

# Effects of habitat patchiness and connectivity on the spatial ecology of the root vole *Microtus oeconomus*

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## Summary

1. The effect of habitat patchiness and connectivity on dispersal distances and spatial aggregation of individuals is investigated in 12 enclosed populations of the root vole, *Microtus oeconomus*, employing a factorial experimental design with three different patch configurations and two distinct geographical root vole strains. The three patch configurations, all with an identical total area, were: two large patches, six small patches and six small patches connected by corridors.

2. The populations were followed for three generations (13 weeks) using live-trapping. Matrilineal relationships, time and place of birth, and weekly home ranges were established for the 1155 individuals in the study.

3. Smaller patch sizes enhanced dispersal, but most for one of the strains. The strain difference is, tentatively, explained by inbreeding avoidance which is known to differ between the strains.

4. The effect of habitat configuration on the dispersion pattern was similar for the two strains. Increased patchiness increased the aggregation of individuals. The two sexes diverged in their response, however, females being more aggregated than males.

5. The spatial pattern of matrilinearity was used as an indication of the resulting effect of habitat configuration on the demic structure in space. Patchiness enhanced and connectivity decreased the substructuring.

*Key-words:* dispersal, aggregation, habitat fragmentation, fission and fusion response, movement corridors, spatial statistics.

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## Introduction

Habitat patchiness is believed to affect most aspects of the biology of a population. Allee effects (Dennis 1989; Burgman, Ferson & Akçakaya 1993), population size and effective population size (Chesson 1981; Boecklen 1986; Lande & Barrowclough 1987; Fahrig & Paloheimo 1988; Pearman & Wilbur 1990; Foster & Gaines 1991; La Polla & Barrett 1993; Diffendorfer, Gaines & Holt 1995), intraspecific competition (Rennau 1991; Bjørnstad & Hansen 1993), immigration/emigration rates (Stamps, Buechner & Krishnan 1987), stability of the dynamics (De Jong 1979; Hassell 1980; Hassell, Comins & May 1991; Kareiva 1990), and, ultimately, extinction rates (Levins 1970; Soulé 1986, 1987; Burgman, Akçakaya & Loew 1988; Burkey 1989; Gilpin & Hanski 1991; Burgman *et al.* 1993) have all been postulated to be functions of habitat patchiness. Much current scientific focus on these issues is centred around the process

of habitat fragmentation by which human-induced disturbances result in smaller, more isolated and 'hard-edged' patches surrounded by a hostile matrix. One fundamental process underlying the demographic and genetic implications of habitat fragmentation is altered spatial pattern of the individuals (dispersion pattern) comprising the population. The change in dispersion is brought about through alterations of the dispersal distance distribution. Two distinct aspects of the fragmentation–dispersal–dispersion relation may lead to reduced population viability.

1. Habitat fragmentation may generate aggregated dispersion patterns if dispersal is restricted. The aggregation may lead to enhanced competition in patches of high density and to inefficient resource utilization in patches of low density. As a result, the overall productivity of the population is diminished.

2. The lowered rates and distances of dispersal may result in a more structured pattern of genes in space. This may, in turn, lead to reduced effective population sizes and elevated levels of inbreeding and genetic drift.

There is a high degree of species-specificity in responses to habitat fragmentation and patchiness (Verboom & van Apeldoorn 1990; Wiens 1990; Opdam 1991; Tschardtke 1992; Ims, Rolstad & Wegge 1993; Wiens *et al.* 1993). The effect for any given species depends on the scale of the fragmentation relative to the 'scale of the individual organism' (Wiens 1989). Differential responses to small-scale fragmentation (fragment sizes close to the size of individual home ranges) may be caused by differences in behavioural mechanisms determining the space use and movement patterns of the individuals (see Ims 1995 for a review). Two different responses with respect to dispersal are conceivable (Ims *et al.* 1993). A 'fission response' is when increased fragmentation leads to increased dispersal frequencies and distances. Conversely, a 'fusion response' to fragmentation is when dispersal is reduced with increasing fragmentation.

The effects of habitat fragmentation on dispersal and aggregation patterns are addressed in the present study using an experimental approach combined with statistical modelling. Twelve experimental populations of two geographical strains of the root vole, *Microtus oeconomus* Pallas, which are known to differ in their social organization (Ims *et al.* 1993; Ims 1994; Aars, Andreassen & Ims 1995), were subjected to varying degrees of habitat fragmentation and patch connectivity at a scale suspected to affect space use and dispersal (Ims *et al.* 1993). The effect of degree of fragmentation was studied by keeping the total habitable area constant while subdividing it either into two large or six small patches (cf. Quinn & Hastings 1987; Burgman *et al.* 1988; Forney & Gilpin 1988; Gilpin 1988; Burkey 1989). The effect of connectivity was investigated by connecting habitat patches by corridors (Simberloff & Cox 1987; Harrison 1992; Hobbs 1992; Inglis & Underwood 1992). Three interrelated topics pertaining to the spatial ecology of root vole populations in fragmented habitats were investigated in this setting. The first relates to *dispersal distances*: what are the effects of patch size and patch connectivity on dispersal, and are such effects sex or strain specific? The other two topics pertain to the manifestations of dispersal and other spacing behaviours on the spatial structuring of the populations: *dispersion pattern*—what are the effects of patch size and patch connectivity on aggregation of individuals? *spatial patterns of relatedness*—are there consistent treatment effects on aggregation of relatives in space at the scale of this experiment? The last question is particularly relevant for *Microtus* populations, as matrilineal structuring has been invoked as a key factor in population regulation (Lambin, Krebs & Scott 1992; Lambin 1994).

Apart from a few attempts to predict social organization in patchy habitats (Ostfeld 1992; Ims *et al.* 1993) the scientific study of the interactions between individual movement/settlement decisions and spatial

structures is still in its infancy (Ims 1995; Lima & Zollner 1996; Ims & Yoccoz 1997). Hence, we prefer at this stage to pose these rather open questions. In this sense, our experiment may be viewed as exploratory, providing information from which more specific experiments addressing mechanistic relations may be designed.

