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Meadow voles (*Microtus pennsylvanicus*) in farm landscapes, II. Movements among habitats

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Two microlandscapes were constructed for use in a live trapping study designed to investigate how meadow vole movement behaviour is affected by landscape structure. Each experimental system was composed of both barley and forage habitats separated by a central habitat of old-field successional meadow. Vole movement patterns in the landscapes were related to differences in the quality and boundary characteristics of each habitat. Habitat quality was shown to be an important determinant of both within- and between-habitat vole movement dynamics. Meadow voles preferred moving within habitats of higher quality and perceived boundaries between habitats of more similar quality as more permeable. Boundaries were in general avoided, thus affecting the voles' spatial distribution. Meadow voles functioning in farm mosaics will be limited in their ability to fulfill their resource needs by the presence of low quality habitats and by increase in the numbers of distinct boundaries.

1. Introduction

Several empirical studies have focused on the effect habitat quality has on movement (e.g., Hansson 1977, Ostfeld *et al.* 1985, Hansson 1987, Dickman & Doncaster 1989, Morris 1992, Pulliam 1988, Szacki *et al.* 1993). Most concentrate on habitat quality, fewer on spatial arrangement (Wiens *et al.* 1985) and fewer still on small landscape features such as habitat size, shape and edge permeability (Buechner 1989). Direct empirical data on edge, boundary or interface permeability of landscape elements or habitats is virtually nonexistent in the literature (Wiens *et al.* 1985, Stamps *et al.* 1987, Buechner 1989, Wiens 1976).

Successful transit among landscape elements rests heavily on the habitat value of the matrix surrounding each habitat of focal interest (Stenseth & Lidicker 1992). Hostile matrices are more likely to be resource (food, shelter from predators, etc.) limited, thus, influencing an individual's behavioral choice to leave its habitat of origin, and its probability of survival during a dispersal event (Hansson 1991). Matrix characteristics, thus, have the potential to limit both a population's spatial extent (Hansson 1991) and its viability (Hanski &

Gilpin 1991).

Connectivity (Merriam 1984) was established to reflect the interaction between behavioral ecology and landscape structure, and thus, identify the functional connection between landscape elements. Landscape matrices that facilitate interhabitat movement are said to have high connectivity. Although interhabitat movements are influenced by, and can even be dependent upon, landscape structural elements such as corridors, connectivity describes the effect landscape structure has on movement, not the movement itself nor the land structure (Baudry & Merriam 1988). Most connectivity studies have, however, centered on corridors and how their structural properties, numbers and juxtaposition affect interhabitat movements (e.g., Merriam 1984, Fahrig & Merriam 1985, Lefkovitch & Fahrig 1985, Henein & Merriam 1990, Merriam & Lanoue 1990, Saunders & Hobbs 1991).

Connectivity has two behavioral components, both of which are influenced by interhabitat quality (*see* Hansson 1991). Individuals moving between habitats must first decide to cross the interface between their home habitat and the interhabitat (Stamps *et al.* 1987). In some cases, this will mean movement into a narrow corridor of suitable habitat; in other cases, individuals will move directly into a dissimilar matrix. An individual's willingness to cross the interface is largely a measure of matrix habitat edge permeability; if two matrices are identical except for their permeability, individuals are more likely to move into the more permeable (Stamps *et al.* 1987). Individuals who have made the choice to cross must then decide whether or not the interhabitat environment is suitable for travel and/or colonization. There may of course be a positive feedback loop between a matrix's potential to ensure survival (higher habitat value), and an individual's decision to proceed after crossing a habitat edge. Habitat boundaries thus have the potential to limit how and where populations interact with and function within a landscape.

In their model of edge dynamics, Stamps *et al.* (1987) defined edge permeability as the proportion of dispersers that reach a habitat edge, and then decide to cross it. In this study, interface permeability is defined as the probability of an individual crossing between two particular landscape elements. In this way, the animal's choice will be influenced by its motive to move, the characteristics of its habitat of origin, the characteristics of its destination habitat, and the characteristics of the interface itself (Wiens *et al.* 1993).

In this study, we use two replicate confined populations of meadow voles (*Microtus pennsylvanicus*) each living in an agricultural landscape composed of meadow, forage and barley habitats. Movements within and between habitats were used to index habitat preference and boundary permeability respectively. Our method of quantifying different meadow vole movement patterns can be modified to describe movement in landscapes at any scale and with any species.

