

# EFFECTS OF HABITAT PATCH SHAPE ON POPULATION DYNAMICS OF MEADOW VOLES (*MICROTUS PENNSYLVANICUS*)

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The geometry of habitat patches may affect population dynamics due to differences in edge-to-area ratios for patches of different sizes and shapes. We conducted a field experiment replicated over 2 years employing four square (40 by 40 m) and four rectangular (16 by 100 m) habitat patches of equal size (1,600 m<sup>2</sup>) to determine the effects of contrasting shapes of habitat patches on population dynamics of meadow voles (*Microtus pennsylvanicus*). We tested the predictions that dispersal rates would be higher, home ranges larger, and population densities lower in rectangular patches compared to square patches. The number of dispersers, but not dispersal rates, was greater in rectangular patches than in square patches only when densities of voles were low. Home ranges were of equal area but different shape in the contrasting shapes of patches. Population density, recruitment, body mass of dispersers, body mass of residents, survival, and age structure were largely unaffected by differences in patch shape. Thus, plasticity of behavior (e.g., changes in shape of home range) appears to have prevented differences in population dynamics between the two patch shapes. We conclude that patch shape does not markedly affect the population dynamics of the meadow vole, and that this species appears to be an edge-tolerant species.

**Key words:** *Microtus pennsylvanicus*, dispersal, edge effects, habitat fragmentation, meadow vole, patch shape, population ecology

Human activities have led to extensive habitat fragmentation and, consequently, patches of natural habitat have become prominent structural features of landscapes (Forman and Godron, 1986). Although scientists have begun to address the biological changes that can occur (e.g., Forman and Godron, 1986; Wilcox and Murphy, 1985), the ecological consequences of habitat fragmentation and isolation remain poorly understood (Simberloff and Abele, 1982). Of particular importance are the effects of changes in geometry of habitat patches (i.e., size and shape of patches—Foster and Haines, 1991; Simberloff, 1988) and connectivity (i.e., habitat corridors—Harris, 1984). Whereas the structure and function

of landscape corridors have received increased attention (Harris and Gallagher, 1989; Lorenz and Barrett, 1990), the role of patch geometry, especially patch shape, remains poorly investigated.

Since Leopold's (1933) initial documentation that edges tend to support greater diversity of wildlife than the interior of patches, edge effects generally have been considered beneficial. However, recent studies of plant and nongame species of animals have revealed many characteristics of edges considered to be undesirable, including increased predation, parasitism, and herbivory (Alverson et al., 1988; Harris, 1988; Laudenslayer, 1986; Temple and Cary, 1988; Yahner, 1988). The geometry

of habitat patches may be an ecologically important factor because patches of different sizes and shapes differ in edge-to-area ratios. Thus, small or narrow patches contain greater amounts of habitat edge per area than do large or square patches, and differ theoretically in the diversity of species they can support.

Even in the absence of vegetational edge effects, the geometry of uniformly high-quality patches of habitat may directly influence population dynamics and dispersal behavior of animals. For example, Stamps et al. (1987a) demonstrated with simulation models that habitat geometry and edge permeability (i.e., edge hardness) can have major effects on rates of emigration from uniformly high-quality patches. These models indicate that the proportion of home ranges at the edge of a patch is positively related to the proportion of dispersers emigrating from that patch (Stamps et al., 1987a). Furthermore, animals in small, elongated, soft-edged patches (i.e., bounded by habitat that emigrants are able to cross) are predicted to defend larger territories (Stamps and Buechner, 1985) and to suffer fewer visits from intruders (Stamps et al., 1987b) than animals in larger, square patches. Detailed field studies are needed to test these simulation models. The degree to which fragmentation affects a population depends, in part, on the dispersal characteristics of that species. Thus, patches may be less isolated in space and time if individuals are able to disperse successfully from one patch to another. Despite general agreement concerning the importance of dispersal (e.g., Soulé, 1980), few studies have specifically examined how it is affected by habitat patches of different sizes and shapes.

Microtine rodents are ideal for evaluating the effects of habitat geometry on dispersal due to the wealth of information regarding the dispersal behavior of these species (see review by Lidicker, 1985). Male voles tend to disperse more frequently than females (Kozakiewicz, 1976; Myers and Krebs, 1971; Tamarin, 1977) and dispersal is bi-

ased in favor of younger individuals (Gaines and Johnson, 1987). Since dispersers often are a nonrandom subset of the population, dispersal can affect the age structure, natality and mortality rates, and sex ratios of the population (Lidicker, 1985). However, we know of no empirical study that has attempted to determine the effects of shape of habitat patches on the dispersal characteristics of microtines.