## Material and methods

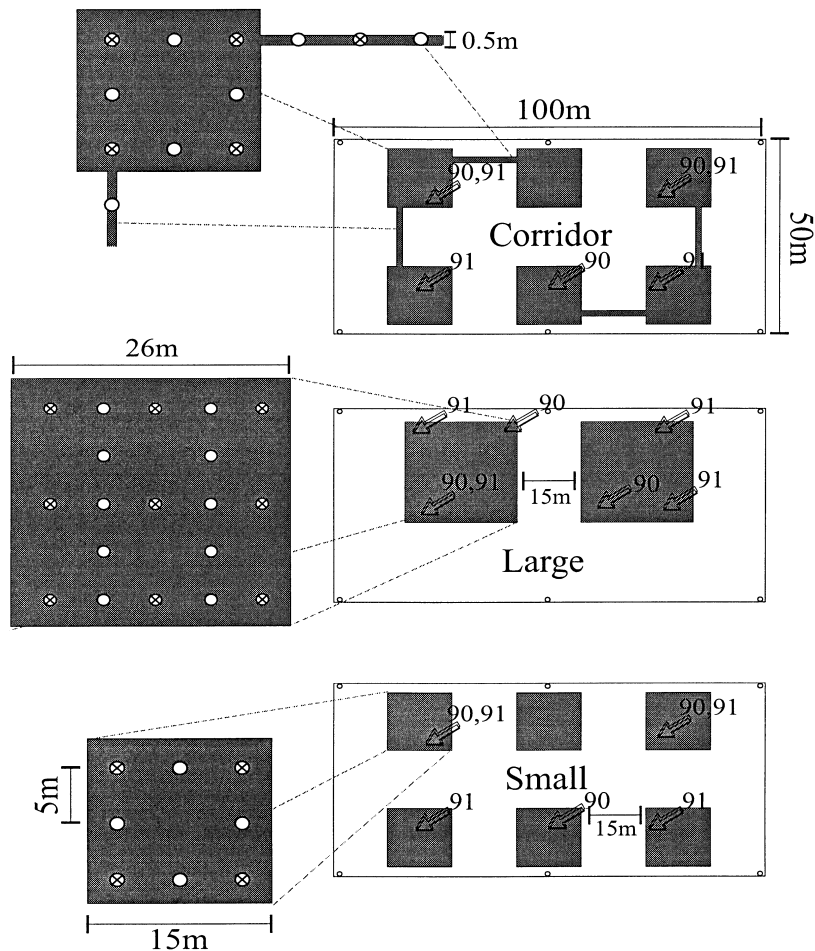
### EXPERIMENTAL PLOTS AND STUDY PERIOD

The experiment was carried out in 1990 and 1991 at Evenstad Research Station as part of the Evenstad Project (Ims *et al.* 1993; Aars *et al.* 1995). Each year six 0.5-ha vole-proof enclosures of meadow habitat (hereafter termed experimental plots) harboured six root vole populations. The 'vole fences' consisted of 1-m wide steel sheets sunk 0.4 m into the ground. All experimental plots were sown with a mixture of *Phleum pratense* L., *Festuca pratensis* Huds., *Agrostis capillaris* L., and *Trifolium pratense* L. seeds, to make the vegetation homogeneous across patches and plots. The plots were thoroughly fertilized every spring to even out possible differences in nutrient levels and to prolong the growth season for the vegetation and the reproductive season for voles (Aars *et al.* 1995).

The plots were experimentally manipulated to yield replicates of three different habitat configurations in both years (Fig. 1). The manipulation was carried out by keeping parts in a lawn-like fashion (height of grass < 5 cm) by mowing throughout the experimental periods. This lawn-like matrix was not included in the home ranges of the root vole (Ims *et al.* 1993). The remaining parts were left to grow freely, forming the habitable area and the habitat fragments (Ims *et al.* 1993). The sum of habitable area was 1350 m<sup>2</sup> in all plots. The experimental area was enclosed by a chicken-wire fence (1.5 m high, sunk 0.2 m into the ground, and with an electric wire along the top) to exclude mammalian predators. Avian predators had free access.

The experiments commenced in early July both years (1 and 4 July, respectively) with the release of animals. Live trapping took place on a regular basis every week until mid-October. To avoid inclusion of artificial behaviour of animals shortly after the release, the first week has been omitted from the analysis. Hence, the study period considered here consists of 13 weeks, which corresponds to three generations of root voles.

The two main experimental factors were habitat configuration (three levels) and geographical origin of the populations (two levels). The levels of habitat configuration were (Fig. 1): two large patches (called 'Large' in the text below); six small patches of which three and three were connected by 0.5-m wide corridors ('Corridor'); and six small isolated patches ('Small'). The levels of geographical origin (termed



**Fig. 1.** The three types of experimental enclosures: 'Corridor', 'Small' and 'Large'. Open circles represent Uggjan traps and circles with crosses represents Uggjan traps and pitfall traps. Note the six Uggjan traps along the fences of each enclosure (edge traps). The arrows indicate the release points of the introduced mothers with litters (matrilines) in the two years (1990 and 1991). Dark-shaded areas are habitable meadow vegetation. The light matrix represents the non-habitable transit areas. Vole-proof fences surround each enclosure. The whole experimental area is surrounded by a predator fence.

'strain' hereafter) were 'Northern' (from Pasvik Valley, Finnmark County, Northern Norway, 69°15'N, 29°25'E, Alt. 100 m) and 'Southern' (from Valdres, Oppland County, Southern Norway, 60°45'N, 9°30'E, Alt. 800 m). The six treatment combinations were replicated twice in time (years: 1990 and 1991). To correct for interannual variation, year was included as an additional (fixed) effect in the analyses. Each plot received a different treatment combination in the 2 years. The experimental and statistical unit was the population (except for the analysis of dispersal distances; see below).

#### STUDY ANIMALS AND CAPTURE REGIME

Each population was established by releasing three or four family groups (matrilines) in each plot (1990: three matrilines; 1991: four matrilines). Each matriline consisted, at the time of release, of one female with her newly weaned litter (age: 16 days) raised in the laboratory. All family groups in a population belonged to the same strain (Northern and Southern), but were selected to maximize within-population gen-

etic variability (as judged by laboratory pedigrees) subject to this constraint. The release points were selected to maximize initial spatial distance between matrilines (Fig. 1).

The two strains have been shown to have distinct characteristics with respect to social behaviour (Santos, Andreassen & Ims 1995; Ims 1997), body size (Ims 1997), sex allocation (Ims 1994; Aars *et al.* 1995) and genetic diversity (Stacy *et al.* 1994). However, both strains exhibit 4-year population cycles and similar habitat requirements in the wild (Wikan 1972; Brekke & Selboe 1983). They are also similar in seasonal timing of reproduction on the experimental plots (Aars *et al.* 1995). In particular, reproduction, sexual maturation and natal dispersal extend into late October in these fertilized meadow plots (Johannesen & Ims 1996), that is, to the end of the experimental period.

