

The Relative Importance of Small-Scale and Landscape-Level Heterogeneity in Structuring Small Mammal Distributions

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Introduction

Landscape characteristics, such as the spatial arrangement and size of habitat patches, can affect localized ecological patterns and processes (Forman and Gordon 1986, Usher 1987, Danielson 1991, Saunders et al. 1991, Wiens et al. 1993, Brown 1995, Turner et al. 1995, Wiens 1995, Holt and Debinski 1999). Small scale patterns in abundance or reproductive performance, therefore, may not tightly match local variation in ecological factors. For example, mobile species can exhibit local densities deviating far from that expected based on local births and deaths (e.g., sink populations, Holt 1985, 1993, Pulliam 1988, Diffendorfer 1998). Even the abundance of sedentary consumers can differ from that expected given local distributions of their resources if their diets are supplemented by spatial flows of nutrients (Polis et al. 1998).

The effects of landscape characteristics vary with the spatial scale at which habitat and resource patchiness are experienced by species (Levin 1992, Robinson et al. 1992, Pearson 1993, Margules et al. 1994, Diffendorfer et al. Chapter 4). Moreover, habitat selection strategies of species respond to several scales of resource aggregation (Kotliar and Wiens 1991, Ward and Saltz 1994, Pedlar et al. 1997). Many studies have suggested that small mammal distributions and habitat selection strategies are sensitive to variance in local vegetative structure (e.g., Dueser and Shugart 1978, Cockburn and Lidicker 1983, Rosenzweig 1989, Swihart and Slade 1990, Hanski 1991). Other studies have shown that large-scale features of habitat can affect the spatial distribution of small mammals (Foster and Gaines 1991, Harper et al. 1993, La Polla and Barrett 1993, Barrett et al. 1995, Diffendorfer et al. 1995a,b, Bowers et al. 1996, Dooley and Bowers 1996, Collins and Barrett 1997, Wolff et al. 1997); however, the relative utility of these two scales of spatial structure in describ-

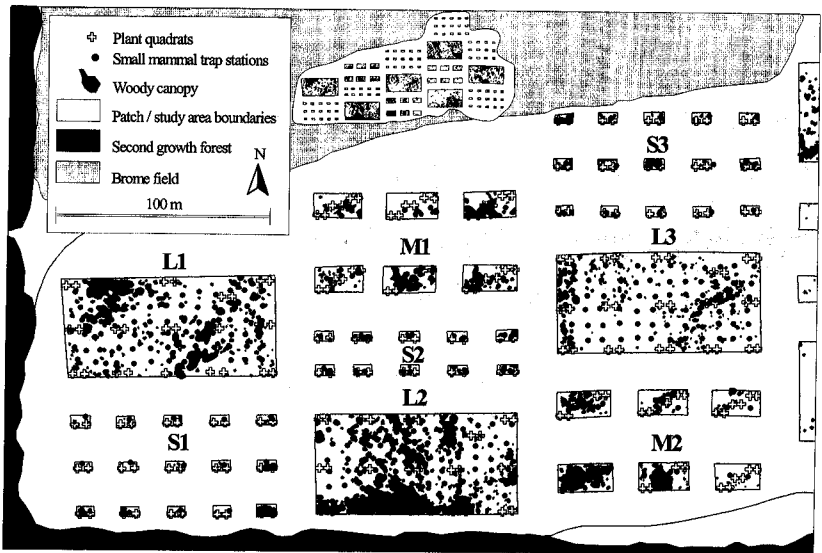


FIGURE 9.1. Map of the 7-ha west half of the Kansas Fragmentation Project site, 12 km northeast of Lawrence, Kansas. The entire 12-ha area is shown in the small inset. The map was generated within a GIS derived from a set of 1994 orthophotos. Features within the GIS mapped here include patch boundaries, small mammal trap stations, plant quadrats, woody canopy within each patch, oak–hickory forest to the west and south of the site, brome field to the north of the site, and a road on the south and east side of the grid. The eastern edge of the site is bordered by mixed forest and pasture. Codes for each block are shown within or immediately above each block (S = small block, M = medium block, L = large block).

ing species distributions is largely unresolved (Morris 1987, Pearson 1993, Bowers and Matter 1997, Pedlar et al. 1997). In this chapter, we will use 2 years of data from a long-term experimental study of habitat fragmentation (Fig. 9.1) to examine the relative influence of local and landscape-scale habitat features on the spatial distribution of prairie voles (*Microtus ochrogaster*), deer mice (*Peromyscus maniculatus*), cotton rats (*Sigmodon hispidus*), harvest mice (*Reithrodontomys megalotis*), and white-footed mice (*P. leucopus*).

Landscape Context and Patch Content

Analyses of data collected from our site during 1984–1992 focused on the effects of patch size on small mammal distribution, movement, and community composition (Foster and Gaines 1991, Gaines et al. 1992a,b, Diffendorfer et al. 1995a,b, 1996, Chapter 4, Schweiger et al. unpublished manuscript), without close consideration of small scale variance in vegetation structure (but see Foster and Gaines 1991). These studies concluded that patch size had

strong, species-specific effects on a suite of small mammal population and community measures. Focusing on patch size in these analyses was reasonable because during the early successional stages of our study vegetation composition and structure did not vary systematically with patch size (Foster and Gaines 1991, Holt et al. 1995).

Analyses of data collected on our site during 1994–1997 suggest factors other than patch size may account for some of the variance in small mammal density and distribution (see also Dooley and Bowers 1996). For example, during 1994–1996, the density of deer mice was highest in medium, followed by large, and small patch size classes (for averages of all patches within a size class, see Figs. 9.1 and 9.2A). When individual blocks of patches within a size class were examined separately, however, mean deer mouse density fell into distinct, statistically separable groups, independent of patch size (Fig. 9.2B). If patch size was the only factor explaining deer mouse density and distribution, then we would expect all medium patches to have the highest mean density, followed by all large patches, then all small patches (the rank order of mean density with data aggregated by patch size). The variance in mean density within each patch size class suggests that patches are not immune to their surrounding landscape context and that local features are not homogeneous across patches within a size class.

