

Familiarity of breeding field vole (*Microtus agrestis*) females does not affect their space use and demography of the population

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We livetrapped enclosed field vole populations with either familiar or unfamiliar founder females in a twofold replicated experiment. The familiar females were kept together in small arenas for two months before the experiment. The unfamiliar ones had no former experience of each other. Home range size, nearest neighbour distance and the behaviour towards other breeding females was similar between the treatments. The same was true for the number of recruits produced, maturation rate and persistence probabilities. Our results suggest that familiarity between breeding females has no important effects in *Microtus agrestis*.

1. Introduction

Social interactions and their effects on population dynamics has been one of the great focuses in the population studies of voles since the work of Chitty (1967). Kin selection hypothesis by Charnov and Finerty (1980) emphasized the significance of the kinship between the interacting individuals: Individuals that are relatives should be more tolerant towards each other and each other's offspring compared to non-relatives. On the basis of several studies with rodents (e.g. Porter et al. 1981, Holmes 1984, Gavish et al. 1984, Halpin & Hoffman 1987, Dewsbury 1988) and other mammalian species (Bekoff 1981) it seems, that familiarity of the individuals and not the coefficient of kinship plays a more important role in mediating the nature of social interac-

tions. Familiarity may also be the mechanism to identify close kin (Ferkin & Rutka 1990).

Ferkin (1988) has shown in laboratory conditions that encounters between familiar females of *Microtus pennsylvanicus* were less agonistic than encounters between unfamiliar females. However Boonstra and Hogg (1988) found no difference in demography of two compared *M. pennsylvanicus* populations with either related or unrelated founder females. In our former study (Pusenius & Viitala 1993ab) we found that reproductive success of *Microtus agrestis* females decreased simultaneously with breaking up of clusters with likely mutually familiar females. Ylönen et al. (1990) found in an enclosure experiment that related and familiar *Clethrionomys glareolus* females had a better reproductive success than unrelated and unfamiliar ones. On the

basis of the differences in the type of habitat and social structure between the two last mentioned species (see e.g. Viitala & Hoffmeyer 1985), they hypothesized that no such effect should be found in *Microtus agrestis*. To test this idea we made a similar field experiment in enclosures with either mutually familiar or unfamiliar founder females. In addition to the demographical parameters we examined also spacing behaviour of the animals with two methods: live trapping was used to study the space use and behavioural trials in small arenas within enclosures were done to assess the significance of familiarity on the level of behavioural acts between individuals.

2. Material and methods

The experiment was carried out at Konnevesi in Central Finland (62°N) in summer 1993. We used four 0.25 ha outdoor enclosures surrounded by metal fence: 1m below and 1m above the ground. The habitat of each enclosure is mainly old field with bushes (for details see Ylönen et al. 1990) and the enclosures are reasonably homogenous in this respect.

Seven females and three males were introduced to each enclosure, so the initial breeding-density was a moderate one for *M. agrestis* (c.f. Pusenius & Viitala 1993a). The familiarity was manipulated by keeping the familiar females (from now on Friends) together in 1 × 2 m arenas for two months before the experiment. The unfamiliar females (from now on Strangers) were raised separately although they lived until the experiment with an other female in a small 0.5 × 0.5 m arena. So the opportunities to social contacts and stress were approximately the same between the animals of the both treatments before the experiment. Some of the familiarized females were also kin: There were two sister-sister pairs and one mother-daughter pair in the Friends1 population and two mother-

daughter pairs and one sister-sister pair in the Friends2 population. The members of the kin groups had, however, overwintered separately before the familiarizing period. The males had also lived with another male in 0.5 × 0.5 m arenas before the experiment. In the Strangers treatment none of the males had former experience of each other, but in the Friends treatment two of the males in both populations had been kept in the same arena and in Friends2 population these two were brothers. The males were in breeding condition induced by increasing light in spring. The females were in reproductively inactive phase after overwintering period, but all of them were ready to be induced to breeding condition by males. The age-structure of all the populations was similar. These four experimental populations were randomly assigned to the four enclosures.

