

The effects of confinement on demography and spacing behaviour in the bank vole *Clethrionomys glareolus*

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Demography and space use were compared between an enclosed and an open bank vole population during a peak year breeding season in Central Finland. A metal fence confined the enclosed population. The enclosed population grew faster and reached a higher and earlier annual peak density. The pooled monthly persistence probabilities and the number of recruits per female did not differ between the populations. More females matured in the open population than in the enclosed one. The difference was likely caused by lower density of breeding females in the open population. Female home range sizes did not differ between the populations. The breeding females in the open population were at times more territorial than those in the enclosure. No fence effect, expressed as overexploitation of food resources as previously documented in genus *Microtus*, was observed supporting the ideas of differences in population regulation between these genera.

1. Introduction

A lot of work on population and behavioural ecology of voles has been carried out with island or otherwise confined (e.g. enclosure) populations (Bujalska 1973, Gliwicz 1980, 1990, Tamarin et al. 1984, Ylönen et al. 1988, 1990, Ylönen & Viitala 1987). This method has advantages in determining actual population sizes, level of carrying capacity of the environment and mechanisms of population regulation (Boonstra & Krebs

1977, Ylönen et al. 1988), but generalization of the results to open populations is problematic (see Gliwicz 1980, for a review).

The absence of the opportunity for dispersal affects the conclusions drawn from the enclosure studies. The importance of dispersal is indicated in the fencing experiments made with some *Microtus* species. The vole-proof fenced populations exhibited abnormally high densities, depleted their food resources, and consequently their numbers crashed (Krebs et al. 1969, Boonstra & Krebs 1977).

In a long-term study with an enclosed bank vole (*Clethrionomys glareolus*) population Ylönen et al. (1988) got interesting results concerning the plasticity of spacing behaviour. The aim of the present paper is to examine if the behaviour of the population in that enclosure is decisively different from the behaviour of the surrounding free-living population. So the study is not purely experimental and is lacking replicates. We define confinement as a restriction of migration but not as a total absence of it (c.f. Gliwicz 1980). That is because the fence of our enclosure was not totally vole proof due to deep ground frost, which lifted parts of the fence during spring. After spring thaw the fence was repaired to prevent dispersal.

Gliwicz (1980) reviewed data from various confined rodent populations. Her generalizations apply to island populations of *C. glareolus* and form the basis of our analysis. We could expect, that:

1) Due to restricted dispersal opportunities, the confined population should grow more rapidly (see Gliwicz 1990, too) and attain a greater peak density earlier in the breeding season than the open population.

2) Because the losses from the confined populations result almost entirely by mortality and negligibly by dispersal, the persistence probability of individuals should be greater in the confined than in the open population.

3) Breeding should stop earlier and, as a consequence, the total number of recruits per female should be lower in the confined population.

4) Due to female territoriality in *C. glareolus* (Bujalska 1973, Saitoh 1981, Gilbert et al. 1986), restricted space leaves few opportunities to the newcomers. Thus, the maturation rate of young females should be lower in the confined population.

5) Home range size of females should be smaller under the more crowded conditions of the confined population. This allows the females to avoid increasing the number of agonistic interactions with the surrounding females. Among the nonterritorial males the effect should not be as pronounced and therefore the difference between home range size of males and females should be greater in the confined population.

2. Study area, material and methods

The study was carried out at Konnevesi Research Station in the peak density year 1985 of the cyclic bank vole populations of Central Finland (Ylönen et al. 1988). The study area consisted of spruce forest and abandoned field; the enclosed area of 0.8 ha is described thoroughly by Ylönen & Viitala (1985) and Ylönen et al. (1988), and the adjacent open study area of 1.0 ha by Pusenius & Viitala (1993). The habitat distributions of the compared study areas were reasonably similar. A difference worth mentioning between the compared areas was the presence of field vole (*Microtus agrestis*) in the open study area. The field voles inhabited mostly the margins of the open area and their number was small (Pusenius & Viitala 1993).

The confined population was established in spring 1983 and was live-trapped monthly since then until the summer 1987. Due to long-lasting confinement the initial spring population density in the enclosure was higher than in the adjacent natural population at the beginning of the present study. In addition to the impact of confinement the effect of spring breeding density is compared between the populations. The enclosure population was live-trapped during the previous winter, too. However, it is very unlikely that there had been an effect of supplementary feeding on the enclosed population as the food from the traps was thoroughly removed after each trapping period and the amount of baiting consumed by the voles was very low: less than 1 kg oats per each trapping period (see Ylönen & Viitala 1985).

