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Social organisation of the male field vole (*Microtus agrestis*): a case of transient territoriality?

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The social organisation of a population of *Microtus agrestis* was studied by trapping and radiotracking in southern England. There was no significant variation in male home-range size during the breeding season or between years but there was significant variation in core areas between years but not during the breeding season. There was no significant relationship with male density and core area size but there was a significant increase in home range size as density decreased. There were no significant correlations between home-range size and body mass. In both 1995 and 1996, there was an increase in mean exclusivity of core areas that coincided with an increase in nearest neighbour distances as the breeding season progressed suggesting a territorial social system. Male residency was transient and recruitment of female offspring influenced residency.

Introduction

Breeding systems of species are the outcome of reproductive strategies of individuals rather than evolved characteristics of species (Clutton-Brock 1989). In male microtines these are dependent on a number of factors including the spatial and temporal distribution of receptive females, which in turn depends on variation in resource distribution, predation pressures and male intra-sexual competition (Perrin 1971, Myllymäki 1977a, Ostfeld 1985, Ims, 1987, Pusenius and Viitala 1993a, Nelson 1995a, 1995b, Agrell *et al*. 1996).

This study sets out to examine the spacing behaviour and dynamics of male field voles over the breeding season in a population in southern England. Ostfeld (1985) proposed that male social organisation is determined by the spatial distribution of breeding females. If breeding females are clumped in distribution then males should exhibit territoriality, defending access to females and thus increase their reproductive success. In contrast if females are evenly distributed (territorial) or widely spaced then males should not be territorial.

Ims (1987) pointed out that the distribution of oestrus females varies both spatially and temporally. Breeding females are only receptive for short periods and often exhibit post partum oestrus (Myllymäki 1977a), which will influence the cost–benefit of territoriality. Ovulation and receptivity in the field vole are complex being influenced by social environment, for example, response to social cues such as contact with males as well as following coitus (Milligan 1974). Chitty (1957) and Milligan (1974) suggested that both short ovulatory cycles lasting between 3 and 4 days and a longer cycle of between 6 to

8 days may occur. Thus any synchrony is likely to be imprecise lasting over a period of two or three days. If females exhibit synchronous reproduction and are clumped in distribution then a territorial system should be the most effective system to defend females. However, if females attain oestrus asynchronously then males should only defend females for short periods whilst they are receptive to fertilisation which may lead to a breakdown in territoriality.

Agrell *et al*. (1996) noted that the changes in male spacing behaviour could not be fully predicted by synchrony and distribution of reproductive females and identified the involvement of other factors such as sex ratio and male dominance. In *Microtus agrestis* male home-ranges are generally larger than those of females and spacing behaviours have been shown to vary between sexes, cohorts, habitats, seasons and density (Myllymäki 1977b, Erlinge *et al*. 1990a, Pusenius & Viitala 1993a). Non-territorial systems operate outside the breeding season but both non-territoriality and territoriality have been reported in males over the breeding season (Perrin 1971, Viitala 1977, Myllymäki 1977a, Erlinge *et al*. 1990b, Pusenius & Viitala 1993a, 1993b, Agrell *et al*. 1996).

Methods

Study site

The study was carried out at Alice Holt Research Station in Hampshire, England (51°17´N, 0°84´W) between March 1994 and September 1996. Four trapping grids were established in an area of rough ungrazed grassland as part of a larger study that experimentally altered the food resource base by addition of fertiliser (Loughran 1999). Field cover was assessed monthly with minimum of 60% of the habitat having vegetation greater that 10 cm in height at the lowest point in early spring and varied seasonally. Habitat description and changes, field cover and food resource assessment that included biomass, protein, alkaloids and tannin assays are reported in Loughran (1999). *Holcus lanatus, Festuca rubra, Festuca rubra commutate* and *Festuca arundinacea* were common grass species on all study areas with patchy distribution of *Agrostis gigantea, Anthoxanthum odoratum, Dactylis glomerata, Deschampsia sespitose* and *Poa trivialis*.