Patch Content

Recruitment of woody species from forests to the south and west of our study site increased dramatically beginning in 1990. The influx of woody stems directly and indirectly affected many components of our system, including local vegetative cover and structural heterogeneity (see Fig. 9.3A,B for selected examples). Moreover, rates of woody species colonization were influenced by patch size (Fig. 9.4A), with variance in stem density across patch size contributing to the emergence of patch size effects on the distribution and abundance of herbaceous life form groups (e.g., Fig. 9.4B; for more detailed analyses see Holt et al. 1995). Woody species colonization of our experimental system has resulted in a dynamic habitat mosaic, characterized by at least two scales of spatial heterogeneity in habitat structure and composition: (1) variation in local vegetative structure and composition across patch size and (2) variation in landscape-scale characteristics among patches. We use the terms *content* and *context*, respectively, to describe these two scales of habitat heterogeneity.

If context has a more important impact on small mammal distribution, then we expect patterns in distribution to reflect larger-scale habitat features, partially independent of local vegetation structure (Holt 1984, Songer et al. 1997). For example, a patch may be too small, or too isolated (regardless of its content), to maintain a persistent consumer population. On the other hand, if patch content is more important in structuring the distribution of a species, then patterns in distribution should be tightly correlated with measures of local vegetation structure. Local abundance may be so strongly influenced

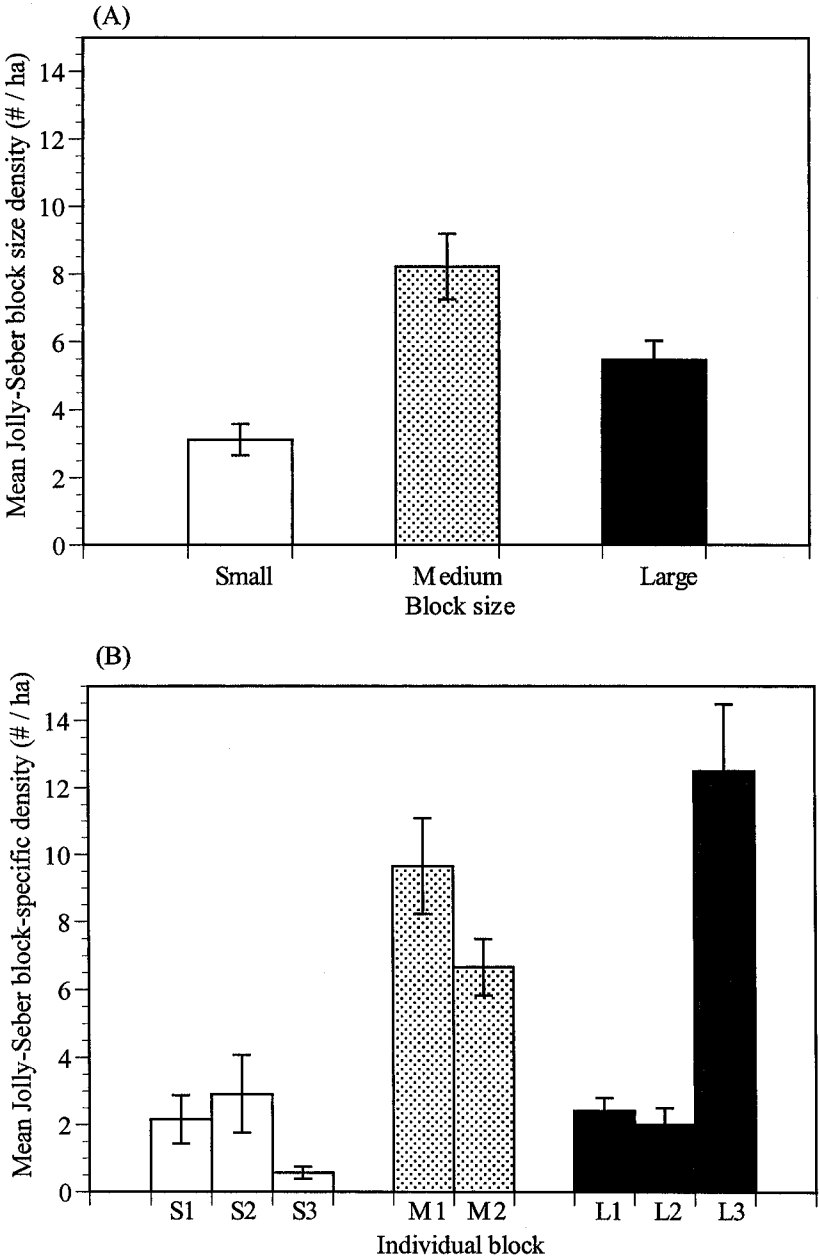


FIGURE 9.2. Mean (± 1 SE) deer mouse density by block size (A) and individual block (B). Densities (numbers / ha) were calculated using a modified Jolly-Seber index and data from 36, 3-day trapping sessions between 1994 and 1996. Block size had a strong effect on mean density [$F(2, 107) = 13.32, P < 0.001$], with peak density in medium blocks. Individual block also had a strong effect [$F(7, 287) = 16.46, P < 0.001$], with peak densities in large block B3, and medium blocks C2 and A3. The lowest density was in small block C3.

