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Effects of corridor width and presence on the population dynamics of the meadow vole *(Microtuspennsylvanicus)*

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Abstract

We tested the effects of increased landscape corridor width and corridor presence on the population dynamics and home range use of the meadow vole *(Microtuspennsylvanicus)* within a small-scale fragmented landscape. Our objective was to observe how populations behaved in patchy landscapes where the animals home range exceeded or equaled patch size. We used a small-scale replicated experiment consisting of three sets of two patches each, unconnected or interconnected by l-m or 5-m wide-corridors, established in an old-field community (S.W. Ohio). Control (O-m) treatments supported significantly lower vole densities than either corridor treatment. Females were the dominant resident sex establishing smaller home ranges ($<150 m^2$) than males ($>450 m^2$). Significantly more male voles dispersed between patches with corridors than between patches without corridors. However, no difference was observed regarding the number of male voles dispersing between patches connected by corridors when compared to the number dispersing across treatments. Dispersal between connected patches was restricted to corridors based on tracking tube data. Corridor presence was more important than corridor width regarding the movement of male voles within their home range.

1. Introduction

There exists a paucity of information regarding the function of landscape corridors on dispersal behavior (Noss 1983; Harris 1985; Forman and Godron 1986; Harris and Gallagher 1989). Wegner and Merriam (1979) observed that birds and small mammals utilized fencerows of various types. Fahrig and Merriam (1985) concluded that small mammal populations within isolated woodlots have lower rates of population increase than populations within woodlots interconnected by fencerows. Henderson *et al.* (1985) observed that chipmunks (*Tamias striatus)* readily recolonized woody patches following local extinctions if patches were connected by fencerows. Although corridor use has been investigated, spatial factors affecting corridor use have been poorly documented.

Investigations of corridor use by small mammals have been performed through modeling (Fahrig and Merriam 1985; Henein and Merriam 1990) and, recently, through field experiments (Lorenz and Barett 1990). Models of population stability within various landscape matrices, generated from and tested against field observations (Lefkovitch and Fahrig 1985; Fahrig and Merriam 1985), predict that population density would be proportional to the number of corridors connecting a patch (*i.e.*, connectivity; Fahrig and Merriam 1985) and increased corridor quality (survival within the corridor; Henein and Merriam 1990). Lorenz and Barrett (1990) found that *Mus musculus* utilize human-made corridors (*i.e.*, split-rail fencing) more frequently than natural corridors (*i.e.*, old-field vegetative strips). Also, Ogilvie and Furman (1959) found that *Microtus montanus* preferred weedy fencerows to bare or shrubby ones as corridors. Geometric features of corridors (*e.g.*, width, length, and height) and their effects on small mammal population dynamics and dispersal behavior have rarely been investigated.

We hypothesized that the presence of corridors and increased corridor width would significantly increase the rate of small mammal dispersal between experimental landscape patches. Here, we define dispersal as the movement by an animal between source and sink patches. Dispersal through a corridor and its relationship to corridor width may be described by random walk theory (Berg 1983) and by patch geometry models (Buechner 1987; Stamps *et al.* 1987a; Stamps *et al.* 1987b; Buechner 1989). Random walk theory (Berg 1983) predicts that a population within a patch consists of potential dispersers that will disperse across random locations along the edge of the patch. Patch geometry models predict that edge permeability is the main determinant of dispersal across the edge of a patch (*e.g.*, Buechner 1987; Stamps *et al.* 1987a). Dispersal from a patch occurs more readily when a patch edge is more permeable to dispersers (*i.e.*, by attaching corridors to the patch edge; Buechner 1987; Stamps *et al.* 1987a, 1987b). However, microtine species infrequently cross edges (*e.g.*, Swihart and Slade 1984) and must, therefore, be provided with an extension of patch habitat to safely disperse between patches. Landscape corridors, theoretically, increase patch edge permeability by extending patch habitat. Connecting patches with a corridor of similar habitat quality would, therefore, extend patch habitat and, theoretically, increase the rate of dispersal. Dispersal between patches by a microtine species should also increase as corridor width increases since the availability of patch habitat within the corridor increases (*i.e.*, as edge permeability increases for this species).

The purpose of this study was to conduct a small-scale replicated field experiment to determine the effects of corridor presence and corridor width on the population dynamics and home range use of the meadow vole (*Microtus pennsylvanicus*) and to evaluate a hierarchy of dispersal routes available to meadow voles in a fragmented landscape. In essence, we were interested in how populations behaved in patchy landscapes where the animals home range exceeded or equaled patch size. The meadow vole was selected as the test species because (a) there exists an abundance of literature describing meadow vole life-history (see Tamarin 1985), (b) meadow voles characteristically produce run-ways (Wolff 1985) in which corridor use by voles could be measured through tracking tube analysis (Fahrig and Merriam 1985), and (c) meadow voles have been identified as interior species of dense grassland habitats (Getz 1985). The effects of corridor width and presence on *Microtus* dispersal behavior should provide a better understanding of small mammal population dynamics within fragmented landscapes.

2. Materials and methods

2.1. Study area

The study was conducted in a 2.5-ha old-field community dominated by goldenrod (*Solidago* spp.) and alfalfa (*Medicago sativa*) located at the Miami University Ecology Research Center near Oxford, Ohio, U.S.A. (Fig. 1). The old-field was heavily seeded with red clover (*Trifolium pratense*) and orchard grass (*Dactylus glomerata*) on 15 April 1990 using a no-till planter to assure dense cover and vegetative homogeneity between patches and treatments and provide a high-quality food source. Litter was virtually absent due to previous agricultural activity. Straw was spread (one bale per patch) to compensate for the scant litter. No fertilizers, insecticides, or herbicides were used during the study. Resident small mammals were live-trapped and removed from each experimental patch between 1–8 July 1990.