Trapping

The dimensions of grids 1 and 2 were 32 × 36 m with 25 traps per grid and grids 3 and 4, 28 × 36 m with 20 traps per grid, with a minimum distance of 4 m between each of the grids. Voles were monitored by live trapping every 10 days using one Longworth trap placed at each trap station with an inter-trap station distance of 8 m. Traps were a permanent feature of the environment and were left out and locked open when not in use. Traps were moved after each trap check to a position 4 m. from the last in a square clockwise rotation around the main inter-trap station; this gives a better definition of trap revealed movement and reduces the 'trap position' effect (Stanford 1995). Each trapping period consisted of between 8 and 10 trap checks and generally lasted three days unless radiotracking was in progress, in which case the trapping period was extended to five days. Traps were only set during the day and were locked open during the night to minimise the risk to pups of lactating females detained in traps. They were baited with whole oats and contained hay bedding. Trap revealed home ranges were calculated using Minimum Convex Polygon analyses for each animal using the Ranges V program (Kenward & Hodder 1995). Each animal was individually marked using ear tags in both ears (Le Boulenge-Nguyen & Boulenge 1986). For each capture the following data were recorded: tag number, trap station, mass, sex, and breeding condition. Breeding condition was assessed by inspection of testes recording whether scrotal or abdominal. If an animal had scrotal testes then it was considered to be capable of breeding and considered non-breeding if testes were abdominal. Attainment of breeding condition in males occurred between January and March and was asynchronous. Vole numbers were estimated using Minimum Number Alive.

Telemetry

Radiotracking was carried out for one week every month during the breeding seasons of 1995 and 1996. Radiocollars (Biotrack Ltd., Wareham, Dorset) weighed approximately 2.5 g and had a battery life of approximately 14 days. Collars may interfere with movement and behaviour (Ostfeld 1986, Varty 1987, White & Garrett 1990, de Mendonça 1999 and references therein). To reduce these effects, 'dummy' collars consisting of a plastic tie coated with heat shrink tubing were applied to animals approximately 10 days prior to radiotracking so that they could get used to them. The weight of the collar may also have energetic considerations and the collars should not exceed 10% of body mass (White & Garrett 1990), but *see* Berteaux *et al*. (1996). This did not present any problems in selecting subjects with most breeding males attaining weights greater than 25 g. The application of collars usually caused some hair loss around the neck but no animal suffered any serious wounds or injury. Some animals had collars applied for extended periods (> 2 months), again with no noticeable injury.

Voles were tracked over a period of six to seven days. Collars were attached for approximately three days after which they were removed and attached to another group of subjects. A minimum of 30 fixes were recorded for each animal (Kenward & Hodder 1995). A maximum of seven animals were tracked at anyone time. The position of an animal may not be independent of its previous location, i.e. fixes may be autocorrelated, which may underestimate range size. White and Garrett (1990) described a general rule to determine statistical independence of observations and considers locations to be independent if enough time has elapsed for the animal to move from one end of its range to the other. Rooney *et al*. (1998) suggested that as short a time interval as possible between fixes should be used over an extended period of time for best estimation of range size. Fixes were taken at minimum time intervals of 30 minutes during the day, (between 07:00–19:00, no tracking was carried out at night) both the above criteria were satisfied. Each animal was located to an area 4 m^2 using paths worn between trap points and its location recorded as the centre of this square. One individual was radiotracked in different months but was treated as independent samples. Radiotracking was mainly carried out on grid 2 but on occasions overlapped onto other grids and data were pooled across grids. Range areas were calculated using Kernel analyses for each animal using the Ranges V program (Kenward & Hodder 1995). Kernel analyses were calculated using fix density and a 40 × 40 grid with a smoothing factor of 1 because this gave the most accurate picture of the fix data (Worton 1989). Core area was defined as the proportion of the home range, which is most heavily utilised, determined from utilisation distributions. Core areas were estimated from utilisation distributions by the change in area when outlying observations were excluded representing the peripheral areas of the ranges, which generally fell between 75% and 85% of the total range areas (Samuel *et al*. 1985). In this study, core areas were standardised at the 80% isopleth and home ranges were estimated using the 95% isopleth, to exclude exploratory sorties out of the range area.

Nearest neighbour analyses were conducted using the Ranges V program (mean distance to nearest neighbour = Σ[distance to nearest neighbours]/[number of individuals in study area]) (Kenward & Holder 1995). Calculation of standard error of mean distance and t values are similar to the standard normal deviate z-test (*see* Krebs 1999) but the length of the boundary is calculated as half mean nearest neighbour distances. Indices of aggregation (R) were calculated from the mean distance to nearest neighbour/expected distance to nearest neighbour (Krebs 1999). If the spatial pattern is random then $R = 1$. If animals are clumped in distribution the R approaches zero but if evenly distributed R approaches an upper limit of approximately 2.15. One way analyses of variance were used to test between fixed factors of month and year. Correlation analyses were used to examine home range and core areas with male numbers (MNA) and mass.

