

Varying spacing behaviour of breeding field voles, *Microtus agrestis*

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Spacing behaviour of breeding field voles (*Microtus agrestis*) was studied by live-trapping wild populations in an abandoned field and a grassy spruce forest in Konnevesi, Central Finland. Spacing behaviour varied between sexes, cohorts, habitats and in time. Females in the field had the most extensive home range overlap. Overwintered females had overlapping home ranges in late spring on the edges of the field, but became more territorial in early summer as they colonized the open field. Later, as females of the year outnumbered overwintered females, the home range overlap correlated positively with population density. In the suboptimal habitat, the spruce forest, the home ranges of females were larger and overlapped less than those in the field. Also the males had overlapping home ranges in late spring but became subsequently more territorial. The overlap between their home ranges responded on the spatial distribution of females in early summer but on temporal distribution of oestrous females later as the breeding was synchronized. The plasticity of spacing behaviour allows field voles to cope with changing habitats.

1. Introduction

In their review on social structures of microtines Viitala & Hoffmeyer (1985) presented a hypothesis that food scarcity and the stability of habitat result in social mechanisms that limit sexual maturation and reproduction during high density. No such mechanisms are expected in a population living on rich food resources and/or in an ephemeral habitat. Thus social behaviour

affects individual life histories and provides one way to adapt to a particular type of environment.

Ostfeld (1985, 1990) pointed out the importance of key resources and population density on the social behaviour. Due to the high energetic costs of maternal care the spacing behaviour of a reproductive female largely depends on the quality, quantity and distribution of food. Scarce and slowly regenerating food and low population density result in territorial behaviour. In an op-

posite situation the home ranges should overlap. Because of the lack of paternal care the key resource for reproductive males is receptive females. Males should be territorial when females have overlapping home ranges (Ostfeld 1985) or breed in synchrony (Ims 1987a). In an opposite situation males should have overlapping home ranges. These expectations are generally supported by data from interspecific comparisons (see Ostfeld 1985).

Evidence for changes in behaviour according to changes in the environment has been reported. Home range size seems to be inversely related to food quantity and quality, and population density (Mazurkiewicz 1971, Viitala 1977, Madison 1985). Phenotypic plasticity in territorial behaviour has been reported in female *Clethrionomys* (Ims 1987b, Ylönen et al. 1988) and in some *Microtus* (Madison 1990).

In previous studies on *Microtus agrestis* Koponen (1972), Myllymäki (1970, 1977b) and Viitala (1977) have found reproductive males to be intrasexually territorial and reproductive females generally non-territorial although overwintered females behave territorially towards each other. The mating structure is polygynous.

The aim of the present study is to examine the spacing behaviour of reproductive field voles (*Microtus agrestis*, L.) in a Central Finnish population during a breeding season of a peak density year. Behaviour in different age classes and habitats is compared. A demographical study on the same population (see Pusenius & Viitala 1993) forms the background.

2. Study area, material and methods

The study was carried out in Konnevesi, Central Finland (62°N), in summer 1985. The study areas were an abandoned field with its margins (0.7 ha) and a thinned moist grassy spruce forest with its edges (1 ha). These habitats correspond to optimal and suboptimal-marginal habitats, respectively, as defined by Stenseth et al. (1977).

We had 10 live-trapping periods in each study area from May to the end of October. Each five-day period consisted of 8 to 10 trap checks. Ugglan special multiple capture traps were set in

a grid with 10 m intervals. For a detailed description of the study areas, material and trapping methods, see Pusenius & Viitala (1993).

The trappability index of different categories was calculated according to Viitala (1977) as the probability of an animal to be captured during one inspection of the traps. The index of home range size for females was the number of traps visited during a trapping period, as the catch points of a given female were mostly adjoining traps. The males were more mobile and we used the largest distance between captures during a trapping period as an index for them, as also in the comparisons between the sexes. The percentage of home range overlap was calculated as a weighted proportion of traps used by two or more individuals from the total number of traps used by the category in question. I.e the number of traps used by three individuals was weighed by two, that used by four by three etc.

