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Behavioural dominance of grey-sided voles over bank voles in dyadic encounters

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Bank voles (*Clethrionomys glareolus*) and grey-sided voles (*C. rufocanus*) occur sympatrically in northern Europe and are considered competitors. Due to its larger size, the grey-sided vole is believed to be dominant. In this study, arena tests were used to study the inter-specific dominance relationship between reproducing *C. glareolus* and *C. rufocanus* females early in the breeding season. The study was conducted in the natural environment of the two species, in an area where they occur sympatrically. We found that the two species behaved similarly in dyadic tests meeting a conspecific, but that grey-sided voles behaved more dominant and bank voles more defensive in interspecific tests.

Introduction

Interspecific competition between microtine rodents may be an important determinant of the variation in population and community dynamics in the Northern Hemisphere (Hanski & Henttonen 1996, Hansen *et al*. 1999). Interspecific dominance relationships are unfortunately difficult to study directly because of the small size and cryptic way of life of microtines. Therefore, dyadic encounters in arenas (small enclosures), where individual animals can be observed directly, have proved useful for studying behaviour and dominance relationships of small mammals (e.g. Ims 1987, 1989, Bondrup-Nielsen *et al*. 1993, Harper & Batzli 1997, Lanctot & Best 2000).

Bank voles and grey-sided voles occur sympatrically in central and northern Fennoscandia (Henttonen & Viitala 1982), and are potential competitors as they have similar requirements for food and shelter (Hansson & Henttonen, 1984). The heavier grey-sided vole (Bondrup-Nielsen & Ims 1990) is assumed to be dominant over the bank vole (Henttonen & Hansson 1984). This dominance relationship is also indicated by the habitat use of the two species. Both Løfgren (1995a), and Johannesen and Mauritzen

(1999) showed that sympatric *C. rufocanus* and *C. glareolus* use different microhabitats and that *C. glareolus* expands its habitat use when the number of *C. rufocanus* decreases. Females of the two species are territorial whereas males have overlapping home-ranges (Viitala & Hoffmeyer 1985). Therefore, interspecific competition should be more intense for females than for males. Accordingly, Løfgren (1989) showed that bank voles and grey side vole females reproducing sympatrically have home ranges that are both intra- and interspecifically exclusive. To our knowledge, no one has used arena tests to explore the dominance relationship between the two species. We ran arena tests and recorded both interspecific and intraspecific behaviours of reproducing female bank voles and grey-sided voles. We predicted that grey-sided voles should be dominant over bank voles.

Material and methods

Study area and vole trapping

This study took place in Arabygdi, Telemark County, southern Norway (59°44´N, 7°43´E), approximately 700 m a.s.l., in subalpine birch forest and boulder fields. The voles were trapped on 25 and 26 June 1998. At this time of the year reproduction had started, but no young had yet appeared in the traps. Animals were trapped with 80 Ugglan traps baited with oats, alfalfa pellets and bits of carrot. The traps were set at 10 p.m. and checked at 7 a.m. the next morning. All males were released upon capture, and all females were carried in the traps from where they were caught to where the arena tests were conducted. The traps were transported in boxes lined with newspaper that was changed between captures to prevent scent contamination. After the arena tests, the females were released where they had been trapped, after a small patch of fur was cut to avoid reuse of animals. All females caught were lactating. Five of them were visibly pregnant (two grey-sided voles, three bank voles), but their pregnancy was not found to affect their behaviour (E. Johannesen unpubl.).

The arena tests

The arena was bottomless and made of transparent Plexiglas. The size (50 × 30 cm) was chosen so that the animals did not have to be in constant contact but could not avoid each other all the time (Bondrup-Nielsen *et al.* 1993). The arena was located on flat ground covered with grass and dead leaves. Tall vegetation that could impede observation was removed before the trials. The trials were conducted under trees to give the voles a sense of protection from above. The arena was moved between trials to avoid scent contamination on the ground from previous trials. The arena tests were conducted on neutral ground, up to 500 m from the place of capture of the voles, far enough to avoid performing the tests inside a home-range of one of the animals (approximate home-range diameter of reproducing bank vole females is ca. 75 m, and grey-sided voles ca. 40 m, Løfgren 1985). Before the arena tests, animals were left undisturbed for at least 30 min after transportation in the traps where they were caught, with carrots and oats *ad libidum*.

The voles caught participated in two dyadic tests, one intraspecific and one interspecific. Half the voles were randomly assigned first to an interspecific test, and the other half first to an intraspecific test. Contestants were assigned randomly to each other.