Results

Core and home range areas

Core areas (Kolmogorov-Smirnov: $Z = 0.95$, $p > 0.05$) and home ranges (Kolmogorov-Smirnov:

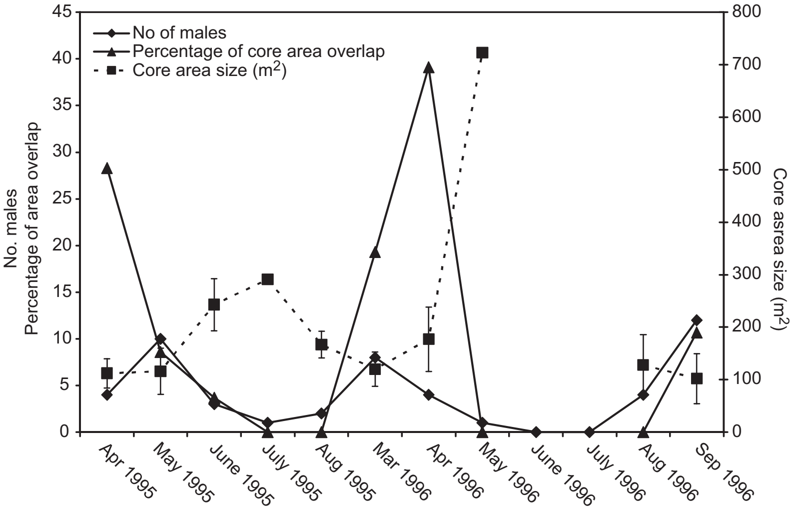

Fig. 1. The number of resident breeding males (MNA), mean and ±1 SE core area size and percentage mean overlap of core areas for males overlapping other males during the breeding seasons of 1995 and 1996. No radiotracking was conducted in June and July 1996 because of low densities.

$Z = 1.105$, $p > 0.05$) determined from radiotracking were not significantly different from normal distributions. There was no significant variation in male home-range size during the breeding season ($F_{6,22} = 2.05$, $p > 0.05$) or between years ($F_{1,27} = 3.37$, $p > 0.05$) but there was significant variation in core areas between years ($F_{1,27} = 4.84$, $p < 0.05$) but not during the breeding season ($F_{6,22} = 1.69$, $p > 0.05$) (Table 1). Trap-revealed home ranges gave comparable estimates to radiotracking homes ranges ($t = 1.69$, d.f. = 30, $p > 0.05$) but were dependent on the number of captures and significantly underestimated home range area if based on fewer than 5 captures ($t = 2.18$, d.f. = 8, $p < 0.05$). Variation in range size may be related to the density of males. Correlation analyses on core areas did not show a significant relationship with male density ($n = 10$, $r = -0.560$, $p > 0.05$) but when home ranges were examined there was a significant increase in home-range size as density decreased ($n = 10$, $r = -0.635$, $p = 0.048$). Range size may also be influenced by weight that may give an indication of dominance but there were no significant correlations for home range size ($n = 36$, $r = 0.095$, $p > 0.05$) or core areas ($n = 36$, $r = 0.049$, $p > 0.05$).

Table 1. Mean home range and core area estimates for male voles (CV = coefficient of variation). Data pooled for months within years.

Year			*n*	Mean area (m^2)	CV (%)
1995					
	Core	Radiotracking	15	159	59
	Range	Radiotracking	15	305	59
	Range	Trap revealed	14	211	78
1996					
	Core	Radiotracking	21	157	103
	Range	Radiotracking	21	259	91
	Range	Trap revealed	15	169	83

Social organisation

In both 1995 and 1996, as the breeding seasons progressed there was a increase in mean exclusivity of core areas which suggests a territorial system was maintained during most of the breeding season, but the low densities during both summers make interpretation difficult (Figs. 1 and 2). Nearest neighbour distances also tended to increase as the breeding season progressed which coincided with a decrease in density of males in 1995 (Table 2). At the start of the breeding season there was a greater degree of overlap in core areas although some males were territorial and this was related to female distribution (Fig. 2 and Table 3). The indices of aggregation were consistent with a random distribution with a tendency to increase towards an even distribution and reflect changes in social organisation with an increase in territoriality in males as the breeding season progressed. In 1996 there was a similar pattern with male mean distances increas-