The animals were released simultaneously at the midpoint of each enclosure on 18th of June. After 10 days adaptation-period we started to monitor the populations by live-trapping. In each enclosure 25 Ugglan Special multiple capture traps were set in a 5 × 5 grid 10 m apart. The traps were baited with potato and oats. We had three trapping periods: in June-July, early August and mid September similarly to the trapping schedule of Ylönen et al. (1990). Ten trap checks was performed during each two week trapping period. Traps were checked twice a day: in the morning, and in the evening. At each capture the following data were recorded for the individual vole: identity, trap location, weight and sexual status. The animals were individually marked by toeclipping. All the animals were removed immediately after the last trapping period using both livetraps and snaptraps. This removal trapping was done until the catch was zero; it lasted for two weeks.

Trappability of the animals was calculated as the mean number of captures of the individuals present during a trapping period. The number of individuals present during a given trapping period was estimated by the minimum number alive (MNA) method. In practice it means that the individuals caught during the last trapping period and during the removal trapping and weighing ≥ 25 g were assumed to be present in the trappable population already in August according to the growth curves of different cohorts of *M. agrestis* by Myllymäki (1977a). As a consequence the trappability during a certain trapping period may be under 1.

Table 1. Trappability ($\bar{x} \pm SD$) of breeding females (bf) and immature individuals (im) in different enclosures. Number of animals within brackets. *P*-values are based on one-way ANOVA performed between the four enclosures.

		Friends1	Friends2	Strangers1	Strangers2	<i>P</i>
June-July	bf	1.57 ± 1.62(7)	4.00 ± 2.52(7)	3.00 ± 1.10(6)	1.33 ± 1.97(6)	0.057
	August	bf	4.64 ± 3.35(11)	3.64 ± 2.30(22)	3.93 ± 2.87(15)	3.82 ± 2.09(11)
September	im	0.89 ± 1.21(36)	0.48 ± 1.02(29)	0.63 ± 1.08(38)	0.63 ± 1.03(30)	0.502
	bf	5.58 ± 2.64(12)	3.59 ± 2.28(22)	4.74 ± 2.64(19)	4.19 ± 2.34(21)	0.138
	im	0.92 ± 1.46(74)	0.55 ± 0.91(91)	0.55 ± 1.25(120)	0.21 ± 0.60(72)	0.002*

*The difference between Friends1 and Strangers2 was significant (Tukey, $p < 0.05$).

Reproductive success during a trapping period on a given month (t) was estimated as follows: the number of recruits during a trapping period one month later ($t+1$) was divided by the number of breeding females during the trapping period on month t . As an index of maturation rate the number of newly matured animals was used. Persistence probabilities between two consecutive trapping periods were calculated. Home range size of breeding females was estimated as the largest distance between capturepoints of an individual captured at least twice during a trapping period. Nearest neighbour distance was used as the index of territoriality of the breeding females (see Saitoh 1985). The statistical analyses of the demographical variables and the variables describing spacing behaviour were performed using independent sample t -tests (when possible) and population as an experimental unit ($n = 4$).

Behavioural trials were performed on 0.5×0.5 m arenas during the first trapping period. The arena, with an open bottom, was placed on the home range (= used trap station) of the other participant of the trial to simulate the nature of contacts in the wild. The other participant was from the same enclosure. The participants were released from tubes on the opposite corners of the arena after calming down for 1 minute. The trials lasted for 10 minutes during which the number of different behavioural acts (aggressive, amicable, approach) of the participants was recorded. Each pair of voles was used only once.

3. Results

As trappability affects the estimates of the variables compared between the treatments we first tested the equality of trappability among the populations (Table 1). Trappability of breeding females was similar in the different populations. Among immature individuals trappability in Friends1 population was better than in Strangers2 population in September. Population dynamics did not differ between the treatments (Fig. 1). The growth of the individual populations was very similar until August. Thereafter there seems to be some differentiation: Strangers1 grew most rapidly and Friends1 most slowly (Fig. 1). Recruitment success per breed-