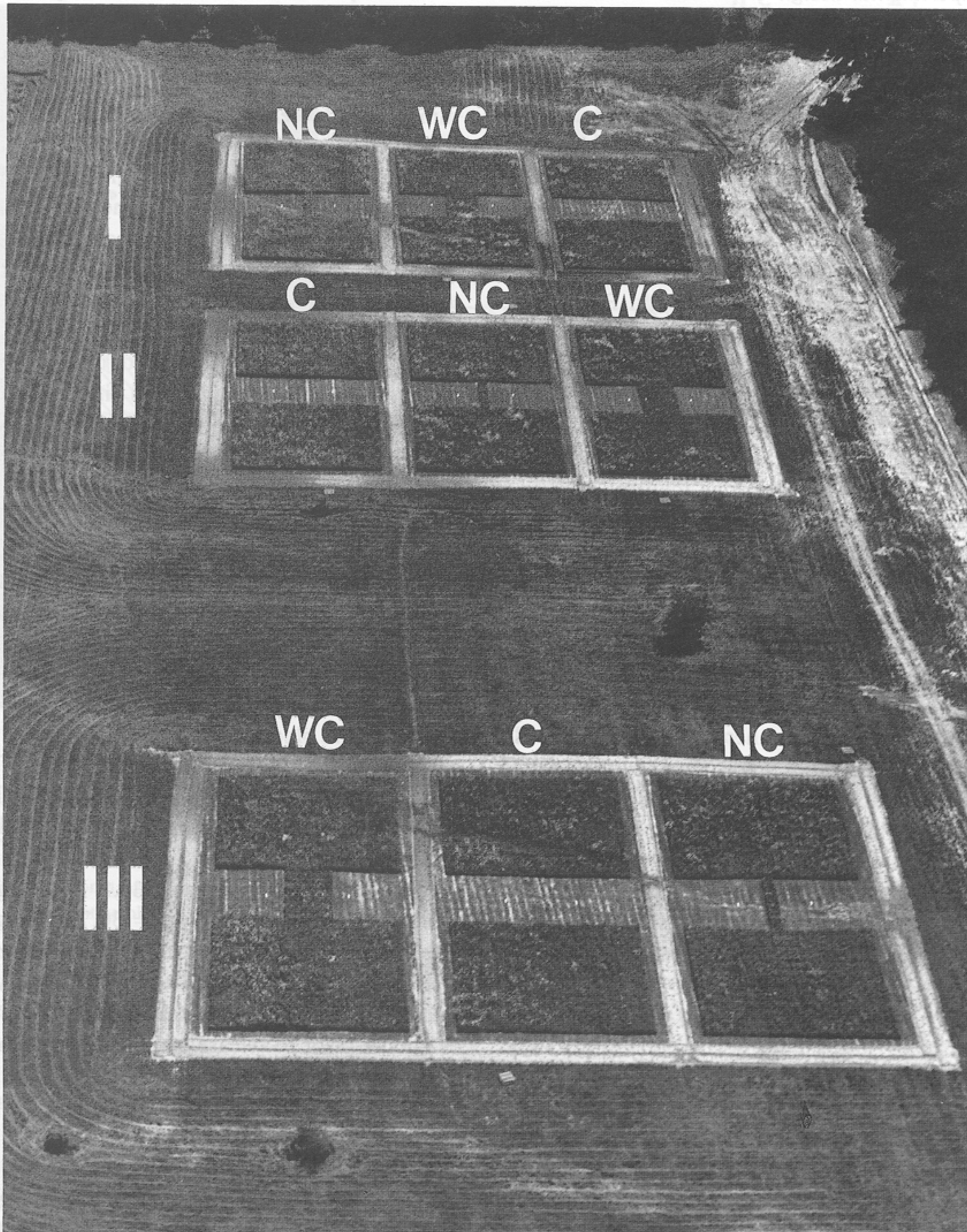

Fig. 1. Aerial photograph depicting the replicated experimental design used to evaluate the effects of corridor width and presence on the population dynamics of the meadow vole. Roman numerals identify treatment blocks. Treatment type is designated by the following; C = controls (no corridor), NC = narrow-corridor (1-m), and WC = wide-corridor (5-m). Distance between blocks I and II was 20 meters and between blocks II and III was 75 meters.

2.2. Experimental design

A three by three randomized complete block design was used (Fig. 1; Hurlbert 1984). Treatments were randomized within the three blocks. A treatment consisted of two patches (one 20-m x 20-m source patch and one 20-m x 20-m sink patch) unconnected or interconnected by a 10-m long corridor (Fig. 2). The patch where voles were initially released was identified as the source patch whereas the empty patch was identified as the sink patch. Patch size ($400 m^2$) was approximately equal to reported minimum home range size ($405 m^2$) for male voles, and greater than minimum home range ($160 m^2$) for females (VanVleck 1969). Source patches alternated between treatments within blocks. Treatments differed based on corridor type (control, no corridor; narrow-corridor, 1-m wide; and wide-corridor, 5-m wide). A treatment, hereafter, is defined as two patches either unconnected or interconnected by a 1-m or 5-m wide corridor.