In general, we predict that differences in edge permeability and potential to promote transit exist among experimental habitats. All the habitats are identical in terms of their size and shape but differ in vegetation type. Greater movement into a given habitat indicates its higher permeability. Greater movement within a habitat indicates the meadow voles' preference for its vegetation and its greater capacity to contribute to landscape connectivity. Differences in preference and boundary permeability of a habitat are related to each habitat quality as outlined in Basquill and Bondrup-Nielsen (1999).

2. Methods

Data were obtained from a replicated capture-mark-recapture study of the meadow vole living within two 105 × 35-meter enclosures. Three 35 × 35-meter plots were established within each enclosure, consisting of a central undisturbed meadow (M), with an adjacent cultivated crop of barley (B) and a second of forage (F). A 7 × 7 grid of Ugglan multiple live-capture traps were created in each plot. Vole populations were trapped on a weekly basis between May and October 1994. Complete details on the enclosure design and the trapping regime can be found in Basquill and Bondrup-Nielsen (1999).

Each time a vole was caught, its plot location was noted. Pairs of sequential trappings, served to categorize between- and within-plot movement events by direction. For example, a movement event originating and ending in the meadow plot would be categorized as MM. A movement event from the meadow to forage plot would be categorized as MF. All movement events could thus be categorized using one of the following movement categories: MM, MF, MB, FF, FM, FB, BB, BF and BM. This was done separately for each vole.

We obtained independent estimates of the mean observed number of voles exhibiting each particular category of movement (hereafter referred to as the observed distribution) in the following manner. We randomly drew a single movement from each vole's capture history event (to maintain independence of the data). This was done for the entire population. This randomization procedure was repeated 15 times, and the average number of events falling into each category was determined. Capture data from both enclosures were pooled, thus, controlling for enclosure effect. The data employed were collected after 8 August, the capture date determined, a priori, as the first date after which voles were consistently found in all plots of both enclosures (Basquill & Bondrup-Nielsen 1999).

To reveal whether or not meadow vole within-plot movement (plot preference) and between-plot movement (boundary crossing) events were influenced by the structural features (plot type and boundary types) of the experimental landscape, a χ^2-analysis was employed to test for statistical differences between the observed distribution of movement categories and an expected random distribution. Values for the expected distribution of the nine movement categories were estimated with a computer simulation set up to randomize movement events and categorize them by direction. Each simulated movement event's origin was randomly selected on the trapping grid; its end point was determined by randomizing the angle and distance of the movement. Random distances were selected from a normal distribution with a mean equal to the mean movement distance observed for the experimental vole population and its corresponding standard deviation. This simulation was repeated 8 000 times to generate the mean expected distribution of movement events that was used for statistical testing.

To determine plot preference, we compare the relative observed frequencies of each within-plot movement category (FF, MM and BB) with the expected frequencies generated from the computer simulation. Higher observed frequencies were assumed to reflect relative preference for movement within a given plot. Plot preference indices thus correspond to the plot's potential for promoting transit and for increasing landscape connectivity. Relative differences in inter-plot preference were related to each plot's habitat quality as indexed in Basquill and Bondrup-Nielsen (1999).

We tested the response of each sex and reproductive class (juvenile male, juvenile female, adult male and adult female), as well as the total population's response. Males with scrotal testes and females with evidence of either pregnancy or lactation were classed as reproductively active.

To determine boundary crossing, we focus on the observed frequencies of between-plot movement categories (FM, FB, MF, MB, BF and BM) relative to the expected frequencies. Measures were employed to control for the influence population density may have had on the relative number of edge crosses originating from each given plot. Thirty-five percent of voles were determined to live in the forage, 58% in the meadow and 7% in the barley plots, as calculated from population density data collected after 8 August (Basquill & Bondrup-Nielsen 1999). These relative proportions were used to weight the number of simulated movement events originating in each plot. The simulation was otherwise similar to the one described above. This analysis was designed to show that meadow vole inter-plot movements were not randomly directed; by controlling for inter-plot differences in density and movement distance, we tested for the influence of boundaries on movement patterns. The expected inter-plot movement distribution was derived from two different computer simulation algorithms. Distribution *A* was based on an algorithm assuming voles in the two end plots, forage and barley, enter the meadow if they "bumped" into the end walls of the enclosures. Distribution *B* was based on an algorithm assuming voles in the end plots would stay in their respective end plots if they "bumped" into the respective end wall of the enclosures.

To determine boundary permeability we compared within-plot movements with between-plot movements to see if voles are deterred by landscape boundaries. We tested for the influence(s) the plot characteristics of the two focal plots (source and destination of movement), and the structural discontinuity imposed by their interface, had on the movement behaviour of voles from different life history classes.