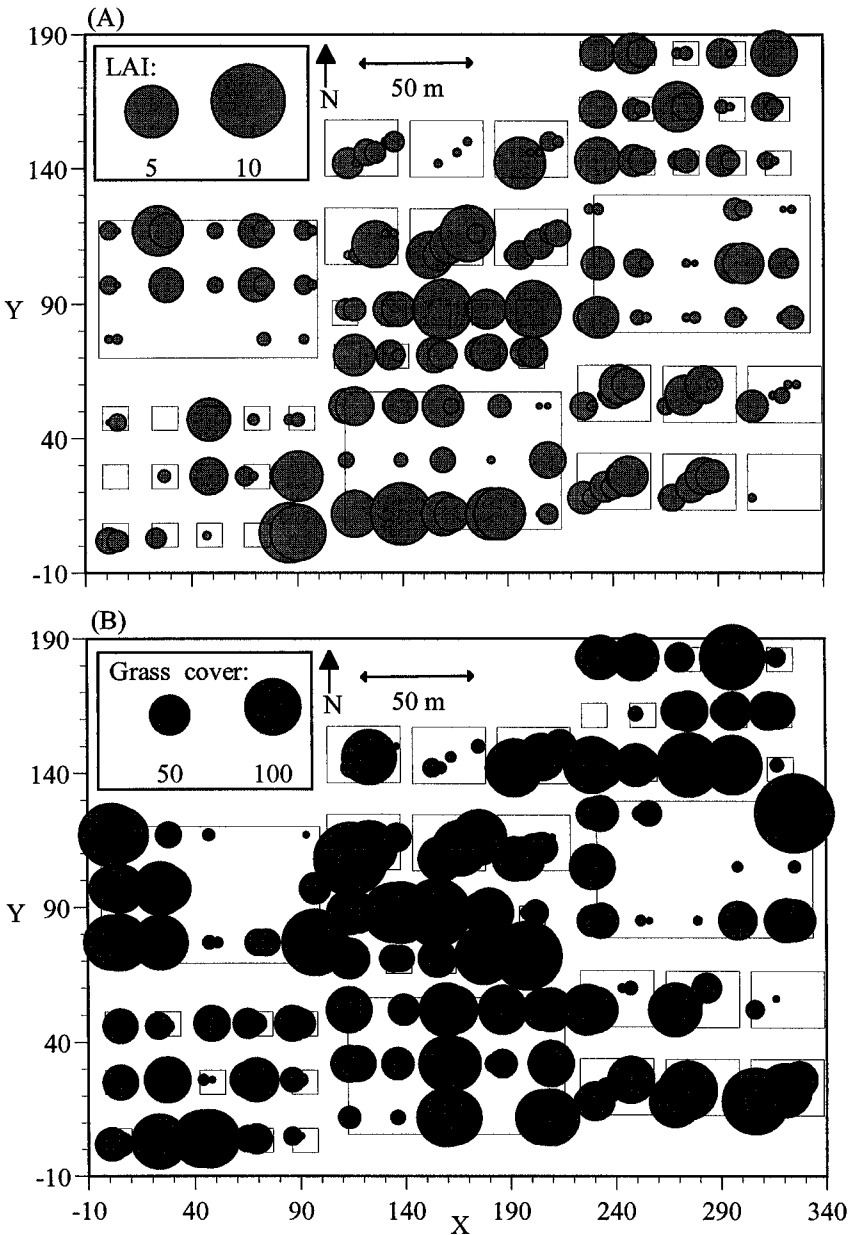


FIGURE 9.3. Select bubble plots of vegetation *content* features. (A) Leaf area index measured at 1.0 m from ground level in the summer of 1996 with a Sunscan 2000 (Delta-T Devices, Ltd., Cambridge, England). (B) Estimates of grass cover (square centimeters; all species combined) at each quadrat. Because cover estimates for individual grass species were summed, values may exceed 100 cm² (total area of quadrat). The diameter of each circle in both figures is proportional to the value at each sampling point. Note the different scales in the two figures. Patch size, shape, and location are approximate.