The whole study area of 1.8 ha was covered with 184 Uggland-Special live traps set at 10 m intervals. The traps were covered with a trap chimney of galvanized metal sheet. The study began in the mid May and lasted until the end of August. Both parts of the study area were monitored monthly by live trapping during one week with approximately ten trap checkings. During the checking periods in May, late June, and August, trapping started a few days earlier in the enclosed than in open population. The traps were generally set in the morning and checked two or three times a day at four to five hour intervals. Thus the trapping was done mostly in the daytime and in the evenings except for one night during every trapping period.

All captured voles were individually marked by toe-clipping. During each capture we recorded trap position, identity of vole, weight, sexual status, and lactation. From these data we could determine the monthly population density, spatial distribution, and home range size of individual voles, breeding parameters, and movements between the enclosure and the surrounding open study area. A correlation analysis between different parameters was performed.

The index of home range size was the largest distance between captures during a trapping period. Crude index was used as the goal was to make comparisons, not to measure areas. The overlapping percentage of home ranges was calculated as a weighted proportion of the traps used by two or more individuals from the total number of traps used by the category in question. This means that the number of traps used by three individuals was multiplied by two, the number used by four by three etc.

The spatial distribution was assessed by the clumping index: $I_{DM} = (s^2/\bar{x} - 1)$, where s^2 = the variance of the number of individuals caught in different traps and \bar{x} = the mean of the number of individuals caught in different traps. The deviation from random distribution can be tested by $I_D = s^2(n-1)/\bar{x}$, where s^2 and \bar{x} are as above and n = the number of traps. The distribution is random if the value of I_D fits between the critical values (95% and 5%) of χ^2 -distribution with $n-1$ degrees of freedom. Smaller values indicate even distribution and greater values contagious distribution (see Southwood 1978).

3. Results

3.1. Demography

The densities were estimated simply as the number of captured individuals, because of the high trappability of the species (see e.g. Ylönen et al. 1990). The enclosed population grew more rapidly than the open population (Fig. 1) and reached its peak density of 137 voles/ha at the end of July. The open population reached a peak density of 100 voles/ha at the end of August (Fig. 1). During that time the density in the enclosure had decreased to the same level as in the

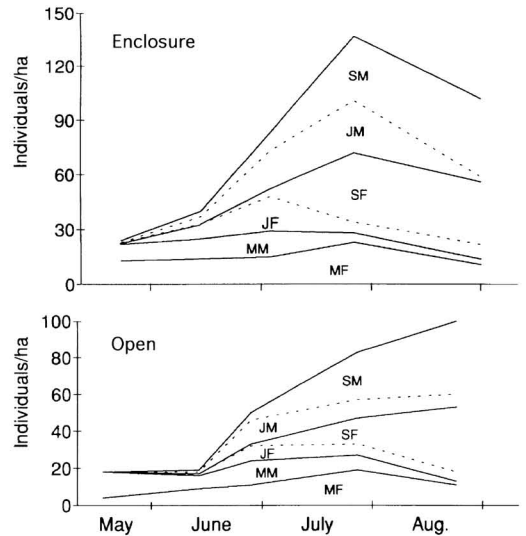


Fig. 1. Population density (voles/ha) and the proportion of different categories of the population in the enclosure and in the open study area. MF = mature females, MM = mature males, JF = juvenile females, SF = submature females, JM = juvenile males, SM = submature males.

open population. Breeding ceased in early August in the enclosure and one month later in the open population.

Persistence probability (Table 1) was determined as the proportion of the animals captured during two successive trapping periods of the animals captured during the former trapping period. The persistence probability of males was greater in the enclosure than in the open population in May. The persistence probability of females tended to be greater ($P < 0.1$) in the open population than in the enclosure in August. The persistence of females correlated negatively with both the population density (open: $r = -0.98$, $df = 2$, $P < 0.01$; enclosed: $r = -0.99$, $df = 2$, $P < 0.01$) and the density of breeding females (open: $r = -0.90$, $df = 2$, $P = 0.05$; enclosed: $r = -0.91$, $df = 2$, $P < 0.05$). The migration from the enclosure to the open population (14 individuals) was greater than the reverse (3 individuals) ($\chi^2 = 7.37$, $df = 1$, $P < 0.01$).

Reproductive success — determined as the number of juvenile recruits (i.e. voles in juvenile pelage) per breeding female — (Table 2) did not

deviate between the populations. More females matured in the open than in the enclosed population (Table 2). In the open population the maturation rate correlated negatively with the actual population density ($r = -0.99$, $df = 2$, $P < 0.001$) and the density of breeding females ($r = -0.93$, $df = 2$, $P < 0.05$). As a consequence of the greater maturation rate in the open population the density of mature females was similar in both populations since June.