Experimental treatments were maintained by mowing the surrounding vegetation of each patch and corridor weekly. Treatments within blocks were isolated from each other by a 3-m wide tilled strip (Fig. 2). Each block was isolated from the surrounding habitat by a 6-m wide strip tilled bimonthly. A 10-m wide area of vegetation was mowed periodically around each block to increase block isolation. Tilled (Harper 1990, Mader 1984) and mowed (Cole 1978) strips have been shown to be effective barriers for isolating small mammal populations.

2.3. Census procedures

Nine Sherman live-traps were placed, diagonally, two meters from nine regularly spaced markers (one trap per marker) within each patch (Fig. 2). Traps were rotated alphabetically between diagonals (see enlargement, Fig. 2) on a weekly schedule to prevent trap habituation (VanVleck 1969). Traps were baited weekly with crunchy peanut butter. Non-absorbant cotton was also added for bedding. Traps were set at 1900h and checked at 0700h three times weekly on alternating nights beginning on Sunday of each week between 9 July and 28 October 1990.

Live trapping was used to identify individual dispersers and residents (Verner and Getz 1985), to estimate mean weekly population densities using the calendar-of-catches method (Petrusewicz and Andrzejewski 1962), and to estimate home range size using the minimum-area method (VanVleck 1969). No trapping was conducted within corridors because we were concerned that traps might affect dispersal behavior or the frequency of corridor use (VanVleck 1969). Instead, tracking tubes (Fahrig and Merriam 1985) were used to monitor vole movement between source and sink patches (Fig. 2). Although individual vole identification was not possible using this technique, corridor use was quantified as to the presence or absence of visible prints (per checking period) left on a 5-cm x 27-cm sheet of white paper placed within each tube. Prints were made legible by placing black powdered paint in the middle of the paper. One tube was placed per meter of width within each corridor; two tubes were placed in the mowed areas between patches and near each corridor. Thus, an equal number of tubes ($N = 6$) were placed within corridors as were placed outside of corridors within each block of treatments (Fig. 2). Tubes were maintained continuously throughout the study and checked 3–4 times weekly.

Three adult male (mass = 38.8 ± 12.5 g **S.D.**) and three adult female (mass = 30.7 ± 9.6 g **S.D.**) lab-bred meadow voles (***Microtus pennsylvanicus***) were released in each source patch on 9 July 1990. Voles were acclimatized to field conditions for 12 hours prior to release by placing them in open-bottom cages (560 x 560 x 40-cm) located within each source patch. Toe-clipping was used to identify individual voles. Live-trapped voles were identified, weighed, sexed, breeding condition determined, and released at site of capture. Weight was used to age voles (Getz ***et al.*** 1978) and detect the onset of pregnancy (Krebs ***et al.*** 1969). Breeding condition (Hasler 1975) for males was either scrotal or non-scrotal and for females was either perforate vagina, non-perforate vagina, pregnant, or lactating mammae. Non-microtine mammals captured during the study were removed. Voles were re-