An index was used to determine which movement category had the greatest probability of occurring. These were calculated as the proportion of movement events into each plot type relative to the total number of movements from each source plot.

For example, vole X might have the following movement categories: MM, MM, MF, FM and MF. Four of this vole's movements originated in the meadow (MM, MM, MF and MF). One half (0.5) of these were movements within the meadow (MM, MM), the other half involved a border cross into the forage area (MF, MF). Therefore, if this vole is in the meadow plot its chance of remaining in the meadow is 0.5, and its chance of leaving for the forage plot is also 0.5. By the same logic, if the vole is in the forage plot, its next move has a chance of 1.0 of ending in the meadow. When calculated for the entire vole population one then obtains the observed probabilities of all possible movement types.

To test for differences in spatial patterns of the voles, all movement data were subdivided separately by voles' age and sex classes. The data were blocked to control for differences in the tendency to cross a plot boundary among individuals. The blocked design also controlled for the additional variability created by pooling the data from both enclosures. A Friedman test was used for each age and sex class, as a non-parametric alternative to ANOVA for randomized blocks, to test for differences between movement events originating in the same plots (e.g., FF versus FB versus FM, etc.). Groups showing significant differences were followed-up with a multiple comparison analysis comparable to the Tukey operation used for ranked data in a one-way ANOVA (Zar 1984).

3. Results

Meadow voles showed the greatest preference for moving within the meadow plot, followed by the forage and lastly the barley plots (Table 1). The meadow voles of both life-history classes and sexes appeared to use the forage plot as expected from the simulation. The meadow plot was generally preferred, having double the number of voles expected and the barley plot was not used extensively.

Vegetative boundaries affected the movement patterns of the voles. The observed distributions differed from both expected distributions (*A* and *B*; Table 2). The meadow vole movement is not randomly directed.

Boundary permeability was analysed by determining whether or not voles in a plot would be more likely to make a move within that same plot or cross a boundary (Table 3 and 4). High values in Table 3 reveal those groups of individuals whose inter- and intra-plot movement probabilities did not have a large chance of differing. Such high values were exhibited by adult, and to a lesser extent juvenile males in the forage area; they had a similar probability of remaining there as of leaving to the meadow or barley plots. A similar scenario exists for individuals of every life history class moving in the barley plot (Table 3).

The results of the multiple range test (Table 4) allow for comparison of all movement probabilities for each source plot, thereby providing a better picture of the meadow vole's spatial pattern. All individuals, regardless of age-sex class, have a similar probability of moving within the forage plot as crossing its boundary to the meadow (Table 4, FF vs. FM column). The voles from both life history groups and sexes, except adult females, were more likely to cross to the meadow plot than they were to the barley plot (Table 4, FM vs. FB). All the types of voles are more likely to move within the forage crop than they are to cross to the barley except for adult and juvenile males (Table 4).

Table 1. Plot preferences indexed by mean number of individuals exhibiting within-plot movement events compared with the expected within-plot movement of 1:1:1, tested with χ^2-test.

Group	Forage	Meadow	Barley	χ^2	$p <$
All indiv.	35.8	62.4	2.9	54.05	0.001
Adult females	14.9	22.7	2.0	17.04	0.001
Adult males	7.2	23.4	1.0	29.32	0.001
Juvenile females	19.2	23.7	0.4	24.72	0.001
Juvenile males	7.6	15.4	0.0	14.22	0.001

The results from the meadow plot are more consistent among the sex and life history groups. The voles from all the categories are more likely to travel within the meadow than to cross into forage (Table 4, MM vs. MF column) or into the barley (Table 4, MM vs. MB). Only when the voles from all the life history and sex categories are considered together (total category), is it apparent that meadow voles are more likely to move from the meadow to forage plot rather than meadow to barley (Table 4, MF vs. MB column).

The results of the BB vs. BF vs. BM movement categories are based on only a few voles and therefore lack statistical power. However, by virtue of these low numbers alone, it is apparent that few voles chose to cross into the barley area (the sum number of recorded FB and MB movement vents totaling 8, less than 1% of all moves). Most of the small numbers of voles that did move into the barley did not return often if at all. The barley plot thus has a very low edge permeability.

4. Discussion

Populations have been traditionally defined by ecologists as groups of interacting individuals of a common species. In landscape systems, populations function within a diversity of habitats, each serving their life history differently, together shaping their dynamics. The level of interaction among individuals may change depending on the habitat of focus, its location in relation to other habitats, and a functional relationship individuals have to all habitats in the surrounding landscape. Thus, to understand landscape ecology, we must understand population dynamics occurring within and among habitats. Movement behaviour, which is easily measured, is an ideal parameter with which to investigate these ecological flows. As the area of an extreme spatial change, boundaries offer ecologists an opportunity to use movement behaviour to measure the functional separation and interaction among individuals in different habitats.

