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Social organization of an enclosed winter population of the bank vole *Clethrionomys glareolus*

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Overwintering of a *Clethrionomys glareolus* (Schreb.) population was studied in an enclosure of 0.77 ha in Konnevesi in late winter 1983 and during the winter 1983/84. Trap-chimneys were used during the snowy period.

The population was started in late September 1982 with six females and eight males and in late 1983 with nine females and seven males. During October before both winters the population aggregated in the parts of the enclosure covered by brush-vegetation. These sites had also the thickest snow cover during mid-winter. In 1983, two overwintered females and one post-breeding summer born female remained on that parts of their summer home ranges, which overlapped brush-vegetation; immature animals aggregated with these individuals.

Post-breeding females remained significantly heavier in mid-winter than males, which again were significantly heavier than summer-born females remaining immature during the summer of their birth. Food availability is suggested as one reason for the beginning of breeding already in January. Survival of the population was high, especially for females. In late spring of 1983 the population crashed to zero either because of predation or because of some other environmental conditions during the spring thaw.

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1. Introduction

Winter ecology of voles of the genus *Clethrionomys* is not yet well known, especially not in regions with permanent snow cover during several months. Most studies concentrate on the main breeding season in summer.

Most studies on winter populations of *Clethrionomys* species in North America and Fennoscandia concentrate on such ecological factors as weight decrease, winter breeding, mortality and survival (e.g., Fuller et al. 1969, Kaikusalo 1972, Stebbins 1976, Larsson et al. 1973, Larsson & Hansson 1977). Only few studies deal with social structure and intra- and interspecific interactions during winter (West 1977, Merritt & Merritt 1978, Henttonen & Viitala 1983, Viitala 1984). Here we report observations on the winter ecology of *C. glareolus* with emphasis on the social organization.

Clethrionomys rufocanus is reported to stay on territories during winter (Viitala 1977), whereas *C. rutilus* probably can change between territoriality and aggregation in different geographical regions and also between different winters (West 1977, Viitala 1984). The overwintering strategy of *C. gapperi* is unclear, but territoriality is reported by Merritt & Merritt (1978). Communal nesting in winter is finally considered the common pattern in *C. glareolus* (e.g., Gebczynski 1969, Christiansen et al. 1978) even though Henttonen & Viitala (1983) were unable to recognize any winter aggregations in Finnish Lappland.

2. Study area, material and methods

The study was carried out in an enclosure of 0.77 ha near the Konnevesi Research Station of the University of Jyväskylä. The enclosure consists of 0.25 ha of oligomesotrophic spruce forest, 0.35 ha abandoned field with some small pockets of bush vegetation and of 0.17 ha of power line through the spruce forest growing brushwood (Fig. 1A).

The fence surrounding this area goes 20-40 cm into the ground and is about 80 cm high. Hence, during mid-winter the snow is deeper than the fence is high. Snow conditions in mid-winter 1983/84 are shown in Fig. 1B and Table 1.

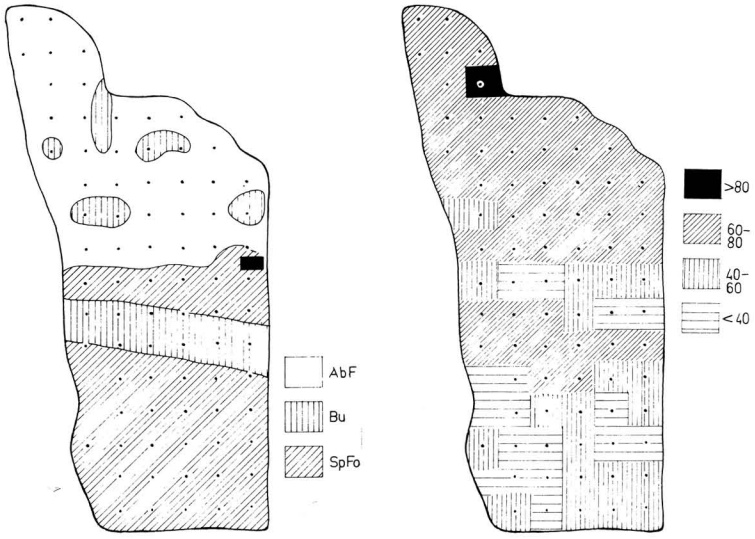

Fig. 1. A: Vegetation of the enclosure area. AbF = abandoned field; Bu = brushwood; SpFo = spruce forest. Trap sites are marked with a dot. — B: Average snow cover thickness in the enclosure during January 1984.