The spatial distribution pattern was studied using the clumping-index of David & Moore (1954, see Southwood 1978):

$$I_{DM} = (s^2/\bar{x}) - 1,$$

where s^2 = the variance in the number of individuals caught in different traps, and \bar{x} = the mean number of individuals caught in different traps. Positive values of I_{DM} indicate clumping and negative territoriality. Deviation from random distribution can be tested by index $I_D = s^2(n-1)/\bar{x}$, where n = the number of traps. The distribution is random if the value of I_D falls between the critical values (95% and 5%) of χ^2 -distribution with $n-1$ degrees of freedom. Smaller values indicate even distribution (territoriality) and greater values aggregated distribution.

The timing of parturitions were estimated on the basis of weight changes of the females. The number of parturitions per five days was obtained. The ages of individuals recruiting to the population were estimated on the basis of weight curves presented by Myllymäki (1977a). The animals were divided in cohorts K_1 to K_8 according to the estimated time of birth (see Pusenius & Viitala 1993). The K_1 cohort consisted of overwintered animals and possibly of some individuals born in winter or in early spring. Other reproducing animals belonged to cohorts K_2 (born in May) and K_3 (born in June).

In the forest the number of reproducing animals was too small for comparisons between the cohorts.

$df = 9$, $P > 0.05$) and clumped during the latter part of the breeding season ($I_D = 34.79$, $df = 9$, $P < 0.001$).

3. Results

3.1. Trappability, operational sex ratio and synchrony of parturitions

The trappability was similar in both habitats and for both sexes (Table 1). However, for females it varied between the cohorts.

The operational sex ratio (the number of reproductive females per a reproductive male) was significantly female biased in the field from early July onwards. The bias increased during the summer peaking at 7 females to one male in September (see Fig. 3).

The parturitions were asynchronous in spring and early summer, but seemed to be more synchronous after July (Fig. 3). The synchronization occurred simultaneously with the recruitment of the cohorts K_2 and K_3 to the reproductive population (Fig. 4). The distribution of the number of parturitions per five days was tested using the I_D index (see methods). The breeding season was divided into two periods: 1) from late May to mid July and 2) from late July to early September (i.e. the period when the young of the year form the majority of the breeding females). The distribution of parturitions was random during the former part of the breeding season ($I_D = 16.66$,

3.2. Spacing behaviour

3.2.1. Home range size

The index of home range size of reproductive animals was calculated for each trapping period and cohort (Fig. 1), as well as the mean for the breeding season (Table 2). Home range size of reproductive females correlated positively with their trappability in the field ($r = 0.69$, $df = 7$, $P < 0.05$). Trappability is thus included as a covariate in the comparisons between different female groups and standardized in calculations of correlations.

In the field the home range size and density of all reproductive females correlated positively (partial correlation, $r = 0.76$, $df = 6$, $P = 0.014$). In the cohort K_1 the home range size correlated positively with both the density of reproductive females (partial correlation, $r = 0.92$, $df = 6$, $P = 0.001$) and the total population density (partial correlation $r = 0.76$, $df = 6$, $P = 0.014$). In the cohort K_2 home range size correlated with the total population density (partial correlation $r = 0.96$, $df = 4$, $P = 0.001$). Cohort K_1 had larger home ranges than the cohorts K_2 and K_3 (Table 2). The differences were most pronounced in August (Fig. 1). The mean home range size of fe-

Table 1. Trappability as a probability (mean \pm SD) of an animal to be captured during one inspection of the traps. n = number of individuals. The values of different cohorts are calculated since middle of July, when the cohorts existed together. K_1 and K_2 were more trappable than K_3 (ANOVA, paired comparisons by contrasts, $F_{1,40} = 9.52$, $P = 0.004$ and $F_{1,40} = 5.70$, $P = 0.022$, respectively). Mature voles were more trappable than immature ones (Mann-Whitney's $U = 7809.5$, $n_1 = 304$, $n_2 = 117$, $P < 0.001$).

| | Field | n | Forest | n |
|------------------------|-----------------|-----|-----------------|-----|
| Breeding males | 0.32 \pm 0.14 | 19 | 0.35 \pm 0.19 | 11 |
| All breeding females | 0.32 \pm 0.12 | 71 | 0.29 \pm 0.17 | 16 |
| Breeding K_1 females | 0.47 \pm 0.15 | 10 | | |
| Breeding K_2 females | 0.41 \pm 0.18 | 16 | | |
| Breeding K_3 females | 0.28 \pm 0.12 | 17 | | |
| Immatures | 0.19 \pm 0.09 | 256 | 0.19 \pm 0.12 | 48 |