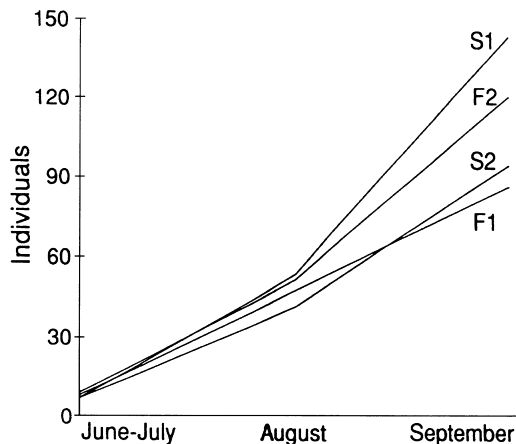


Fig. 1. Number of individuals (MNA-estimate, see methods) in different populations. F1 = Friends1, F2 = Friends2, S1 = Strangers1, S2 = Strangers2.

ing female (Table 2) was similar between the treatments, although in August it tended to be better in the Strangers treatment ($t = 3.25$, $df = 1.85$, $P < 0.1$). Number of matured females (Table 2) did not differ between the treatments. However, it seems that more females matured in the Strangers treatment in August. Survival of both founder females and new recruits (Table 3) was similar in both treatments during the study. However there was one founder female in the both Strangers populations that was not captured after the introduction. Of the three males introduced to each enclosure only one per enclosure was captured again except in the Friends2 population where two males were captured during the first trapping period. Thereafter one founder male was captured in each enclosure until the end of the study.

Home range size of breeding females (Fig. 2) was similar in both treatments during the different trapping periods (t -tests, $P > 0.1$ in all

Table 2. Recruitment success (recruits per a breeding female) and number of matured females. Number of breeding females within brackets. P -values are based on t -tests performed between the two treatments.

		Friends1	Friends2	Strangers1	Strangers2	P
Reproductive success	July	5.71(7)	6.14(7)	6.71(7)	5.00(7)	0.948
	August	4.09(11)	3.27(22)	6.46(15)	5.36(11)	0.092
Number of matured females	July	4	15	9	5	0.710
	August	5	4	12	17	0.144

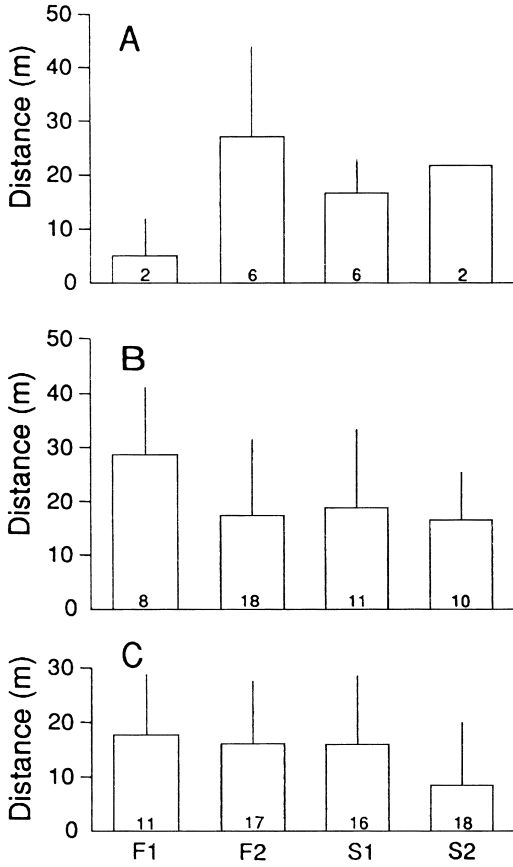


Fig. 2. Home range size ($\bar{x} \pm SD$) of breeding females measured as the largest distance between capturepoints of a given individual in June-July (A) in August (B) and in September (C). Number of individuals within columns. For other symbols see the legend of Fig. 1.