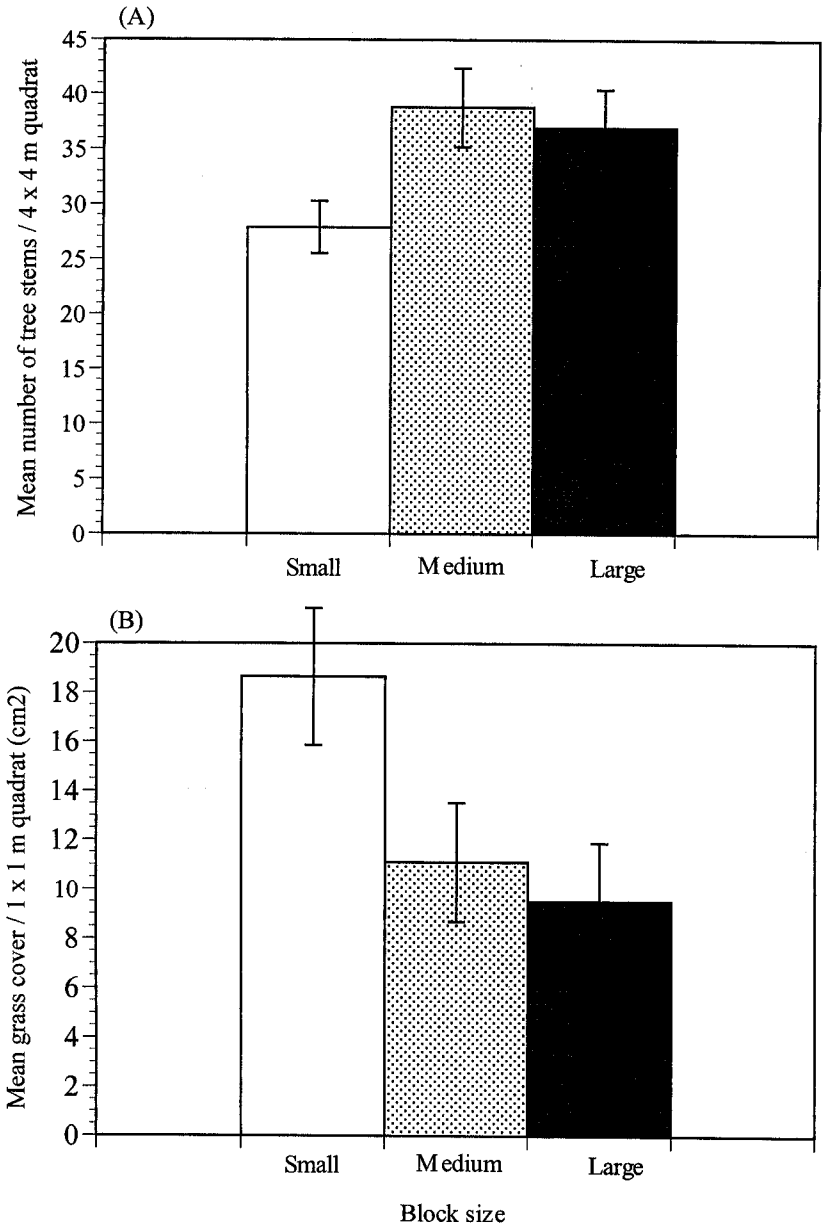


FIGURE 9.4. Plots of select vegetation features by block size. (A) Mean (± 1 SE) woody stem counts (all species) in 4×4 m quadrats measured in 1995. Block size had an effect on mean stem density [$F(2, 241) = 4.21, P = 0.016$], with higher densities in larger blocks. (B) Mean (± 1 SE) 1995 grass cover (all species) in 1×1 m quadrats. Because cover estimates for individual grass species were summed, values could exceed 100 cm^2 . Block size had an effect on mean grass cover [$F(2, 241) = 3.85, P = 0.023$], with higher densities in small blocks. Note the different scales in the two figures. Patch size, shape, and location are approximate.

by patch content that any landscape effects on small mammal demography are not measurable.

Methods

Overview

We used stepwise multiple regressions to examine the effect of vegetative structure (content), heterospecific small mammal abundance (content), and a suite of landscape features (context) on the distribution of small mammal captures (see also Morris 1987, Pearson 1993, Kelt et al. 1994, Dooley and Bowers 1996, Seamon and Adler 1996, Pedlar et al. 1997). We will begin by briefly describing our study site and field methods. We will then describe the dependent, content, and context variables used in the regressions. Finally, we will describe the details of the regression analyses. All analyses (except where noted) were conducted in STATISTICA version 5.1 or MINITAB version 11.1 (Minitab 1996, Statsoft 1997).

Study Site and Field Method Summary

Our study area consists of 104 patches arrayed within a 12-ha old field located 12 km northeast of Lawrence, Kansas (Fig. 9.1). The patches have been allowed to undergo succession since their creation in 1984, while the intervening interstitial areas have been regularly mown. The patches are grouped into 50 × 100 m experimental units or “blocks” of either one, 50 × 100 m patch (“large blocks”), six, 12 × 24 m patches (“medium blocks”), or 10–15, 4 × 8 m patches (“small blocks”). We use the term *block size* to refer to archipelagos of similarly sized patches. We consider the study area proper—the patches and interstitial habitat—plus the surrounding forest and brome fields that are potential sources of dispersers, to comprise a “landscape” (Wiens et al. 1993, Lidicker 1995, Krohne 1997).

There are 280 trap stations and 242 plant quadrats distributed among the 55 patches on the 7-ha, west half of the study area (from which all data for the analyses presented here are drawn). Small mammals have been trapped biweekly or monthly for two to three consecutive mornings using standard protocols since the project's inception (for details, see Foster and Gaines 1991). In this chapter, we will use data spanning January 1995 to December 1996, because these were years in which comprehensive vegetation and landscape composition data were collected. Identification, height, and the percentage of cover estimates for all plant taxa within the 1 × 1 m quadrats have been collected one to three times per year using standard point-intercept or visual cover techniques (Goodall 1952). In 1990, we began woody stem count and diameter measurements in 4 × 4 m quadrats (centered on the 1 × 1 m quadrats). For more details on the plant sampling protocol see Holt et al. (1995).

Dependent Variable

Models were calculated for each species using two dependent variables, (1) the cumulative number of first-time captures in each trap station (e.g., Kelt et al. 1994), and (2) all captures of each individual within each trap station (e.g., Dueser and Porter 1986, Schweiger 1998). Both of these measures are spatially referenced point estimates of populations as they expand and contract over a landscape, and both measures approximate relative habitat use by each species at each trap station; however, using all captures of each animal may confound individual and population-level responses (e.g., captures at a given trap may be multiple captures of a single individual or of several different animals). When possible, therefore, we used first-time capture models; however, if for rarer species using first-time captures prohibited generating a final model with an acceptable r^2 (Menard 1995), then we used the less statistically robust, all-captures based models.

Content Variables

In the following sections we briefly describe and justify our 21 (1995) and 24 (1996) vegetation content measures. Space limits preclude presenting each variable in detail.

Vegetative Cover

Small mammals tend to forage on assemblages of species within plant life-form groups (e.g., forb, grass, and woody species). For example, prairie voles require dense, high-quality forb cover to reach peak densities (Kaufman and Fleharty 1974, Hjältén et al. 1996), whereas white-footed mice favor seed-bearing woody species (Kaufman and Fleharty 1974, Bergeron and Jodoin 1987, Adler and Wilson 1989). To describe the distribution of plant life-form groups we used summations of the total cover of species within five classes at each quadrat (annual and perennial grasses, annual and perennial forbs, and woody species, see Huntly and Inouye 1987, Holt et al. 1995). We also used the height of the tallest plant stem within each group as an estimate of local vegetative structure.

Woody Stem Density

The density of woody stems and variance in stem height structure can also influence the distribution and behavior of small mammal species (Dueser and Shugart 1978, Cockburn and Lidicker 1983, Rosenzweig 1989, Swihart and Slade 1990). For example, white-footed mice in eastern Kansas tend to favor areas with dense woody structure. In addition, areas with dense woody stems often have reduced herbaceous vegetation (Bazzaz 1990, 1996) and are avoided by species such as deer mice (Kaufman and Fleharty 1974). To describe these habitat features at each plant quadrat, we calculated the fre-

quency of woody stems (all species) within five height classes, the total basal area of woody stem, the total height of woody stem, and the coefficient of variation in woody stem height.

Canopy Structure

Nonliving vegetative structures (e.g., dead snags), which are not included in our quadrat based samples, can also influence small mammal distribution (Cockburn and Lidicker 1983, Kelt et al. 1994). We estimated canopy structure at each quadrat with a leaf-area index (LAI, Chen and Black 1992) and output from a hemispherical photo-based canopy gap model (Norman and Campbell 1989, Rich 1990).

