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Shifting spacing behaviour of male field voles (*Microtus agrestis*) over the reproductive season

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Spacing behaviour of male field voles was studied by radio-telemetry during spring and autumn. Spacing patterns were different during the two periods with great overlap between ranges in spring, and exclusive ranges during autumn. Regarding movement activity males were stationary and made regular excursions in the surroundings during spring, whereas they continuously moved around in their exclusive ranges during autumn. Contradictory to the theoretical models on male spacing behaviour, the shift in male spacing behaviour could neither be attributed to distribution of females nor to female reproductive synchrony. Instead female density seemed to be the most influential factor, although sex ratio, dominance relations and predation may also be important.

1. Introduction

In small mammals a large interspecific variation in social organization and in spacing patterns have been reported during the last decades. The factors behind this variation has received great interest (reviews in Ostfeld 1985, 1990, Wolff 1985). Even within the single genus Microtus a remarkable variation has been demonstrated. In some species males tend to have exclusive ranges while female ranges overlap (e.g. *M. californicus* (Peale): Ostfeld 1986). In other species males have overlapping ranges while females occupy almost exclusive areas (e.g. *M. pennsylvanicus* (Ord): Madison 1980, Ostfeld *et al.* 1988, and *M. brewer*i (Baird): Zwicker 1989). Group territories have been reported from *M. pinetorum* (Le Conte) (FitzGerald & Madison 1983), and trapping data indicate a system were both males and females have intrasexually exclusive ranges in *M. montanus* (Peale) (Jannett 1982).

One proposed explanation for male spacing patterns, and the resulting mating system, is that male behaviour is determined by the spatial and temporal distribution of reproductive females (Trivers 1972, Emlen & Oring 1977, Clutton-Brock & Harvey 1978). Ostfeld (1985, 1990) has presented a detailed application of this hypothesis to microtine rodents, where he predicts overlapping ranges among males when females are evenly distributed (territorial), whereas exclusive ranges between males are expected when females are spatially clumped as a result of being nonterritorial.

Ims (1987a) proposed that the spacing system of male microtines can be predicted from the temporal distribution of receptive females, i.e. the degree of reproductive synchrony between females.

He predicted that males should have overlapping home ranges when females are asynchronous and exclusive home ranges when females are synchronous.

The general view has been that the mating system and spacing pattern are species specific, and in interspecific comparisons each species has been assigned to a single social system. However, several reports of intraspecific variation in small mammal spacing patterns have appeared (Viitala 1977, Madison & McShea 1987, Ylönen *et al.* 1988, Viitala & Pusenius 1990, Wolff & Cicirello 1990, Pusenius & Viitala 1993, Agrell 1995), and a need to reconsider current predictive models is emerging (Ostfeld & Klosterman 1990).

The spacing system of male field voles, Microtus agrestis (Linnaeus), has been studied earlier by use of the capture-mark-recapture method (Viitala 1977, Viitala & Pusenius 1990, Pusenius & Viitala 1993). Data showed that males are quite flexible in their spacing behaviour, although the factors behind the various spacing systems remains unclear. The purpose of this study was to examine male spacing and movement patterns, by use of intense radio-tracking, during the breeding season. By quantifying female spatial and temporal distribution we were able to analyse male spacing behaviour in relation to predictions derived from current theory on male spacing patterns and mating systems (Ostfeld 1985, Ims 1987a).

2. Study area and methods

The study was carried out in the Revinge area in southern Sweden (55°42′N, 13°25′E) during 1986 and 1987. The study area is a homogeneous wet meadow dominated by *Poacae* spp., *Urtica dioica*, *Anthriscus sylvestris*, and *Cirsium arvense*.

The field voles were trapped by the use of "Ugglan" traps placed in an open grid of about 1 ha with the traps 7 m apart. During each tracking period we radio-marked all reproductively active individuals captured within a limited part of the study area. We used implanted transmitters with a weight of about 2.5 g (5–8% of body weight). After surgery the animals were allowed to recover for 12–24 h before release.