Uggjan and pitfall traps activated 2 days per week were dispersed at 5 m intervals throughout the habitable areas of the experimental plots (Fig. 1) to ensure high capture rates and that young animals were caught shortly after weaning (16 days) (Aars *et al.* 1995). In

in addition, six Ugglan traps were placed at 50-m intervals in the mowed area along the fences (edge traps). These traps were kept activated every night throughout the study period so that frustrated emigrants were repeatedly captured in the edge traps (Aars *et al.* 1995; Johannesen & Ims 1996), and could be removed to prevent 'fence effects' (Krebs, Keller & Tamarin 1969; Ostfeld 1994). None of the populations reached abnormally high densities (Fig. 2). Upon capture of an animal, location (on a  $10 \times 20$  reference grid), reproductive status and weight were recorded. Average biweekly trappability of adult females, as estimated from Cormack–Jolly–Seber models, was  $0.97 \pm 0.03$  (mean  $\pm 2$  SE) in 1990 and  $0.92 \pm 0.03$  in 1991 (Johannesen, Andreassen & Steen 1997; Johannesen & Andreassen, unpublished data). The figures for adult males are similar. Average biweekly trappability estimates for juveniles were  $0.91 \pm 0.04$  (1990) and  $0.80 \pm 0.07$  (1991). Any unmarked animals were marked by toe-clipping. Mother–offspring relationships were established by means of fluorescent pigment marking of lactating mothers in combination with growth curves of young and mothers (to establish birth dates). In addition 120 young were marked in nests found by radio tracking mothers. The mother of three of 1155 individuals could not be determined. These are excluded from the analyses. For a full description of the methods to determine matrilineal relations in the populations see Aars, Andreassen & Ims (1994) and Aars *et al.* (1995). The total numbers of animals and litters recorded for the 12 populations are given in Table 1.

Natal dispersal is the most common form of dispersal in microtines (Boonstra *et al.* 1987; Stenseth & Lidicker 1992) and is seemingly linked to puberty (Ims 1989). Isaksen (1993) found root vole emigrants from the age of 22 days. Animals older than 30 days are assumed to have completed juvenile dispersal events

and are called adult in the present study. This classification refers to dispersal only. On average, females of the plots reach sexual maturity at the age of 33 days and males at the age of 38 days (Isaksen 1993).

#### HOME-RANGE CENTRE AND LOCATION OF BIRTH SITES

A 'home-range centre' was assigned to all animals alive during the 13 weeks considered. Home-range centres were selected as the main home ranges descriptor (Andreassen *et al.* 1993) because a univariate measure of an individual's 'home site' was required for the subsequent analyses. The centre was estimated from the capture data using the harmonic mean method (Dixon & Chapman 1980), because this is more robust to scarce trapping data than the geometric centre. The centre was generally found to be close to the centre of activity from radio tracking. The nest, when uncovered by radiotelemetry, was always found in the vicinity (mean = 3.6 m, range = 0.0–7.7 m,  $n = 9$ ) of the home-range centre as estimated from captures. Animals alive were captured 0–8 times a week. A total of 10 722 captures were recorded for this study. Biweekly home-range centre estimates were calculated based on more than three captures spanning the shortest possible interval. In this way, the data set consisted of 2800 home-range centres for the 1155 animals. For the intervals in which an animal was never captured, but known to be alive, a location was interpolated from the estimates in the previous and the subsequent interval. A total of 191 interpolations were required for the trappable part of the population. Home-range analyses were carried out using Ranges IVa (Kenward 1990).

Dispersal distances were estimated for all marked individuals that survived to at least 30 days of age during the experimental period. The analysis of dis-

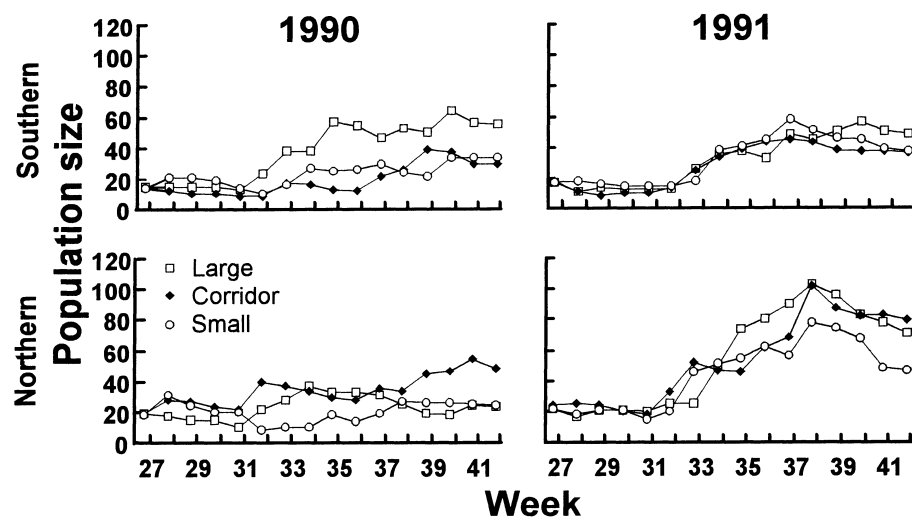


Fig. 2. Population trajectories of the 12 root vole populations by strain, year and fragmentation pattern from the time of release of the founding animals (matrilines) until the time of termination of the experiments (week 42). Population sizes are based on numbers of animals known to be alive. □, Large fragment plots; ○, Small fragment plots; ◆, Corridor plots.

**Table 1.** The total number of individuals and litters included in the analyses. The numbers in brackets gives the number of litters. 'Configuration' represents the levels of habitat configuration: L = Large; C = Corridor; S = Small

Strain	Year	Configuration			Totals		
		L	C	S	Subtotals	Strain	Grand
Northern	1990	62 (10)	101(18)	63(12)	226(40)	647(112)	1155(222)
	1991	135 (26)	154(25)	132(21)	421(72)		
Southern	1990	114 (18)	71(11)	83(15)	268(44)	508(110)	
	1991	85 (16)	71(14)	84(16)	240(46)		

persal distances thus embraced 821 animals from 202 litters. The dispersal distance was measured as the distance between the estimated birth site and the average home-range centre from trappable age.

#### ANALYSIS OF DISPERSAL DISTANCES

Dispersal is known to be correlated within litters in small mammals (Hilborn 1975; Beacham 1979; Massot *et al.* 1994). To avoid violation of the assumption of independence of observations underlying statistical testing (Massot *et al.* 1994) the litter was used as the statistical unit. To assess differences between the sexes the average of any females in the litter and the average of any males were calculated separately. In this way, 259 means were calculated from the 821 individuals and 202 litters. These were investigated using a linear model with: habitat configuration (three levels); strain (two levels); year (two levels); sex (two levels); and date of birth (continuous). The latter variable is a covariate in time that may be seen as a fudge factor of the unmanipulated and uncontrolled seasonal aspects. Included in this will be effects of increased density through the experimental period. Trying to separate these effects is not statistically permissible because all these uncontrollable latent variables are likely to be highly multicollinear (Kleinbaum, Kupper & Muller 1978). Pairwise interactions were eliminated by stepwise selection ( $p_{\text{crit}} = 0.10$ ). The dependent variable (mean dispersal distance) was log-transformed to stabilize the variance. The analysis was carried out using SAS version 6.08 (SAS Institute 1990).