Heterospecific Small Mammal Captures

Finally, because of the many well-documented interactions between the small mammal species within our study area (Abramsky et al. 1979, Glass and Slade 1980, Dueser and Porter 1986, Morris 1987, Swihart and Slade 1990), we also included the number of captures per trap of each small mammal species as additional content variables in each regression.

Trap-Plant Quadrat Association

The spatial distribution of our trap stations and plant quadrats varies slightly (see Fig. 9.1); therefore, we estimated the content variables at each trap station using inverse distance weighting (IDW) interpolation. IDW interpolation estimates unknown values using coefficients derived from an inverse function of the distances between known sample points (Watson and Philip 1985, Burrough 1986). The interpolated vegetation-content values were qualitatively checked for accuracy. In summary, comparisons with GIS coverages and select ground truthing suggested that the estimates conformed well with actual vegetative composition and structure at each trap station. IDW interpolation was calculated with Arc/Info version 7.1 (Environmental Systems Research Institute 1997). All subsequent references to vegetation-content measures refer to the interpolated values.

Factor Analyses of Vegetation Variables

Small mammals respond to multivariate combinations of local habitat structure and vegetation composition (Cockburn and Lidicker 1984, Adler and Wilson 1987, Kelt et al. 1994). We therefore produced composite predictor variables from our original vegetation content measures using principal axis factor analysis (FA, Seamon and Adler 1996, Dueser and Shugart 1978, Belk et al. 1988). Because of their fundamentally different nature, the heterospecific small mammal capture variables were not included in the factor analyses. All vegetation content variables were first examined for univariate normality

and transformed as needed. Correlation matrixes were used to equalize the influence of variables with highly different absolute ranges (James and McCulloch 1990). Resulting factors were retained based on standardized protocols (Kachigan 1982). Factors were rotated using an equamax normalized procedure to improve the ability to name each composite variable.

Context Variables

Buffer Zones

To assess the impact of landscape features at spatial scales larger than the typical small mammal home range (Diffendorfer et al. 1995a), we created two "buffer zones" around each trap station within a Geographic Information System (GIS, see Fig. 9.1 and Schweiger et al. unpublished manuscript). The first buffer zone was a circle 75 m in radius, and the second was a ring between 75 and 125 m. Two buffer zones were used in an attempt to describe the effects of landscape features at variable distances from trap stations. We chose these buffer zone sizes to ensure that areas used by individuals for daily foraging activity and small-scale movement would be smaller than either zone. Few animals move between blocks on our site. For example, out of 27,162 captures of all species from 1984 to 1996, less than 15% were recaptures on a block other than that of first capture (Diffendorfer et al. 1995a, Diffendorfer et al. Chapter 4, E. W. Schweiger, unpubl. data). In addition, estimates of mean home range size on our site range from 120 to 750 m² (Slade and Swihart 1983, Diffendorfer et al. 1995a, Slade and Russell 1998, E. W. Schweiger, unpubl. data), which suggests that the majority of movements are less than 15 m (radius of the average home range). Only long-distance dispersers, therefore, would likely encounter habitats at the scale of the buffer zones. Finally, the buffer zones were also designed to average over local heterogeneity (content) and to include landscape features on the periphery of the study area (e.g., forest and brome field).

To describe each buffer zone quantitatively we calculated the percentage of composition of 10 major habitat features within each area (see Pearson 1993 for a similar analysis). The categories included interstitial area, heavily forested area outside the study site, brome field area outside the study site, road area on the border of the study site, woody area in each block size, and nonwooded area in each block size.

Factor Analyses of Buffer Zone Composition Variables

We used factor analyses (identical to those used on the vegetation content data) to remove all covariance structure among the original independent variables and to create synthetic axes of buffer zone habitat composition. Because the percentages of each habitat type within each buffer zone summed to 1.0, the measures were not independent. Following Aebischer et al. (1993), therefore, the buffer zone composition measures were transformed by dividing

by the rarest category (woody canopy area within small blocks) and taking the natural log of these proportions. To eliminate problems with matrix elements of zero, 0.0001 was first added to all values. This transformation reduced the perfect linear dependency among the buffer zone measures.

Distance Measures and Block Indicators

Three additional context variables were included in the regression models: (1) the distance from each trap station to the nearest patch edge, (2) the distance from each trap station to the nearest study area boundary defined by the limits of the mowing regime and surrounding continuous forest, and (3) block-specific categorical dummy variables (see Fig. 9.1, Hardy 1993). Using block-specific indicator variables permitted us to interpret effects due to both patch size and block position within the landscape. We arbitrarily chose block S1 as the reference category in coding the dummy variables (necessary to avoid singular matrixes, Draper and Smith 1981).

Regression Details

The cumulative number of captures per year at each trap station was regressed on the set of previously described predictor variables using forward stepwise procedures. Separate models were generated for first-captures and all captures. Square-root transformations of the number of captures were used to reduce negative binomial skews in the distributions. Models were generated following two strategies. First, we generated models that included both content and context measures in a single set of predictor variables. This was done despite weak correlations between select content and context variables in order to preserve our designation of predictor variables being either content or context in nature (e.g., we did not remove this collinearity in a factor analysis that included both types of variables). Following Pedlar et al. (1997), our second strategy involved regressing small mammal captures on content and context predictor variables in separate models, followed by a third stepwise procedure that combined the final variables from the content and context models. This three-step process potentially included variables masked by correlations between context and content variables (which was a possible outcome in the first strategy). We qualitatively compared the models produced by these two techniques and will discuss the implications of any differences in the two sets of final models.

In both strategies, insignificant predictor variables (included by the stepwise procedure) were manually removed one at a time until all variables in the model were significant at the $P \leq 0.05$ level of probability. At each step in the model selection procedures, residual plots, N -scores, Mallow's $C(p)$ tests, and experimental lack-of-fit tests were used to validate variable selection (Draper and Smith 1981). All residuals from the final models were tested for serial autocorrelation with a Durbin-Watson test and plotted against the

original predictor variables to test for nonlinear relationships between the dependent and independent variables. Only models that fit these assumption tests are reported (Draper and Smith 1981, Kachigan 1982).