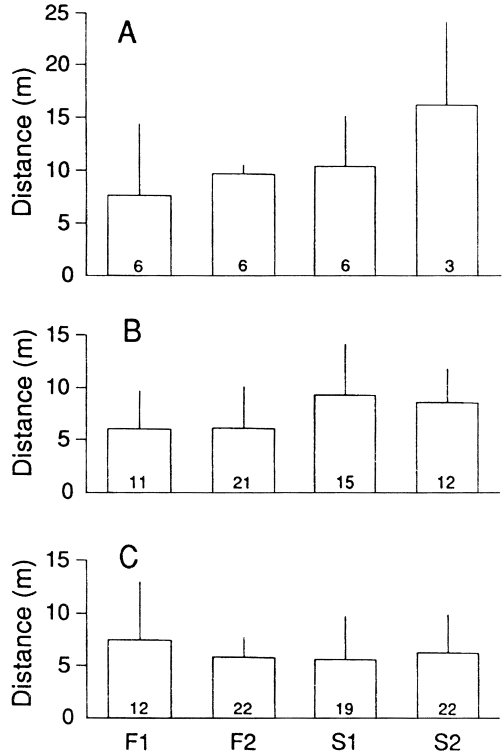


Fig. 3. Nearest neighbour distance ($\bar{x} \pm SD$) between breeding females in June-July (A) in August (B) and in September (C). Number of individuals within columns. For other symbols see the legend of Fig. 1.

cases). Nearest neighbourhood distances between breeding females (Fig 3) were similar in both

treatments in June-July and September, but seemed to be greater in the Strangers treatment in August ($t = -8.49, df = 1.04, P < 0.1$). The number of different behavioural acts between the breeding females did not differ between the treatments (Table 4).

Table 3. Persistence probabilities of founder females (ff) and recruits (re). The first time interval (June) is from the start of the study to the first trapping period. Number of animals in the beginning of the period within brackets. *P*-values in June and July are based on Mann-Whitney's *U*-tests (no variance within the treatments) and in August on *t*-tests performed between the two treatments.

		Friends1	Friends2	Strangers1	Strangers2	<i>P</i>
June	ff	1.00(7)	1.00(7)	0.86(7)	0.86(7)	0.083
July	ff	1.00(7)	1.00(7)	1.00(6)	1.00(6)	1.000
August	ff	0.71(7)	0.86(7)	1.00(6)	0.83(6)	0.370
	re	0.93(40)	0.98(43)	0.94(47)	0.86(35)	0.383

4. Discussion

We found no clear demographical or behavioural differences between the treatments. The experiment had only twofold replication. This means that slight differences are not found by this design (see e.g. Hurlbert 1984). However in most of the parameters analyzed there is so much overlap between and variability within the treatments that it seems that few more replicates, which could be possible to arrange in practice, could not change the situation. In addition very low trappability in Friends1 and Strangers2 restricted the opportunity for comparisons during the first trapping period. One could also assume that the treatment effect may have diluted in time. There is however evidence (see Frank 1954), that voles may not change their attitude towards their neighbours after becoming to breeding condition.

The results indicate some tendencies possibly connected with the treatment. The early disappearance of founder females in the Strangers populations may have been due to the unfamiliarity, which should promote aggressivity. Ferkin (1988) made behavioural tests with *M. pennsylvanicus*, which is genetically and ecologically very closely related to *M. agrestis* (Anderson 1985, Ostfeld & Klosterman 1990), and found that unfamiliar females behaved more aggressively towards each other than the familiar ones. However, the results of our behavioural trials are contradictory as we found no differences between the Friends and the Strangers. The results of behavioural trials made by De Jonge (1982) with *M. agrestis* suggest that this species may not have mechanisms that enable differential reactions to familiar and unfamiliar individuals: In an environment, unknown to at least one of the two voles which met each other, they started fighting irrespective of familiarity.

Reproductive success tended to decrease more and maturation processes tended to slow down more from July to August in the Friends populations than in the Strangers (see Table 2). These trends may be more or less due to chance. The tendency towards more pronounced territorial behaviour in the Strangers populations in August is not easily interpreted. It may have something to do with relatively more intensive reproduction in the Strangers populations during that time (see e.g. Pusenius & Viitala 1993b, Wolff 1993). An interpretation that Strangers should be more territorial is probably too simple, because there were a lot of newly recruited breeding animals during that time and they should stay near their mothers especially in the Strangers populations (see e.g. Lambin & Krebs 1991).