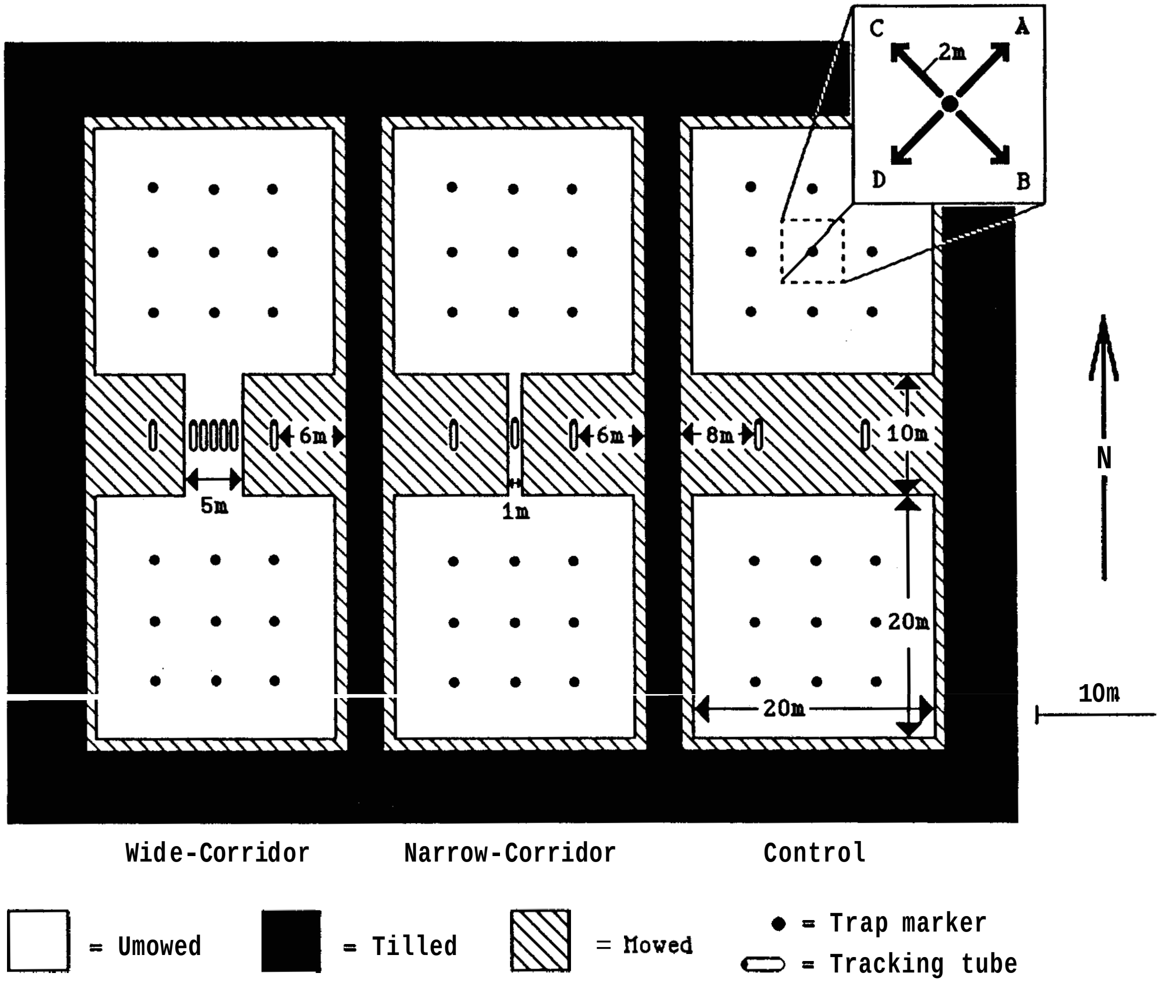

Fig. 2. Trap location, trapping regime (letters within enlargement), tube placement, and treatment dimensions for patches and corridors within **a** representative block.

moved from all experimental patches between 28 October and 10 November 1990.

2.4. Vegetation sampling

Vegetation and litter within each patch and corridor were sampled to estimate plant cover density, patch homogeneity, and ground litter. Vole population dynamics have been found to be related to changes in plant density (see Getz 1985; Birney *et al.* 1976). Vegetation within each patch and corridor was sampled twice (17–18 July and 28–30 August 1990) using the point-contact method (Levy and Madden 1933). **A** Levy and Madden (1933) sampler was modified to accommodate the robust vegetation within the patches and corridors. Five metal pins (0.5-cm dia x 92.5-cm long dowel) were inserted (20-cm apart) through a three-sided frame (1 x 1 x 1-m) placed vertically within the vegetation. Nine samples **(45** points) per patch and three samples (15 points) per corridor were taken on each sampling date. Each component of vegetation contacting a pin was counted and identified to species. Cover contributed by litter was estimated by scoring whether a dowel made a final contact with soil or litter.

A Relative Importance Value (RIV) was calculated for each plant species based on the formula:

$$\mathrm{RIV} = \frac{(\mathrm{PCS} + \mathrm{ACS})/2}{\Sigma(\mathrm{PCS} + \mathrm{ACS})/2} \times 100,$$

where Σ is the summation over all species within the sample. PCS (percent cover per species) was estimated on the number of times each species (including litter) contacted a pin divided by the total number of times all species (including litter) contacted a pin. ACS (percent area covered per species) was estimated based on the number of pins contacted by each species (including litter) divided by the total number of pins sampled. Simpson's inverse (1/C) and Shannon's exponentiated (exp H') diversity indices (Peet 1974), based on PCS, were used to describe vegetative composition within each patch and each corridor. RIV, 1/C, and exp H' were compared for patches within treatments, between treatments, and between blocks.

2.5. *Statistical analysis*

Voles were classified as residents, dispersers, or recruits. A resident was a vole that resided within a patch for a minimum of five consecutive days as determined by the calendar-of-catches method (Petrusewicz and Andrzejewski 1962). A disperser was a vole that dispersed from a patch regardless of destination. Dispersers were subclassified as to where they dispersed: alpha-disperser, to patches within treatments; beta-disperser, to patches between treatments; and gamma-disperser, to patches between blocks. Wild or unmarked juvenile voles were defined as recruits. Since most juvenile and sub-adult voles were trapped once, only an age comparison between recruits was possible. Voles were pooled by sex for all other analyses, because few juvenile and sub-adult voles were retrapped to permit adequate comparisons between age groups. A two-way ANOVA (SAS 1985) was used to compare differences between treatments, sexes, and interactions between treatments and sexes for residents, recruits, and dispersers. A second two-way ANOVA was performed to compare disperser-types between sexes and treatments. Duncan's multiple range test was performed on each single effect to identify significant pairwise differences. Bonferroni adjusted t-tests were used to isolate significant interactions. Differences in home range size between male and female voles were tested using a Student t-test. A MANOVA repeated measures analysis (SAS 1985) was used to test the hypothesis that vole population densities did not differ between treatments.

Tracking tube data were compared between treatments and between tube location (Fig. 2) based on the average number of tubes per treatment containing identifiable prints. A second analysis was used to compensate for differences in the number of tubes used within narrow and wide corridors. Tubes within the wide corridors were collectively treated as one tube and not averaged (*i.e.*, at least one tube in the corridor showed evidence of use). A two-way ANOVA was used to test the hypotheses that there was no difference in tracking tube use between treatments, between tube position, and the interaction between treatments and tube position.

Chi-square test of homogeneity (McClave and Dietrich 1985) was used to test the null hypothesis that vegetative cover was homogeneous between patches, treatments, and blocks of treatments. Homogeneity tests were based on the number of pins contacted by each plant species (*i.e.*, the best measure of cover distribution; Levy and Madden 1933). Species were pooled based on RIVs to decrease the amount of error in the Chi-square homogeneity test. Four pooled categories were constructed: dominants (species with the top three RIVs), non-dominants (remaining species), standing dead, and litter. Simpson's (1/C) and Shannon's (exp H') diversity indices were compared using a Student t-test for comparisons between patches and a one-way ANOVA for comparisons between treatments and blocks.