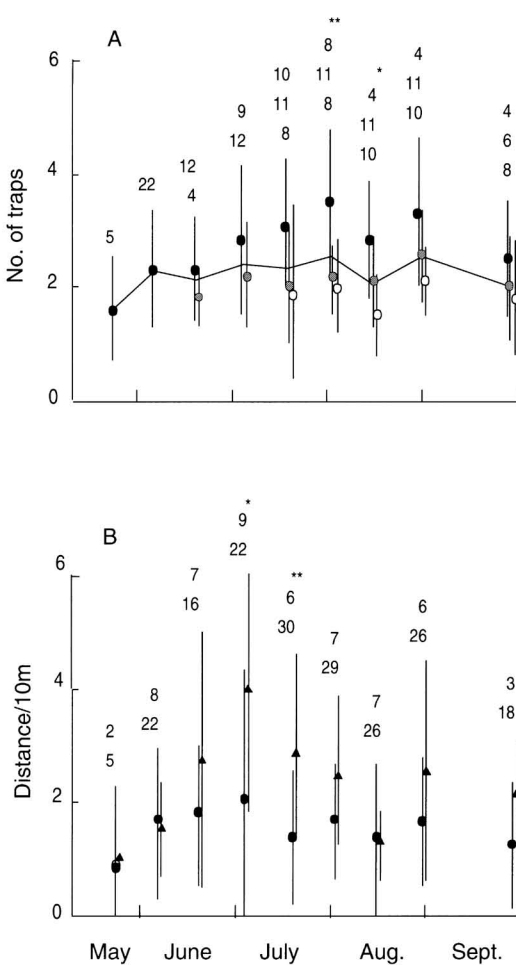


Fig. 1. Temporal variation in the index of home range size of reproductive animals in the field measured as the number of traps visited during a trapping period (upperpart, A), and as the largest distance between captures during a trapping period (lowerpart, B). Line in A = all breeding females. Dots in A: filled = K₁ females, shaded = K₂ females, open = K₃ females. Dots in B = all breeding females. Triangles in B = all breeding males. The vertical bars denote $\pm SD$, figures denote sample size: in A from above K₁, K₂, K₃ and in B from above males, females. Asterisks in A: ** K₁ had bigger home ranges than K₂ and K₃ (ANCOVA, paired comparisons by contrasts, $F_{1,24} = 11.20$, $P = 0.003$ and $F_{1,24} = 6.20$, $P = 0.019$, respectively), * K₁ had bigger home ranges than K₃ (ANCOVA, contrast, $F_{1,22} = 7.81$, $P = 0.011$). Asterisks in B: males had bigger home range than females. * $t = 2.41$, $df = 29$, $P < 0.05$ and ** $t = 2.91$, $df = 34$, $P < 0.01$.

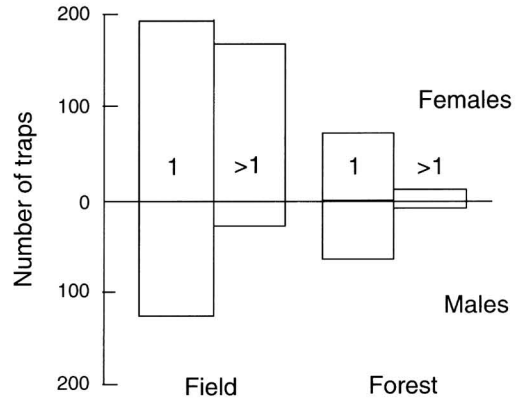


Fig. 2. The number of traps visited by only one individual (1) and the number of traps visited by more than one individuals (>1) of the same category summed from different trapping sessions. Differences exist between females of field and (i) males of field ($\chi^2 = 37.21$, $df = 1$, $P < 0.001$) (ii) females of forest ($\chi^2 = 32.67$, $df = 1$, $P < 0.001$) (iii) males of forest ($\chi^2 = 27.90$, $df = 1$, $P < 0.001$).

males was smaller in the field than in the forest (Table 2). The home ranges of reproductive males were bigger than those of females in the field in July (Fig. 1B).