Data were collected during two radio-tracking periods from a spring situation and two from a late summer/autumn situation. Spring data were collected from two different reproductive seasons, since the spring situation in this field vole population is very similar between years (Agrell *et al.* 1992). Autumn densities, on the other hand, show great intra-annual variation (Agrell *et al.* 1992). To obtain data on male spacing behaviour from comparable autumn situations, i.e. with similar male and female densities, we therefore performed two radio-tracking sessions within the same year. However, these sessions were separated by a four week interval and were carried out with different individuals in different parts of the study area (about 60 m apart). Since the turnover rate of adult field voles is very rapid (Agrell *et al.* 1992) and individuals are extremely philopatric (Sandell *et al.* 1991), we consider that this set-up ensured that possible effects of pseudoreplication were kept to a minimum. The spring periods were 4–18 May, 1986 and 7–15 May 1987. In 1986 five males were radio-marked and we took one position every hour 24 hours per day for 14 days (283 ± 79 [$x \pm S.D.$] positions per individual [one animal was predated after one week]). In May 1987 we took one position per hour 18 hours per day on six individuals for eight days (138 ± 0 positions per individual). The autumn studies were performed 13–27 August 1986 (six adult males) and 27 September–11 October 1986 (four adult males). During September–October 1986 we also radio-tracked three subadult males (body mass < 23 g) present in the study area, but these were not included in the statistical analyses. During both periods the animals were located every hour for 14 days (August: 313 ± 45 positions per individual, September: 333 ± 0 positions per individual). During radio-tracking the position of each animal was determined to the closest square meter. In this field vole population the reproductive season lasts from April to late October or early November (Nelson *et al.* 1991), and during all radio-tracking periods more than 50% of the adult females present in the study area were reproductively active (being pregnant and/or lactating).

Home range sizes were calculated as 95% minimum convex polygons. The 5% of positions that were deleted were the ones with highest harmonic mean distance to all other positions. For our tracking-data home range analysis with convex polygons resulted in less unused areas than did the harmonic mean method. Overlap between adjacent ranges was calculated from these 95% convex polygons. Daily ranges were calculated as 100% minimum convex polygons. As a measure of variance we used coefficient of variation (*c.v.*). For statistical analyses we used the Mann-Whitney *U*-test, two-tailed. There were no significant differences in any examined aspect between the two spring materials and no differences between the two autumn materials (Mann-Whitney *U*-test, $p > 0.10$ in all cases), so in the analyses data from each season were pooled.

To analyse the distribution of females in the area during the time when males were radio-tracked we calculated the average trapping coordinates (central position) for all females present. From parallel radio-tracking studies during 1986 and 1987 the average home range size of free ranging females during the spring and autumn periods was known to be 183 and 171 m^2, respectively (Sandell *et al.*, unpubl. results, see also Agrell 1995). For each period we then constructed a map of the female distribution by drawing circles with the average range area around the central position of each female. This observed distribution of females was then compared with 100 distributions were the central positions of the females had

been randomly located within the trapping area (see details in Agrell 1995). If the observed female overlap was either higher or lower than in all of the 100 random distributions, the observed female distribution was significantly different from a random distribution ($p < 0.01$).

We also analysed how female reproductive synchrony changed over the reproductive season in this field vole population. Data for this analysis were obtained during 1984–1985. Trapping was then performed in two weeks out of three in the study area. For each week of trapping we calculated the proportion of adult (> 23 g body weight) females that were pregnant. If the synchrony is high there should be a high variation between weeks in this measure, whereas a perfectly asynchronous pattern would give the same proportion pregnant females each week, and thereby a low variation (cf. Ims 1986). The degree of reproductive synchrony was estimated for a spring period (late April to early June) and an autumn period (late July to early September). The obtained estimates of reproductive synchrony, although crude, can be expected to be representative; in southern Scandinavia field vole density patterns are usually very similar between years (Hansson & Henttonen 1988), as are the seasonal changes in female reproductive patterns (Nelson *et al.* 1991).

Total density, estimated as the minimum number of animals alive, during the radio-tracking sessions in May were 30 and 34 individuals/ha for 1986 and 1987, respectively. During the autumn sessions in 1986 densities were 50 individuals/ha in August, whereas the corresponding figure for September–October was 59. Average densities (individuals per ha) of reproductive animals during radio-tracking were 9.5 females and 8.6 males in May 1986, 9.8 females and 10.0 males in May 1987, 28.3 females and 8.7 males in August 1986, and 31.3 females and 9.5 males in September–October 1986. Thus, male densities were about the same in both spring and autumn but female densities were 2–3 times higher in autumn. In this field vole population, sex ratio show great and irregular variation between years, as well as between seasons, although adult sex ratio is usually female biased when density is high (Erlinge, unpubl. data). We have no data on previous dispersal/residency for the radio-tracked individuals, but an extensive analyses on the field voles present in the study area during the years 1983–1986 have revealed that adult dispersal is extremely infrequent (Sandell *et al.* 1991). None of the radio-tracked individuals dispersed during the study.