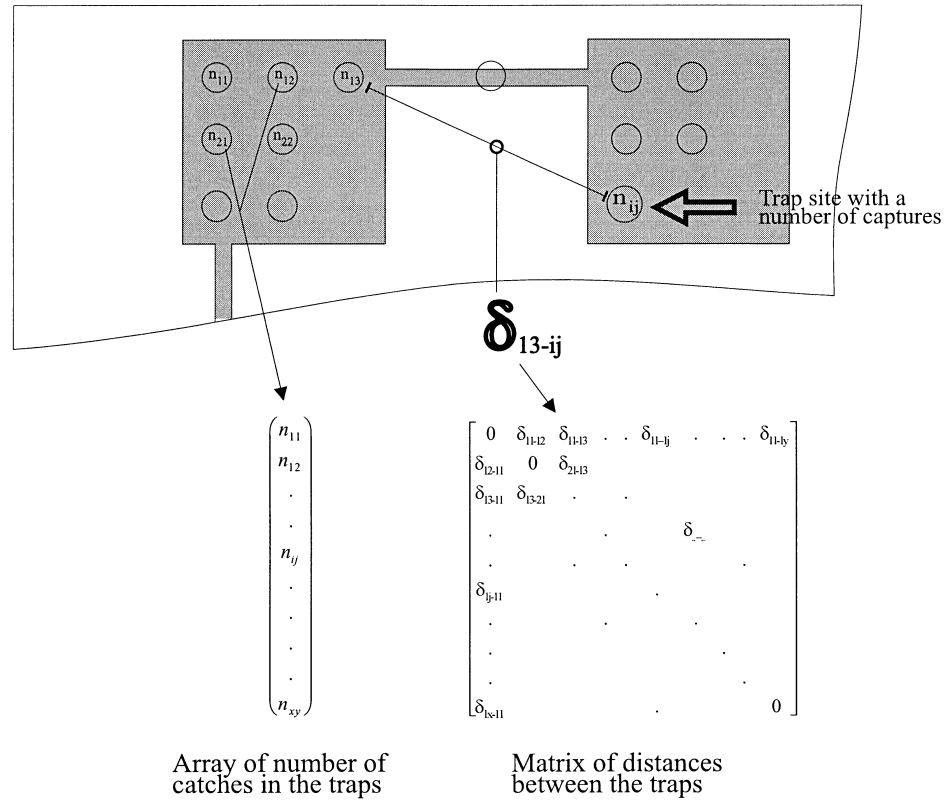
#### ANALYSIS OF DISPERSION PATTERNS

To investigate the overall dispersion pattern of the root vole populations, all captures ( $n = 10\,722$ ) were partitioned in biweekly intervals. Two different counting schemes for quantifying dispersion patterns were employed, one summing up all captures during each biweekly interval regardless of identity of the trapped vole, the other summing the number of different animals captured. The first emphasizes the space use of the individuals and, hence, measures aggregation in

the population. The second emphasizes the identity of the individuals and is more in line with the conventional way of measuring aggregation of individuals (Myers 1978). The sexes were treated separately in both counting schemes.

The metric distance between traps was calculated to give a matrix of distances, and the captures were arranged to give an array consisting of the counts at each trap station for the biweekly interval (Fig. 3). The spatial patterns in the data were investigated using the Moran's index (Gloaguin & Gautier 1981; Carpenter & Chaney 1983) as calculated by 'R' for the Macintosh (Legendre & Vaudor 1991). The degree of correlation within the neighbourhood of 20 m was used as the index of dispersion—positive values of the coefficient signify an aggregated pattern and negative values signify a regular pattern. The advantage of this index as the measure of dispersion is that it will allow comparison between the different habitat geometries. Such would not be the case using a quadrature-based method with the fragment as a quadrature.

Biweekly estimates of the aggregation coefficients were produced for each experimental plot and arranged into a time series. The series were investigated with respect to the experimental factors strain and habitat configuration. They were also investigated with respect to difference between the two years and differences between the sexes. The analysis was carried out with a repeated measure ANOVA (PROC GLM; SAS Institute 1990). Time was modelled as the within-subject effect (as a polynomial as suggested by Littell, Freund & Spector 1991) and treatment, strain, year and sex were modelled as between-subject effects. As for the analysis of dispersal distances, the time variate is a fudge factor of a variety of correlated non-controllable factors, such as season, photoperiod and density. Mauchly's test criterion for the validity of univariate *F*-test for within-subject effects (changes in time) was employed (LaTour & Miniard, 1983). This revealed strong departure from the assumptions ( $\chi^2$ -approximation = 41.74, d.f. = 20,  $P = 0.003$ ). Hence, a multivariate test statistic was used to evaluate any changes in time. Pillai's trace was chosen, as this is the multivariate test with greatest robustness to the assumption of normality (Olson 1974).