The purpose of this study was to determine the effects of patch shape on the dispersal behavior and population dynamics of the meadow vole (*Microtus pennsylvanicus*). We employed equal-area square and rectangular patches of habitat to test three hypotheses. First, based on the hypothesis that patches with high edge-to-area ratios have increased rates of dispersal (Stamps et al., 1987a), we predicted that a greater proportion of individuals would disperse from rectangular patches than from square patches. Second, based on the hypothesis that home ranges increase within patches with high edge-to-size ratios (Stamps et al., 1987b), we predicted that home ranges would be larger for residents in rectangular patches compared to square patches. Third, due to increased rates of dispersal and sizes of home ranges, we hypothesized that fewer individuals could be supported within patches with high edge-to-size ratios; therefore, we predicted that rectangular patches would have lower population densities compared to square patches.

#### MATERIALS AND METHODS

This study was conducted during 1989 and 1990 at the Miami University Ecology Research Center, located near Oxford, Ohio (39°30'N, 84°44'W). A 2.2-ha field (104 by 212 m) was tilled and fertilized (14:14:14, N:P:K; 224 kg/ha) in early May 1989. To establish suitable habitat for meadow voles (e.g., Zimmerman, 1965), the entire field was sown on 19 May 1989 with the following grass-legume mixture (per ha): 8.98 kg meadow fescue (*Festuca elatior*); 4.49 kg timothy (*Phleum pratense*); 3.37 kg red clover (*Trifolium pratense*); 7.85 kg alfalfa (*Medicago sativa*).

Eight 0.16-ha experimental patches were es-

tablished, four patches were square (40 by 40 m; edge-to-area ratio = 0.100) and four patches were rectangular (16 by 100 m; edge-to-area ratio = 0.145; Fig. 1). We wanted to establish patches large enough so that moderate population densities could be supported but small enough to also insure that voles encountered an edge. Based on typical estimates of home ranges for male and female meadow voles (ca. 690 and 160 m<sup>2</sup>, respectively—Gaulin and FitzGerald, 1988), a spatial scale of 1,600 m<sup>2</sup> was selected. Patches were separated by dispersal barriers, with each patch bounded by 3-m-wide strips of mowed vegetation and 2 m of tilled soil. Grassy and tilled strips were maintained by mowing and tilling at weekly intervals throughout the study. The entire study area was bounded by a 5-m tilled border and a ditch (15 cm wide by 60 cm deep).

One disadvantage of isolating populations by using barriers of any type is that immigration and emigration are disrupted; however, populations can still increase via in situ reproduction and decrease if sources of mortality are unaltered. In hard-edged enclosures such as metal-fenced pens, emigration is prevented and dispersal movements must be defined in some artificial manner (e.g., Desy and Batzli, 1989). In soft-edged enclosures, such as the mowed barriers used in this study, emigration can still occur if an individual is motivated to disperse. Because the habitat surrounding the study area was not homogeneous and the arrangement of experimental patches may bias immigration rates, we reduced immigration by establishing a wide-tilled border and ditch around the entire study site. Thus, our experimental design incorporated replicated populations isolated by soft-edged borders to study the effects of shape of habitat patches on within-population processes (recruitment, survivorship, growth rates, sex ratios, age structure) and emigration.

Vegetation was sampled two times each in 1989 (19 July and 25 September) and 1990 (25 June and 2 August). Four samples, each 0.25 m<sup>2</sup>, were harvested from each of the eight experimental patches on each sampling date. Within each patch, two circular quadrats were randomly located in the interior of the patch (i.e.,  $\geq 2$  m from the patch edge) and two were randomly located  $< 1$  m from the patch edge. Standing vegetation was clipped at ground level, sorted to species, oven dried at 80°C for 72 h, and weighed to the nearest

g.

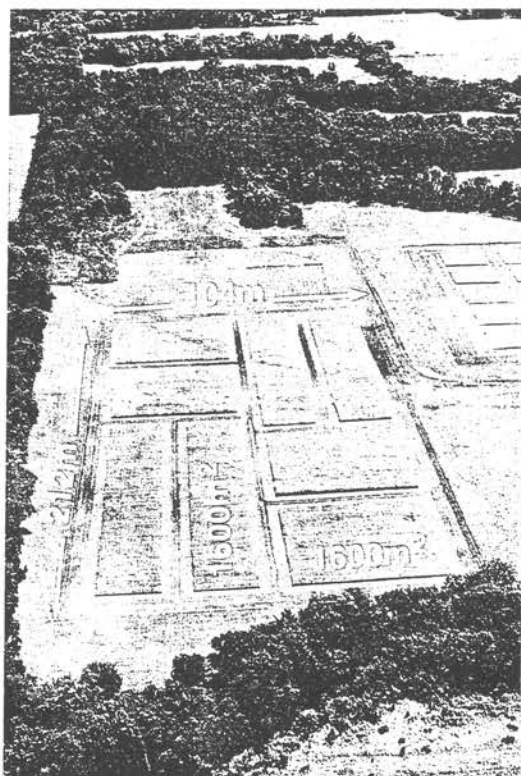


FIG. 1.—Aerial photograph of eight 1,600-m<sup>2</sup> experimental patches of contrasting shape located at the Miami University Ecology Research Center, Oxford, Ohio ( $n =$  four replicates per shape; photograph taken 8 August 1989).