Individuals that show no preference for interor intra-plot movement did not appear to be spatially limited by the boundaries imposed in this landscape. The adult and juvenile males found in the forage and barley areas exhibited this type of the movement pattern. As microtine males are most influenced in their spatial organization by the distribution of fertilizable females (Ims 1987), it is not surprising that nonterritorial males exhibit more free ranging movement in their efforts to find estrous females (Madison 1980, 1985). Ostfeld and Klosterman (1986) also found such spatial substructuring between the sexes for *Microtus californicus* living in a landscape composed of varying quality habitats.

The voles in the barley plot (from every life history class) showed no preference for inter- or intra-plot movement. This is quite surprising because one would expect females entering a low quality habitat to want to leave in search of "greener pastures". The live trapping records indicate the animals entering the barley plot had a tendency to stay a while (often until their total disappearance). Considering the proximity of a higher quality habitat, it is possible that the distinct boundary

Table 2. Boundary crossing indexed by mean number of between-plot movement events compared with two expected random distributions *A* (assuming voles in the two end plots, forage and barley, would have twice the probability of entering the meadow than voles leaving the meadow (M) for the barley (B) or forage (F)) and *B* (assuming voles in the end plots would have the same probability of enering the meadow as voles in the meadow plot entering the forage or barley) with the χ^2-test (analysis based only on FM, MF, MB, and BM).

	FM	FB	MF	MB	BF	BM	χ^2	$p <$
All Indiv.	9.5	0.0	8.6	1.2	0.0	0.8		
Expected *A*	12.2	0.1	8.9	11.4	0.0	2.3	10.78	0.025
Expected *B*	6.5	0.1	9.5	12.2	0.0	1.2	11.48	0.005

Table 3. A three way Friedman analysis comparing edge permeability indeces (proportions of all moves from each source plot (proportion of all moves from each source plot averaged among individuls within each life history class) for voles originating in the forage, meadow, and barley plots respectively. Indices from 246 individuals were used (54 adult females, 69 adult males, 65 juvenile females and 43 juvenile males); F = forage, M = meadow, and B = barley (the first letter represents the source plot of a movement event and the last letter represents he destination plot).

				χ^2	p
	FF	FM	FB		
Total	0.9 ± 0.4	0.2 ± 0.3	0.004 ± 0.06	18.08	< 0.0001
Adult female	0.3 ± 0.4	0.2 ± 0.3	0.02 ± 0.2	6.70	0.035
Adult male	0.2 ± 0.3	0.2 ± 0.3	0 ± 0	4.05	0.132
Juvenile female	0.3 ± 0.4	0.2 ± 0.3	0 ± 0	10.39	0.006
Juvenile male	0.2 ± 0.4	0.9 ± 0.4	0 ± 0	5.04	0.081
	MF	MM	MB		
Total	0.1 ± 0.3	0.5 ± 0.5	0.01 ± 0.1	100.36	< 0.0001
Adult female	0.2 ± 0.3	0.6 ± 0.5	0.04 ± 0.2	31.03	< 0.0001
Adult male	0.1 ± 0.2	0.7 ± 0.4	0.02 ± 0.1	58.40	< 0.009
Juvenile female	0.2 ± 0.3	0.6 ± 0.5	0.005 ± 0.03	32.40	< 0.0001
Juvenile male	0.07 ± 0.2	0.6 ± 0.5	0.006 ± 0.03	22.37	< 0.0001
	BF	BM	BB		
Total	0.004 ± 0.06	0.02 ± 0.1	0.02 ± 0.1	0.22	0.895
Adult female	0.001 ± 0.009	0.01 ± 0.07	0.06 ± 0.2	0.40	0.819
Adult male	0 ± 0	0.009 ± 0.07	0.05 ± 0.2	0.22	0.894
Juvenile female	0 ± 0	0.02 ± 0.1	0.008 ± 0.06	0.07	0.966
Juvenile male	0 ± 0	0.05 ± 0.2	0.05 ± 0.2	0.14	0.933

between these two areas served as a barrier for potential emigrants. A boundary's distinctness (as perceived by a particular individual) could be measured according to the relative differences (social, physiognomic, diet and/or moisture influences) between its two component habitats, and by the width of the transition area separating them (boundary thickness). Gradual transitions between similar quality habitats would be less distinct and more permeable. Although the high density of voles in the meadow could have also served as a barrier to potential barley immigrants (*see* Madison 1980, 1985), it was dismissed as the isolating factor because the voles inhabiting the forage plots did not show the same aversion.