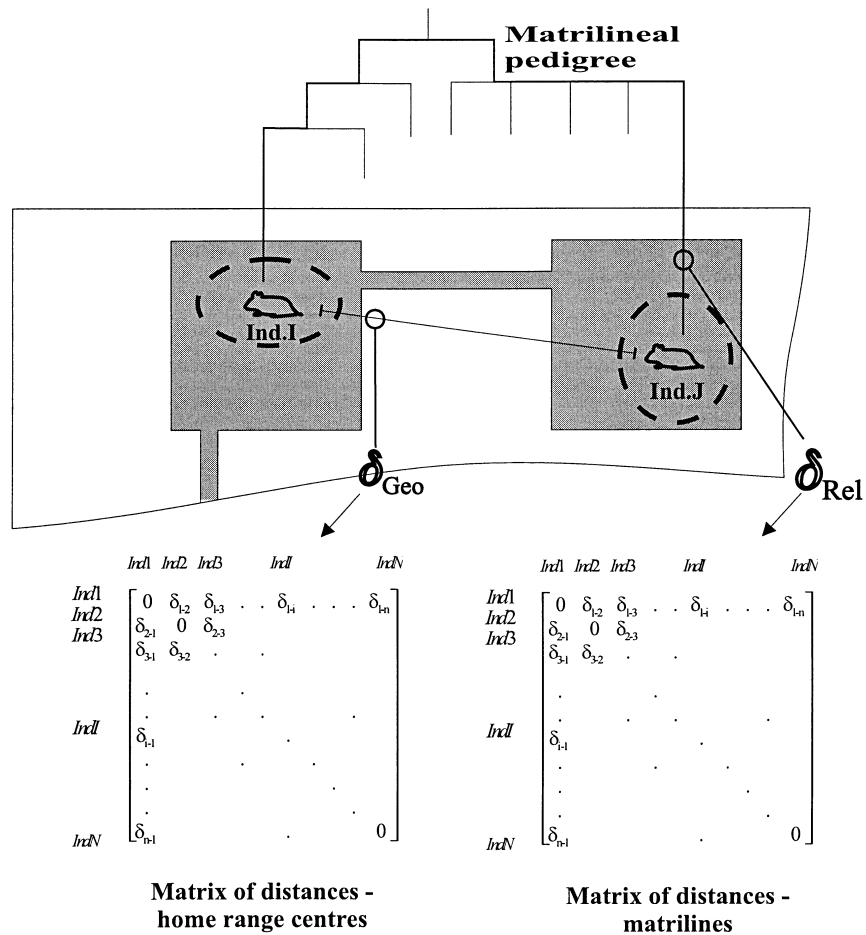
**Fig. 3.** A graphical representation of the analysis of the dispersion patterns. The number of captures in each trap ( $n$ ) is counted and sorted to produce an array of numbers. The distances between all traps ( $\delta$ ) are calculated and arranged in a distance matrix. The autocorrelation analysis consists of measuring spatial dependence between points at different distances apart. Spatial dependence between traps at a distance of zero to 20 m is used as the index of dispersion.

#### ANALYSIS OF SPATIAL PATTERNS OF RELATEDNESS

The low genetic variability of these two strains of root voles, documented from natural populations (Stacy *et al.* 1994) prohibited the use of biochemical markers for establishing paternity in the experimental populations so 'relatedness' is taken to mean matrilineal proximity. This quantity was measured by the distance between the animals in the matrilineal pedigree. Mother-offspring and full sibs (first-order relatives) were given a value of  $1/2$ , 'half sibs' (the same mother but different litter) were assigned a distance of  $1 - (1/2)^2$ . Generally the genetic distance between two animals was assigned the value of  $1 - (1/2)^n$ , where  $n$  is the number of branches separating the two in the family tree. Animals of different matrilineal were consequently considered of distance 1 from each other. Mantel correlograms, the multidimensional analogue of the standard correlograms (Legendre & Fortin 1989; Legendre 1993), were applied to investigate the extent to which patterns of relatedness (matrilineal relationships) were clustered in space. For this analysis, all matrilineal distances were assigned to three discrete classes (first-order relatives, more distant relatives and different matrilineal). Aggregation

of relatives will show up in the correlogram as positive, significant correlation for the first classes. The analysis was carried out on all adult animals at the week of peak density (sexes separate).

The mantel correlation coefficient (Manly 1991; Legendre 1993) was used to measure the correlation between the matrilineal and spatial proximity of individuals (Fig. 4) as calculated by 'R' for the Macintosh (Legendre & Vaudor 1991). The correlation coefficients were computed for biweekly intervals for the two sexes separately. The time series of mantel correlation coefficients were investigated with respect to strain, habitat configuration, year and sex using a repeated measure ANOVA (in the same way as for the analysis of dispersion pattern). Due to the low number of adult animals in some of the experimental plots, the analysis could only be carried out on correlation coefficients estimated from adults and juveniles pooled together. Data for weeks 33–34 was excluded due to missing values. The univariate test for significance of the within-subject effect (time) was employed, as Mauchly's test criterion for its validity did not prohibit such an approach ( $\chi^2$ -approximation = 21.22, d.f. = 14,  $P = 0.09$ ). The Greenhouse–Geisser correction for heterogeneous variance was employed (LaTour & Miniard 1983).



**Fig. 4.** A graphical representation of the analysis of spatial pattern of relatedness using bivariate Mantel analysis. Two measures of proximity between individuals were correlated using mantel correlation: matrilineal distances ( $\delta_{rel}$ ) and distances between home-range centres ( $\delta_{geo}$ ). Correlations were carried out for every biweekly interval in the full analysis.

## Results

### DISPERSAL DISTANCES

The patterns of dispersal were found to be both strain and habitat specific (Fig. 5). Date of birth of the litter was, furthermore, found to be an important covariate. Dispersal distances showed a general decrease through the season, and more so in 1991 than 1990 (possibly as an effect of increasing density being most pronounced in 1991; Fig. 2). The interaction terms persisting in the model after variable selection were those between date-of-birth and year (date-of-birth\*year:  $F_{1,250} = 3.69$ ,  $P = 0.056$ , partial  $r^2 \approx 1.5\%$ ), strain and year (strain\*year:  $F_{1,250} = 3.23$ ,  $P = 0.074$ , partial  $r^2 \approx 1.3\%$ ), and strain and habitat configuration (strain\*habitat configuration  $F_{1,250} = 2.7$ ,  $P = 0.070$ , partial  $r^2 \approx 2.1\%$ ). All the main effects in the model except sex (sex:  $F_{1,250} = 0.68$ ,  $P = 0.51$ , partial  $r^2 \approx 0.5\%$ ) were of some importance (habitat configuration:  $F_{2,250} = 10.75$ ,  $P < 0.0001$ , partial  $r^2 \approx 8.5\%$ ; strain:

$F_{1,250} = 6.45$ ,  $P = 0.012$ , partial  $r^2 \approx 2.5\%$ ; year:  $F_{1,250} = 3.4$ ,  $P = 0.066$ ; date-of-birth:  $F_{1,250} = 89.93$ ,  $P < 0.0001$ , partial  $r^2 \approx 22\%$ ). In general, the longest dispersal distances were attained in the plots with small fragments (irrespective of corridors or not) (Fig. 5). The Southern strain attained generally longer dispersal distances than the Northern strain, in particular in plots with small fragments. In total 40% of the variation in dispersal distances was explained by the model, of which habitat configuration and strain together accounted for 13%.

### DISPERSION PATTERN

The two counting schemes for quantifying the dispersion pattern, one counting number of captures per trap, the other counting number of individuals per trap gave virtually identical values of the Moran index. The data for the first counting scheme were used for further analyses.