Species richness, species diversity, and indices of community similarity were computed for each patch. Species richness was based on the mean number of species/0.25-m<sup>2</sup> sample. Species diversity was based on the Shannon-Wiener index (Shannon and Weaver, 1964),  $H' = -\sum P_i \log_2 P_i$ , where  $P_i$  is the proportion of total biomass belonging to the  $i^{\text{th}}$  species. Community similarity was based on the Renkonen index (Krebs, 1989),  $RI = \sum \text{minimum}(P_{1i}, P_{2i})$ , where  $P_{1i}$  is the percentage of species  $i$  in community sample 1 and  $P_{2i}$  is the percentage of species  $i$  in community sample 2. Additionally, mean total aboveground biomass of plants, preferred-forage biomass (*Medicago* + *Trifolium* biomass), and litter-mass values were calculated for each patch. Because no edge effects of vegetation were detected, interior and edge samples were pooled. Two-way analysis of variance was used to test for differ-



ences between patch shapes and between study years for each vegetation parameter.

Live-trapping was used to remove any resident voles from all patches before the study was initiated in 1989 and 1990. Traps were set daily until no voles were captured for 5 consecutive nights. Four adult pairs of meadow voles were released into the center of each patch on 29 June 1989 and on 24 April 1990. One additional pair of voles was released into each patch on 26 July 1989 due to low survivorship. Following a local extinction in one rectangular patch, three additional pairs were introduced into this patch on 28 August 1989 to restore its population density to the mean density of the other rectangular patches. Voles were introduced into hardware-cloth cages (1 by 1 by 0.4 m) for 24 h in 1990 to reduce immediate dispersal or predation prior to acclimation. However, low survivorship was again observed and we released three additional pairs into each patch during May 1990. The mean body mass of voles we released did not differ significantly between patch shapes or between study years for either males or females (range, 32–46 g; two-way analysis of variance, all  $F < 1.91$ ,  $P > 0.2$ ). All voles were in breeding condition (i.e., males had descended testes and females had perforate vaginas) prior to release.

Released and newly-captured voles were marked by toe-clipping, sexed, and weighed to the nearest 0.5 g. Breeding condition was determined for males (testes scrotal and non-scrotal) and for females (vagina nonperforate or perforate; embryos present or absent). Animals were classified as juveniles, subadults, and adults based on body mass (<22 g, 22–30 g, and >30 g, respectively—Getz et al., 1978). Age structures of populations within each patch shape were determined weekly and repeated-measures analysis of variance was used to test for differences between patch shapes and between study years for each age class.

Nine trapping stations were permanently located within each patch and two Sherman-type live-traps were located at each trapping station in 1989. Four traps were placed at each trapping station in 1990 due to increased population densities. Trapping stations were located 11-m apart and arranged in a 3 by 3-grid pattern in square patches and a 1 by 9-grid pattern in rectangular patches. Traps were rotated systematically to known distances around each trapping station. Traps were set twice weekly, on consecutive nights

when possible, for 18 weeks in 1989 (until 8 November) and for 26 weeks in 1990 (until 25 October). Traps, baited with peanut butter, were set early in the evening and checked the following morning, cotton was provided for nesting material, and traps were locked open between trapping sessions.

Young voles (<30 g) previously unmarked were classified as recruits (Boonstra, 1985; Dueser et al., 1981). A vole captured in a patch different from the patch where it was previously released or marked was classified as a disperser. By definition, we needed to capture an individual in two patches to classify it as a disperser. This method is more conservative than classifying individuals that are relatively heavy (>30 g) at time of first capture as dispersers (Dueser et al., 1981), and does not confound low trappability of juveniles with dispersal. Voles that remained within the patch where first released or marked were classified as residents. Residents and recruits were released at the capture site, whereas dispersers were removed permanently. By not allowing dispersers to remain within the patch where captured, we prevented these individuals from affecting the dynamics of populations within these patches. Thus, known immigration from one population into another was prevented, just as immigration into the study site had been reduced by the surrounding tilled barrier and ditch.

Per capita rates of dispersal (number of dispersers divided by the number of voles present) and recruitment rates (number of recruits divided by the number of voles present) were calculated weekly and compared between patch shapes and between study years using repeated-measures analysis of variance (SAS Institute Inc., 1982). Mean body mass of residents and dispersers was compared between patch shapes and between study years using two-way analysis of variance for males and females. Similar analyses were performed to test for differences between body masses of residents and dispersers. Overall sex ratios (percent males) were determined for dispersers, residents, and recruits. Chi-square contingency analysis was used to test for significant differences in sex ratios between patch shapes in each study year.