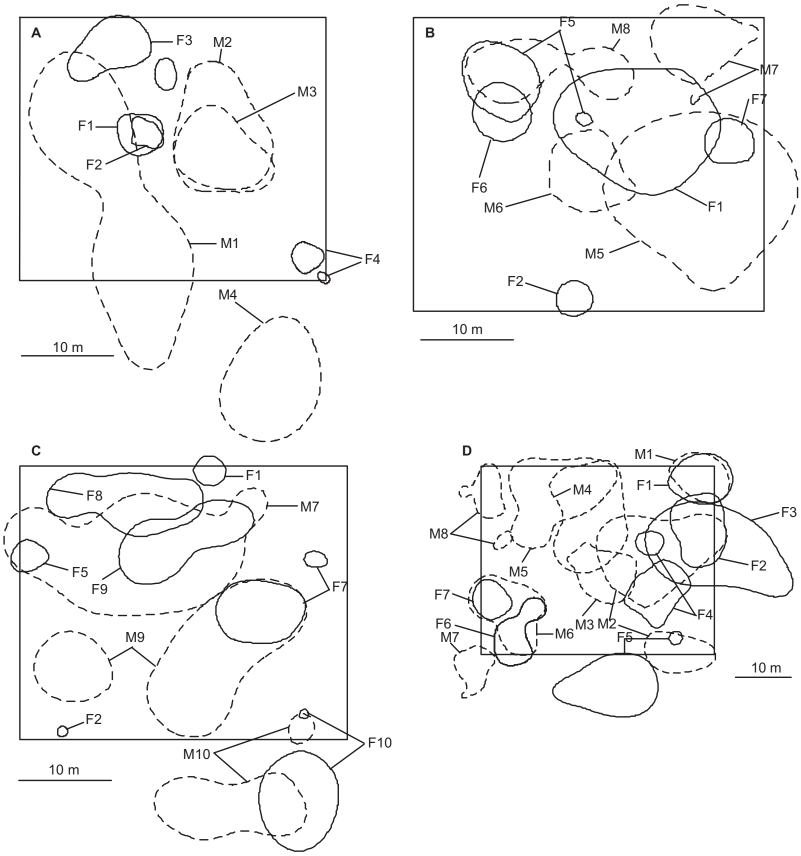

Fig. 2. Kernel analyses of core areas (80% isopleth) calculated from radiotracking data of males (dashed lines) and females (solid lines) in (**A**) April 1995, (**B**) May 1995, (**C**) June 1995 and (**D**) March 1996.

ing over the spring. At lower densities, aggregation indices were generally not significant from random distributions. Distances were greatest in August which is thought to be associated with low density of animals. However, mean distances declined markedly during September although males showed little overlap of core areas suggesting territoriality was still operating. Mean male nearest neighbour distances showed significant negative correlations with adult male density ($r = –0.808$, $n = 7$, $p = 0.028$).

Female home ranges (95% isopleth) tended to be overlapped by more than one male home range (n = 15, mean number of overlaps per

Table 2. Nearest neighbour analyses showing mean distance, expected distance and aggregation indices for males. Standard error of mean distance and *t* values shown. Distributions significantly deviating from a random distributions indicated with an asterisk.

	n	Mean distance (m)	Expected distance (m)	SE	Index of aggregation	*t*
1995						
April	4	14.83	10.05	3.22	1.47	1.48
May	4	16.34	10.05	3.22	1.63	1.95
June	3	18.66	12.21	4.46	1.53	1.45
1996						
March	8	13.05	6.55	1.48	1.99	4.38*
April	4	19.90	14.48	4.70	1.37	1.15
August	4	20.19	14.53	3.29	1.39	1.72
September	6	12.33	9.45	2.15	1.30	1.34

female = 2.1, SE = 0.24). Male residency changed over the summer of 1995 on grids 1 and 2. Males disappeared after 5–6 weeks which in terms of female reproduction equates with approximately two breeding events (Table 4). This coincided with recruitment of young females and may indicate that breeding male residency is dependent on the 'female environment'. A different pattern was found on grids 3 and 4 where male residency extended for a longer period where there was little change in the female composition of the population. Recruitment was male biased on these grids and would serve to increase intra-sexual competition but there was no female recruitment and no dispersal of overlapping breeding males from these grids. Female recruitment occurred in May that was accompanied by a subsequent change in overlapping males. It was not possible to follow these dynamics past June 1995 and during the early part of the breeding season of 1996 due to disruption by weasel predation.