Measures of habitat composition in the buffer areas were included in multiple sampling units because the buffer zones around adjacent trap stations overlapped. This resulted in buffer-zone composition estimates that were not perfectly independent at each trap location (e.g., Hurlbert 1984). The values of the regression coefficients in our final models are probably robust to this problem; however, the overlap did reduce the variance in the estimates of landscape composition around each trap station and lowered the standard errors around each regression coefficient. We therefore cautiously interpret buffer zone composition axes using a Bonferroni adjusted α level of > 0.003 (Draper and Smith 1981); however, because the beta coefficients of nonbuffer zone predictor variables were probably not markedly affected by the reduced standard errors around the buffer zone factor axes variables, we included the contribution of buffer zone factor axes with $0.003 > P > 0.05$ in the calculation of the final model r^2 and other diagnostic statistics.

To determine the influence of content or context variables as a group, we calculated the proportion of the sum of all beta coefficients (regression coefficients in standardized z-score form) accounted for by the sum of all content or context beta coefficients. All variables included in the final models were used to calculate the proportions. The percentages are not exact estimates because each beta value includes variance explained by other predictor variables. This procedure is appropriate, however, for assessing the relative proportion of explained variance accounted for by a group of predictor variables when there is also an interest in individual predictor variables (Kachigan 1982).

Results and Discussion

Factor Analyses

Vegetation

In 1995, 77.5% of the variation in the 21 original measures was explained by six factors (Table 9.1). In 1996, 65.5% of the variation in the 24 original measures was explained by five factors (Table 9.2). For both years, the majority (~35.0%) of the explained variance was accounted for by axis (V1), highly correlated with woody stems > 0.50 m, total height and basal area of woody stems, woody cover, and (in 1996) LAI and (negatively) canopy-gap measures. The remaining variation within both years was partitioned among a set of axes characterized by high loadings of herbaceous vegetation life form groups, woody stem counts < 0.50 m, and species richness (see Tables 9.1 and 9.2 for details). The equamax rotations of the axes did not produce any significant correlations among factor scores (all $r < 0.01$).

TABLE 9.1. Results from factor analysis of 1995 vegetation content variables.

Axis code*; Principle loading variables; "Axis name"	Eigenvalue	% Experiment variance
V1; Number of stems >0.50 m in height, total woody stem height and basal area, woody cover; "Woody canopy"	7.57	35.26
V2; Perennial grass cover and height; "Perennial grass"	2.62	11.89
V3; Number of stems <0.25 m in height, -CV in woody stem heights; "Short woody stem vs. variance in woody stem height"	2.29	10.41
V4; Annual grass cover and height; "Annual grass cover"	1.78	8.08
V5; Total herbaceous cover, height of perennial forb; "Herbaceous cover"	1.48	6.73
V6; -Perennial forb cover; "-Perennial forb cover"	1.12	5.10

*Axis code corresponds to the symbol used for each factor axis in the regression equations (Appendix 9.1) and text. Predictor variables with the highest loadings ($P > 0.70$) were used to name each axis. A "-" indicates a negative correlation between a predictor variable(s) and a factor axis. The proportion of the total variance explained by each axis is shown in the last column. The analysis explained 77.48% of the total variation in the 21 original content measures.

Buffer Zones

Factor analysis of the buffer zone composition data reduced the original landscape composition variables to six factors explaining 80.7% of the original

TABLE 9.2. Results from factor analysis of 1996 vegetation content variables.

Axis code*; Principle loading variables; "Axis name"	Eigenvalue	% Experiment variance
V1; Number of stems >1.0 m in height, total woody stem height and basal area, woody cover, LAI, -GAP; "Woody canopy"	8.67	34.69
V2; Woody stems 0.25-1.0 m in height; "Short woody stems"	2.65	10.59
V3; Perennial grass cover and height; "Perennial grass"	2.24	8.97
V4; Annual grass cover; "Annual grass"	1.52	6.06
V5; -Annual forb cover, -herbaceous species richness; "-Annual forb and -herbaceous species richness"	1.29	5.18

*Axis code corresponds to the symbol used for each factor axis in the regression equations (Appendix 9.1) and text. Predictor variables with the highest loadings ($P > 0.70$) were used to name each axis. A "-" indicates a negative correlation between a predictor variable(s) and a factor axis. The proportion of the total variance explained by each axis is shown in the last column. The analysis explained 65.5% of the total variation in the 24 original content measures.

variance (Table 9.3). The equamax rotations resulted in insignificant correlations among the factors (all $r < 0.025$); therefore, we treated the rotated factors as orthogonal.

Interpretations of the axes were facilitated by using maps of the distribution of factor score values on each axis. For each trap station, a large negative factor score indicated a relatively low frequency of the habitat types in the surrounding buffer zones characterized by each axis, and a large positive score indicated a relatively high frequency. Almost one third of the explained variance was accounted for by axis Bu1, which arranged trap stations by proportions of forest and road area within 75 and 75–125 m, as well as the proportion of wooded large patch within 75 m (Table 9.3). Traps with positive scores on axis Bu1 were in large blocks L1, L2, S1, and M2 (located near the forest on the western and southern side of the study area, see Fig. 9.1). Axis Bu2 explained 20% of the original variation and displayed trap stations according to proportions of interstitial area, nonwoody large patch, and woody large patch habitat at a distance of 75–125 m. Trap stations with positive scores on axis Bu2 tended to be on the edges of blocks. Axis Bu3 (15% of the original variation) arranged trap stations by wooded and nonwooded medium patch within 75 m. Traps with positive scores on axis Bu3 were typically within medium blocks and on the edges of small and large blocks that directly abutted a medium block. Axis Bu4 displayed trap stations according to proportions of woody and non-woody medium patch 75–125 m away (10% of

TABLE 9.3. Results from factor analysis of buffer zone habitat composition variables.