Populations were censused using the calendar-of-catches method (Petrusewicz and Andrzejewski, 1962). Calendars were updated at the conclusion of each year by continuous removal-trapping until no previously marked voles were

captured for  $\geq 3$  consecutive nights. Weekly trapping efficiencies were calculated for each patch by dividing the number of voles captured each week by the number of voles known to be present that week (Krebs et al., 1973). We tested for differences between patch shapes and between study years using repeated measures analysis of variance.

Survival was determined using two methods, survivorship and persistence. Weekly survivorship was calculated as the proportion of animals present at a given week that survived to the next week. Persistence was defined as the number of weeks individuals within a given monthly cohort were present within the same patch. Survivorship curves were computed for each of two monthly cohorts in 1989 (29 June–5 August and 6 August–2 September) and in 1990 (24 April–24 May and 25 May–20 June). Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf, 1981) were used to compare survivorship curves for each monthly cohort of males and females between square and rectangular patches. Animals that dispersed and consequently were recaptured were not included in these analyses.

Home ranges were computed for resident voles captured at least eight times using minimum-convex polygons (Hayne, 1949). Estimates of home range were not affected by the number of captures when eight or more locations were used. Only home ranges of females were analyzed in 1989 because no males were recaptured the minimum number of times. Observed length of range, defined as the maximum linear distance between two capture points (e.g., Renzulli et al., 1980), was determined from trap-location data. Two-way analysis of variance was used to test for differences between patch shapes and between study years for both estimates of home range for males and females.

## RESULTS

Plant communities within square and rectangular patches did not differ significantly between patch shapes with regard to species richness (mean range, 4.94–7.81;  $F = 0.04$ ;  $d.f. = 1,24$ ;  $P > 0.8$ ), species diversity (mean  $H'$  range, 0.56–1.14;  $F = 1.39$ ;  $d.f. = 1,24$ ;  $P > 0.2$ ), total aboveground biomass (mean range 84.8–171.7 g;  $F = 0.28$ ;  $d.f. = 1,24$ ;  $P > 0.5$ ), preferred-forage biomass (mean range 10.4–128.7 g;  $F = 0.47$ ;

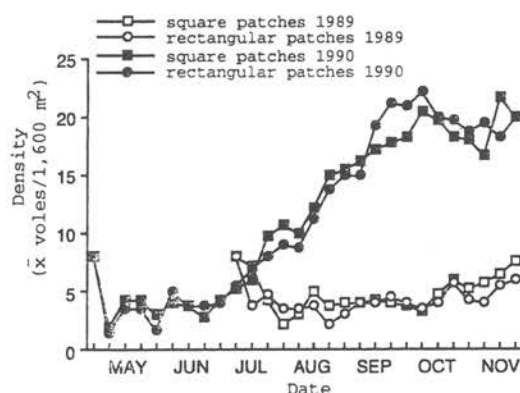


FIG. 2.—Population densities of meadow voles (mean number of voles/1,600 m<sup>2</sup>) in square and rectangular patches during the 18-week study in 1989 and the 26-week study in 1990 ( $n =$  four replicates per shape). Multiply densities by 6.25 to get voles/ha.

$d.f. = 1,24$ ;  $P > 0.4$ ), and litter mass (mean range 2.7–133.8 g;  $F = 0.22$ ;  $d.f. = 1,24$ ;  $P > 0.6$ ). As expected, these variables differed significantly between sampling dates; no significant interactions were detected. Comparisons of community similarity among replicates and between treatments (28 comparisons per sampling date) indicate that all patches were similar with regard to vegetative composition (mean  $RI = 76.5$ ; range, 45.8–98.3).

Population densities of voles declined to low levels (ca. 2 voles/1,600 m<sup>2</sup>) within 3 weeks of release in 1989 and 1990. In 1989, densities remained relatively low throughout the study in both patch shapes. Densities in 1990 were similar to densities in 1989 during the first 9 weeks; however, densities reached levels about three times greater than those attained in 1989 in both patch shapes (Fig. 2). Population densities did not differ significantly between square and rectangular patches ( $F = 0.09$ ;  $d.f. = 1,616$ ;  $P > 0.7$ ), but were significantly greater in 1990 than in 1989 ( $F = 73.77$ ;  $d.f. = 1,616$ ;  $P > 0.001$ ). Because mean values of trapping efficiency each week were relatively high during both years for males (74% in 1989; 59% in 1990) and females (77% in 1989; 73% in 1990),

TABLE 1.—Body masses (g) of dispersing and resident voles in square and rectangular patches.