The inter-plot transfer probabilities of the voles living in the meadow plot were fairly consistent among the life history classes. Our results clearly indicated the voles' strong preference for within meadow plot movement. Not surprisingly, the voles (total category) that do make the decision to cross into the cultivated areas show preference for the higher quality forage. This is consistent with results of other studies of voles living in heterogeneous areas (Hansson 1977, Ostfeld *et al.* 1985, Ostfeld & Klosterman 1986, Adler & Wilson 1988, Bergeron *et al.* 1990, van Apeldoorn *et al.* 1992).

The meadow voles inhabiting the forage plot did not show the same preference for remaining within the vegetative boundaries of their plot, as did the individuals living in the meadow habitat. The voles (from all life history classes) were just as likely to stay within the forage as leave for the meadow. Therefore, even though the forage populations performed similarly to the meadow ones, their residents still frequented the meadow area. We have no way of telling whether or not this is the result of dispersal to the meadow habitat, resource supplementation (Dunning *et al.* 1992), the occurrence of disjunct home ranges (*see* Madison 1985) and/or home range shifts between the two areas (*see* Myllymäki 1977). No matter the cause, it indicates that voles in the forage area used the meadow habitat to fulfill some aspect of their life history.

In using a probability index to measure edge permeability, we assumed that the voles had an equal probability of exhibiting any given type of movement event. In other words, the null hypothesis tested was that voles from any given plot had the same probability of moving within that plot as leaving for one of the other two. Deviations from this distribution were related to differences in boundary characteristics. The problem with this assumption is that it did not control for the influence plot population density, physical distance (at this scale) or habitats relative juxtaposition (within the landscape) may have on movement patterns. In other words, a vole's location within the landscape could have influenced its probability to move somewhere else. We address this problem by comparing our empirical data to an expected distribution of movements from a computer simulation. As the two sets of distributions were shown to differ strongly, we conclude that the habitat boundary characteristics were the main parameter influencing the experimental population.

This landscape study elucidated an interest-

Table 4. Multiple pairwise statistical analysis of inter- and intra-plot movement categories were used to compare boundary permeability indices for the forage and meadow plots (non-parametric version of the Tukey test, test statistic = q).

	q	p	q	p	q	p
	FF vs. FM		FM vs. FB		FF vs. FB	
Total	1.21	> 0.5	4.97	< 0.001	6.18	< 0.001
Adult Female	1.10	> 0.5	2.72	< 0.1	3.81	< 0.01
Juvenile Female	2.23	< 0.2	3.00	< 0.005	5.21	< 0.001
	MF vs. MM		MM vs. MB		MF vs. MB	
Total	12.37	< 0.001	16.32	< 0.001	3.95	< 0.01
Adult Female	7.10	< 0.001	8.98	< 0.001	1.91	< 0.2
Juvenile Female	7.10	< 0.001	9.55	< 0.001	2.48	< 0.01
Adult Male	10.47	< 0.001	12.40	< 0.001	1.93	< 0.2
Juvenile Male	6.71	< 0.001	7.62	< 0.001	0.92	> 0.5

ing and potentially detrimental boundary dynamic. It seems apparent that vegetative boundaries served as a deterrent for the voles living in every plot. Boundary distinctness appeared to be the greatest predictor of its permeability. For example, in the low quality barley plot, the distinct boundary it shared with the higher quality meadow served as an effective isolating mechanism. In farm landscapes, barley areas may therefore serve as giant mousetraps, spatially and functionally severing their occupants. More generally, as the number of edges multiply with increased fragmentation, overall landscape connectivity may decrease. Kozakiewicz *et al.* (1993) found contrasting results for bank voles traveling among elements of a mixed agricultural/forest landscape in Poland. However, despite having shown bank voles to move further in mixed habitats, they indicated neither variety nor habitat quality of a single agricultural crop the voles crossed nor did they measure the influence of its edge permeability.

Most landscape studies focus on suboptimal inter-patch habitats only so far as it concerns an animal's utilization of component patches (e.g., Merriam 1984, Schreiber 1988, Hansson 1991, Saunders & Hobbs 1991, Taylor *et al.* 1993, Lidicker 1995). By de-emphasizing the importance and abundance (Andrén 1994) of matrix habitats, such an approach glosses over a potentially significant element(s) of landscape level dynamics (Wiens *et al.* 1993). Matrix habitats can make important contributions to animal survival (Szacki *et al.* 1993) and further understanding of their role in landscape ecology is needed.

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