3.2. Spacing behaviour

Home range size of breeding animals (Table 3) was similar in the two populations. The males

had larger home ranges than the females in both populations. The difference between the sexes was of the same magnitude in the compared populations. Pooled home range overlap did not deviate between the populations (Table 3). However, the breeding females of the enclosure overlapped more than those of the open population in late June ($\chi^2 = 4.50$, $df = 1$, $P < 0.05$) and in August ($\chi^2 = 4.32$, $df = 1$, $P < 0.05$) (Fig. 2). The values of the clumping index (I_{DM}) of breeding females of the enclosed population indicated random spatial distribution during the study (Fig. 2). In the open population the breeding females were distributed evenly in July and August ($I_D = 72.9$, $df = 102$, $P > 0.975$; $I_D = 73.1$, $df = 102$, $P > 0.975$, respectively) (Fig. 2) and I_{DM} values cor-

Table 1. Monthly persistence probabilities (p). n = number of animals in the beginning of a monthly trapping period, F-E = Fisher's exact test, * = $P < 0.05$, O = $P < 0.10$, 1) = Difference between the sexes in enclosure ($\chi^2 = 6.17$, $df = 1$, $P < 0.05$), 2) = Difference between the sexes in both populations (enclosure: $\chi^2 = 3.94$, $df = 1$, $P < 0.05$; open: $\chi^2 = 7.09$, $df = 1$, $P < 0.01$). Pooled values are formed by dividing the sum of survivors over trapping periods by sum of n over trapping periods.

	Females					Males				
	Enclosure		Open		χ^2	Enclosure		Open		χ^2 or F-E
	p	n	p	n		p	n	p	n	
May	1.00	11	1.00	4		1.00	8	0.50	14	F-E *
June	0.89	18	1.00	8	0.96 NS	0.50	16	0.80	10	2.32 NS 1)
July	0.64	33	0.72	18	0.39 NS	0.42	38	0.53	30	0.85 NS
August	0.40	53	0.58	40	2.92 O	0.42	59	0.37	46	0.32 NS
Pooled	0.60	115	0.69	70	1.38 NS	0.47	121	0.48	100	0.02 NS 2)

Table 2. Maturation percentage and reproductive success of females. Maturation percentage (%) is calculated as a proportion of matured females of the potentially maturing females (n) between two consecutive trapping periods. For the symbols of the tests see Table 1. Reproductive success for a given trapping period measured as juvenile recruits per breeding female (r/f) is determined as follows: The number of juvenile recruits in a trapping period a month later is divided by the number of breeding females (n) in trapping period in question.

	Maturation					Reproductive success				
	Enclosure		Open		χ^2 or F-E	Enclosure		Open		χ^2 or F-E
	%	n	%	n		r/f	n	r/f	n	
May	0.0	5	50.0	2	F-E NS	0.90	10	0.50	4	F-E NS
June	0.0	14	50.0	6	F-E *	2.91	11	2.33	9	0.17 NS
July	10.3	29	25.0	20	1.86 NS	2.33	12	1.45	11	0.82 NS
August	0.0	26	2.4	42	0.61 NS	0.44	18	0.60	20	0.29 NS
Total	4.4	68	18.3	60	6.34 *	3.95	22	3.12	25	0.51 NS

related negatively with population density ($r = -0.93, df = 3, P = 0.01$). The home range overlap between the breeding males of both populations was greater than that of the breeding females (Table 3).

4. Discussion

The characteristics of the dynamics of our confined population were in accordance with those of island populations reported by Gliwicz (1980, 1990): i.e. more rapid growth, an earlier peak density and subsequent decrease in the confined population in comparison with the open population.

In the beginning of the breeding season population density was nearly twice as high and number of breeding females more than twice as high in the enclosure as in the vicinity. In addition the voles of the confined population were obviously familiar with each other after having overwintered mainly in aggregations (Ylönen & Viitala 1985). These facts probably contributed to the rapid start of breeding and the higher population peak. The earlier termination of breeding in the enclosure was probably connected with density. High density seems to shorten the breeding season (Bujalska 1983, Ylönen et al. 1988), although Ylönen et al. (1990) found no such effect in experimental populations composed of mutually familiar individuals. After the end of the recruitment of neonatals the population den-

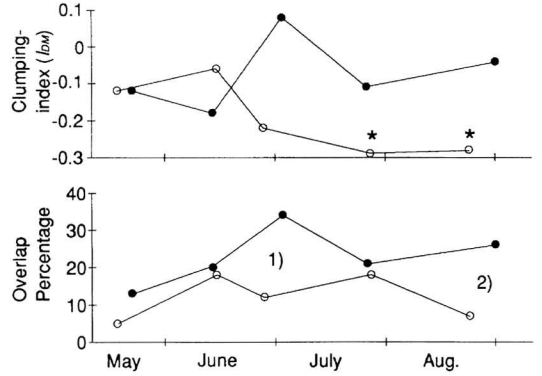


Fig. 2. Clumping index (I_{DM}) and percentage of home range overlap of breeding females in the enclosure (filled dots) and in the open population (open dots). Positive values of I_{DM} indicate clumping and negative values territoriality (see Southwood 1978). Asterisks (*) denote deviation from random spatial distribution ($P < 0.05$ in both cases, see text). 1) and 2) difference between the populations ($P < 0.05$ in both cases, see text).

sity in the enclosure decreased to the same level as in the open population until the end of August.

