

Different demography of friends and strangers: an experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*

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Received October 23, 1989 / Accepted January 4, 1990

Summary. We examined demographic effects of familiarity and relatedness in the bank vole *Clethrionomys glareolus* (Schreber) in four 0.5-ha enclosures in Central Finland. In two enclosures were mature voles which had overwintered together and some of their mature offspring (hereafter referred to as “Friends”), and in the other two individuals of the same species captured from different localities near the study area (“Strangers”). The experiment lasted from June to September. The populations of Friends reached densities twice as high as those of Strangers with a significantly higher rate of recruitment and survival of the young. This may have been due to mutual familiarity decreasing antagonism towards the juveniles. The conflicting results obtained from studies of *Clethrionomys* and *Microtus* are discussed. We believe that these genera represent behavioural adaptations to different habitats and ways of life. Most behavioural population regulation hypotheses are based on studies of *Microtus*. We conclude that these results should be applied with great caution to other rodent genera.

Key words: *Clethrionomys* – Demography – Kin selection – Familiarity

Since the 1960s the ability of small rodents to recognise individual conspecifics has been studied (e.g. Bruce 1960; Kalkowski 1967; Halpin 1976, 1980; Porter et al. 1984; Gavish et al. 1984; Caley and Boutin 1987; Ferkin 1988a). Familiarity has been found to have a strong effect on the functioning of priming pheromones (e.g. Bruce 1960; Clulow and Clarke 1964; Clulow and Malloy 1970). The demographic effects of familiarity have attracted particular attention in recent years (Armitage 1984, 1986; Kawata 1987; Boonstra and Hogg 1988; Rodd and Boonstra 1988).

Species inhabiting rich but ephemeral habitats show low philopatry, dispersal being the basic means of population limitation. Species living in a less productive but

predictable environment, however, exhibit both high philopatry and strict sociophysiological regulation of breeding during high population density (see Viitala and Hoffmeyer 1985 for review). Typically, most *Microtus* species live in unpredictable habitats, but all *Clethrionomys* species are mainly granivorous forest dwellers and have poorer but more predictable resources. Therefore familiarity and perhaps also kin selection (c.f. Charnov and Finerty 1980) may play different roles in *Clethrionomys* and *Microtus*.

In the summer of 1988 we studied the effect of familiarity on the reproduction, growth, and survival of enclosed populations of the bank vole *Clethrionomys glareolus* (Schreber) in four large outdoor enclosures located in Central Finland. Two of the enclosures were inhabited by mutually familiar animals, some of which were related, which were called “Friends”, and two others by individuals collected from many different locations, called “Strangers” following Boonstra and Hogg (1988), who published an experiment on *Microtus pennsylvanicus* with an almost identical procedure. Thus we can compare the results of these two experiments, which may also enable us to evaluate hypotheses on behavioural population regulation.

We made the following predictions for *Clethrionomys* populations:

1. Recruitment of young in the Friends populations should be higher than among Strangers.
2. Young should survive better among Friends than among Strangers.
3. As a consequence of the first two predictions, the population density should grow more rapidly among Friends than among Strangers.
4. The trappability of the young – an index of social tolerance between the individuals of the population, see e.g. Viitala (1977) – should be lower among the Strangers than among Friends.

Methods

The experiment was carried out at Konnevesi in Central Finland (62° N) in summer 1988. It was the peak year for the local microtine cycle. In the previous year, four 0.5-ha enclosures had been erected

on a field that had been abandoned 5 years earlier. We knew abandoned fields to be the preferred habitat of bank voles if the main competitor, the field vole *Microtus agrestis*, was excluded (Ylönen et al. 1988). There were small thickets of *Alnus incana* and *Salix* spp. growing along the old ditches, and heaps of rocks which had been removed when the field was reclaimed. In one of the enclosures were the stony ruins of a country house now overgrown with *Rubus idaeus* and *Cicerbita macrophylla*. In other respects the habitat was as homogenous an old field as was possible to find in which the 2-ha area could be fenced.