Table 2. Home range size (mean $\pm SD$) of breeding females as a mean from different trapping periods. n = number of individuals. The values of different cohorts are calculated since middle of July when the cohorts existed together. Cohort K₁ had bigger home ranges than cohorts K₂ and K₃ (ANCOVA, paired comparisons by contrasts, $F_{1,33} = 19.27$, $P < 0.001$; $F_{1,33} = 19.51$, $P < 0.001$, respectively). The forest females had bigger home ranges than the field females (ANCOVA, $F_{1,69} = 9.76$, $P = 0.003$).

| Habitat | Category | Home range size | n |
|---------|----------------|-----------------|-----|
| Field | All | 2.19 \pm 0.67 | 59 |
| | K ₁ | 2.92 \pm 0.50 | 10 |
| | K ₂ | 2.17 \pm 0.43 | 13 |
| | K ₃ | 1.89 \pm 0.49 | 14 |
| Forest | All | 2.81 \pm 0.97 | 13 |

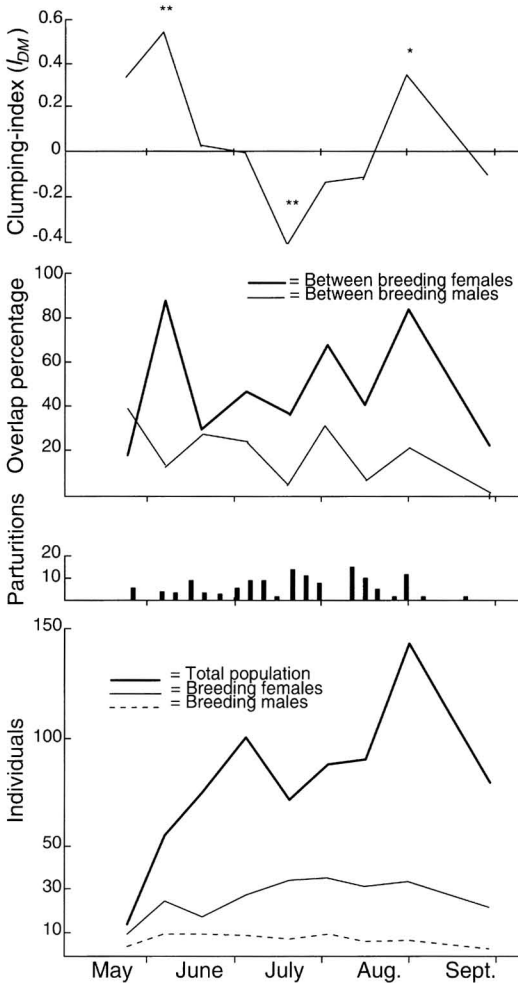


Fig. 3. Temporal variation in clumping index of breeding females (I_{DM}), home range overlap percentage of breeding females and males, number of parturitions and number of animals in field. Asterisks denote deviation from random spatial distribution (** = $P < 0.01$, * = $P < 0.05$). Positive values of I_{DM} (see methods) indicate clumping and negative territoriality.

3.2.2. Home range overlap and spatial distribution

Home range overlap, indicating the degree of territoriality, varied between the sexes, cohorts, habitats and in time (Figs. 2, 3 and 4). The females in the field had the greatest home range overlap (Fig. 2). Their spacing behaviour changed