According to Gliwicz (1980), the persistence of individuals is better in confined populations. The poorer persistence of females in the enclosure in August was probably affected by the greater population density as indicated by the negative correlation between persistence and density. A contributing factor may have been the difference in the phase of reproduction of the

Table 3. Mean home range size and overlap of breeding animals. Mean home range size is calculated as a mean from different trapping periods and measured as the longest distance between the captures of an individual during a five day trapping period. n = number of individuals captured only in one or the other study area. Two-way ANOVA gives the following effects: population, $F_{1,51} = 0.79, P = 0.38$; sex, $F_{1,51} = 5.54, P = 0.02$; population x sex, $F_{1,51} = 0.42, P = 0.52$. Home range overlap is measured as the proportion of the traps that are visited by more than one individuals ($pr. >1$) of the same sex. Values from different trapping periods are summed. (1) number of traps visited by only one individual, (>1) number of traps visited by more than one individual, *** = $P < 0.001$.

	Home range size					Overlap					χ^2
	females		males		females			males			
	mean \pm SD	n	mean \pm SD	n	1	>1	pr.>1	1	>1	pr.>1	
Enclosure	3.52 \pm 1.46	14	4.28 \pm 2.07	10	139	29	0.17	67	41	0.38	14.88***
Open	2.83 \pm 1.29	17	4.21 \pm 2.17	14	167	25	0.13	103	58	0.36	25.77***

populations, in the enclosed population breeding stopped earlier, too (see Ylönen et al. 1988). The similar recruitment of juveniles per breeding female in our study populations do not fit either with the results of studies with confined bank voles populations reviewed by Gliwicz (1980). The probable familiarity of the breeding females in the enclosure may have enhanced the juvenile survival as found by Ylönen et al. (1990).

Clethrionomys-females need a territory of their own in order to mature (e.g. Bujalska 1973, Saitoh 1981, Gilbert et al. 1986, see Ylönen et al. 1988, for an exception). This view is supported also in our study. In the more densely populated enclosure the maturation rate was low compared to the open population, where the opportunities for young females to achieve a territory should have been better. The increasing densities of both the whole population and the breeding females, however, decreased the maturation also in the open population as less space was available.

The reduction of the home range size of females or the greater difference in home range size between the sexes in confined populations reported by Gliwicz (1980), were not found in our study. Mutually familiar females of the enclosure should tolerate the increased number of interactions caused by their greater density (H. Ylönen, pers. obs.). That is indicated also by the greater home range overlap in the enclosure at times. Low density of breeding females early in the breeding season seems to induce some kind of social cohesion in the open population (c.f. Lambin & Krebs 1991) indicated by clumping of the home ranges during spring and early summer despite of available space. When the female densities increased, the home ranges were spaced out. The greater home range overlap in males than in the females in both populations is in accordance with the general view of spacing behaviour of genus *Clethrionomys* (see e.g. Viitala & Hoffmeyer 1985, Ostfeld 1985, Cockburn 1988).

We conclude, that much of the observed differences between the confined and the open population can be related to the difference in the density of breeding females in the beginning of the breeding season. The field vole may potentially have affected reproductive success and growth of the population in the open study area, but because of its low numbers and distribution

in the margins of the area (Pusenius & Viitala 1993), the effect have to be of secondary importance.

The earlier termination of reproduction in a confined population suggests some kind of density-dependent inhibition of reproduction in addition to the regulation of breeding density based on territoriality of females. We suggest that these regulatory systems prevent overgrazing of the habitat as in the case of vole-proof confinement of *Microtus*-species (Krebs et al. 1969, Boonstra & Krebs 1977). On the basis of these studies with vole-proof enclosures and island studies with *Clethrionomys* and *Microtus* it is obvious that these genera have different social systems as adaptations to different environments. We suggest that even with totally vole-proof enclosures and different confinement times we would not be able to create a "fence effect" in a study with *Clethrionomys* populations. Finally it can be mentioned that both populations crashed simultaneously in the next year 1986 (Ylönen et al. 1988) suggesting that the mechanisms behind the crash should be the same in and outside the fence.

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