The fence was constructed by embedding a 1-m galvanized steel sheet into the ground to a depth of about 50 cm, giving it a height of 50 cm. No posts were used. The entire fence was constructed of two rolls of sheet metal, measuring 1200 m in total. We tried to avoid seams which could act as escape routes for climbers as good as bank voles. The fence prevented immigration and emigration relatively well. Some bank voles did move from one enclosure to another, but not a single field vole from the surrounding dense population was caught inside the enclosures.

Another experiment had been conducted in the enclosures during the previous winter. The populations were monitored by live trapping throughout the winter (Ylönen and Viitala 1990). Two such populations and their offspring were selected randomly for the experiment. From both of these populations five mature females and five males of about the same weight and age (according to the winter trapping data) were introduced into the Friends populations. These two populations are referred to as "Friends 1" (F1) and "Friends 2" (F2). The population of F1 consisted of a mother, her three daughters and a son, one unrelated female, and three unrelated males which had overwintered together in the same enclosure, with one new male introduced from the neighbouring enclosure. The population of F2 consisted of a mother and her four daughters and three sons from two consecutive litters, with two new males introduced into the population.

In the last week of May we begun trapping bank voles in six localities in the Konnevesi area. These individuals and those remaining from enclosure populations of the previous experiment were used to form two populations comprising five females and five males who were unfamiliar with each other. The weights and ages of the animals were similar to those in the friends populations. They are referred to as "Strangers 1" (S1) and "Strangers 2" (S2). By accident, six females and four males were released into S2, instead of a 1:1 sex ratio.

These four experimental populations were randomly assigned to the four enclosures, with the condition that each Friends population had to be transferred from its original enclosure. The four enclosures were located beside each other so that the two outermost had one common fence of 100 m with a neighbour and the two central enclosures had two walls in common with neighbours. The Stranger populations were founded in the two central enclosures and the Friends populations in the outermost enclosures.

On 18 June the animals were released simultaneously at the same coordinate point of each enclosure. In each enclosure we used 50 Ugglan Special multiple capture live traps in a 5 × 10 grid 10 m apart. Each trap was covered by a winter snow chimney (Ylönen and Viitala 1985). These were made of galvanized sheet and protected the traps from heat during the exceptionally hot summer.

The first live trapping started after 1 week's acclimatisation time. Every individual was marked by toe-clipping. Trapping was carried out at the end of June – early July, late July, late August, and late September. During each trapping the traps were checked about 15 times over 1½ weeks. They were set in the morning and checked two to three times at 5-h intervals and again the following morning. Because of the hot weather in June and July we trapped mainly in the evening and at night. At each capture the following data were recorded for the individual vole: identity, time, trap location, sex, weight, and sexual status. Young voles were toe-clipped when captured for the first time when they weighed between 8 and 14 g. From the trapping data we calculated the growth of the population and the survival of the founder individuals and their young for each population. Trappability of the voles was

calculated as the percentage of captures of individual voles of the total number of trap controls (in average 15 per trapping session) during the time that each vole was present in the population.

Results

Population changes

The initial population density in each enclosure of ten individuals (= 20 animals/ha) is similar to a spring population in a peak year of cyclically fluctuating populations in Central Finland (Ylönen et al. 1988). Thus the phase of the cycle in the enclosures was the same as for adjacent unenclosed populations. At the end of the experiment the density of the Friends population averaged 116 voles/ha (Fig. 1), which was twice that of the Strangers, averaging 55 voles/ha. The slope of the growth curve of the two Friends populations (17.34 voles/month, S.E. 2.51) was significantly steeper than that of the Strangers (6.12 voles/month, S.E. 1.47; $t=10.78$, $p<0.001$, $df=12$) (Fig. 1).

Until late July there was no difference in the population growth of the Friends and Strangers grids. This, however, may have been caused by numerous harvest mice *Micromys minutus* (Pallas) on the Friends 2 grid. We left harvest mice in two enclosures until mid-July, expecting the voles, which were three times heavier, to exclude the harvest mice. However the voles avoided the areas inhabited by the harvest mice (Ylönen 1990). After the harvest mice had been removed in July the growth of that vole population was as rapid as in the Friends 1 as the voles took over the area previously inhabited by the harvest mouse (see Ylönen 1990). In the enclosure Strangers 2 the population grew as rapidly as the Friends populations during the first month of the experiment (six females in the founder population of S2), but the poor survival of the young had already caused decline of the population density by August (Fig. 2).

