Fig. 3.** Least square means estimates with error bars of the PC1 and PC2 scores for grey-sided voles and bank voles. The arrows show the direction of change in habitat from 1995 to 1996. The mean PC1 and PC2 score for all traps on each plot is zero.

winter survival (Karlsson 1988).

If the observed pattern in habitat selection was due to competition, bank voles should be forced out of areas preferred by grey-sided voles, i.e., areas dominated by boulders/lichen or *Vaccinium* spp. In Løfgren's (1995) study, bank voles started to use areas rich in *Vaccinium* spp. when grey-sided voles disappeared, and this was interpreted as a result of competitive release. In our study area, bank voles used more areas rich in *Vaccinium* spp. in the north-faced plot 1996 compared to 1995, as it became numerically dominant over grey-sided voles. The same tendency was apparent on the south-facing plot over the season during both years, consistent with the lack of population growth over the season for grey-sided voles and the pronounced population growth over season for bank voles, both years. In our study, the bank vole tended to be found in areas richer in boulders in 1996 when it was the numerically dominant species in both plots compared to 1995 (Fig. 2). This is consistent with competition with the grey-sided vole as an underlying cause of its habitat selection. There is, however, an alternative explanation. If more bank voles survive in areas rich in boulders over the winter from 1995 to 1996 (Karlsson 1988), the same pattern would emerge. However, there was no evidence that survival of bank voles over the winter 1995 to 1996 to be affected by the amount of boulders ($F_{(1,45)}$ = 0.02, $p = 0.88$).

In conclusion, using findings from other studies, we had no a priori reason to expect a negative association between bank voles and boulder/lichens and *Vaccinium* spp. It, therefore, seems likely that this negative association is enforced by competition from grey-sided voles. Our results are correlative, and to untangle the role of local survival, season, and inter- and intra-specific densities on habitat selection, would require more specific experiments or more comprehensive studies.

Small agile generalists can coexist with competitively stronger specialists that are more susceptible to predation (e.g. Morris 1996). The more specialised folivourous diet of the grey-sided vole as compared with that of the bank vole gives it a blunt and heavy body, which may render it more susceptible to predation (e.g. Hanski & Henttonen 1996). The bank vole and grey-sided vole thus pertain to this theoretical notion, to which the result of the present study lends some support. However, obviously something limits the potential for grey-sided voles to co-exist with bank voles (and to exist!) south-wards. Both parasitism and predation are possible candidates. Ticks (*Ixodes* spp.) are not found in northern Fennoscandia, and can be detrimental to grey-sided voles (Viitala *et al.* 1986). They are usually found in places with moist and dense vegetation, habitats that were avoided by grey-sided voles in our study area. Also, the number of generalist predators increase with decreasing latitude (Erlinge *et al.* 1983, Hanski & Henttonen 1996). Boulder areas may represent spatial refuges from predation and parasitism for the grey-sided vole at the periphery of its range.

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