Axis code*; Principle loading variables; "Axis name"	Eigenvalue	% Exp. variance
Bu1; Forest (75 m), road (75 m), woody large patch (75 m), forest (75 - 125 m), road (75–125 m); "Forest, road, and woody large patch"	5.26	29.21
Bu2; Non-woody and woody large patch (75–125 m), interstitial (75–125); "Large patch and interstitial"	3.58	19.87
Bu3; Non-woody and woody medium patch (75 m); "Medium patch (near)"	2.69	14.95
Bu4; Non-woody and woody medium patch (75–125 m); "Medium patch (far)"	1.75	9.70
Bu5; Brome field (75–125 m); "Brome field"	1.26	7.00

*Axis code corresponds to the symbol used for each factor axis in the regression equations (Appendix 9.1) and text. Predictor variables with the highest loadings ($P > 0.70$) were used to name each axis. Values in parentheses correspond to the maximum distance from the trap station the feature was measured at, or the radius of each buffer zone. A "-" indicates a negative correlation between a predictor variable(s) and a factor axis. The proportion of the total variance explained by each axis is shown in the last column. The analysis explained 80.7% of the total variation in the 21 original buffer zone composition measures.

original variance). These traps tended to be in the southwest corner of the grid (most removed from medium blocks within our landscape). Axis Bu5 displayed trap stations according to proportions of brome field at a distance of 75–125 m (7% of original variance). These traps were located in the southeast corner of the study area (most removed from the brome field). Details of all factor analyses, including loadings and factor scores, are available upon request.

Regression Models

First-Captures Versus All Captures

From January, 1995 to December 1996, 20160 trap nights with 3656 total captures of 1907 individuals of the five most common species were logged on the study area (18.1% trap occupancy). Just over half of all individuals were captured once (52.1%). Only 21.1% of animals (all species) were captured three or more times.

Acceptable models could not be generated for harvest mice in either year (both $r^2 < 0.05$), cotton rats in 1996, or for white-footed mice in 1995, regardless of whether the first-capture or all captures of each individual were used. Nevertheless, context effects were paramount in the harvest mice models, accounting for close to 100% of what little variance the models did explain (see later for other species). We were able to use first-captures for five of the remaining six year–species combinations (Appendix 9.1). Moreover, for most year–species combinations, the models using first-captures and all captures were similar (the first-capture models did have marginally lower r^2). The two types of dependent variables, therefore, appeared to describe similar responses to local and landscape scale habitat structure. See Schweiger (1998) for interpretations of the all capture models for each species.

Model Construction Strategies

Virtually identical results were obtained from the two model construction strategies we used (including content and context measures in a single group of predictors versus separate stepwise treatment of the two types of independent variables). This suggests that correlations between content and context variables did not strongly affect the final composition of each model; therefore, only the results from the models that used all independent variables together (the first strategy) are reported.

All final regression models were highly significant, with r^2 between 0.23 and 0.47 (Appendix 9.1). Many (but not all) buffer zone factor axis predictor variables in the final models were significant at the Bonferroni level of 0.003. The relationships inferred by the models are complex and we do not claim that a significant predictor variable necessarily implies a mechanistic relationship. Certain patterns, however, do make sense in light of what is known about the natural history of the small mammal species in our system. In the following sections we summarize and interpret each model.

Prairie Voles

The first-capture and all capture models for prairie voles were similar, with nearly identical final predictor variables, r^2 values, and proportion of the total explained variance accounted for by context variables. Prairie vole populations on our site have always been characterized by high turnover (Foster and Gaines 1991, Diffendorfer et al. 1995b), and the majority of animals (55%) are only caught once.

Almost 50% of the variance in the distribution of first-time captures of voles per trap station in 1995 was explained by eight predictor variables (final model $r^2 = 0.47$, Appendix 9.1). Two buffer zone factor axes variables were included in the final model, however, neither were significant at the Bonferroni-adjusted alpha value. Context accounted for the majority (85.8%) of the variance explained by the model. Vole captures were positively associated with edge habitat (DP) and negatively associated with large blocks L1, L2, and L3 (as compared with the relatively high number of vole captures in reference block S1). Voles were positively associated with traps that were greater than 75 m from brome field (Bu5), and negatively associated with traps that were between 75 and 125 m from medium patches (Bu4), although because of their P values, the real effect of these buffer zone variables on prairie vole distribution is unclear. Content features in the final model included a positive association with cotton rat captures, and a (marginal) negative correlation with the woody canopy factor axis (V1).

More than 40% of the variance in the distribution of the number of captures of prairie voles per trap station in 1996 was explained by six variables (final model $r^2 = 0.41$, Appendix 9.1, Fig. 9.5A). Of the explained variation in capture distribution, 84.9% was due to context. As in the 1995 model, vole captures were positively associated with edge habitat (DP) and negatively associated with large blocks L1, L2, and L3 (as compared with the relatively high number of vole captures in reference block S1). This suggests these context features had consistent impacts on vole distributions, partially independent of other temporally variable factors. Only two content variables appeared in the final model. First-time vole captures were negatively associated with woody canopy (axis V1), and positively associated with low annual forb cover and plant species richness (axis V5). Given the marginal P value and small beta coefficient for V5, however, we consider the local vegetation features described by this factor axis relatively unimportant in predicting prairie vole distribution.

To indirectly examine prairie vole space use in more detail, we measured vole runway density surrounding each patch during the winter and summer of 1996. On average, we found 0.52 runways per meter of edge leaving small patches and 0.05 runways per meter of edge leaving large patches (R. Anderson and E.W. Schweiger, unpubl. data). This suggests that voles actively use the interstitial areas close to small patches (they are rarely caught in interstitial traps spaced more than 10 m from a patch). The close proximity of cover providing patch habitat and ideal foraging in nearby interstitial areas (see

also Hyman et al. 1991, Lidicker et al. 1992) may produce a habitat mosaic favorable to prairie voles. In large, and to a lesser extent, medium blocks, the lower edge-to-interior ratios may have limited the number of voles with high quality edge territories and reduced the number of captures in these areas relative to small blocks. Other studies also indicate that voles prefer edges and have higher fitness in edge habitat (Dooley and Bowers 1996, Collins and Barrett 1997).