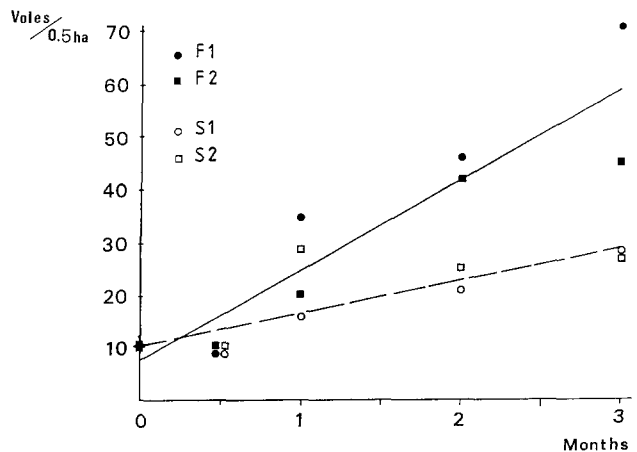


Fig. 1. Growth of the Friends and Strangers populations of the bank vole *Clethrionomys glareolus* during the experiment (between 18 June and 28 September). Founder populations with individuals familiar with each other (F 1 and F 2) are pooled (solid line), and populations with individuals unfamiliar with each other (S 1 and S 2, broken line). Immigrants are not included (see text)

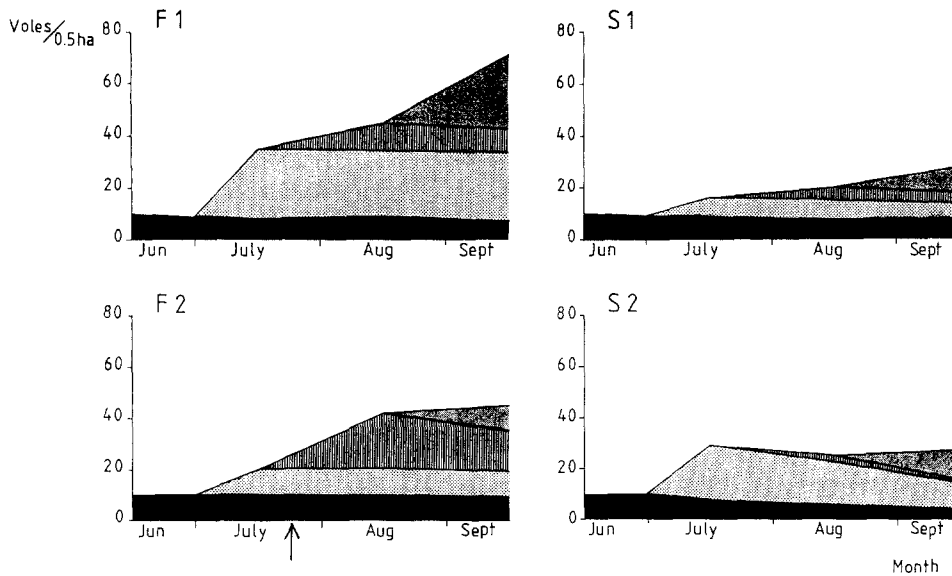


Fig. 2. Survival of the founder populations (black) and recruitment and survival of the young during the experiment. Recruitment of the young is shown as the number of new animals captured during trapping periods of July, August, and September. *F 1* and *F 2* are the enclosures with founder voles familiar with each other; *S 1* and *S 2* are enclosures with voles unfamiliar with each other. The arrow in *F 2* indicates the removal of harvest mice from the enclosure

Young bank voles moved between the enclosures in August and September. Most movements (14 in August and 7 in September) were between the two Stranger populations, obviously due to the existence of a single hole under the fence separating the two populations. Only three trans migrants were captured among the Friends in August and a single one in September. The movements had no effect on the difference in the growth of the populations. The sex ratio of the migrants was male biased (19 males: 5 females) ($\chi^2 = 8.167$; $P < 0.01$, $df = 1$).