Discussion

Male home range size was stable over the breeding season and between years but there was a

Table 3. Mean core area estimates and mean exclusivity of male voles core areas (proportion of core area not overlapped by another male) by month (CV = coefficient of variation).

	Number of males	Number of overlapping pairs	Mean core area (m^2)	CV(%)	Mean exclusivity (%)
1995					
April	4	1	112	50	63
May	4	1	116	85	90
June	3	1	243	35	95
July	1	0	291	–	100
August	2	0	167	22	100
1996					
March	8	4	120	72	80
April	4	1	177	69	69
May	1	0	723	–	100
August	4	0	128	91	100
Sepember	6	2	120	105	87

Table 4. Examples of differential social dynamics on grids from March to July 1995. Time periods represent 14 days. Cohort (*C*) set in italics.

Date	Grids 1 and 2		Grids 3 and 4	
	Females	Males	Females	Males
18 Mar. 2005	Onset of breeding		Onset of breeding	
1 Apr. 1995	Pregnancies	Stable associations *C1*	Pregnancies	Stable associations *C1*
15 Apr. 1995	Births — lactation *C2*	Stable associations *C1*	Births — lactation *C2*	Stable associations *C1*
30 Apr. 1995	Pregnancies /lactation	Stable associations *C1* Unstable associations *C2*	Pregnancies	Stable associations *C1*
13 May 1995	Recruit females Births — lactation *C3*	*C1* disperse/range shift Stable associations *C2*	Births — lactation *C3*	Stable associations *C1*, increase in males
24 May 1995	Pregnancies /lactation	Stable associations *C2* Unstable associations *C3*	Recruit females Pregnancies/lactation	Stable associations *C1* Unstable associations *C2*
10 June 1995	Recruit females Births — lactation *C4*	*C2* disperse/range shift Stable associations *C3*	Births — lactation *C4*	*C1* disperse/range shift Stable associations *C2*
24 June 1995	Pregnancies /lactation	Stable associations *C3*	Pregnancies /lactation	Stable associations *C2*
8 July 1995		Predation	Births — lactation *C5*	Stable associations *C2*

significant inverse linear relationship with density. At low densities males may increase range size to incorporate other female ranges or search for new females at low cost in respect of competitive interactions. Erlinge *et al.* (1990a) demonstrated an increase in range size in response to low density which has also been recorded for *M. californicus* (Ostfeld 1986, Heske 1987). Nelson (1995a) found a relationship between male home-range size and body weight, which was suggested to be associated with competitive ability, but no such relationships were evident in this study. Ranges sizes were comparable with those given by Nelson (1995a, 1995b) for radiotracking although these were conducted in enclosures, but when compared to trapping estimates, range sizes were smaller (Myllymäki 1977a).

Some males were non-territorial at the beginning of the breeding season in both years, overlapping other males but no females. At the same time, a few could be considered to have been territorial and these overlapped females. Female distribution was variable at this time with some females being clumped but others were more evenly distributed. Female reproduction was asynchronous (Loughran 1999) which would predict a non-territorial system according to Ims (1987). The distribution of males at this time would be more consistent with a dominance hierarchy and the majority of initial breeding males would have been familiar having overwintered in the same area (Loughran 1999). The patterns of distribution at the beginning of the breeding season do not support Ims (1987) hypothesis that territoriality in males was determined by synchrony in female receptivity, although male spacing appeared to have been influenced by the distribution of females and was dominated by a few males and supports Ostfeld's hypothesis (1985, 1990).

Studies demonstrating that male spacing behaviour and social organisation are influenced by female distribution have used caged females which may not accurately reflect natural dynamics (Ims 1988, Nelson 1995a, 1995b). Nelson (1995a) manipulated female density and distribution and found that at low density there was a high degree of overlap among males and concluded that male spacing behaviour was influenced by female density. At low density, if females are clumped as they were in April 1995, then a high degree of overlap due to competition might be expected according to Nelson (1995a). However, this was not the case with one male monopolising overlap. A similar situation was evident in March 1996 although the density was higher suggesting that there were large variations in individual competitive abilities among males. Thus, spacing behaviour of females appears to be important and may also influence distribution and residency in males but asymmetrical intrasexual competition may also be important.

