Social organization of *Clethrionomys rutilus* (Pall.) at Kilpisjärvi, Finnish Lapland

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The social organization of the vole, *Clethrionomys rutilus* (Pall.), was studied by extensive live trapping at Kilpisjärvi, Finnish Lapland.

Strict female territoriality was demonstrated. In males the territorial behaviour was not as strict as in females. The territories and home ranges of both sexes were extremely large.

Strict regulation of maturation by territorial behaviour in females and by territorial behaviour and/or dominance in males was demonstrated.

Both the social status of males and territory size and breeding in females of *C. rutilus* was severely affected by increasing numbers of *C. rufocanus*.

The ecological consequences of social organization in *C. rutilus* are discussed.

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1. Introduction

All *Clethrionomys* populations so far studied have been characterized by female territoriality and large male home ranges. Territoriality regulates female maturation (Kalela 1957, Bujalska 1970, 1971, Viitala 1977, Saitoh 1981, Bondrup-Nielsen 1987, Gilbert et al. 1986). *C. rutilus* has exceptionally large home ranges and territories in the Kilpisjärvi area, probably implying food scarcity (Viitala 1980).

It has been suggested that microtine social organization may respond both evolutionarily and phenotypically on different environmental factors (Viitala & Hoffmeyer 1985, Viitala et al. 1986). *Clethrionomys rutilus* (Pall.) when compared with the more generalist *C. rufocanus* (Sund.) and *C. glareolus* (Schreb.) is in many parts of its geographical range a specialist granivore, also eating fungi and lichens (Koshkina 1957, Hansson 1986, Bangs 1984). *C. rutilus* depends greatly on plants belonging to the genus *Scrophulariaceae* (Kalela & Peiponen 1972, Henttonen & Peiponen 1982). Thus, I assume that low plant productivity resulting in food scarcity — especially seeds — in a subarctic environment near the arctic-alpine tree line affects the social regulatory mechanisms of such a specialist.

C. rutilus is the smallest microtine species in the Kilpisjärvi area. It has been shown that the interspecific dominance order among rodent species depends on size (Miller 1967, Grant 1972, Morse 1974, Henttonen et al. 1977). The different rodent species cycle in synchrony at Kilpisjärvi (Tast & Kalela 1971). In the cyclic peak the habitat niche of *C. rutilus* is included in those of the stronger rival species (Viitala 1987). Thus an interesting aspect to be studied is the effect of *C. rufocanus* and *Microtus agrestis* (L.) on the social processes of *C. rutilus,* and how it can survive in such a situation where it should become extinct on the basis of the competitive exclusion principle (Miller 1967).

The present paper is an attempt to examine these questions by following the fate of each individual using extensive live trapping, by comparing *C. rutilus* with other species (Viitala 1977), by using studies made of more southern areas (Henttonen unpubl.) and by comparing the demography of a population under heavy interspecific interaction with that of a population living without competition.

2. Study area, materials and methods

The material was collected by extensive live trapping on a 6.7 ha study area, below the tree line in arctic-alpine birch forest at Kilpisjärvi, Finnish Lapland (69°5′N, 20°47′E). The vegetation of the study area was a mosaic of oligomesotrophic and mesotrophic heath woods, eutrophic meadow woods, small
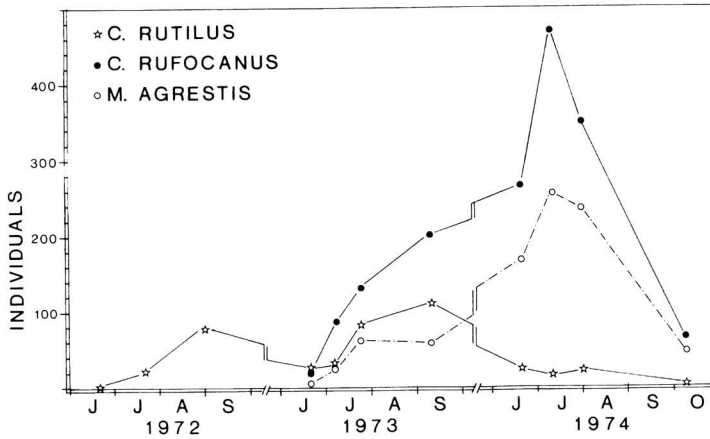
Fig. 1. Numbers of voles (*Clethrionomys, Microtus*) known to be present in the study area.