Recruitment and survival of the young

Since we did not use the spooling technique (Boonstra and Craine 1986), or any other technique to locate the nests of lactating females, we can deal only with the numbers of young appearing in the population during each trapping session. In the population of territorial females, it is often possible to determine which young belong to which particular female according to their spatial occurrence and time of birth (Mappes et al. unpublished work).

The recruitment of the juveniles per lactating female (Boonstra 1985) was similar in all populations during July (4.1 in Friends, 4.0 in Strangers). By August there were 4.7 new young per lactating female in the Friends but 1.1 in the Strangers. This poor recruitment suggests a high juvenile mortality. The survival of the young cap-

tured in July was 100% until September among the Friends but 57% among the Strangers (Fisher's exact test, $p < 0.0001$). Furthermore in September the number of new young among the Friends was higher (38 compared with 22 among the Strangers, $\chi^2 = 4.267$; $P < 0.05$, $df = 1$) although the number of juveniles per lactating female in the Strangers (5.5) was higher than that of the Friends (3.5).

Three young females had litters among the Friends during the late breeding season but only one among the Strangers.

Trappability

There were no significant differences in trappability among the founder populations of Friends and Strangers (approximately 70%, Table 1). The trappability of the young born during the experiment was significantly higher in the Friends grids. The greatest difference was found in the group of summer-born voles, which showed signs of maturation and were the heaviest of the young voles. Here the trappability of Friends was 75% compared with 41% for Strangers (Mann-Whitney U-test, $n_F = 13$, $n_S = 11$, $U = 24$, one-tailed $p = 0.003$). The juveniles had trappabilities between 40% and 50%, also with a significantly higher trappability among the Friends (Mann-Whitney U-test, $n_F = 43$, $n_S = 27$, $U = 435$, one-tailed $p = 0.040$).

Table 1. Mean trappability of the bank voles in Friends and Strangers populations. Trappability is calculated for the time during which each individual was present in the population (from the appearance of a vole in the population until its disappearance or the end of the experiment in September). The group Mature and Submature consists of individuals born during early July and having shown signs of maturation during their first summer (nine males and four females among the Friends, six males and five females among the Strangers), including also the young females which had litters. The group Juveniles includes the rest of the young voles marked during this study (18 males and 25 females in the Friends, 14 males and 13 females among the Strangers)

	Founder females		Founder males		Mature and submature		Juveniles	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Friends	71.6 ± 4.5	10	70.3 ± 3.8	9	75.4 ± 1.8	13	48.8 ± 2.4	43
Strangers	73.2 ± 1.8	10	64.8 ± 4.5	9	41.2 ± 8.7	11	40.2 ± 2.6	27

Discussion

All four predictions we made were confirmed. As predicted (1) more young were recruited in the Friends populations, and (2) their survival was better than that of the Strangers. The obvious explanation for these observations is that there is more agonistic behaviour among unrelated and unfamiliar individuals than among kin and familiar ones (c.f. Frank 1954; Crowcroft and Rowe 1957, 1963; Rowe and Redfern 1969; Boonstra 1984; Ferkin 1988a; Rodd and Boonstra 1988). Familiarity as a factor decreasing aggression between individuals can increase the overlap of home ranges (Ferkin 1988b; Ylönen et al. 1988, unpublished work), promote communal nesting, and influence the composition of overwintering groups (Ferkin 1988b; Wilkinson and Baker 1988). If infanticide plays a role in *Clethrionomys*, as observed for other genera (Mallory and Brooks 1980; Boonstra 1984), one would expect a higher incidence among Strangers. This could be an explanation for the low recruitment of young in the Stranger populations in spite of similar numbers of lactating females to the Friends populations.

The trappability of young born during the experiment (prediction 4) was significantly lower among Strangers than among Friends. No differences were found between the founder groups of the experiment. As shown by Viitala (1977) and Hoffmeyer (1983), trappability measures social dominance. The availability of food in the traps seems to make them favoured spots in the habitat. Therefore they may be more odour-marked by dominants (Hoffmeyer 1983). If subordinates are subject to greater aggression from unfamiliar dominants, they are also expected to avoid these sites more than those sites visited by familiar adults.