3. Results

3.1. *Vegetation analysis*

Percent relative cover per patch increased significantly ($P < 0.05$) between sampling periods for all treatments, but did not differ significantly ($P > 0.25$) between treatments for the July ($F_{2,15}$ =

Table 1. Mean (± S.E.) cover density (%), mean (± **S.E.**) Simpson diversity index (1/C), mean (± S.E.) Shannon apportionment index (exp H'), and Chi-square test of homogeneity of pooled species composition† between treatments (control, narrow-corridor, and wide-corridor) and blocks of treatments (I, II, III; Fig. 1) for 17–18 July and 28–30 August 1990. Statistical results are for comparisons within treatments and between blocks of treatments (Duncan Multiple Range test).

	Treatment			Block		
	Control	Narrow Corridor	Wide Corridor	I	II	III
17–18 July 1990						
Cover Density (%)	209.0 ± 9.6	218.3 ± 14.7	222.2 ± 15.4	213.2 ± 14.5	222.3 ± 10.4	214.0 ± 15.2
Simpson's Diversity	3.33 ± 0.24	4.41 ± 0.42	4.43 ± 0.54	3.90 ± 0.20	4.57 ± 0.55	3.68 ± 0.50
Shannon's Diversity	4.89 ± 0.35	6.43 ± 0.58	6.25 ± 0.76	5.66 ± 0.35	3.37 ± 0.85	5.35 ± 0.59
Chi-square (df)		5.79 (6) NS ††			11.10 (6) NS	
28–30 August						
Cover Density (%)	236.5 ± 6.3	250.3 ± 19.0	272.0 ± 14.5	240.2 ± 19.1	265.3 ± 12.6	253.7 ± 12.4
Simpson's Diversity	3.24 ± 0.24	3.68 ± 0.39	3.87 ± 0.39	3.67 ± 0.46	3.33 ± 0.21	3.80 ± 1.35
Shannon's Diversity	5.05 ± 0.52	5.28 ± 0.46	5.63 ± 0.47	5.80 ± 0.63	4.82 ± 0.26	5.35 ± 0.43
Chi-square (df)		4.77 (6) NS			8.16 (6) NS	

† Based on the number of pins a plant species contacted per treatment or block.
†† NS = not significant ($P > 0.05$).

0.27) or August ($F_{2,15} = 1.60$) sampling periods (Table 1). Vegetative cover during July was dominated by red clover (***Trifolium pratense;*** RIV = 41.4%, 31.4%, and 31.1%) and goldenrod (***Solidago*** spp.; RIV = 12.9%, 19.6%, and 14.5%) for control, narrow-corridor, and wide-corridor treatments, respectively. In August, contribution to the cover by ***T. pratense*** decreased (RIV = 32.1%, 24.8%, and **30.3%),** whereas *Solidago* spp. (RIV = 22.4%, 23.9%, and 16.1%) and standing dead (RIV = 14.7%, 16.4%, and 18.1%) increased for each treatment, respectively. No differences in species composition or total vegatative cover were observed between blocks of treatments (Table 1). Plant community diversity (1/C, exp H') did not differ between treatments or blocks of treatments (Table 1). Chi-square analysis between patches within treatment replicates revealed no significant differences between patches (Table 2). Source and sink patches within treatment replicates were pooled for final analysis since no significant differences were found between patches.

3.2. Vole population dynamics and home range use

Source and sink patches were pooled since no differences in vole densities between patches were observed beginning on 29 July 1990 (Fig. 3). Each treatment significantly increased in mean vole population density ($F_{28} = 3.02$; $P < 0.001$) over the duration of the study (Fig. 4). Both narrow and wide-corridor treatments had consistently higher mean densities of voles than controls, and maintained significantly higher mean densities during the last three weeks of October (narrow: F,,,, = 137.7, $P < 0.001$; wide: $F_{2,12} = 94.71$, $P < 0.001$). No difference in vole densities was evident between narrow and wide-corridor treatments ($F_{2,12} = 0.73$; $P > 0.40$) throughout the study.

Overall (8 July–28 October 1990) mean number of recruits per patch did not differ significantly between control (% = 1.9), narrow-corridor (% = 2.4), and wide-corridor ($\bar{x} = 2.6$) treatments ($F_{2,61} = 2.01$; $P > 0.05$). There was no significant difference between the number of male and female recruits within treatments $F_{2,61} = 0.08$; $P > 0.05$). No differences between adult, sub-adult, and juvenile recruits were observed for control and

Table 2. Chi-square test of homogeneity for species composition between patches within control, narrow-corridor, and wide-corridor treatments regarding the number of pins contacted by each species (pooled).

Treatment	Control (N = 3)			Narrow-Corridor (N = 3)			Wide-Corridor (N = 3)		
July 17–18									
No. of pins contacted									
χ^2 =	2.21	1.18	0.37	6.62	1.78	1.02	2.50	2.22	3.93
df =	3	3	3	3	3	3	3	3	3
P =	NS	NS	NS	NS	NS	NS	NS	NS	NS
August 28–30									
No. of pins contacted									
χ^2 =	0.64	2.76	2.46	0.97	1.46	1.05	7.45	2.74	1.31
df =	3	3	3	3	3	3	3	3	3
P =	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS = not significant ($P > 0.05$).