A population was, on September 30, 1982 (the transition between summer and winter) started with six females and eight males, and 1983 with nine females including two overwintered and one post-breeding summer born female and seven immature males. Eighty trap stations in a grid with 10 m between stations were covered with chimneys to make it possible to trap during the snowy season. Each month, trapping was done during a five day period. The following data were recorded: trap station and time, body weight, sex and sexual status, wounds and scars, and behaviour in the trap (particularly in the case of multiple captures). One handful of oats per trap was used as bait; in early November all trap chimneys were once supplied with two handfuls of oats. No deaths were observed in traps even though some animals spent up to twelve hours in traps. After the onset of reproduction the time animals spent in traps was reduced in order to avoid death of the nestlings.

Twenty additional traps were set outside the enclosure with one trap line on the forested side of the enclosure.

Table 1. Average thickness of snow cover during the 1983/84 winter. (SpFo = meso-oligotrophic spruce forest, Bu = brushwood, AbF = abandoned field; numbers in parentheses, *n*, are the numbers of trap stations in the particular type of vegetation; means and standard deviations are given).

	December	January	February
Spruce forest (n=33)	14.9±4.6	41.7±9.5	46.0±12.3
Brushwood (n=16)	26.0±4.0	66.3±6.0	71.6± 8.6
Abandoned field (n=31)	29.5±4.2	72.2±4.3	83.6± 3.6

3. Results

Mainly data from the winter 1983/84 are reported below; whenever appropriate additional data from late winter 1983 are referred to.

3.1. Aggregations

During summer, the population used the entire enclosure; territories of reproductively active females did hardly overlap at all, whereas mature males moved around the whole area and immature animals moved in rather small areas overlapping with both mature females and males (Kojola, unpubl.).

In early October voles moved their activity areas closer to each other with a concentration on the brushy parts of the enclosure (i.e., in pockets of bushes on the abandoned field and to the bush belt of the power line). Already in late October/early November distinct aggregations of voles could be observed in these areas, even though the ground was still free of snow (Fig. 2). All the frequently visited traps were used by many individuals. Both male and female home ranges overlapped extensively.

In the first half of the winter the "field aggregation" was composed of five females and two males. The area underneath the powerline was used primarily by two females and some immigrants. Throughout the period, three females were rather independent of these