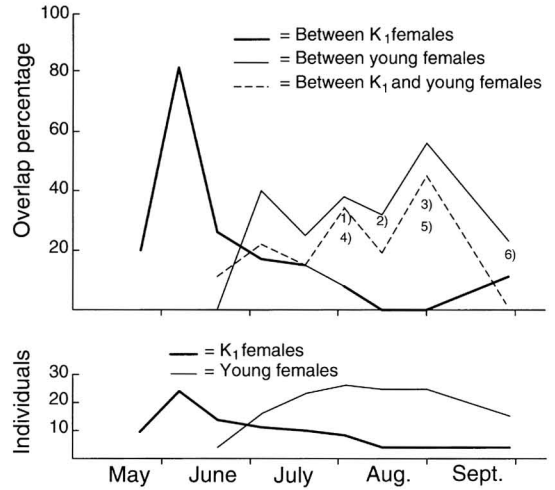


Fig. 4. Temporal variation in home range overlap percentage and number of breeding females of cohort K_1 and cohorts K_2 and K_3 combined (young females) in field. Home range overlap between the young females was greater than that between the K_1 females (1: $\chi^2 = 6.65$, $df = 1$, $P < 0.01$; 2: $\chi^2 = 4.66$, $df = 1$, $P < 0.05$; 3: $\chi^2 = 10.26$, $df = 1$, $P < 0.01$). Home range overlap between the age groups was greater than that between the K_1 females (4: $\chi^2 = 5.59$, $df = 1$, $P < 0.05$; 5: $\chi^2 = 7.43$, $df = 1$, $P < 0.019$). Home range overlap between the young females was greater than that between the age groups (6: $\chi^2 = 4.39$, $df = 1$, $P < 0.05$).

significantly in time (Figs. 3 and 5). They were aggregated in small groups in early June ($I_D = 109.13$, $df = 70$, $P < 0.01$, overlapping 89 percent) and again in the end of August during the maximum density ($I_D = 95.65$, $df = 70$, $P < 0.05$, overlapping 85 percent). Between these peaks of group behaviour there was an even distribution in mid July ($I_D = 41.43$, $df = 70$, $P > 0.99$, overlapping 39 percent) indicating more territorial behaviour. At other times the degree of overlap varied between 30 and 70 percent and the clumping index indicated random spatial distribution. There was a negative Pearson correlation between the clumping index values and the number of parturitions during and one week after a trapping period ($r = -0.82$, $df = 5$, $P < 0.05$). One should also notice the parallel profiles of the curves of clumping index and population size from beginning of July ($r = 0.96$, $df = 4$, $P < 0.01$) (Fig. 3).

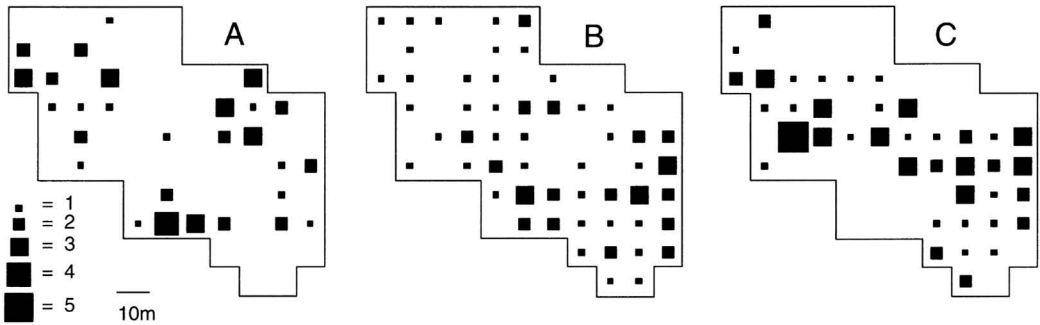


Fig. 5. Spatial distribution pattern of breeding females in field in early June (A), mid July (B) and late August (C). Size of the squares refers to number of individuals visited in a given trap.

The dynamics and the magnitude of home range overlap of the breeding females in cohorts K_2 and K_3 was very similar, so these cohorts are treated together and called the young females. The overlap among the young females and their overlap with the K_1 females was greater than the overlap among the K_1 females in August. In September the overlap among the young females was greater than their overlap with the K_1 females (Fig. 4). Early in the breeding season the reproductive females were all from the cohort K_1 . After living in coherent groups in the early summer, these females behaved territorially towards each other for the rest of the reproductive season (Fig. 4). The overlap percentage among the females of K_1 correlated with the number of females in that cohort ($r = 0.94$, $df = 7$, $P < 0.01$). In the group of young females, which formed the majority of the reproductive females after July (Fig. 4), the overlap percentage correlated with both the density of that group ($r = 0.79$, $df = 5$, $P < 0.05$) and the total population density ($r = 0.81$, $df = 5$, $P < 0.05$). The overlap percentage between the age groups also correlated with the population density ($r = 0.81$, $df = 5$, $P < 0.05$).

The females in forest had little home range overlap and were randomly distributed (Fig. 6). There was a positive correlation ($r = 0.81$, $df = 8$, $P < 0.01$) between the overlap percentage and number of breeding females.