patches of paludified Korpi woods and small open fens. 672 trap stations at 10 metre interwalls were marked in a grid. The traps were set at 20 metre interwalls and moved every second day to the next station. Thus during an 8-day trapping session every station had a trap for two days i.e. for 4 checks. This procedure was developed because of the low density and large home ranges of *C. rutilus* and because of the lack of man power. A detailed description of the study area and trapping procedures are given elsewhere (Viitala 1987). During the study, 1966 rodent individuals were captured and released 7640 times, among them 286 individuals of *C. rutilus* were recorded 1647 times (cf. Viitala 1987: table 1).

The study began on 12 June 1972 and ended, by snap trapping for three days, in October 1974. The end was during the decline after the peak density of *C. rufocanus* and *M. agrestis* in early July 1974. The populations were followed using montly trappings from June to early September 1972 and 1973, but only to early August 1974.

3. Results and discussion

3.1. Population fluctuations

In 1972 *C. rutilus* was the only species in 6.7 ha study area. The first specimens of *C. rufocanus* and *M. agrestis* appeared in June 1973, attaining their greatest density in July 1974. Thus, I was able to examine the social organization of *C. rutilus* alone and under increasing interspecific pressure (Fig. 1).

3.2. Home ranges and territories

C. rutilus is characterized by large home ranges and territories at Kilpisjärvi (Fig. 2). There were 10 to 80 trap stations inside the territories of mature females estimated by the inclusive boundary strip method (Hayne 1950). I could get no more than 14 catches per female during one trapping period of eight days. Thus, sizes of the territories may have been severely underestimated by the trap spacing used. Even so, the two home range sigma radius method (Myllymäki 1977), including about 93 per cent of catches, gave the mean territory size of females as 0.65 ha during low competition but high population density in 1972 and 1973, but 0.42 ha in high interspecific pressure and low population density in 1974. The difference was statistically significant (*t*-test; $P<0.05$). Even though the home range measures based on live trapping should be treated as indexes of the real home range sizes, (Hayne 1950, Stickel 1954, Faust et al. 1971) the results suggest that interspecific interaction may restrict the movements of the female *C. rutilus*.

The home ranges of males, even though much larger than the territories of females, could not be estimated because all ranges touched the margins of the study area, thus probably reaching outside it.

The territory system exhibited by females seems to be very similar to other *Clethrionomys* species (Bujalska 1970, 1971, Viitala 1977, Saitoh 1981, Bondrup-Nielsen 1987). The great need for space may be an adaptation to food scarcity. A female from Kilpisjärvi, introduced in an enclosure in Central Finland, was reproducing on an area of 0.05 ha even though it had the opportunity to extend its territory (Viitala 1984b). Thus the geographical variation in the home range size of *C. rutilus* (Henttonen, pers. comm.) seems to be related to habitat and food. In northern Finnish taiga, territories of *C. rutilus* are distinctly smaller than in subarctic birch forest at Kilpisjärvi.
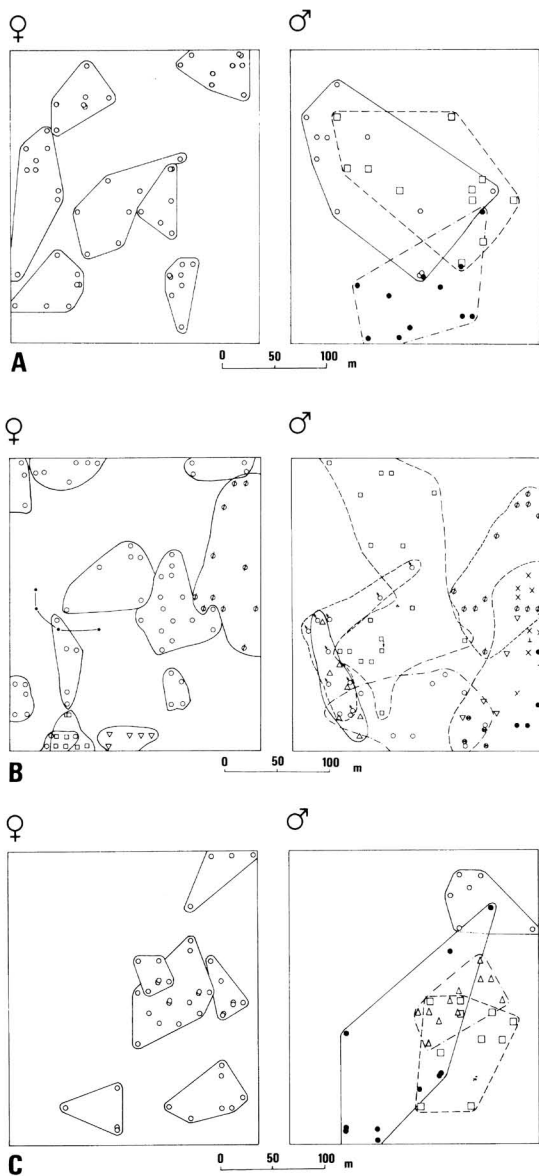
Fig. 2. Capture sites of mature *C. rutilus* females and males in one trapping session of each summer as an example. A = females and males, respectively, in July 1972, B = females and males in late June 1973 and C = females and males in early July 1974.