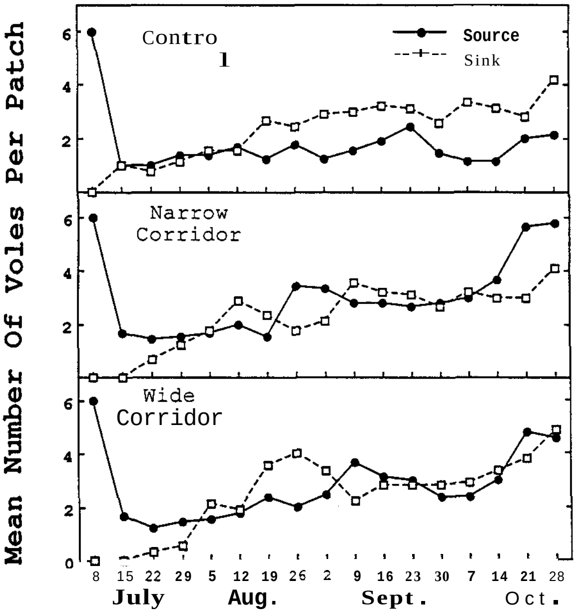

Fig. 3. Mean weekly density of voles for both source and sink patches within control, narrow-corridor, and wide-corridor treatments between 8 July and 28 October 1990.

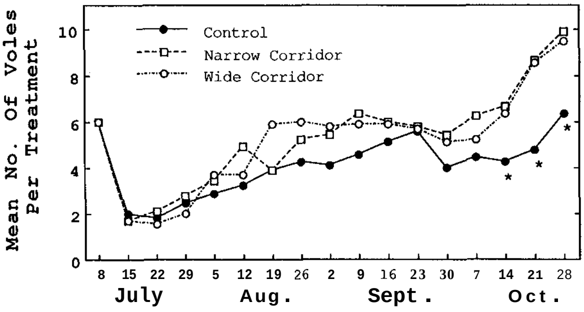

Fig. 4. Mean weekly meadow vole population density estimates for control, narrow-corridor, and wide-corridor treatments between 8 July and 28 October 1990. Asterisks denote significant differences ($P<0.01$) between control and both corridor treatments.

narrow-corridor treatments. In wide corridor treatments, however, significantly more male and female adults were recruited than juvenile males or sub-adult females (Fig. 5).

Over the duration of the study significantly more males ($\bar{x} = 2.4, 3.6, 2.8$) than females ($\bar{x} = 1.3, 1.1, 1.3$) dispersed between patches on all treatments ($F_{1,77} = 31.22$; $P < 0.05$). No significant difference was observed between treatments for females concerning the number of alpha, beta, and gamma-dispersers (Fig. 6). Significantly more males dispersed from patches between treatments (beta-dispersal) than from patches within treatments (alpha-dispersal) for control treatments. No differences were observed concerning the number of male alpha- and beta-dispersers between corridor treatments. Male alpha-dispersal, however, was significantly greater in narrow-corridor treatments than wide-corridor or control treatments. Gamma-dispersal by male and female voles was rare (Fig. 5); however, more females than males dispersed between blocks.

There was no significant difference ($F_{2,98}$ =

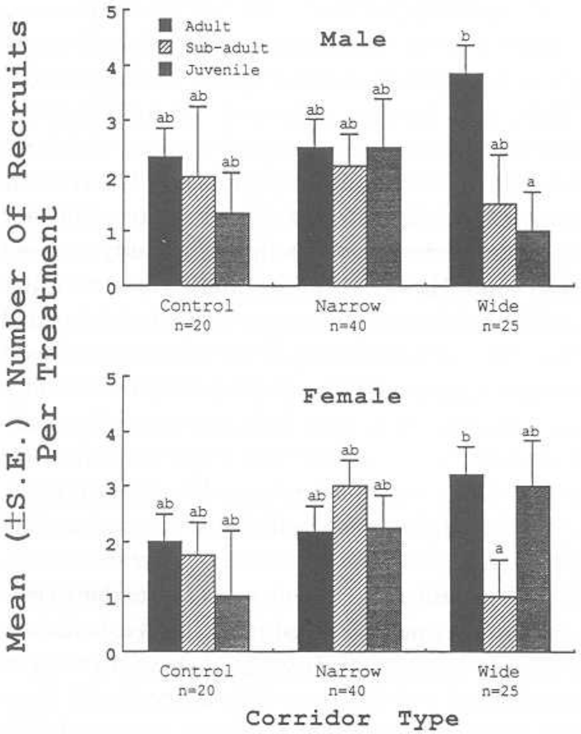

Fig. 5. Mean (± S.E.) number (per patch) of male and female adult (>28.1 g), sub-adult (19.1–28.0 g), and juvenile (<19.0 g) voles recruited within control, narrow-corridor, and wide-corridor treatments. Bars with same letters are not significantly different (P>0.05).

1.55; P > 0.05) in the mean number of residents per source or sink patch within treatments, either for males ($\bar{x}$ = 3.8, 4.2, 4.0) or females ($\bar{x}$ = 3.3, 4.8, 4.3). Females resided in patches more frequently than males in all treatments, but this was significant only in narrow-corridor treatments (Fig. 7). The number of male and female residents did not differ significantly between treatments. Male voles resided in source and sink patches for shorter durations than females. Resident males also had significantly (t = 4.15, df = 55, P < 0.001) larger home ranges (N = 26; $\bar{x}$ = 463.6 ± 85.0 m^2 ± S.E.) than females (N = 31; $\bar{x}$ = 136.0 ± 13.1 m^2 ± S.E.). Also, most male voles established home ranges consisting of two or more patches (N = 24, 92%), whereas most females established home ranges within a single patch (N = 22, 71%). Mean male home range was 12.5% larger than patch size whereas mean female home range was 66.0% smaller than patch size.