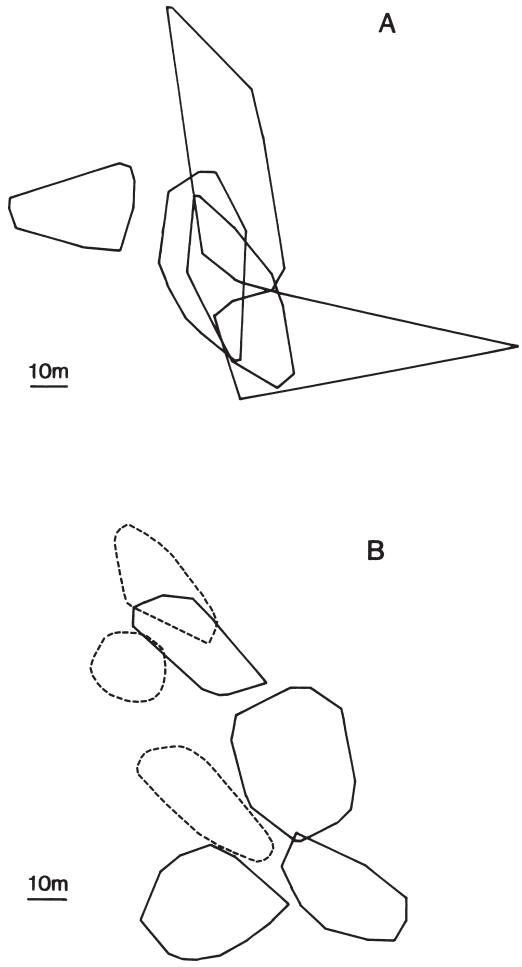

Fig. 1. Home ranges (95% convex polygons) of males in (A) May 1986 and (B) September 1986. Broken lines show ranges of subadult males. Home-ranges are calculated from intense radio-tracking data obtained during two weeks.

3. Results

There was a clear difference in male spacing behaviour and movement patterns between spring and autumn. Range sizes (95% convex polygons) were not significantly different between seasons, but there was a large difference in the degree of overlap between adjacent ranges. In spring male ranges overlapped on average 25%, whereas in autumn ranges were almost exclusive (Table 1, Fig. 1). The differences in movement patterns were pronounced. In spring males spent most of their time close to some resting places and made extended movements out in the surroundings. In autumn they moved constantly over their whole range. These patterns showed no differences in average daily range size (100% convex polygons), but the variance in daily range size (calculated as *c.v.*) differed significantly between seasons (Table 1). Also mean distance moved between consecutive telemetry positions and the variance (*c.v.*) in this measure were significantly different between spring and autumn (Table 1).

The limited radio-tracking data on the subadult males present during September 1986 ($n = 3$) were not possible to analyse statistically, but indicated that these individuals had comparably small ranges and moved in the periphery of the home-ranges of adult males (Fig. 1).

During the time when radiotracking of males was carried out the females present in the area showed a similar distribution; the males experienced an even distribution of females during both spring and autumn (difference from random distribution; $p < 0.01$ in all cases).

Analyses of the seasonal variation in female reproductive synchrony revealed differences between spring and autumn. During spring the *c.v.* was 59.5% (the proportion pregnant was 0.52 ± 0.31 [$x \pm S.D.$], $n = 10$, range 0.10–1.0) indicating a relatively high synchrony, whereas the autumn value was 27.0% (0.42 ± 0.11, $n = 10$, range 0.16–0.42), which suggests that the general pattern is that breeding is more asynchronous during autumn than during spring.

4. Discussion

Our extensive radio-telemetry data demonstrate a shift in male spacing behaviour over the reproductive season. This is in agreement with previously published trapping studies on microtines (e.g. Viitala 1977, Pusenius & Viitala 1993). Together, these results show that voles have an extremely flexible social behaviour, and suggest that much of the interspecific differences reported in the literature are conditional.

What factors promoted the shift in male spacing pattern during the breeding season? Ostfeld (1985, 1990) predicted overlapping ranges among male voles when females are evenly distributed (territorial), whereas exclusive ranges are expected when females are spatially clumped as a result of being nonterritorial. In this study the males experienced an even distribution of females during both spring and autumn, but female density was higher during autumn, which should make it possible for a male to include more females within a territory of a given size. It should be noted, though, that female field voles normally show a reversed seasonal shift in their spacing behaviour, i.e. have exclusive home ranges in spring, but more overlapping ranges in autumn (Agrell 1995). Consequently it is possible that the males in this study exhibited an autumn spacing behaviour primarily adapted to a system with overlapping female ranges, although the females within the area studied were overdispersed. If so, our data show agreement with Ostfeld's (1985, 1990) predictions. However, if the observed male spacing behaviour was adapted to the actual situation, which seems likely since microtine rodents quickly respond

Table 1. Differences between spring and autumn spacing and movement patterns of male field voles ($x \pm S.D$). Ranges within parentheses. Statistical comparisons are performed with Mann-Whitney *U*-test, two-tailed.