Table 1. Spring populations in 1973 and 1974. Survivors = animals marked in previous year, New = animals first marked in the same spring and Previous = population of the previous autumn.

| | 1973 | | 1974 | | |
	Males	Females	Males	Females	Total
Survivors	4	3	1	8	16
New	9	9	13	4	35
Total	13	12	14	12	51
Previous	45	53	56	67	221

41 females and 32 males at the end of summer 1972 and to 55 females and 43 males in 1973 (Fig. 1, Table 1). In 1972 all reproducing females were young of the year, indicating that the young are fully capable of reproducing in their season of birth given enough space (c.f. Gilbert et al. 1986). In 1973, among the fourteen mature females recorded during the summer, two were young of the year. In 1974 all mature females had overwintered. Thus the territorial limitation of reproducing female numbers was quite evident, exactly as in other *Clethrionomys*-species (Bujalska 1970, 1971, 1985, Viitala 1977, Saitoh 1981, Gilbert et al. 1986). In females the stabilization was probably a result of territorial behaviour. I never captured two mature females simultaneously in a multiple capture trap and there were almost no traps visited by two mature females during the same trapping period (Fig. 2).

The maturation and dispersal of males in most microtines studied so far is regulated by dominance (for a review see Viitala et al. 1987); aggressive behaviour blocking maturation and stabilizing the male density on a lower level than that of females (Stein 1952, Kalela 1971, Anderson 1970, Viitala 1977). The picture was not so clear in *C. rutilus* males. Due to the much larger home ranges of males, the effective trapping area may have been larger for males than for females. Thus the real density may have been lower for mature males than for breeding females and the sex ratio of mature animlas in high population density may have been biased in favour of females, as in other small rodents of the area (Tast 1966, Kalela 1971, Viitala 1977).

Because of the difficulties in determining the real home range size of either sex, the actual density has not been calculated. It could be estimated to be about one per hectare for mature females.

3.3. Population regulation

The number of mature animals known to be present in the study area was 12–14 every year for both sexes. The number of immature animals increased to
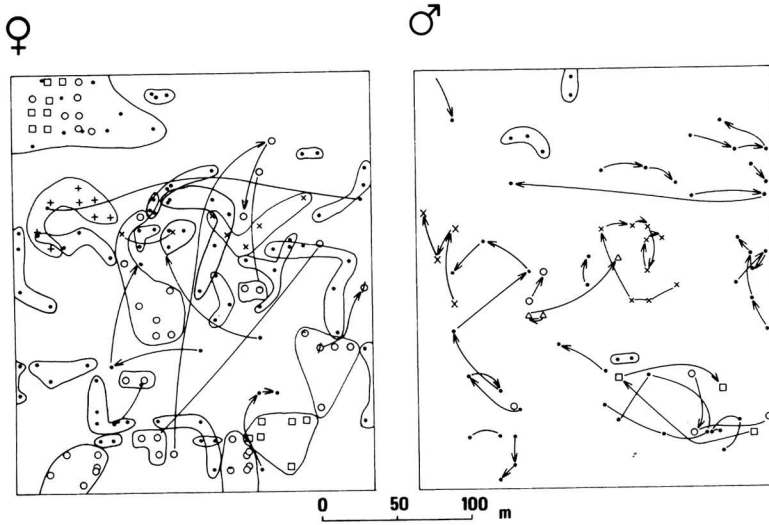
♀   ♂