Year	Sex	Category	Body mass (g)			
			Square		Rectangle	
			$\bar{X} \pm SE$	(n)	$\bar{X} \pm SE$	(n)
1989	male	disperser	40.7 $\pm$ 9.1	(3)	36.2 $\pm$ 2.7	(10)
		resident	31.1 $\pm$ 1.8	(54)	28.1 $\pm$ 1.5	(60)
	female	disperser	31.2 $\pm$ 2.9	(3)	35.0 $\pm$ 2.8	(4)
		resident	31.8 $\pm$ 1.2	(75)	28.9 $\pm$ 1.3	(73)
1990	male	disperser	37.7 $\pm$ 1.6	(26)	39.3 $\pm$ 1.9	(21)
		resident	30.4 $\pm$ 0.9	(168)	31.3 $\pm$ 1.0	(159)
	female	disperser	34.1 $\pm$ 3.3	(11)	32.6 $\pm$ 2.0	(18)
		resident	27.1 $\pm$ 0.8	(164)	27.2 $\pm$ 0.8	(195)

we believe that enumeration methods accurately reflect population densities. Furthermore, trapping efficiencies each week did not differ significantly between square and rectangular patches ( $F = 2.67$ ;  $d.f. = 1, 166$ ;  $P > 0.1$ ).

Populations within both patch shapes were female-biased in 1989 (41.9% male in squares, 45.1% male in rectangles) and differed from a 1:1 sex ratio ( $\chi^2 = 4.69$ ,  $P < 0.05$ ). Populations did not differ from a 1:1 sex ratio in 1990 (50.6% male in squares, 44.9% male in rectangles;  $\chi^2 = 3.71$ ,  $P > 0.05$ ).

The mean number ( $\pm SE$ ) of voles recruited per patch into populations in square patches (12.3  $\pm$  4.2 in 1989, 43.5  $\pm$  9.5 in 1990) and rectangular patches (15.5  $\pm$  3.2 in 1989, 36.3  $\pm$  6.9 in 1990) did not differ significantly ( $F = 0.09$ ;  $d.f. = 1, 12$ ;  $P > 0.7$ ). Significantly more voles were recruited in 1990 than in 1989 ( $F = 16.19$ ;  $d.f. = 1, 12$ ;  $P < 0.01$ ). Per capita recruitment rates, calculated to account for changes in density, were not different between patch shapes ( $F = 0.89$ ;  $d.f. = 1, 537$ ;  $P > 0.3$ ), but were significantly greater in 1990 than in 1989 ( $F = 19.27$ ;  $d.f. = 1, 537$ ;  $P < 0.01$ ). The sex ratios of voles recruited into the populations did not differ from a 1:1 ratio in 1989 (49.7% male in squares, 48.9% male in rectangles;  $\chi^2 = 2.61$ ,  $d.f. = 7$ ;  $P > 0.9$ ) or in 1990 (49.2% male in squares, 44.8% male in rectangles;  $\chi^2 = 5.46$ ,  $d.f. = 7$ ;  $P > 0.6$ ).

The mean number ( $\pm SE$ ) of voles per patch that dispersed from square patches 1.5  $\pm$  0.6 in 1989, 11.3  $\pm$  1.9 in 1990) and rectangular patches (3.5  $\pm$  0.3 in 1989, 10.3  $\pm$  1.5 in 1990) did not differ significantly ( $F = 0.16$ ;  $d.f. = 1, 12$ ;  $P > 0.7$ ). Significantly more voles dispersed in 1990 than in 1989 ( $F = 42.16$ ;  $d.f. = 1, 12$ ;  $P < 0.001$ ). Although the interaction term for the two-way analysis of variance was not significant ( $F = 1.39$ ;  $d.f. = 1, 12$ ;  $P > 0.2$ ), we found that the numbers of dispersers differed between patch shapes in 1989 when each year was analyzed separately using Student's one-tailed  $t$ -tests. Significantly more voles dispersed from rectangular patches than square patches in 1989 ( $t = 2.83$ ;  $d.f. = 6$ ;  $P < 0.02$ ), but not in 1990 ( $t = 0.30$ ;  $d.f. = 6$ ;  $P > 0.03$ ). Per capita rates of dispersal, calculated to account for changes in density, did not differ significantly between patch shapes ( $F = 3.39$ ;  $d.f. = 1, 538$ ;  $P > 0.1$ ), but were significantly greater in 1990 than in 1989 ( $F = 12.03$ ;  $d.f. = 1, 538$ ;  $P < 0.001$ ). Dispersal was male-biased compared to the expected sex ratios of resident voles in the populations in 1989 (50.0% male in squares, 71.4% male in rectangles;  $\chi^2 = 4.11$ ,  $P < 0.05$ ) and in 1990 (70.3% male in square, 53.9% male in rectangles;  $\chi^2 = 5.46$ ,  $P < 0.05$ ).