After the first waves of reproduction a territorial social organisation was maintained. A change from non-territoriality to territoriality occurred when the resident males changed. New males were immigrants and were likely to have been unfamiliar. Generally the degree of wounding among males was low and this may be associated with avoidance strategies. Females were only territorial whilst lactating; at this time their core areas were small (Loughran 2006). Male ranges were larger than females which would allow territorial males to overlap a number of lactating females, the pattern observed in this study. However these data would also fit the resource-defence polygyny model for 'stayers' of Sandell and Liberg (1992) in which a system of males with non-overlapping ranges maximise the number of females within their home range as opposed to the second strategy, to 'roam' or scramble competition polygyny.

I consider that familiarity (length of temporal and spatial associations) and intra-sexual competition are both important in males in determining space use, particularly at the beginning of the breeding season. This will lead to a social dominance hierarchy at beginning of the breeding season, and territoriality later in the breeding season when the length of associations shorten, but this will also be influenced by female distribution rather than asynchrony in female reproduction.

Of note in this study were the dynamics in 1995 in respect to male residency. Distinct changes in male residency appeared to coincide with recruitment of young females into the breeding population. Patterns of overlap found in this study revealed that females were overlapped by a number of males which was particularly evident when females were perforate and suggests a polygynous or promiscuous mating system (Myllymäki 1977a, Cockburn 1988, David-Gray 1996). In polygynous or promiscuous mating systems assessment of relatedness may utilise proximate cues where offspring mature within or near their natal range (Myllymäki 1977b, Sandell *et al.* 1990). Kin discrimination in males appears to be associated with location and female associations (Wolff & Cicirello 1989, Cicirello & Wolff 1990) but may dissipate rapidly if not reinforced (Lambin & Mathers 1997). If males adjacent to or overlap the home range of a female they have copulated with, they may behave amicably or neutrally towards young appearing in their home range (Wolff & Cicirello 1989, Wolff & Cicirello 1991). If space is available, female offspring often remain close to or overlapping their natal range (Sandell *et al.* 1990, Viitala *et al.* 1994). Generally outbreeding systems are considered to occur in mammalian systems (Greenwood 1980, Moore & Ali 1984, Bollinger *et al.* 1993) and this appears to be the case *in M. agrestis* (Frykman 1988, David-Gray 1995). Natal dispersal is male biased in field voles with a higher percentage of females being philopatric (Myllymäki 1977b, Sandell *et al.* 1990). Therefore young females entering the population will be at risk of inbreeding and/or competition with resident adults and should disperse (Trivers 1974, Emlen & Oring 1977, Emlen 1995). Young females entering the population may use familiarity as a basis for discriminating kin in respect of overlapping males, and *vice versa,* males may use location or association to distinguish possible offspring. This factor has the potential to influence range shifts or dispersal in breeding males as access breeding females may be compromised by recruitment of female offspring into the breeding population if outbreeding is maintained. In the early part of the breeding season, if space was available then recruitment of young females occurred and male residency changed with dispersal of breeding males. However this may only be applicable to the early part of the breeding season when young matured rapidly into the breeding population. Clutton-Brock (1989) noted that, if females form kin groups, then the average tenure of reproductive males in particular groups was generally less than the average age of females at first breeding. If females disperse, average male tenure usually exceeds the age of females at first breeding and is thought to be associated with minimising inbreeding. During the latter part of the breeding season maturation rates were slower which may affect these dynamics and Pusenius *et al.* (1998) found the number of young breeding females in kin clusters decreased as the breeding season progressed. Viitala *et al.* (1994) looked at dispersal in field voles and found that females matured on their natal range and dispersed when breeding (pregnant) after approximately two months. However, they suggest inbreeding may occur among some females with resident dominant males. These patterns require further investigation but may be important in elucidating some of the social mechanisms which occur in field vole populations.

From a female perspective, a polygnous mating strategy may be advantageous. If overlapping males are stable over one or more breeding events, then risks of infanticide from males may be reduced by copulation (Wolff & Cicirello 1989, Cicirello & Wolff 1990). Female choice may also be a factor affecting social environment for males. However, genetic quality of a mate would be unlikely to have substantial genetic advantages unless there are large heritable differences in fitness among males, for which there is no evidence among microtines (Boonstra & Boag 1987).