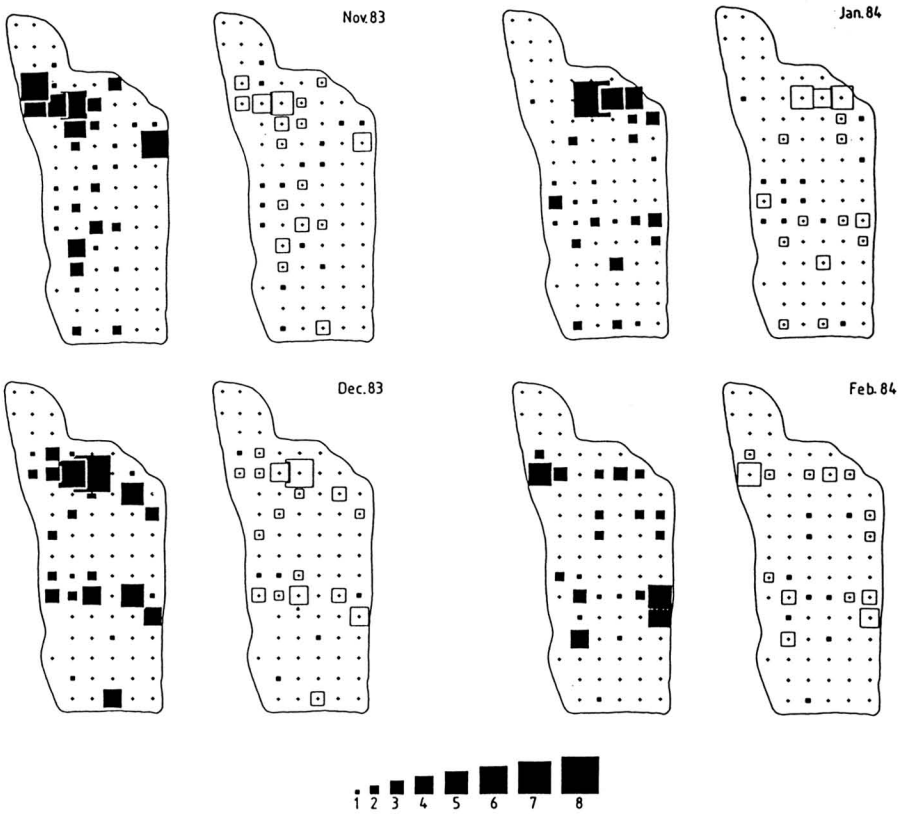

Fig. 2. Trapping frequencies in each trap (black squares) and the number of individuals which have visited these traps (open squares) during each trapping period in mid-winter 1983/84.

groups; finally one female stayed alone on a large "winter territory" in the spruce forest below the powerline.

In January the aggregations became less homogeneous, although they still could easily be recognized. In February the area inside and around these aggregations was almost completely divided between mature females (see Fig. 3). Again, there was negligible overlap between territories of mature females. Males used at this time greatly overlapping areas which in some cases were separated by those habitats which were not used by the population during winter (Fig. 4).

3.2. Winter weight and winter breeding

The development of the weight structure of the population during mid-winter is shown in Fig. 5; only members of the founder population from September 1983 are considered. The immigrants, which were always among the lightest individuals, are excluded.

Individuals' weight and reproductive condition depend on each other. The weight of each cohort reaches (synchronously) its minimum just prior to maturation. The gain of weight of males and adult females as well as the growth of testes of males began in early-mid December. In January almost all females were mature and the first litter was born in the third week of January: the first three juveniles (slightly above 12 g) were marked February 14. In mid February the female giving birth to the first litter, was pregnant for the second time, three more females were lactating: all females were mature. Of the seven males in the enclosure (five from the original population and two immigrants), two were mature and one prepubertal at this time.