Fig. 3. Capture points of females and males at the end of the breeding season (September) 1973. Open symbol = mature or post-breeding animal; closed, small dot, cross etc. = immature animal.

0   50   100 m

3.4. Overwintering

There seems to be great difference in home range size between breeding season and winter (Fig. 3). In contrast, the breeding territories of *C. rufocanus* females are of about the same size as the autumn territories of both sexes (Viitala 1977). The shape of the *C. rutilus* autumn home ranges gives an impression of a single, long track.

The decrease in territory size in autumn could indicate decrease in energy requirements after the cessation of breeding or a change to a more abundant food source. The animals remain active throughout the winter. The stomach analyses which are needed to determine the winter foods of *C. rutilus* at Kilpisjärvi are lacking, however. They eat mostly lichens in winter in the northern taiga at Pallasjärvi, (Henttonen & Peiponen 1982). Thus, the latter case seems possible.

3.5. Philopatry

Significantly more females were found in their former autumn territories in spring 1974 than in spring 1973 (Table 1, $\chi^2 = 4.196$; $P<0.05$). Also the females behaved more philopatric than males in the latter winter ($\chi^2 = 7.656$; $P<0.01$) but not in the former (Table 1). Thus, considerable dispersal is evidenced both for males and females during winter without heavy interspecific interaction but for males, only during winter with presence of competing spe-

cies (c.f. Viitala 1984a). *C. rufocanus* individuals are philopatric in all situations except for males at the beginning of the breeding season and especially male subadults in summer (cf. Viitala 1977).

There may have been considerable dispersal in spring because of the great increase in need of space at the beginning of the breeding season. There were 98 and 123 individuals in autumn 1972 and 1973, respectively, but there was space for about 25 animals only in the spring population (Table 1). The excess animals are obviously forced to disperse. However, females surviving as breeding individuals remained mostly in and around the home ranges adopted when immature in the same or in the previous year (Fig. 4). After that only minor territory changes took place. Thus, the established sedentary breeding population was as philopatric as that of any *Clethrionomys* population (c.f. Viitala 1977). In increasing interspecific interaction in summer 1973 even the juveniles and subadults exhibited considerable philopatry.

3.6. Interspecific interactions

The territory size in females seems to be affected by interspecific interaction (Fig. 5). The large territory size, together with small body size, makes *C. rutilus* vulnerable to interspecific competition. Territorial behaviour between *C. rutilus* and *C. rufocanus* has been indicated (Viitala 1987). In the high density situation of competing species in 1974, the habitat niche of *C. rutilus* was included in that of the