	Spring ($n = 11$)	Autumn ($n = 10$)	p
Range size (m^2) (95% convex polygons)	749 ± 358 (363–1460)	647 ± 264 (306–1074)	0.526
Overlap between adjacent ranges (%)	25.6 ± 23.4 (0–73.8)	4.8 ± 7.5 (0–23.8)	0.014
Daily ranges (m^2) (100% convex polygons)	260 ± 92 (136–399)	340 ± 140 (158–516)	0.181
Variance (*c.v.*) in daily range size (%)	106 ± 25 (72–160)	43 ± 19 (20–73)	< 0.001
Mean distance between subsequent positions (m)	4.1 ± 1.2 (2.8–7.0)	8.3 ± 1.9 (5.9–10.7)	< 0.001
Variance (*c.v.*) in distance between positions (%)	223 ± 27 (164–268)	105 ± 15 (87–124)	< 0.001

to changes in their social environment (Ostfeld 1986), then female density, and not female distribution, is the primary influential variable. This view also receive strong support from an experimental study on the field vole, which demonstrated that manipulations of female density caused shifts in male spacing behaviour, whereas manipulations of female distribution did not (Nelson 1995a).

What then is the influence of female reproductive synchrony? Ims (1987a) predicted a nonterritorial system when females are asynchronously receptive and a territorial system when females are synchronous. In this field vole population the reproductive synchrony of females was found to decrease over the reproductive season. This finding seems reliable since the potential for reproductive synchrony can be expected higher when reproduction is initiated and when all individuals belong to the same cohort (spring situation), than when reproduction has been going on for long and several female cohorts exist at the same time (autumn situation). We found male field voles to have a nonterritorial system during the part of the season when females were relatively synchronous (spring) and a territorial pattern when females had more asynchronous breeding (autumn), which goes directly against the predictions by Ims (1987a). The degree of breeding synchrony may nevertheless have influenced some aspects of male spacing behaviour. Movements were shorter and more irregular during spring than during autumn. Female synchrony is high during spring, which means that there will be periods when few or no females are receptive, which may cause reduced male activity. During autumn, on the other hand, there are almost always receptive females available, which could explain the high movement activity of males during this period. An alternative/additional explanation to these observations is that predation is more intense during spring than during autumn (Erlinge *et al.* 1983), and that male movements were influenced by the seasonal variation in predation (cf. Anderson 1986, Brown *et al.* 1988).

The observed changes in male spacing behaviour could not be fully predicted from any of the present hypotheses. One reason for this may be that factors other than the distribution of reproductive females changed during the season, e.g. sex ratio changed from around one female per male in spring to 2–5 females per male in autumn. The relative dominance between males had probably changed, e.g. from a situation in spring with overwintered males of about equal body size and status to an autumn situation with a male population consisting of individuals of unequal body size and dominance. Differences in spacing behaviour between male field voles of unequal dominance status have previously been demonstrated (Nelson 1995b). Also, in the present study data indicated that subadult males occupied small, peripherical ranges. Sex ratio and male dominance relations have been shown theoretically to have a large effect on the spacing pattern and mating system (Sandell & Liberg 1992), and a change in any of these factors may change the outcome as predicted by the spatial or temporal distribution of females alone.

To conclude, male field voles show a shift in spacing behaviour over the reproductive season. This study, together with others (Viitala 1977, Madison & McShea 1987, Ims 1987b, 1988, Ylönen *et al.* 1988, Wolff & Cicirello 1990, Lambin & Krebs 1991, Pusenius & Viitala 1993, Agrell 1995), demonstrates that small mammals have very flexible behaviours. Spacing patterns and mating systems are obviously not species-specific attributes, but instead conditional systems adapted to the current environmental conditions. In this study female density seemed to have a large influence on the resulting male spacing system. Animal mating systems are, however, complex phenomena influenced by many different factors. It therefore seems unlikely that predictive models can be developed from only one or two factors such as spatial or temporal distribution of receptive females, or female density. Other variables, like oestrous length, sex ratio, and dominance relations between males may change the outcome predicted by the spatial or temporal distribution of females (Sandell & Liberg 1992). Although single (or two) factor explanations may give some general correlations, which Ostfeld's (1985, 1990) hypothesis has made quite successfully, a more complete understanding will probably have to consider multifactorial models.

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