In each test, the two voles were released simultaneously into the arena. In order to distinguish the voles easily, one was marked with a small spot of coloured powder on its head before the trial. One observer watched each vole. To avoid observer bias, four observers alternated among observing grey-sided voles in intraspecific tests, bank voles in intraspecific tests, grey-sided voles in interspecific tests and bank voles in interspecific tests. Each test lasted 6 minutes. During each trial, the number of Avoidances (the vole moving away from its contestant) and the number of Approaches (the vole moving towards its contestant) were recorded. These behaviours are easy to observe, are common in *Clethrionomys* females (e.g. Ims 1987, 1989), and can easily be interpreted as aggressive (Approach) or defensive (Avoidance).

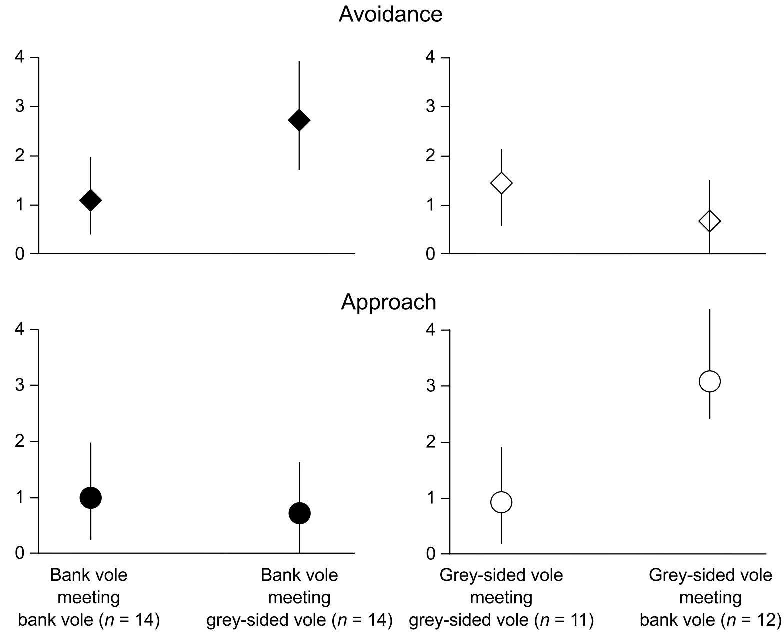

Fig. 1. Back-transformed least square mean estimates and confidence intervals of mean number of recorded Avoidance and Approach bouts per vole per encounter.

Statistical analysis

The number of Avoidance and Approach bouts per vole per encounter was transformed to obtain normality (square root of the number of bouts + 0.5; *see* Bondrup Nielsen *et al*. 1993). Because the behaviours of the two contestants within one test were not independent (Approach by one vole will tend to be followed by Avoidance by the contestant), each encounter was used as one independent observation (three tests in which only one of the contestants was observed had to be excluded from the analysis). We combined the information from one encounter by using the ratio of each behaviour for the two voles. Then the two behaviours observed in each test were combined by taking the average of the ratio for each behaviour:

Independent observation interspecific encounter $n = i$:

$$x_i = (y_i\text{-Avoid} + y_i\text{-Approach})/2$$

where y_i-Avoid = (transformed Avoidances by the bank vole)/(transformed Avoidances by the grey-sided vole), and y_i-Approach = (transformed Approaches by the grey-sided vole)/(transformed Approaches by the Bank vole).

In the intraspecific encounters we used the ratio of the two conspecific contestants based on a random order of the two contestants.

In interspecific encounters ($n = 12$) the average ratio was expected to be greater than one, whereas in intraspecific encounters ($n = 12$) the ratio was expected to be equal to one. To test for difference in behaviour in intra- and interspecific tests, a randomisation test was applied as follows: 12 intraspecific and 12 interspecific test types were allocated randomly 1000 times into the 24 observations, creating 1000 new data sets (Manly 1997). The distribution of the difference in ratio of behaviours for intraspecific and interspecific encounters from the randomised samples was compared with the difference observed from our data.

Results

Bank voles avoided more and grey-sided approached more in interspecific tests as compared with intraspecific tests (Fig. 1).

The difference between intraspecific tests and interspecific tests in the ratio of behaviours was 1.1 (ratio of behaviour — interspecific test: 2.1, intraspecific test: 1.0). Such an extreme difference was only found in 1 of the 1000 random subsamples (i.e. the difference was significant at the α-level = 0.001).