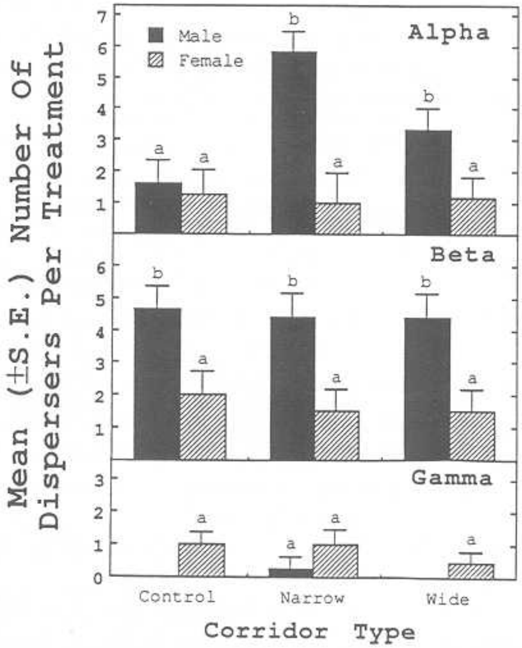

Fig. 6. Mean (± S.E.) number of male and female voles dispersing between patches within treatments (alpha), between treatments (beta), and between blocks (gamma). Bars with same letters are not significantly different (P>0.05).

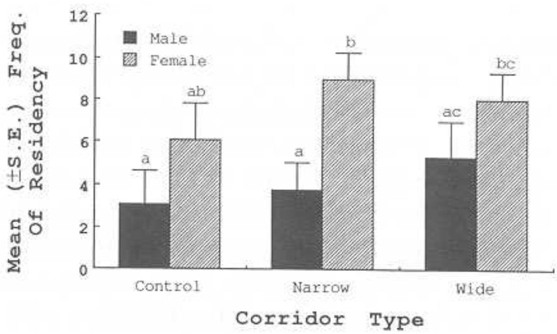

Fig. 7. Mean (± S.E.) frequency of residency for male and female voles in control, narrow-corridor, and wide-corridor treatments. Bars with same letters are not significantly different (P>0.05).

3.3. Tracking tube results

Tracking tubes within narrow corridors were used more frequently than tubes in wide corridors. However, tubes in both corridors were used more frequently than all exterior tubes. When tubes in wide-corridors were corrected for differences in tube density per corridor, no significant difference

Table 3. Mean percent (± S.E.) of tubes with prints for corridor interior and exterior tube checked between 8 July and 28 October 1990 (in parentheses) for all treatments. Values with different letters are significantly different ($P < 0.05$).

	Tubes	
Corridor Type	Interior	Exterior
Control	NA† (N = 0)	0.8 ± 0.4 A (N = 96)
Narrow	32.1 ± 0.7 B (N = 48)	0.0 A (N = 96)
Wide	21.3 ± 1.9 C (N = 240)	0.5 ± 0.3 A (N = 96)
Wide††	30.3 ± 2.2 B (N = 48)	

† No interior tubes existed for controls.
†† Tubes in wide-corridors were treated collectively as one tube.

in tube use was found between corridor types (Table 3). Evidence of tube use between control patches was rare ($\bar{x} = 0.8$); tubes located outside corridors were never used.

4. Discussion

The use of controlled replicated field experiments to study small mammal population dynamics and home range use at the simulated landscape level has rarely been performed (but see Lorenz and Barrett 1990). Such experiments are difficult to perform since landscapes often encompass a number of diverse ecosystems (*i.e.*, landscape patches) which are difficult to duplicate (Risser 1985). However, to test and evaluate landscape principles (Risser *et al.* 1984), investigations at small landscape scales are needed. The use of landscape corridors as dispersal conduits for movement within a home range, including factors affecting this use, can be evaluated by performing field experiments within replicated small-scale landscapes (*i.e.*, patches with variable connectivity). Our study employed a controlled replicated field experiment using a two-patch system, unconnected or interconnected by a single corridor, to evaluate the effects of corridor width and presence on the population dynamics and home range use of the meadow vole (*Microtus pennsylvanicus*).

The immediate loss of voles initially released into source patches may have been attributed to exploratory behavior, habitat quality, and predation. Voles used in this study were lab-bred and unfamiliar with the experimental patches which enhanced the likelihood of exploratory behavior. It may be possible to suppress exploratory behavior by either increasing the scale of the study or using wild voles. However, further study is needed. Litter and vegetative cover were sparse in all experimental patches early in the study when voles were released despite seeding and the addition of straw. The lack of vegetative cover may have hampered the establishment of nests and "run-way" tunnels. Getz (1960, 1985) observed lower dispersal of *M. pennsylvanicus* from habitats dense in vegetative cover compared to habitats less dense in vegetative cover. Poor vegetative cover made voles vulnerable to predators (*e.g.*, the red-tailed hawk, *Buteo jamaicensis;* American kestrel, *Falco sparverius;* coyote, *Canis latrans*; and feral cat, *Felis domesticus*). Pearson (1966) observed that predators consumed 88% of the peak density (308 per ha) and 27% of the lowest density (3 per ha) of *Microtus californicus*. Although the density of released voles was considered intermediate (18 per ha; this study), the sparse cover early in the study, made voles susceptible to high rates of predation (89% lost).

Vole population densities were greater in treatments with corridors than without corridors. Similar results have been found from model simulations concerning patch connectivity (Fahrig and Merriam 1985) and corridor quality (Henein and Merriam 1990). Fahrig and Merriam (1985) predicted that patches with low connectivity (*i.e.*, few connecting corridors) supported lower densities than patches with high connectivity (*i.e.*, many connecting corridors). Henein and Merriam (1990) also noted that patch densities were higher (including increased survivorship) when patches were connected with high-quality as opposed to low-quality corridors.