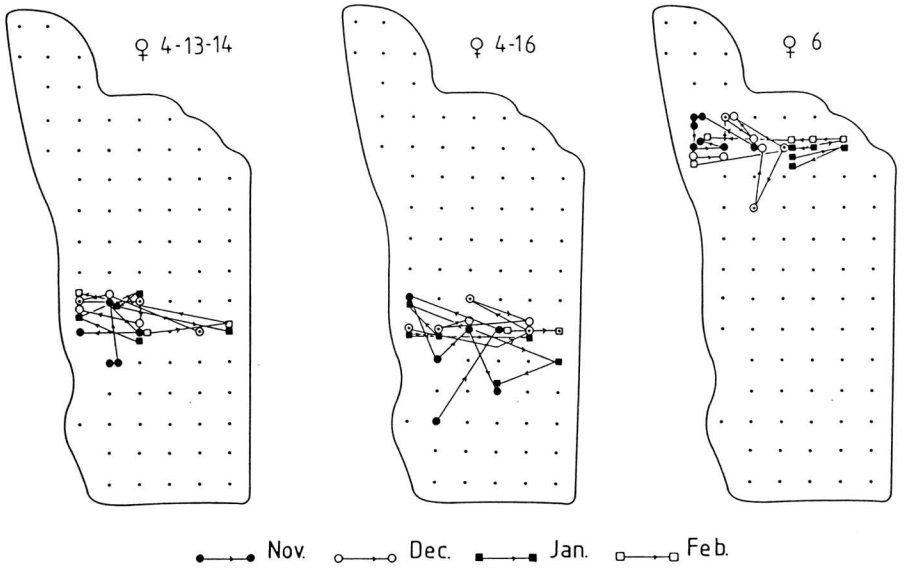

Fig. 3. Movements of three females in mid-winter 1983/84 in areas characterizing main aggregations in the enclosure.

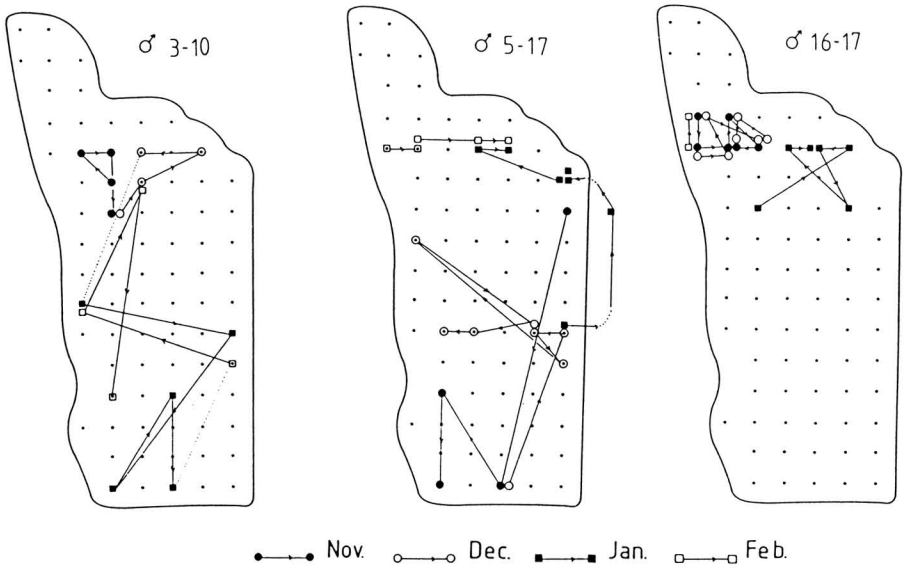

Fig. 4. Movements of three males during mid-winter. The two first ones with wide movements became mature at earliest in December.

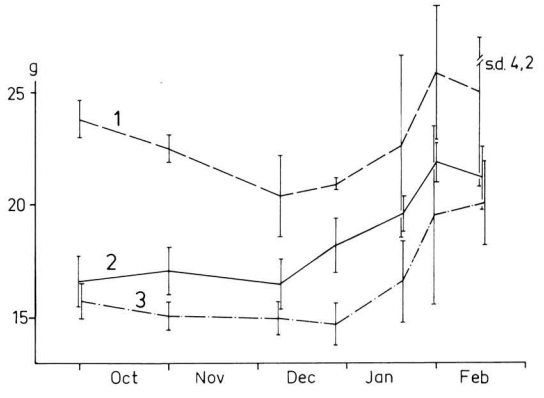

Fig. 5. Mean weights and standard deviations of different cohorts of the enclosure population during the 1983/84 winter. 1 = overwintered females and one post-breeding female; 2 = all males; 3 = immature females of the summer.

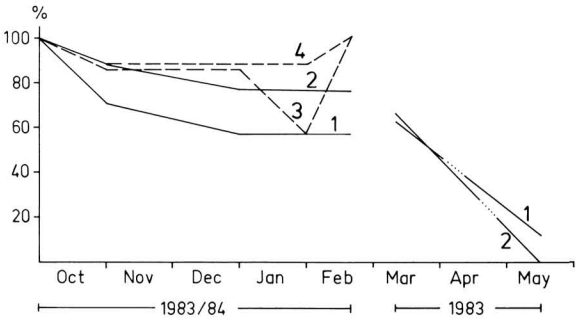

Fig. 6. Survival of the enclosure population of *C. glareolus* in late winter 1983 and during the 1983/84 winter. 1 = males; 2 = females; 3 = males with immigrants; 4 = females with immigrants.