Discussion

Despite the restricted sample size, and consequent low statistical power of the analysis, our results provide clear evidence supporting earlier assumptions and indirect findings about the dominance relationship between grey-sided voles and bank voles (Henttonen & Hansson 1984, Løfgren 1995a, Hansen *et al*. 1999, Johannesen & Mauritzen 1999). Grey-side voles behaved more aggressively, and bank voles behaved more defensively in interspecific tests. In contrast, the behaviour of the two species was similar in the intraspecific contests serving as a control for the interspecific behaviour.

The dominance relationship of the species found here could be influenced by the unnatural setting imposed on the animals, e.g. confinement and neutral ground (although Harper and Batzli (1997) found results from arena tests to be robust in a variety of settings). If the tests had been performed in the home-ranges of individual females, the results could have been different, as it has been shown that individuals behave more dominantly within their own territories (Ims 1987). The neutral ground might mimic an area where over-wintering females establish territories at the onset of reproduction. At the time of these tests all females were lactating and in various stages of pregnancy, and therefore in a different hormonal condition and potentially behaving differently than at the onset of reproduction (e.g. Cushing 1985). However, we have no reason to believe that seasonal differences in hormone levels should affect the dominance relationship between the species *per se*. Finally, the confinement of the arena forced the animals to interact more than they would have under natural circumstances. Even so, short fights occurred in only four of the 27 tests that were run in total (the fights being short and with no injures), and the results were in accordance with the avoid-and-flee behaviour of small mammals found in natural, unconfined conditions (Lambin & Bauchau 1989).

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References

Bondrup-Nielsen, S., Lambin, X. & Fredga, K. 1993: An overview of dyadic behaviour encounters with an example: behaviour of female wood lemmings (*Myopus schisticolor*). — In: Stenseth, N. C. & Ims, R. A. (eds.), *The biology of the lemmings*: 619–631. Academic Press, London.

Bondrup-Nielsen, S. & Ims, R. A. 1990: Reversed sexual size dimorphism in microtines: are females larger than males or are males smaller than females. — *Evol. Ecol*. 4: 261–272.

Cushing, B. S. 1985: Estrous mice and vulnerability to weasel predation. — *Ecology* 66: 1976–1978.

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. — *PNAS* 96: 986–991.

Hanski, I. & Henttonen, H. 1996: Predation on competing rodent species: a simple explanation of complex patterns. — *J. Anim. Ecol*. 65: 220–232.

Harper, S. L. & Batzli, G. O. 1997: Are staged dyadic encounters useful for studying aggressive behaviour of arvicoline rodents? — *Can. J. Zool*. 75: 1051–1058.

Henttonen, H. & Viitala, J. 1982: *Clethrionomys rufocanus* — Graurötelmaus. — In: Niethammer, J. & Krapp, F. (eds.), *Handbuch der Saugetiere Europas*: 147–164. Akademische Verlagsgesellschaft, Wiesbaden.

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

Ims, R. A. 1987: Responses in the spatial organization and behaviour to manipulation of the food resources in the vole *Clethrionomys rufocanus*. — *J. Anim. Ecol*. 56: 555–596.

Ims, R. A. 1989: Determinants of of natal dispersal and space use in the grey-sided vole *Clethrionomys rufocanus*, a combined laboratory and field experiment. — *Oikos* 57: 106–113.

Johannesen, E. & Mauritzen, M. 1999: Habitat selection of grey-sided voles and bank voles in two subalpine populations in southern Norway. — *Ann. Zool. Fen-*

nici 36: 215–222.
Lambin, X. & Bauchau, V. 1989: Contest competition between wood mice and bank voles: is there a winner? — *Acta Theriol*. 34: 385–390.
Lanctot, R. B. & Best, L. B. 2000: Comparison of methods for determining dominance rank in male and female prairie vole (*Microtus ochrogaster*). — *Can. J. Zool*. 81: 734–745.
Løfgren, O. 1989: Do intrisic or extrinsic factors limit reproduction in cyclic populations of *Clethrionomys glareolus* and *C. rufocanus*? — *Hol. Ecol*. 12: 29–35.
Løfgren, O. 1995a: Niche expansion and increased maturation rate of *Clethrionomys glareolus* in the absence of competitors. — *J. Mammal*. 76: 1100–1112.
Løfgren, O. 1995b: Spatial organization of cyclic *Clethrionomys* females: occupancy of all available space at peak densities? — *Oikos* 72: 29–35.
Manly, B. F. J. 1997: *Randomization, bootstrap and Monte Carlo methods in biology*. — Chapman & Hall, London.
Viitala, J. & Hoffmeyer, I. 1985: Social organization in *Clethrionomys* compared with *Microtus* and *Apodemus*: social odours, chemistry and biological effects. — *Ann. Zool. Fennici* 22: 359–371.