The repeated-measures analysis of variance of the

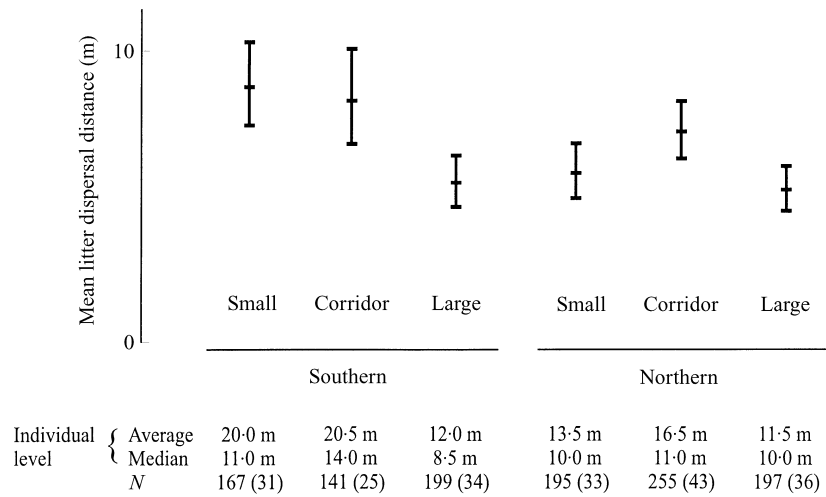


Fig. 5. Dispersal distances of the voles classified by strain and habitat configuration. The least-square mean estimates of (litter-averaged) dispersal distances with 95% error bars obtained from the model described in the text. The medians and means are given at the bottom with number of individuals and, in brackets, the number of litters.

biweekly estimated dispersion indices revealed that habitat configuration significantly altered the mean level of aggregation (habitat configuration:  $F_{2,16} = 12.18$ ,  $P < 0.001$ , partial  $r^2 \approx 42\%$ ; Table 2, Fig. 6). The two sexes responded differently to the habitat configurations, indicated by the interaction term (sex:  $F_{1,16} = 0.49$ ,  $P = 0.49$ , partial  $r^2 \approx 0.8\%$ ; habitat configuration\*sex:  $F_{2,16} = 6.39$ ,  $P = 0.009$ , partial  $r^2 \approx 22\%$ ). The pattern of aggregation of females with respect to habitat configuration was Large < Corridor  $\leq$  Small, whereas that of males was Large  $\leq$  Small < Corridor (Table 2). Habitat configuration and sex together explained 65% of the population level (between-subject) variation in aggregation. None of the other main factors had significant effects on the dispersion pattern (strain:  $F_{1,16} = 2.26$ ,  $P = 0.15$ , partial  $r^2 \approx 4\%$ ; year:  $F_{1,16} = 2.39$ ,  $P = 0.14$ , partial  $r^2 \approx 4\%$ ). Pairwise interaction terms

Table 2. Pairwise contrasts between the levels of the significant effects and interaction in the repeated measure ANOVA of dispersion pattern. Capital letters represent habitat configuration: L = Large, C = Corridor, S = Small, and F = females, M = males. Degrees of freedom are 1, 16 for all  $F$ -tests

Contrasted levels	Difference in Moran I	F-value	P-value
F : L-C	0.03-0.06 = -0.03	3.50	0.078
F : L-S	0.03-0.15 = -0.12	7.04	0.016
F : C-S	0.06-0.15 = -0.09	0.61	0.444
M : L-C	0.04-0.13 = -0.09	3.71	0.070
M : L-S	0.04-0.09 = -0.05	0.00	0.966
M : C-S	0.13-0.09 = 0.04	3.54	0.076
L : F-M	0.03-0.04 = -0.01	0.53	0.476
C : F-M	0.06-0.13 = -0.07	0.55	0.470
S : F-M	0.15-0.09 = 0.06	0.25	0.624

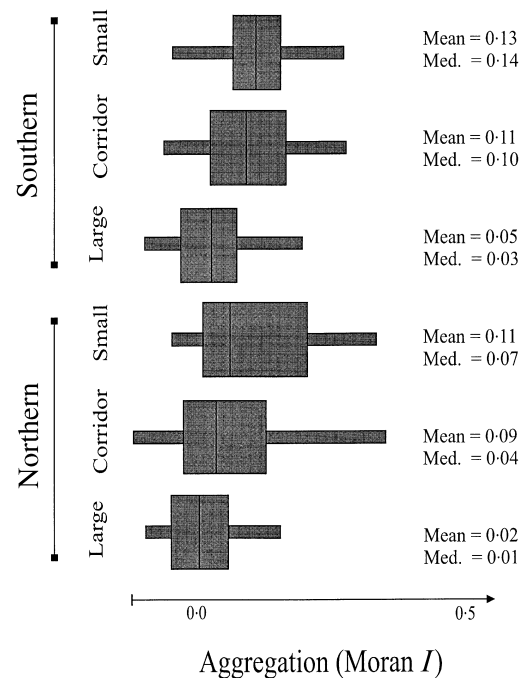


Fig. 6. Box plots depicting the distribution of the indices of aggregation of individuals (Moran I), classified by strain and habitat configuration. Vertical bars represent the medians, the large rectangular boxes represent 25% and 75% quartiles, the horizontal bars represent the 5th and the 95th percentiles. The scale for the box plots is given by the horizontal axis at the bottom of the panel. Each box plot is based on the seven biweekly estimates for each sex for each of the two years ( $n = 28$ ).

(other than strain\*sex) were all insignificant at the 10% level.

The degree of aggregation increased significantly through time for females, but not for males (females: Pillai's trace = 0.99,  $F_{6,2} = 35.31$ ,  $P = 0.02$ ; males: Pillai's trace = 0.81,  $F_{6,2} = 1.42$ ,  $P = 0.46$ ). All interactions between time and the other factors were insignificant.

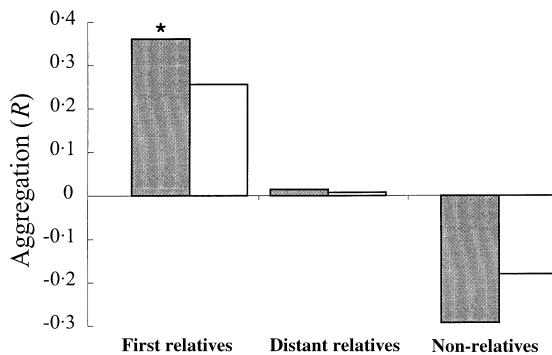


nificant ( $P > 0.3$ ). The data are, hence, consistent with the hypothesis that the dispersion pattern has a qualitatively similar development through time in all treatments.

SPATIAL PATTERN OF RELATEDNESS

The mantel correlograms based on adult animals for the week with highest density for each plot show that matrilineal relatedness was structured in space (Fig. 7). The first-order relatives are significantly spatially clustered and females more than males.

The repeated-measures analysis of variance shows that the matrilineal correlation in space was stronger when estimates were based on all animals (both adults and juveniles) of the populations, as a proportion of these are pre-dispersal animals. However, the trends are qualitatively the same for both data sets (Fig. 8).