3.3. Survival

Survival of the September 1983 population is shown in Fig. 6. Sixty percent of males survived until December; i.e., the monthly survival was about 85 %. The survival of females of the founder population was approximately 80 % until mid-winter; i.e., 93 % per month. All survived through January and February; and survival was good during spring too. Except for one individual, we do not known whether the disappeared animals died or emigrated: however, one overwintered female probably died in December 1983 when it was last caught in very bad condition.

In February and March of 1983 the survival of the September 1982 population was also approximately 70 %. An almost total crash occurred, however, during late spring: in May only one male was caught.

4. Discussion

After summer two overwintered females and one post-breeding female remained in the enclosure population. They formed the centres of the aggregations on the most suitable overwintering areas of their summer home ranges. A loss of aggressiveness among these females was, however, not observed (West 1977, Christiansen et al. 1978). In arena tests performed in November, when the aggregations had already been established, they showed the same kind of aggressive behaviour as is observed in summer. After the time when individuals started to mature (i.e., in December) the aggregations were not so clear anymore; breeding females moved to home ranges in or near to the aggregations and males began to use larger areas.

Winter studies on *Cletrionomys* are rare. However, the few which have been done show the flexible strategy of overwintering *Clethrionomys*. In higher latitudes or elevations the snow cover is sufficiently thick to form stable microhabitat conditions underneath the snow. Due to the food scarcity it may then be profitable to remain territorial in order to secure the food supply during long winter. In areas with unstable snow cover the extreme temperatures necessitates social heat production (through huddling). The higher productivity of these habitats, and thus their better food conditions, provide the conditions for forming aggregations.

Winter weights reached their minimum in November/December but differences between various cohorts of the population were highly significant (see Fig. 5). In Kaikusalo's (1972) study *C. glareolus* reached their minimum weight in February; he was unable to find differences in the weight of immature and post-breeding animals (he could not find overwintered individuals in his material). That the weight minimum was reached as early as in December may have been due to good food conditions and an early start of breeding.

For *Clethrionomys glareolus* there are only very few observations of winter breeding or

signs of maturity during mid-winter on latitudes comparable to those in our study (Kaikusalo 1972, Larsson & Hansson 1973, 1977). Winter breeding seems much more common in *Microtus*, also under snow cover (e.g., Tast & Kaikusalo 1976, Skaren 1978). In the presently described *Clethrionomys* population, winter breeding was common: fourteen young of the winter were found up to early March 1984. In February and March 1983 we did, however, not notice any signs of breeding during the winter 1982/83. The observed winter breeding could, of course, have been induced by the supplementary food (Andrzejewski 1975). The effect of supplementary food was, however, negligible in the present study: Although all the trap chimneys were supplied with oats in November, only 25–30 of them were visited by voles after that time. This means a maximum of about 40 g of supplementary food in 30 traps, which makes a total of 1200 g. In addition comes 20 g in those traps, which were visited and emptied by voles between the trapping periods of each month; this makes a total of $30 \times 20\,g = 600\,g$ each month for the whole population. In this connection it is important to observe that Henttonen (unpubl.) was unable to induce winter breeding in a feeding experiment in Pallasjärvi, Lappland, when using much higher amounts of supplementary food. It is much more likely that the good overwintering circumstances as a whole (good seed crop of spruces and shrubs, thick snow cover and mild winter) produced the necessary conditions for an early start of winter breeding.

The survival of the population was good or very good after the first critical period of autumn freeze (see Kaikusalo 1971, Merritt & Merritt 1978). The population crash in spring 1984 was associated with high numbers of cats, stoats and weasels. There did not exist many predators in late winter and spring 1984 when the population survived well.

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