In earlier papers (Pusenius & Viitala 1993a, b) we suggested that the midsummer population low, "the midsummer crisis", described in *Microtus agrestis* in Finland by Myllymäki (1977a, b), Pokki (1981), and Pusenius and Viitala (1993a) and in *M. pennsylvanicus* in North America by Mihok (1984) may be caused partly by social factors. The familiarity of the females may decrease, when they disperse from overwintering aggregations to their summer home ranges. In the light of the results of our experiment the change in the degree of familiarity should not have any significant demographical effects and the midsummer crisis is likely caused by other factors (see Myllymäki 1977a, b).

Ylönen et al. (1990) found that in *Clethrionomys glareolus* the Friends populations reached densities twice as high as the Strangers populations. The enclosures used and the number of replicates were the same as in our study, but the coefficient of kinship was higher as all the females were kin in one of the Friends population and all except one in the other and also some males were kin with the

Table 4. Mean number \pm SD of different behavioural acts performed by an animal during a 10 minute arena test. FOH = friend on its own home range, FFH = friend on a foreign home range, SOH = stranger on its own home range, SFH = stranger on a foreign home range. Number of arena tests within brackets. *P*-values are based on independent sample *t*-tests between FOH and SOH or FFH and SFH.

Behaviour	FOH	SOH	<i>P</i>	FFH	SFH	<i>P</i>
Aggressive	5.69 \pm 2.15(8)	5.07 \pm 5.62(7)	0.792	4.22 \pm 3.87(9)	5.21 \pm 5.00(7)	0.414
Amicable	0.50 \pm 0.76(8)	0.43 \pm 0.79(7)	0.861	0.56 \pm 0.73(9)	0.29 \pm 0.50(7)	0.661
Approach	6.06 \pm 2.57(8)	4.29 \pm 2.50(7)	0.199	4.67 \pm 2.74(9)	6.00 \pm 4.66(7)	0.485

females and each other. The different degree of relatedness may explain partly the difference to our results. However Ylönen and Viitala (1995) found that in *Clethrionomys glareolus* both familiarity and kinship were equally important and their effects seem to be similar. Thus there seems to be a real difference between these species.

In genus *Microtus* kinship and familiarity has been found to affect demography and breeding success in *M. townsendii* (Lambin & Krebs 1993) but not in *M. pennsylvanicus* (Boonstra & Hogg 1988) and *M. ochrogaster* (Sera & Gaines 1994). Ylönen et al. (1990) suggest that the life style and habitat of the species is crucial in determining its susceptibility to social interactions. The species like *M. agrestis* and *M. pennsylvanicus* living in unstable isolated habitats have a high tendency to disperse (Getz 1985, Viitala & Hoffmeyer 1985) and thus interactions with the neighbours remain shortlived. Whereas the species like *C. glareolus*, *M. ochrogaster* and *M. townsendii* living in large stable habitats should be philopatric (Getz 1985, Viitala & Hoffmeyer 1985) and the effects of social interactions should be more pronounced. The absence of kin and familiarity effects in *M. ochrogaster* however, does not fit in this view. Moreover the different methods used in the different studies makes generalizations difficult. More work is needed on species with different life styles to determine the conditions in which familiarity and kinship of interacting animals may affect their fitness.