The males in the field had clearly overlapping home ranges in May. Compared with the females the degree of overlap varied in opposite phase in early summer but in synchrony from

July onwards (Fig. 3). The forest males also had the greatest home range overlap in May. Later on the two reproductive males in the forest were strictly territorial (Fig. 6).

4. Discussion

The main findings of the study were:

- 1) The pronounced variation in spacing behaviour in time and space.
- 2) The differences in the behaviour of different cohorts.
- 3) The effect of both spatial and temporal distribution of females on the spacing behaviour of males.

Increasing synchrony in breeding, however, seemed to obscure the importance of spatial distribution (see Ostfeld 1990). The variation in the number of trap checks may slightly strengthen the variation in space use. For example the lows in the home range size in mid August (8 trap checks) (Fig. 1) are probably partly due to this. The effect of the number of trap checks on the general trends and the correlations between different variables, observed, is negligible: The direction of the effect on estimates of numbers and space use indices is the same (see also Pusenius & Viitala 1993).

Trappability can be interpreted as an index of social dominance (Gliwicz 1970). That explains the trappability differences between the cohorts. Cohort K_2 approached the trappability of K_1 fe-

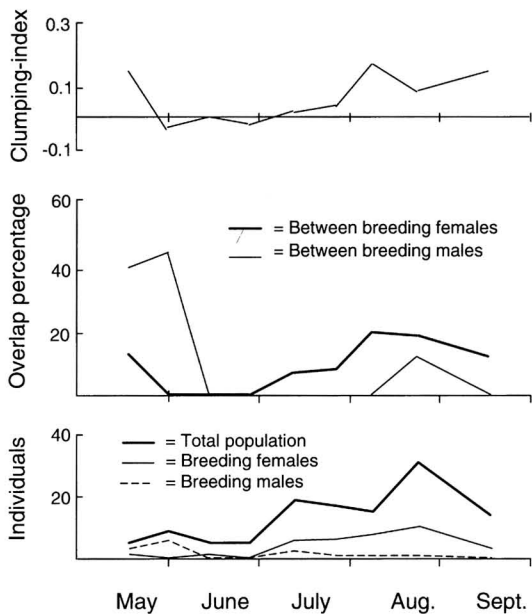


Fig. 6. Temporal variation in clumping index (I_{DM}) of breeding females, home range overlap percentage of breeding females and males and number of animals in forest. Positive values of I_{DM} (see methods) indicate clumping and negative territoriality.

males but K_3 remained subdominant (c.f. Viitala 1977). Trappability affects also the estimates of home range size. Due to the small home range size of field vole relative to the distance between traps, the effect may not be very large (see Hayne 1950).

The positive relationship between the home range size and density in the field is contradictory to results of former studies with *Microtus*: home range size is generally found to decrease with increasing density and intruder pressure (Madison 1985). Erlinge et al. (1990) found that *M. agrestis* females in southern Sweden had smaller home ranges during high than low density during nonbreeding season. The behavioural differences between breeding and nonbreeding season may explain the difference with our results. There may also be differences regarding the impact of the vole population on its food resources. A rapid depletion of food resources by an growing *Microtus*-population has been demonstrated by Boonstra & Krebs (1977) and Myllymäki (1977b). The latter found in southern

Finland an increase in home range size of reproductive *M. agrestis* females during the time of food shortage in midsummer although there was no correlation between home range size and density. According to Lima (1984) territory size may reflect the probability of future resource shortage indicated by density. If the dominant K_1 and to some extent K_2 females try to secure food from a larger area as the density increases, they are probably not strongly affected by the intruder pressure by the younger conspecifics.

The larger female home ranges in the forest than in the field seems to agree with the presumption of a negative correlation between food availability and home range size (see e.g. Mazurkiewicz 1971, Madison 1985). We have no quantitative measurements of the vegetation, but it is likely that for a grazer specialized in monocotyledons, the coniferous and mixed forest provides less food than the abandoned field.