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References

Agrell, J., Erlinge, S., Nelson, J. & Sandell, M. 1996: Shifting spacing behaviour of male field voles (*Microtus agrestis*) over the reproductive season. — *Ann. Zool. Fennici* 33: 243–248.

Berteaux, D., Masseboeuf, F., Bonzom, J., Bergeron, J., Thomas, D. W. & Lapierre, H. 1996: Effect of carrying a radiocollar on expenditure of energy by meadow voles. — *J. Mamm.* 77: 359–363.

Bollinger, E. K., Harper, S. J. & Barrett, G. W. 1993: Inbreeding avoidance increases dispersal movements of the meadow vole. — *Ecology* 74: 1153–1156.

Boonstra, R. & Boag, P. T. 1987: A test of the Chitty hypothesis: inheritance of life-history traits in meadow voles *Microtus pennsylvanicus*. — *Evolution* 41: 929–947

Chitty, H. 1957: The oestrus cycle and gestation period in lactating field voles, *Microtus agrestis*. — *Journal of Endocrinology* 15: 279–283.

Cicirello, D. M. & Wolff, J. O. 1990: The effects of mating on infanticide and pup discrimination in white-footed mice. — *Behav. Ecol. Sociobiol.* 26: 275–280.

Clutton-Brock, T. H. 1989: Mammalian mating systems. — *Proc. R. Soc. Lond. B* 236: 339–372.

Cockburn, A. 1988: *Social behaviour in fluctuating populations*. — Croom Helm Ltd., London.

David-Gray, Z. 1995: *The application of DNA fingerprinting to the study of mating strategies*. — Ph.D. thesis, London University.

de Mendonça, P. G. 1999: Impact of radio-collars on yellow-necked mice, *Apodemus flavicolis* (Mammalia, Rodentia). — *Mammal Review* 29: 129–134.

Emlen, S. T. & Oring, L. W. 1977: Ecology, sexual selection and evolution of mating systems. — *Science* 179: 215–233.

Emlen, S. T. 1995: An evolutionary theory of the family. — *Proceedings of the National Academy of Sciences* 92: 8092–8099.

Erlinge, S., Hoogenboom, I., Agrell, J., Nelson, J. & Sandell, M. 1990a: Density-related home range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. — *J. Mamm.* 71: 597–603.

Erlinge, S., Agrell, J., Nelson, J. & Sandell, M. 1990b: Social organisation and population dynamics in *Microtus agrestis* populations. — In: Tamarin, R. H., Ostfeld, R. S., Pugh, S. R. & Bujalska, G. (eds.), *Social systems and population cycles in voles*: 45–58. Advances in Life Sciences, Birkhäuser Verlag, Basel, Switzerland.

Frykman, I. 1988: Breeding structure in two field vole populations. — *Hereditas* 108: 41–46.

Greenwood, P. J. 1980: Mating systems, philopatry and dispersal in birds and mammals. — *Anim. Behav.* 28: 1140–1162.

Heske, E. J. 1987: Spatial structuring and dispersal in a high density population of the Californian vole *Microtus californicus*. — *Holoarctic Ecol.* 10: 137–148.

Ims, R. A. 1987: Male spacing systems in microtine rodents. — *Am. Nat.* 130: 475–484.

Ims, R. A. 1988: Spatial clumping of sexually receptive females induces space sharing among male voles. — *Nature* 335: 541–543.

Kenward, R. E. & Hodder, K. H. 1995: *Ranges V: an analysis system for biological location data.* — Institute for Terrestrial Ecology, Dorset, UK.

Krebs C. J. 1999. *Ecological methodology*, 2nd ed. — Benjamin/Cummings, Menlo Park, California.

Lambin, X. & Mathers, C. 1997: Dissipation of kin discrimination in Orkney voles, *Microtus arvalis orcadensis*: a laboratory study. — *Ann. Zool. Fennici* 34: 23 – 30.

Le Boulenge-Nguyen, P. Y. & Le Boulenge, E. 1986: A new ear-tag for small mammals. — *J. Zool.* 209: 302–304.

Loughran, M. F. E. 1999: *A study of the demography and social organisation of the field vole, Microtus agrestis, in relation to food resources.* — Ph.D. thesis, London University.