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References

- Anderson, S. 1985: Taxonomy and systematics. — In: Tamarin, R. H. (ed.), *Biology of new world Microtus*. Spec. Publ. Amer. Soc. Mammal. 8: 373–419.
- Bekoff, M. 1981: Vole population cycles: kin-selection or familiarity? — *Oecologia* 48: 131.
- Boonstra, R. & Hogg, I. 1988: Friends and Strangers: a test of the Charnov-Finerty Hypothesis. — *Oecologia* 77: 95–100.
- Charnov, E. L. & Finerty, J. P. 1980: Vole population cycles: a case for kin-selection? — *Oecologia* 45: 1–2.
- Chitty, D. 1967: The natural selection of self-regulatory behaviour in animal populations. — *Proc. Ecol. Soc. Aust.* 2: 51–78.
- De Jonge, G. 1983: Aggression and group formation in the voles *Microtus agrestis*, *M. arvalis*, and *Clethrionomys glareolus* in relation to intra- and interspecific competition. — *Behaviour* 83: 1–73.
- Dewsbury, D. A. 1988: Kinship, familiarity, aggression and dominance in deer mice (*Peromyscus maniculatus*) in seminatural enclosures. — *J. Comp. Psychol.* 102: 124–128.
- Ferkin, M. H. 1988: The effect of familiarity on social interactions in meadow voles, *Microtus pennsylvanicus*: a laboratory and field study. — *Anim. Behav.* 36: 1816–1822.
- Ferkin, M. H. & Rutka, T. F. 1990: Mechanisms of sibling recognition in meadow voles. — *Can. J. Zool.* 68: 609–613.
- Frank, F. 1954: Beiträge zur Biologie der Feldmaus, *Microtus arvalis* (Pallas). Teil I: Gehegeversuche. — *Zool. Jb. Syst.* 82: 354–404.
- Gavish, L., Hofmann, J. E. & Getz, L. L. 1984: Sibling recognition in the prairie vole, *Microtus ochrogaster*. — *Anim. Behav.* 32: 362–366.
- Getz, L. L. 1985: Habitats. — In: Tamarin, R. H. (ed.), *Biology of new world Microtus*. Spec. Publ. Amer. Soc. Mammal. 8: 286–309.
- Halpin, Z. T. & Hoffman, M. D. 1987: Sibling recognition in the white-footed mouse, *Peromyscus leucopus*: association or phenotypic matching? — *Anim. Behav.* 35: 563–570.
- Holmes, W. 1984: Sibling recognition in thirteen-lined ground squirrels: effects of genetic relatedness, rearing association, and olfaction. — *Behav. Ecol. Sociobiol.* 14: 225–233.
- Hurlbert, S. H. 1984: Pseudoreplication and the design of ecological field experiments. — *Ecol. Monogr.* 54: 187–211.
- Lambin, X. & Krebs, C. J. 1991: Can changes in female relatedness influence microtine population dynamics? — *Oikos* 61: 126–132.
- Lambin, X. & Krebs, C. J. 1993: Influence of female relatedness on the demography of Townsend's vole populations in spring. — *J. Anim. Ecol.* 62: 536–550.
- Mihok, S. 1984: Life history profiles of boreal meadow voles (*Microtus pennsylvanicus*). — In: Merritt, J. F. (ed.), *Winter ecology of small mammals*. Spec. Publ. Carnegie Mus. Nat. Hist. 10: 91–102.
- Myllymäki, A. 1977a: Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. — *Oikos* 29: 468–493.
- Myllymäki, A. 1977b: Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. — *Oikos* 29: 553–569.
- Pokki, J. 1981: Distribution demography and dispersal of the field vole, *Microtus agrestis* (L.) in the Tvärminne archipelago, Finland. — *Acta Zool. Fennica* 164: 1–48.
- Porter, R. H., Tepper, V. J. & White, D. M. 1981: Experimental influences on the development of huddling pref-

- erences and "sibling" recognition in spiny mice. — *Devl. Psychobiol.* 14: 375–382.
- Pusenius, J. & Viitala, J. 1993a: Demography and regulation of breeding density in the field vole, *Microtus agrestis*. — *Ann. Zool. Fennici* 30: 133–142.
- Pusenius, J. & Viitala, J. 1993b: Varying spacing behaviour of breeding field voles, *Microtus agrestis*. — *Ann. Zool. Fennici* 30: 143–152.
- Saitoh, T. 1985: Practical definition of territory and its application to the spatial distribution of voles. — *J. Ethol.* 3: 143–149.
- Sera, W. E. & Gaines, M. S. 1994: The effect of relatedness on spacing behavior and fitness of female prairie voles. — *Ecology* 75: 1560–1566.
- Wolff, J. O. 1993: Why are female small mammals territorial? — *Oikos* 68: 364–370.
- Ylönen, H., Mappes, T. & Viitala, J. 1990: Different demography of friends and strangers: an experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*. — *Oecologia* 83: 333–337.
- Ylönen, H., Pusenius, J. & Viitala, J. 1995: Impact of kinship and familiarity on the annual social organisation and population dynamics of *Clethrionomys* and *Microtus* voles. — *Ann. Zool. Fennici* 32: 225–232.