Mean body mass did not differ between square and rectangular patches for either sex ( $F = 0.04$ ;  $d.f. = 1, 23$ ;  $P > 0.8$  for males;  $F$



= 0.69;  $d.f. = 1,19$ ;  $P > 0.4$  for females; Table 1). Similarly, mean body mass did not differ between 1989 and 1990 for either sex ( $F = 1.30$ ;  $d.f. = 1,23$ ;  $P > 0.2$  for males;  $F = 3.18$ ;  $d.f. = 1,19$ ;  $P > 0.09$  for females). Male dispersers were significantly heavier than male residents ( $F = 10.72$ ;  $d.f. = 1,23$ ;  $P < 0.01$ ), while female dispersers did not differ from female residents with regard to body mass ( $F = 2.04$ ;  $d.f. = 1,19$ ;  $P > 0.1$ ).

Weekly survivorship did not differ between square and rectangular patches ( $F = 1.18$ ;  $d.f. = 1,539$ ;  $P > 0.3$ ), but was significantly greater in 1990 than in 1989 ( $F = 34.29$ ;  $d.f. = 1,539$ ;  $P < 0.001$ ; Table 2). Survivorship was significantly greater for females than males ( $F = 29.91$ ;  $d.f. = 1,539$ ;  $P < 0.001$ ). A significant interaction was found between the variables year and sex ( $F = 27.26$ ;  $d.f. = 1,539$ ;  $P < 0.001$ ), as survivorship of males increased more dramatically between years than did survivorship of females.

Survivorship curves were constructed to estimate persistence of voles in the initial two monthly cohorts in 1989 and 1990 (Fig. 3). Due to small samples, replicates were pooled for each patch shape. Survivorship curves were not significantly different for males or females for any monthly cohort when compared between square and rectangular patches (all largest unsigned differences  $< 0.48$ ; all  $P > 0.05$ ).

Age structures of populations were similar within the contrasting shapes of patches during both study years. Square and rectangular patches did not differ in the percentage of voles captured that were juvenile ( $F = 0.12$ ;  $d.f. = 1,515$ ;  $P > 0.7$ ), subadult ( $F = 1.94$ ;  $d.f. = 1,515$ ;  $P > 0.2$ ), or adult ( $F = 0.58$ ;  $d.f. = 1,515$ ;  $P > 0.4$ ). Between study years, the percentage of voles captured that were juvenile did not differ ( $F = 0.10$ ;  $d.f. = 1,515$ ;  $P > 0.7$ ), while subadults increased ( $F = 11.78$ ;  $d.f. = 1,515$ ;  $P < 0.001$ ) and adults decreased ( $F = 4.20$ ;  $d.f. = 1,515$ ;  $P < 0.05$ ) from 1989 to 1990.

The mean observed length of range for residents was significantly larger in rectan-

TABLE 2.—Weekly survivorship (percent surviving until next trapping period) in square and rectangular patches for male and female voles.

Year	Sex	Weekly survivorship (%) <sup>a</sup>	
		Square	Rectangle
		$\bar{X} \pm SE$	$\bar{X} \pm SE$
1989	male	58.5 $\pm$ 6.8	64.9 $\pm$ 6.4
	female	88.9 $\pm$ 2.1	80.2 $\pm$ 3.5
1990	male	88.1 $\pm$ 1.8	85.7 $\pm$ 2.2
	female	88.2 $\pm$ 1.9	86.6 $\pm$ 2.3

<sup>a</sup> Means based on  $n = 72$  in 1989 (18 week by 4 replicates) and  $n = 104$  in 1990 (26 week by 4 replicates).

gular patches than in square patches ( $F = 49.04$ ;  $d.f. = 1,109$ ;  $P < 0.001$ ) and significantly larger for males than females ( $F = 27.76$ ;  $d.f. = 1,109$ ;  $P < 0.001$ ; see Table 3 for means). The interaction between the variables patch shape and sex was significant ( $F = 9.97$ ;  $d.f. = 1,109$ ;  $P < 0.01$ ). Observed range lengths were significantly smaller for females in 1990 than in 1989 ( $F = 16.11$ ;  $d.f. = 1,82$ ;  $P < 0.001$ ).

Estimates of area of home range based on minimum-convex polygons were not significantly different between patch shapes ( $F = 0.01$ ;  $d.f. = 1,109$ ;  $P > 0.9$ ), but were significantly larger for males than females ( $F = 24.9$ ;  $d.f. = 1,109$ ;  $P < 0.001$ ; Table 3). Areas of home ranges were significantly smaller for females in 1990 than in 1989 ( $F = 11.04$ ;  $d.f. = 1,82$ ;  $P < 0.01$ ).