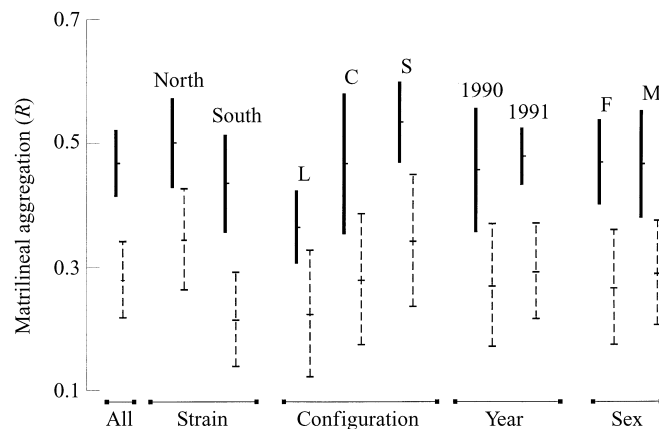
**Fig. 7.** Mantel correlograms of matrilineal distances in space for adult individuals. The correlations ( $R$ ) depicted are averages across all enclosures in the week of peak density for both years. First-order relatives represents mother-daughters and full sibs, distant relative represents animals (other than first-order relatives) of the same matriline and non-relatives represents animals of different matriline. Females are represented by shaded bars and males are represented by open bars. Only the correlation of female first-order relatives is significant throughout (asterix).

All the main effects—possibly excluding sex—were significant (habitat configuration:  $F_{2,14} = 19.17$ ,  $P < 0.001$ , partial  $r^2 \approx 33\%$ ; strain:  $F_{1,14} = 21.97$ ,  $P < 0.001$ , partial  $r^2 \approx 19\%$ ; year:  $F_{1,14} = 19.91$ ,  $P < 0.001$ , partial  $r^2 \approx 17\%$ ; sex:  $F_{1,14} = 3.56$ ,  $P = 0.080$ , partial  $r^2 \approx 3\%$ ). The only significant interaction between the main effect was between habitat configuration and year (habitat configuration\*year:  $F_{2,14} = 8.73$ ,  $P = 0.004$ , partial  $r^2 \approx 15\%$ ; all other:  $P > 0.15$ ). The overall model explains 88% of the (between-subject) variation in the matrilineal structuring of the populations. Habitat configuration and strain have dominant effects on the pattern. The difference between year is, however, also strong.

When contrasting the levels of the main effects (Table 3) the interaction between year and habitat

**Table 3.** Pairwise contrasts of the mantel correlation coefficients for levels of the main effects in the repeated-measure ANOVA of matrilineal clumping in space. The coefficients reflect the degree of clumping of the matriline in space. Capital letters represents habitat configuration: L = Large, C = Corridor, S = Small. Degrees of freedom are 1, 14 for all the  $F$ -tests

Contrasted levels	Difference in mean		$F$ -value	$P$ -value
	mantel $r$			
Female–Male	0.45–0.44 =	0.01	3.56	0.080
Northern–Southern	0.48–0.41 =	0.07	21.97	<0.001
90 : L–C	0.25–0.41 =	–0.16	2.18	0.16
90 : L–S	0.25–0.55 =	–0.30	41.33	<0.001
90 : C–S	0.41–0.55 =	–0.14	19.81	<0.001
91 : L–C	0.47–0.49 =	–0.02	0.38	0.54
91 : L–S	0.47–0.53 =	–0.06	0.98	0.34
91 : C–S	0.49–0.53 =	–0.04	2.33	0.14
L : 90–91	0.25–0.47 =	–0.22	25.80	<0.001
C : 90–91	0.41–0.49 =	–0.08	5.93	0.028
S : 90–91	0.55–0.53 =	0.03	0.13	0.72



**Fig. 8.** Mean matrilineal aggregation in space as measured with the mantel coefficient ( $R$ ) for various experimental factors averaged over experimental season. Solid lines represent estimates and error bars based on all animals of the populations; dotted lines represent estimates based on the adult part of the population. ‘Configuration’ represents habitat configuration, L = Large, C = Corridor and S = Small. F = females and M = males. The error bars are not corrected for the other variables in the fitted models (see text). They are therefore more conservative than the 95% C.I.

configuration is clear: 1990 exhibited large significant differences between the habitat configurations, whereas 1991 did not. Note, however, that the gradient in matrilineal clumping is the same in both years: Small > Corridor > Large (Table 3, Fig. 8). The Northern strain is more aggregated in space with respect to matrilines than the Southern strain, and the year 1991 had a more aggregated pattern than the year 1990. The differences between years may again be associated with the high densities of the Northern strain in the second year (Fig. 2). There was significant increase in the matrilineal aggregation through time (Greenhouse–Geisser corrected:  $F_{5,70} = 9.98$ ,  $P_{adj} < 0.001$ ). The only one significant interaction between time and any of the main effects was between time and year (G–G corrected:  $F_{5,70} = 4.21$ ,  $P_{adj} = 0.01$ ; all other:  $P_{adj} > 0.15$ ).

#### SYNTHESIS OF RESULTS

The main results considering the dispersal and dispersion responses of root voles to the experimental variables (habitat configuration and strain) can be summarized as follows.

1. Dispersal distance distribution was found to be altered by habitat patchiness, but more so for the Southern than the Northern strain. Dispersal distances increased as a response to fragmentation, but seemed relatively less affected by connectivity.
2. Habitat fragmentation increased structuring of populations both with respect to general aggregation of animals and with respect to spatial clumping of matrilines. Populations in small patches exhibited more clumped patterns than those in large patches.
3. Connectivity significantly diminished the spatial aggregation of females and increased the spatial aggregation of males.
4. Connectivity diminished the matrilineal aggregation of both sexes for both strains.

The relationships between population estimates of sex-specific dispersal distances and the two aggregation indices, as well as between the sex-specific dispersal distances and a measure of genetic heterogeneity (matrilineal diversity) of the populations can be summarized as follows (see Table 4).

- (i) Females: longer mean dispersal distances at the population level were associated with less genetic

structuring in space and less matrilineal diversity in the population as a whole.

- (ii) Males: there was an association between dispersal and population level aggregation, supporting the notion that males that move frequently are better at detecting and aggregating around temporal hot-spots (presumably receptive females: see Ims 1987, 1988).

#### Discussion

##### EXPERIMENTAL SETTING: SPATIAL ASPECTS

Population ecological studies in general, and particularly those focusing explicitly on effects of spatial structures, should be designed and interpreted with emphasis on the spatial scaling of the study relative to that of the study animal (Morris 1987; Wiens 1989; Gascon & Travis 1992).