Differences in vole densities between corridor and control treatments were attributed to (a) increased dispersal between patches, thereby increasing the rate of patch colonization (Henderson *et al.* 1985) and decreasing any potential effects due to inbreeding (Batzli *et al.* 1977; Bollinger *et al.* 1991),

(b) additional habitat contributed by the corridor itself (Wegner and Merriam **1979**), and (c) increased use of patches, especially by males, for home range establishment. Henderson *et al.* **(1985)** found that patches devoid of *Tamias striatus* were readily colonized when patches were connected by fencerow corridors. We also found that dispersal between patches was greater for patches connected with corridors than those not connected by corridors, although rates of recruitment did not differ between treatments. Thus, habitation of sink patches was not entirely attributed to dispersal from source patches, but also by immigrants from patches in adjacent treatments and/or habitats.

Additional habitat contributed by the corridor itself does not explain differences in vole densities between treatments because patches connected with wide corridors did not support significantly higher densities of voles than patches connected with narrow corridors (see Fig. **3**). Henderson *et al.* **(1985)** and Wegner and Merriam **(1979)** found that *Peromyscus leucopus* and *Tamias striatus* readily colonized and bred within fencerow corridors three meters in width and > 50-m in length. Therefore, the length of the corridors (10-m) established in this study may not have been long enough to permit corridor colonization by meadow voles.

Mean home range size for male voles was four times larger than the mean home range size for female voles and most often consisted of two or more patches as compared to a single patch for females. Our estimate for home range size for male ($\bar{x}$ = 464 m^2) and female ($\bar{x}$ = **136** m^2) voles are within ranges summarized by Madison **(1985)**. Male voles also inhabited more patches for shorter periods of time (*i.e.*, lower frequency of five-day residency) than females supporting the greater frequency of dispersal (*i.e.*, movement between patches) observed for male voles. Madison **(1980)** and Ostfield *et al.* **(1988)** also found that home range overlap in *M. pennsylvanicus* was more frequent between males alone and between males and females than between females alone. We also noted a greater frequency of home range overlap between males alone and between males and females than between females alone. This finding adds credence to previous reports that female *Microtus* defend their home range against other female voles and are the predominant sex residing within defined patches (Madison **1980,** Wolff **1985,** Ostfield *et al.* **1988). As** a result, voles increased their reproductive fitness by having females defend resources during breeding while males mate with various females within their home range (Emlen and Oring **1977).** Therefore, higher vole population densities in corridor treatments than control treatments was likely related to differences in home range establishment and corridor use between sexes.

Based on our research design, voles dispersing within or outside their home range displayed either alpha (between patches), beta (between treatments), or gamma (between blocks) dispersal. More male voles alpha-dispersed in treatments with connected patches, independent of corridor width, than treatments with unconnected patches, suggesting that corridor use at this scale is more dependent on corridor availability than on corridor width. Lorenz and Barrett **1990** also found that house mice (*Mus musculus*) used corridors rather than mowed habitat in a simulated landscape. Vegetative cover within corridors enabled voles to establish "runway" tunnels (Wolff **1988)** which aided the rate of dispersal between source and sink patches. Consequently, the absence of cover between patches hindered alpha-dispersal in control treatments, especially for female voles.

The absence of cover between treatments, however, did not reduce male beta-dispersal. High rates of beta-dispersal by male voles were observed in all treatments. The number of male beta-dispersers was significantly greater than male alpha-dispersers in control treatments. This suggested that the absence of cover between treatments was compensated for by a reduction in dispersal distance (*i.e.*, the probability of survival was higher in the shorter, but less hospitable, tilled borders than in the longer mowed areas between control patches). Since more male voles were found to be continuously moving between patches connected by narrow-corridors than by wide-corridors and since wide-corridors contained more interior habitat than narrow-corridors, it may be that voles perceived wide-corridors more as an extension of patch habitat than as a corridor, per se. A one-meter-wide corridor, therefore, was sufficient to allow dispersal between source and sink patches at this scale.

Gamma-dispersal was rare during this study but occurred more successfully with female voles. Voles exhibiting gamma dispersal displayed behavior characteristic of "movers" identified in other studies (*e.g.*, Lidicker 1985). These voles have been recognized as unsuccessful breeding adults seeking new home ranges in which to breed (Getz 1960; Krebs ***et al.*** 1969; Verner and Getz 1985). We believe that our gamma-dispersers are of similar origin. The importance of landscape features to the movement of these voles remains uncertain. It is evident from this study that small-scale landscape features are not important or recognized by this group of voles.

In conclusion, the population dynamics and home range use of ***M. pennsylvanicus*** within a small-scale landscape were influenced more by the male vole's response to the availability of a corridor than by corridor width for movement within their home range. To increase home range size within these simulated small-scale landscape patches, male voles utilized several patches and chose dispersal routes in which the probability of survival was highest (*i.e.*, long vegetative corridors or short tilled borders). This suggests that management of ***M. pennsylvanicus*** in patchy small-scale landscapes include the establishment of corridors to increase vole survivorship. Managing small mammal populations within small-scale landscapes will, in turn, benefit predatory species dependent on such species for food (Pearson 1966; Korpimaki and Norrdahl 1991). Landscape studies at varying, replicated scales should provide a better understanding regarding the fluxes and redistribution of organisms among landscape elements.

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