## DISCUSSION

The prediction that square patches would support a greater population density of meadow voles than rectangular patches was not supported during either year of this study. Population densities in square and rectangular patches remained low throughout the 18-week study in 1989, but reached densities three times greater during the 26-week study in 1990 (Fig. 1). These densities range from low to moderately high compared to reported annual ranges of density for meadow voles (Taitt and Krebs, 1985). Thus, we found that population densities of this species were unaffected by shape of hab-

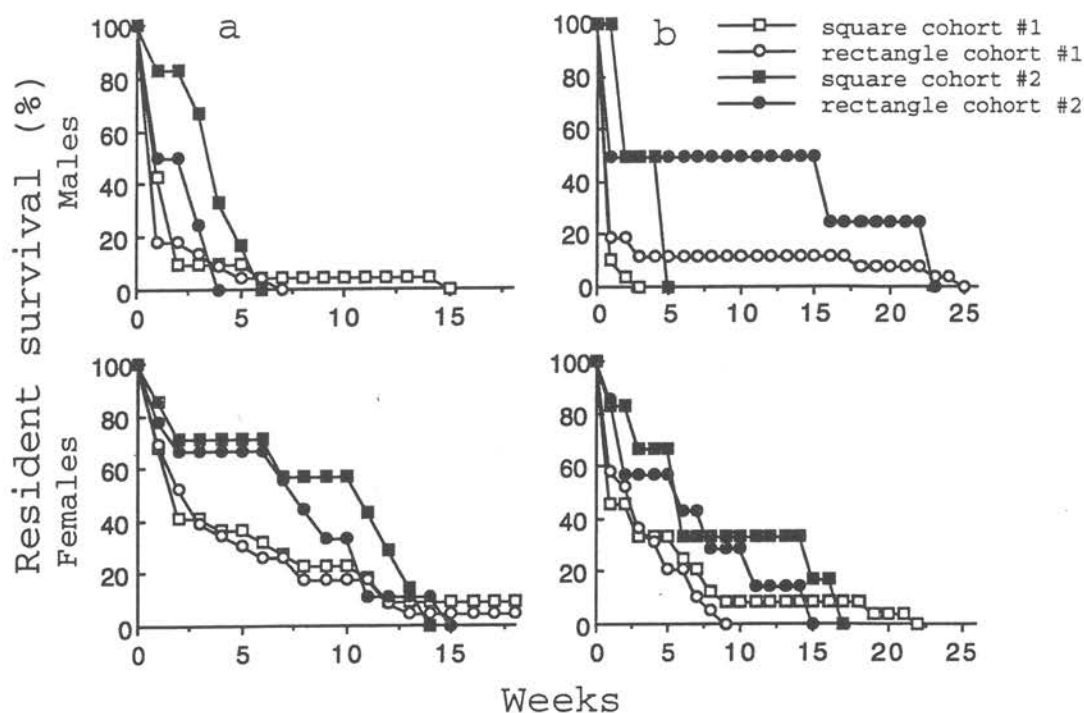


FIG. 3.—Population survivorship curves (percent of known residents surviving) of two monthly cohorts (see text for dates) of male and female meadow voles in patches of contrasting shapes for a, 1989 and b, 1990.

itat patches at this spatial scale. Replication of this study over years of low and high density provided a rigorous test of the prediction that square patches would support higher densities of voles than rectangular patches. We believe that the chosen spatial scale was appropriate to test this prediction. The study design incorporated a difference

in edge-to-area ratio of 45% between square and rectangular patches (0.100 and 0.145, respectively). Furthermore, the width of a rectangular patch was less than typical home-range lengths found for voles in square patches.

One explanation for the lack of difference between population densities in square and

TABLE 3.—Observed length of range and minimum-convex-polygon estimates of home ranges for voles captured in square and rectangular patches.

Year	Sex	Square		Rectangle	
		$\bar{X} \pm SE$	(n)	$\bar{X} \pm SE$	(n)
Observed length of range (m) <sup>a</sup>					
1989	female	27.3 ± 1.6	(16)	58.1 ± 7.1	(9)
1990	female	22.8 ± 1.5	(30)	32.6 ± 3.7	(31)
	male	32.0 ± 1.0	(12)	69.1 ± 5.1	(15)
Minimum-convex-polygon area (m <sup>2</sup> ) <sup>a</sup>					
1989	female	258.8 ± 27.0	(16)	331.3 ± 54.5	(9)
1990	female	188.4 ± 25.1	(30)	178.8 ± 25.5	(31)
	male	361.6 ± 23.7	(12)	360.8 ± 24.2	(15)

<sup>a</sup> Estimates calculated only for individuals captured at least eight times. No males were captured at least eight times in 1989.