Loughran, M. F. E. 2006: Social organisation of the field vole *Microtus agrestis* in a population in Southern England. — *Acta Theriol.* 51: 233-242.

Milligan, S. R. 1974: Social environment and ovulation in the vole, *Microtus agrestis*. — *Journal of Reproduction and Fertility* 41: 35–47.

Moore, J. & Ali, R. 1984: Are dispersal and inbreeding avoidance related? — *Anim. Behav.* 32: 94–112.

Myllymäki, A. 1977a: Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. — *Oikos* 29: 468–493.

Myllymäki, A. 1977b: Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. — *Oikos* 29: 553–569.

Nelson, J. 1995a: Determinants of male spacing behaviour in microtines: an experimental manipulation of female spatial distribution and density. — *Behav. Ecol. Sociobiol.* 37: 217–223.

Nelson, J. 1995b: Intrasexual competition and spacing behaviour in the male field vole *Microtus agrestis* under constant female density and spatial distribution. — *Oikos* 73: 9–14.

Ostfeld, R. S. 1985: Limiting resources and territoriality in microtine rodents. — *Am. Nat.* 126: 1–15.

Ostfeld, R. S. 1986: Territoriality and mating system of Californian voles. — *J. Anim. Ecol.* 55: 691–706.

Ostfeld, R. S. 1990: The ecology of territoriality in small mammals. — *Trends Ecol. Evol.* 5: 411–415.

Perrin, M. R. 1971: *Exploratory behaviour as related to trapping results and population estimation in the vole Microtus agrestis hirtus.* — Ph.D. thesis, University of Exeter.

Pusenius, J. & Viitala, J. 1993a: Varying spacing behaviour of breeding field voles, *Microtus agrestis*. — *Ann. Zool. Fennici* 30: 143–152.

Pusenius, J. & Viitala, J. 1993b: Demography and regulation of breeding density in the field vole *Microtus agrestis*. — *Ann. Zool. Fennici* 30: 133–142.

Pusenius, J., Viitala, J., Marienberg, T. & Ritvanen, S. 1998: Matrilineal kin clusters and their effect on reproductive success in the field vole *Microtus agrestis*. — *Behav. Ecol.* 9: 85 – 92.

Rooney, S. M., Wolfe, A. & Hayden, T. J. 1998: Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. — *Mammal Review* 28: 89–98.

Samuel, M. D., Pierce, D. J. & Garton, E. O. 1985: Identifying areas of concentrated use within the home range. — *J. Anim. Ecol.* 54: 711–719.

Sandell. M., Agrell, J., Erlinge, S. & Nelson, J. 1990: Natal dispersal in relation to population density and sex ratio in the field vole *Microtus agrestis*. — *Oecologia* 83: 145–149.

Sandell, M. & Liberg, O. 1992: Roamers and stayers: a model on male mating tactics and mating systems. — *Am. Nat.* 139: 177–189.

Stanford, W. 1995: The influence of female social behaviour on the population dynamics of the field vole *Microtus* *agrestis*. — Ph.D. thesis, London University.

Trivers, R. L. 1974: Parent offspring conflict. — *Am. Zool.* 14: 249–264.

Varty, N. 1987: *A study of range and activity in the short tailed vole (Microtus agrestis) by live trapping and telemetry*. — Ph.D. thesis, London University.

Viitala, J. 1977: Social organisation in cyclic sub arctic populations of the voles *Clethrionomys rufocanus* and *Microtus agrestis*. — *Ann. Zool. Fennici* 14: 53–93.

Viitala, J., Hakkarainen, H. & Ylönen, H. 1994: Different dispersal in *Clethrionomys* and *Microtus*. — *Ann. Zool. Fennici* 31: 411–415.

White, G. C. & Garrott, R. A. 1990: *Analysis of wildlife radiotracking data*. — Academic Press, Inc., San Diego, California.

Wolff, J. O. & Cicirello, D. M. 1989: Field evidence for sexual selection and resource competition infanticide in white footed mice. — *Anim. Behav.* 38: 637–642.

Wolff, J. O. & Cicirello, D. M. 1991: Comparative paternal and infanticidal behaviour of sympatric white footed mice (*Peromyscus leucopus noveboracensis*) and deermice (*Peromyscus maniculatus nubiterrae*). — *Behav. Ecol.* 2: 38–45.

Worton B. J. 1989: Kernel methods for estimating the utilisation distribution in home range studies. — *Ecology* 70: 164–168.