In the present study, being a manipulative experiment, we drew on previous knowledge of the experimental animals (Tast 1966, 1968; Ims *et al.* 1993) to select appropriate habitat characteristics for the themes in question. A contrasting patch mosaic (with a hostile, uninhabitable matrix habitat) was chosen to maximize the effects of the manipulations within the rather small spatial extent of the study plots. Pronounced habitat contrasts in patchy (fragmented) habitats are, furthermore, an increasingly common setting for root vole populations in parts of its geographical range (Tast 1968; Van Apeldoorn *et al.* 1992; Bergers, Van Apeldoorn & Bussink 1994).

In the present study the experimental scaling was as follows.

1. Fragment size: the total home-range size of females in continuous and homogeneous meadow habitat is comparable to the size of the small fragments (225 m<sup>2</sup>), while the defended part of the female home ranges is one-quarter to one-third the size of a small fragment (Ims *et al.* 1993). Even the small fragments contained several resident breeding females (Andreassen, Hertzberg & Ims 1997).

2. Inter-fragment distance: the shortest distance to adjacent fragments was 15 m for all fragments. Given the locomotory abilities of root voles, this is a short distance. Root voles in the wild can move up to 1 km during one night (Steen 1994). Animals in our enclosed populations were observed crossing the inter-

**Table 4.** Spearman rank correlation between mean dispersal distances, mean aggregation (measured by the Moran I), mean matrilineal clumping (measured by the mantel R) and mean matrilineal diversity (measured by a standardized Shannon index of proportional abundance of the different matrilines; H.P. Andreassen & R.A. Ims, unpublished information). The means are taken across the experimental season.  $n = 12$  for all correlations

	Matrilineal aggregation	Individual aggregation	Matrilineal diversity
Mean dispersal females	$\rho = -0.50$ , $P = 0.10$	$\rho = 0.12$ , $P = 0.72$	$\rho = -0.62$ , $P = 0.03$
Mean dispersal males	$\rho = -0.28$ , $P = 0.38$ ,	$\rho = 0.59$ , $P = 0.05$	$\rho = -0.31$ , $P = 0.33$

fragment area (Andreassen *et al.* 1997). However, adult females and young (predispersal) individuals did not generally include more than one unconnected fragment when maintaining stable home ranges (Ims *et al.* 1993; Aars *et al.* 1994, 1995). Moreover, we have earlier shown that 4-m gaps in linear habitats impede movements significantly (Andreassen, Ims & Steinset 1996a).

**3. Connectivity:** Andreassen, Halle & Ims (1996b) show that narrow lanes of grass are perceived by the root voles as corridors—they move through them more readily than across barren ground, but less readily than through wider habitats. Also, recent experiments on *M. pennsylvanicus* have shown that habitat corridors at a similar scale to the present, increase movement rates between patches (La Polla & Barrett 1993).

**4. Extent (size of enclosures):** enclosures gave complete control of spatial scale of the study populations, in contrast to open populations, which always will be part of a larger system (Holt 1994), such as a source-sink system (Pulliam 1988). However, enclosures impose artefactual constraints on the study populations; for instance, no dispersal distances longer than  $\approx 100$  m were possible. Animals attempting long-distance movement were removed as emigrants and lost from sight. Hence, the dispersal distance distributions is truncated by the spatial extent of the study. The removal of frequently edge-trapped individuals prohibited artificially high aggregations of individuals and/or 'fence effects' due to abnormally high densities (Krebs *et al.* 1969; Ostfeld 1994). No effects of frustrated dispersal were observed; for example, sex ratio (Aars *et al.* 1995), which may reflect sex-biased dispersal (generally found in *Microtus*; Boonstra *et al.* 1987), was within the limits of what is observed in natural populations (Tast 1966; Lambin, Krebs & Scott 1992).

In summary, the scaling of this experiment, allowing frequent but configuration-specific exchanges between patches inhabited by small groups of breeding individuals, resembles a patchy population rather than a metapopulation (Taylor 1991; Burgman *et al.* 1993).

#### PATTERNS OF DISPERSAL AND DISPERSION

The two geographical strains of the root voles had divergent dispersal responses to the habitat configurations. The Southern strain exhibited a 'fission response': when habitat was fragmented, they increased dispersal distances (Fig. 5, below). The increase is evident regardless of connectivity of the patches. In contrast, the Northern strain had more modest dispersal distances, especially in the small fragmented populations, and this strain was generally more aggregated than the Southern strain. Mean dispersal distances of females (at the population level) was negatively correlated with matrilineal diversity in

the populations (Table 4). If the matrilineal component to genetic change in the populations is larger than the paternal, as has been indicated in population genetic studies of *M. pennsylvanicus* (Sheridan & Tamarin 1988), our results may imply that a lower level of genetic variation is preserved in the populations with higher rates of dispersal. This phenomenon has been anticipated by Boecklen (1986). Note, however, that this conjecture remains speculative until more specific population genetic studies have been conducted.

Habitat patchiness was found to change the processes of dispersal of individuals and thereby increase aggregation of relatives and of individuals in general. The findings corroborate earlier theoretical and empirical findings and conjectures (Stamps *et al.* 1987; Ostfeld 1992; Ims *et al.* 1993).

#### INBREEDING, MATRILINEAL CLUMPING AND DISPERSAL

The two strains have shown differences in response to inbreeding in laboratory conditions. The Southern strain exhibits inbreeding avoidance and signs of inbreeding depression, whereas no such phenomenon is apparent for the Northern strain (Santos *et al.* 1995). The present analysis from the field corroborates this pattern: the Northern strain, which is most resistant to inbreeding, naturally exhibited a stronger matrilineal clumping in space. Also detailed studies on home-range use of sexually mature females based on radiotelemetry show that there is more space sharing between related females in the Northern strain (Andreassen *et al.* 1997). The differences between the geographical races were reflections of their dispersal patterns. The Southern strain seemed more compelled to move than the Northern strain if patches were small, regardless of connectivity. Bollinger, Harper & Barrett (1993) recently demonstrated that inbreeding avoidance influences dispersal in meadow voles (*M. pennsylvanicus*).

Ims *et al.* (1993) proposed two classes of responses to increased patchiness. Increased aggregation as home ranges were squeezed and dispersal inhibited was termed a 'fusion response' (see also Ostfeld 1992 for similar scenarios). Less aggregation as individuals incorporate several patches in their home range or increase their dispersal effort was termed a 'fission response'. The Northern strain is found to exhibit a fusion response and the Southern a fission response. These responses may well be adaptive in their natural environments. They are conceivably a result of selection under varying costs of dispersal and inbreeding. Future studies may elucidate which of these two spatial life history strategies renders a population less sensitive to increased fragmentation.

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