rectangular patches is that the meadow vole is an edge-tolerant species. Meadow voles presumably evolved in ephemeral patches of grassland habitat and therefore may not be strongly affected by constraints imposed by patch geometry. Ephemeral patches of habitat likely vary tremendously with regard to size and shape. Because of its evolutionary history, the meadow vole currently may be tolerant of patches with high edge-to-area ratios. Indirect support for this explanation is provided by studies of inbreeding avoidance in microtines. Bollinger et al. (1991) found that the meadow vole demonstrates an intermediate level of inbreeding avoidance compared to several other microtine species (Batzli et al., 1977; Facemire and Batzli, 1983). Because they evolved in ephemeral patches, it may be adaptive for meadow voles to breed readily with any other individual encountered, including a close relative. Both a reduction in inbreeding avoidance and an increase in tolerance for high edge-to-area ratios could be advantageous for individuals inhabiting patchy environments. For these reasons, we believe that *M. pennsylvanicus* may be an edge-tolerant species.

Shape of habitat patches affected the number of meadow voles that dispersed in 1989 when population densities were low, but not in 1990 when densities were high. In contrast, dispersal rates were not affected by shape of habitat patches at either low or high densities. Thus, the prediction that more voles would disperse from rectangular patches than from square patches was only partially supported. These findings indicate that effects of habitat geometry on dispersal may be most dramatic under marginal habitat conditions.

Several methods have been used to identify dispersers (e.g., Desy and Batzli, 1989; Gaines et al., 1979; McShea, 1990). In the present study, we defined a disperser as an individual that crossed at least two 3-m, mowed, grassy strips and one 2-m tilled strip before being recaptured. Thus, voles that crossed these barriers were exposed to an increased risk of predation due to the lack

of cover. Because patches differed in the amount of edge exposed to other patches (i.e., 50–93%), our experimental design potentially biased the classification of dispersers. However, this does not appear to be the case. Dispersers were not always captured in immediately adjacent patches. In fact, 56% of the dispersers from square patches and 54% from rectangular patches actually were captured in patches that were not immediately adjacent to the patch in which they originally were marked. It is possible that some emigration went undetected; however, this is unlikely to have been a large component of total emigration due to the high frequency of trapping. Any undetected losses of dispersers would not be strongly biased by the position of a patch within the study area, given that dispersers move such long distances.

In contrast to dispersal, other major population parameters of voles were not affected by differences in shape of habitat patches at this spatial scale. For example, contrasting shapes of patches were not different with regard to recruitment, weekly survivorship, persistence, body mass of residents, or age structure of population at either low or high densities. It is erroneous to conclude, however, that shape of habitat patches affected only individuals that dispersed. We found that shape of habitat patches affected the space-use behavior of resident voles. Home ranges for individuals in rectangular patches were of equal area but elongated (indicated by longer observed lengths of ranges) compared to home ranges of voles in square patches. Residents in rectangular patches altered the shape of their home ranges but remained active over similar areas despite patch constraints. It is likely that territorial females in rectangular patches incurred increased costs to defend larger perimeters. It appears that residents within rectangular patches adjusted their movements and interactions such that population dynamics in these patches were similar to those in square patches.

Population densities of meadow voles differed markedly between the two years of

study. Low population densities in 1989 likely were due to a combination of factors related to improved quality of habitat. Plant species considered to be high-quality food (i.e., *Medicago sativa* and *Trifolium* sp.—Bergeron and Jodoin, 1987; Lindroth and Batzli, 1984; Thompson, 1965) may have been limiting in 1989, but not in 1990. There was a 10-fold increase in biomass of preferred forage between years of study. Following the initial 1989 growing season, litter mass increased nearly 20-fold and this increased cover likely provided greater protection from predators (Birney et al., 1976). This interpretation is supported by an increase in weekly survivorship for males in 1990 compared to 1989. Male meadow voles are not territorial and tend to have large, overlapping home ranges (Madison, 1980). Increased movement by males probably made them more susceptible than females to predation during conditions of poor cover. Low population densities in 1989 were not attributed to lack of reproductive success; 91% of males captured in 1989 were in active breeding condition (i.e., testes were scrotal; compared to 74% in 1990), while 49% of females captured in 1989 were either pregnant or lactating at least once (compared to 33% in 1990).

In conclusion, our findings indicate that the shape of habitat patches can affect dispersal and within-patch movements under certain conditions. However, meadow voles largely were able to overcome constraints imposed by patch geometry at this spatial scale so that population-level processes were largely unaffected by shape of habitat patches. Since isolated patches of habitat are becoming prominent features of landscapes (Mader, 1984), further empirical studies are needed to investigate how the geometry of these patches can affect populations, communities, and ecosystems at various spatial and temporal scales.

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