Why then the K_1 females had bigger home ranges than the younger ones and were territorial towards each other for most of the summer when the younger breeding females lived in overlapping home ranges? Because of their dominance, as indicated by the trappability, the K_1 females had the best possibilities to respond to the growing density. In addition, because of their own decreasing density, they were able to space out their territories. But it is also possible that there was a true behavioural change related to age and future life expectation. The old females may maintain family territories exclusive of other old females (c.f. Frank 1953, Heske 1987, Lambin et al. 1992). This could benefit the offspring, including the reproducing daughters, by e.g. securing enough high quality food (Bergeron et al. 1990) and protecting against infanticide (Rodd & Boonstra 1988). Because of the lower social status of the younger females, they may not be able to defense territories especially in high density situations (Madison 1985). Koponen (1972) also found indications of density-dependent spacing behaviour of younger females in *M. agrestis*: there was a tendency towards aggregations during high density. In September the association between the young females and the K_1 females weakened.

So there seems to exist an age-dependent continuum in the behaviour. The behaviour of K_1 changes at least in time and possibly because

of aging. The status of K_2 is intermediate as its trappability approaches that of K_1 but spacing behaviour is similar to that of K_3 . The age-specific differences in behaviour are also reflected in the temporal variation in the spacing behaviour of the whole breeding female population.

The pronounced temporal variation in the female home range overlap in the field (Fig. 3) has many possible explanations. They do not exclude each other:

- 1) There may have been a decrease in the degree of familiarity between the mature females early in the breeding season. In May the field was uninhabited due to lack of cover. The animals lived in colonies in the ecotone between the field and the forest (Fig. 5). These may have been winter colonies with a relatively high degree of familiarity between the individuals. As the field became habitable, unfamiliar animals of different colonies came into contact (see Pusenius & Viitala 1993). This may have increased territoriality and decreased female density (Fig. 3, c.f. Ferkin 1988). In southern Sweden the reproductive females of a *M. agrestis* population studied by Erlinge et al. (1990) were territorial from the onset of breeding. These voles were able to use the same habitat throughout the year.
- 2) The density-dependent home range overlap of the younger females contributed to the variation especially since the beginning of July.
- 3) The variation in the number of births may have had an effect. The food demand of pregnant and lactating females more than doubles compared with nonreproducing females (Grodzinski & Wunder 1975). This is a potential explanation when breeding is synchronized and especially in midsummer, when food may also have been scarce (Myllymäki 1977a, b).
- 4) Dispersal of young females to an independent home range before the birth of their second litter observed by Myllymäki (1977a) and Viitala (1980). In our study, this could have been possible in mid June, July and August. Such dispersal was also observed in our unpublished pilot experiment, but was not found by Sandell et al. (1991) in *M. agrestis* in southern Sweden.

- 5) The distribution of resources (Ostfeld 1985) including cover was an uncontrolled but also an affecting variable in this study as the slight changes in microhabitat selection suggests (Fig. 5).

The home range overlap of females was lower in the forest than in the field. A probable explanation for the difference is the lower female density in the forest allowing spacing out of the home ranges. In addition the female population was originated by colonization and the individuals were probably unfamiliar with each other.

The female biased operational sex ratio indicates polygyny in the field. The home range indices of males were larger than those of females especially during the conception of the largest cohort, the K_5 . Assuming postpartum oestrus most of the females were in oestrus during that time. However, in May there were more males than females in the forest and the operational sex ratio was low also in the field, and the mating structure was possibly promiscuous as found by Viitala (1977) in Lapland.

Early in the breeding season the home range overlap of males and females varied in opposite phase but since July in synchrony. Territoriality of males was especially pronounced during the periods when most of the females were in oestrus and less evident when only few females were in heat (Fig. 3). Thus during asynchronous breeding the spatial distribution of females determined the male behaviour (Ostfeld 1985), but with increasing breeding synchrony of females the temporal distribution of oestrous females became more important (Ims 1987a).

Spacing behaviour of *M. agrestis* can be seen as a continuum from territoriality to group behaviour where the position of one particular population and individual may change according to habitat, amount and distribution of key resources, population density and age of the individual. Thus the social organization is multimodal *sensu* Madison (1990). The flexible behaviour makes *M. agrestis* capable to inhabit seasonally and successional changing habitats and to cope with the need for seasonal and annual habitat changes (e.g. Stearns 1976, Fleming 1979). The behavioural flexibility does not, however, induce stability with respect to population cycles as suggested by Madison (1990) as *M. agrestis* is

clearly 'cyclic' in Central Finland (see Hansson & Henttonen 1985).

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