Fig. 4. Capture points of one male and two females in successive trapping sessions in 1972 and 1973 as an example of the philopatry. X = immature at first capture, dotted line = September 1972, shot broken line = June 1973, continuous line = July 1973, longer dash line = August 1973 and dotted broken line = September 1973.
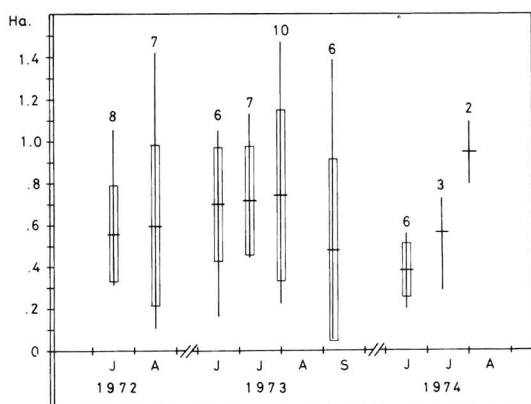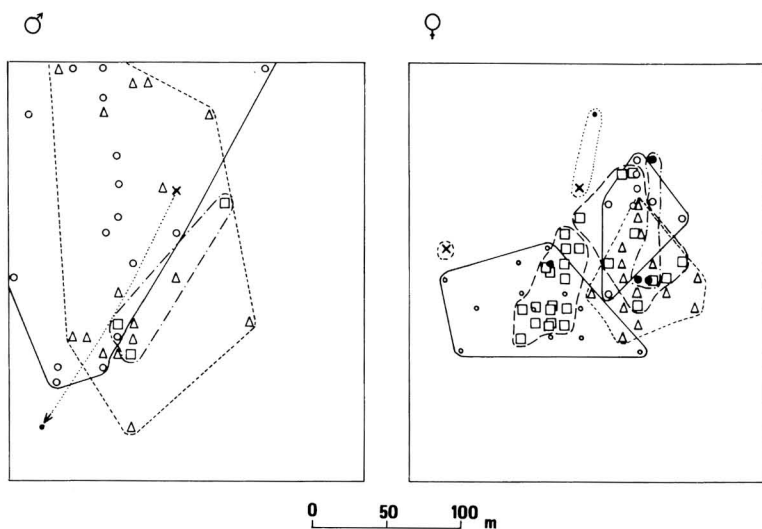

Fig. 5. Home range size indexes of mature females calculated on the basis of the two home range sigma radius (Myllymäki 1977). Mean, standard deviation and range have been given. Sample size indicated above each bar.

superior *C. rufocanus* (c.f. Henttonen et al. 1977), except those parts occupied by *M. agrestis* (Viitala 1987).

In the two first years, mature *C. rutilus* females were reproducing continuously from late May to September indicating post partum oestrus. Out of the 12 females living in the study area in June 1974 only four were pregnant. One more female became pregnant in July. These females produced 12 summer-born animlas belonging to three different litters, when 71 and 120 such animlas were produced in 1972 and 1973, respectively. The females in June

1974 were big (34.3 ± 5.2g) and seemingly mature with perforated vaginae. Two oestrus runs were noticed. Thus the females may have copulated but they did not become pregnant. A total cessation of breeding from mid July 1969 to late July 1970 was observed in a previous study (Viitala 1980). Kaarsalo & Wallgren (1986) found signs of the Bruce effect; a pregnancy block in such animals (c.f. Wallgren et al. 1984, too).

During the present study the survival of the animals with blocked reproduction was about 50 per cent in a month i.e. about twice as high as that of the rival species (Viitala unpubl.). In the previous study (Viitala 1980) an almost 100 per cent monthly survival during the interspecifically induced cessation of reproduction was observed. The lower survival, compared with the previous study, was probably due to a tularemia epizootics observed in 1974 (Viitala in preparation).

Thus, to survive periods of high rival species numbers the strategy of *C. rutilus* seems to be based on increased survival of non-reproducing, old and mature animals, which begin to reproduce after the decline of other species (c.f. Viitala 1980). This kind of strategy could be applicable among highly cyclic populations only and exemplifies how the cyclicity may be responsible for the high number of microtine species in northern Fennoscandia (c.f. Henttonen & Hansson 1984).

There were more interspecific multiple captures, involving mature *C. rutilus* and *C. rufocanus* individuals of the same sex than expected (Viitala, in

preparation). The animals behaved toward each other as toward members of their own species, i.e. neighbouring females by mutual tolerance and males, in about half of the cases, by mutual aggression. Hoffmeyer (1983) has noticed, in the laboratory, that subordinate mature *C. glareolus* males are behaviourally unable to take part in reproduction. In July 1974 all *C. rutilus* males had bitten, shortened tails as signs of lost fights, presumable with *C. rufocanus* males. This was found in that particular year only. Bitten tails have occasionally been observed in subordinate, mature *C. rufocanus* males, too (Viitala 1980). A bitten tail seems to be a sign of subordinance among microtine males. Dominants have their scars, if any, in the anterior parts of the body (Viitala 1977). Thus, it is suggested that the social status of *C. rutilus* males may have been that of a subordinate in 1974. This may be another, probably less important reason for poor reproductive success in late summer 1974.

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