Our results for *Clethrionomys*, obtained in four large (0.5 ha) enclosures, differ from those of Boonstra and Hogg (1988) for *Microtus pennsylvanicus* obtained in two small enclosures (0.145 ha). In their study, there were no demographic differences between Friends and Strangers of *M. pennsylvanicus*, in contrast to the positive effect of relatedness and familiarity on the growth of the *Clethrionomys* populations found in the present study. Thus, kin selection could be of greater importance of *Clethrionomys*.

What should we deduce from these contrasting results? Much of the information needed to understand the differences in behavioural ecology between *Microtus* and *Clethrionomys* is already available (see e.g. Viitala and Hoffmeyer 1985, Table 1; Stenseth et al. 1988, Table 1). There are several studies which establish that population densities of most *Microtus* species are regulated by dispersal (e.g. Myllymäki 1970; Boonstra and Krebs 1977; Viitala 1977; review by Gaines and McClenaghan 1980) whilst those of *Clethrionomys* are regulated by sociophysiological regulation of maturation and breeding (Kalela 1957; Bujalska 1970, 1973; Viitala 1977; Saitoh 1981; Ylönen et al. 1988). Most enclosed *Microtus* populations exhibit the "fence effect", i.e. they reproduce until they destroy the habitat and show a drastic decline in density (Krebs et al. 1969, 1973; Boonstra and Krebs

1977). An enclosed *Clethrionomys* population stops breeding before the destruction of the habitat and survives well (Ylönen et al. 1988). Thus dispersal is not an entirely necessary mechanism of population regulation in *Clethrionomys*.

Clethrionomys and *Microtus* seem to exemplify different evolutionary strategies of behavioural adaptation to different environments. *Microtus* is an inhabitant of rich but often unstable habitats. Due to these rich resources it does not need strict regulation of its breeding density. Because of the unpredictability of the habitat field voles must have evolved a high tendency to disperse (Viitala 1977). Thus the probability that close kin will live and reproduce together may be low. Therefore it may be unlikely that familiarity should play an important demographic role, even though there are some conflicting results (Frank 1953; Boonstra et al. 1987).

Clethrionomys on the other hand, lives on a fairly scarce yet predictable resource, mostly in climax vegetation (Kalela et al. 1971). This may be the evolutionary reason for the high philopatry of mature animals, especially mature females (Viitala 1977). When maturing, the young females disperse to individual territories as close to that of their mother and to each other as possible (Kawata 1987; Ylönen et al. 1988). Instead of *Microtus*-type social and spatial lability, *Clethrionomys* is characterized by high social stability and philopatry. (For a review see Viitala and Hoffmeyer 1985, but also Boonstra et al. 1987.) On the conventional $K-r$ axis *Microtus* seems to be a typical r -strategist but *Clethrionomys* seems to be closer to the K end of the continuum.

Both *Microtus* and *Clethrionomys* (several species) cycle in synchrony in boreal and subarctic Fennoscandia (Henttonen 1986). If *Microtus* is bascially regulated by dispersal but *Clethrionomys* by sociophysiological limitation of reproduction, and if kin selection acts more strongly in *Clethrionomys*, how can this be in agreement with the Charnov-Finerty hypothesis or any other behavioural hypotheses of population regulation? We suggest that there is no basis for generalizing results and ideas obtained in *Microtus* studies to all microtines. If we try to solve a general problem, e.g. the mechanism generating cycles, we should study different kinds of organisms displaying this process. Otherwise we cannot know what is general for all cyclic populations and what is just a species- or genus-specific feature having little or nothing to do with the phenomenon we are investigating. Thus we find that Erlinge et al. (1983), Henttonen (1986), Hansson (1987), Hansson and Henttonen (1988), Heske et al. (1988), Lidicker (1988) and Stenseth et al. (1988) have presented a more comprehensive discussion of causes of microtine cycles by combining data on predation, snow cover (causing time lag for predation), social mechanisms, food, and possible effects of diseases and parasites.

Acknowledgements. We would like to thank Mrs. Johanna Mappes for help in the field work, Mrs. Eeva-Liisa Pakarinen for help in the data management and Jukka Suhonen for statistical advice. Rauno Alatalo, Rudy Boonstra, Pekka Helle and Erkki Pankakoski are acknowledged for their comments on the manuscript. John Calton checked the English of the manuscript.

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