The content variables that appeared in the vole models largely follow from well-known local habitat preferences for this species (e.g., Kaufman and Fleharty 1974, see also Cockburn and Lidicker 1983). Prairie voles prefer habitat characterized by few woody stems, partially because of the higher cover of grass and forb forage species in areas without dense woody canopies (Hjältén et al. 1996). In 1995 and 1996, mean woody stem density per quadrat was almost 1.5 times greater in large blocks than in small blocks, whereas grass cover per unit area in small blocks was approximately twice that of large blocks (Fig. 9.4A,B, see also Schweiger et al., unpubl. data). Similar vegetation is preferred by cotton rats; hence, the positive relationship between vole and cotton rat captures in 1995.

Deer Mice

The first-capture and all capture models for deer mice varied more than almost all other species, perhaps because a relatively high proportion of deer mice were captured more than once (28%). The most important (based on their beta coefficients) predictor variables, however, did occur in both sets of models. Moreover, the models had similar r^2 values and the proportion of the total explained variance accounted for by context variables was nearly identical (see Schweiger 1998).

Almost 40% of the variance in the distribution of captures of deer mice per trap station in 1995 was explained by five predictor variables (final model $r^2 = 0.37$, Appendix 9.1). All of the explained variance was accounted for by context features. Deer mouse captures were positively associated with blocks M1, M2, and S3 (relative to the low number of captures in reference block S1). Deer mouse captures were negatively associated with the southwest corner of the grid (axis Bu4). Finally, deer mouse captures were negatively associated with locations embedded in large blocks L1 and L2 adjacent to the forest on the western and southern edge of our site (axis Bu1).

Almost 30% of the variance in the distribution of 1996 deer mouse captures per trap station was explained by seven predictor variables (final model $r^2 = 0.27$, Fig. 9.5B). The three buffer zone predictor variables, however, included in the final model were not significant using the Bonferroni criterion. As in the 1995 model, context variables accounted for 100% of the explained variance. Deer mouse captures were higher in the three eastern-most blocks (M2, L3, and S3) and in the northeast medium block (M1), relative to the low number of captures in reference block (S1, see Figs. 9.1 and 9.5B). Deer mouse

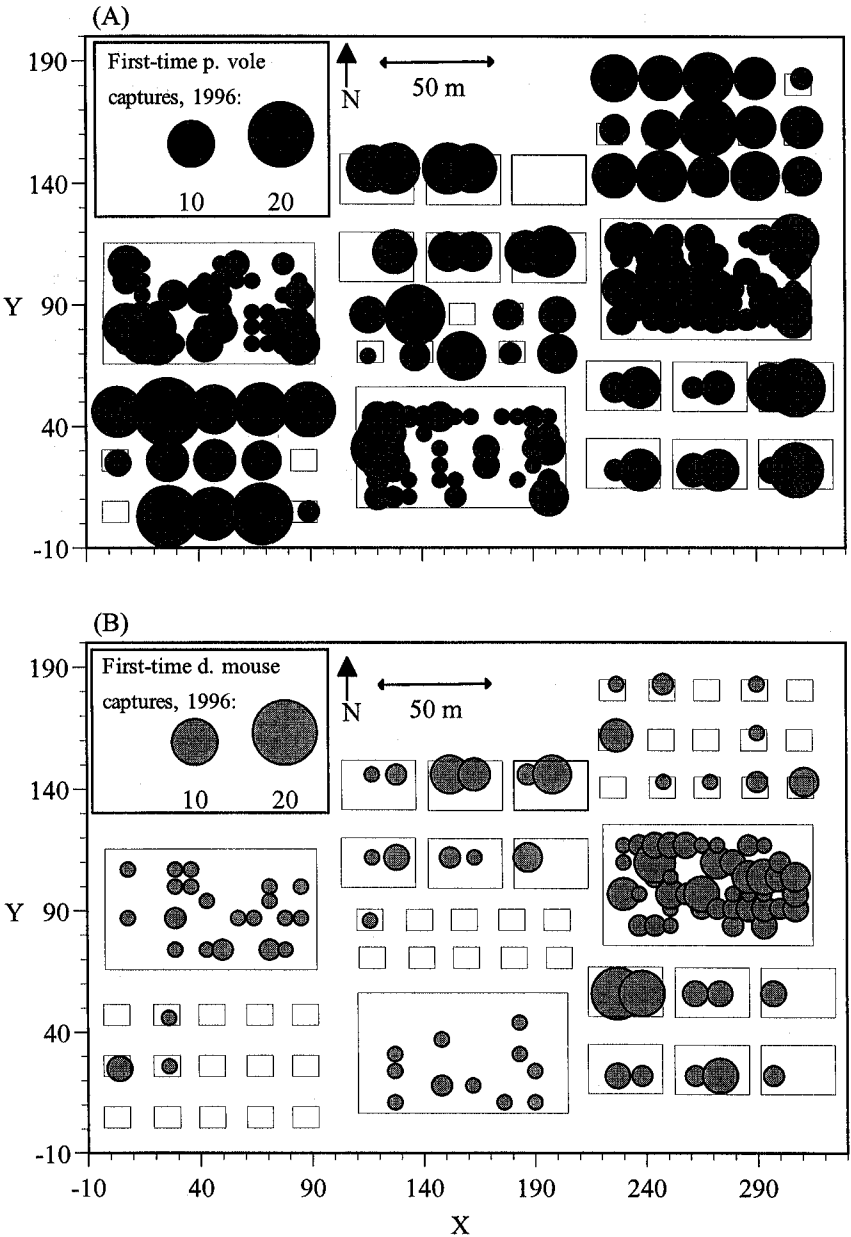


FIGURE 9.5. Select distributions of small mammal captures. Each circle is proportional to the cumulative number of captures at each trap station location. (A) First-time captures of prairie voles in 1996; (B) first-time captures of deer mice in 1996; (C) first-time captures of cotton rats in 1995; (D) all captures of white-footed mice in 1996. Patch size, shape, and location are approximate.

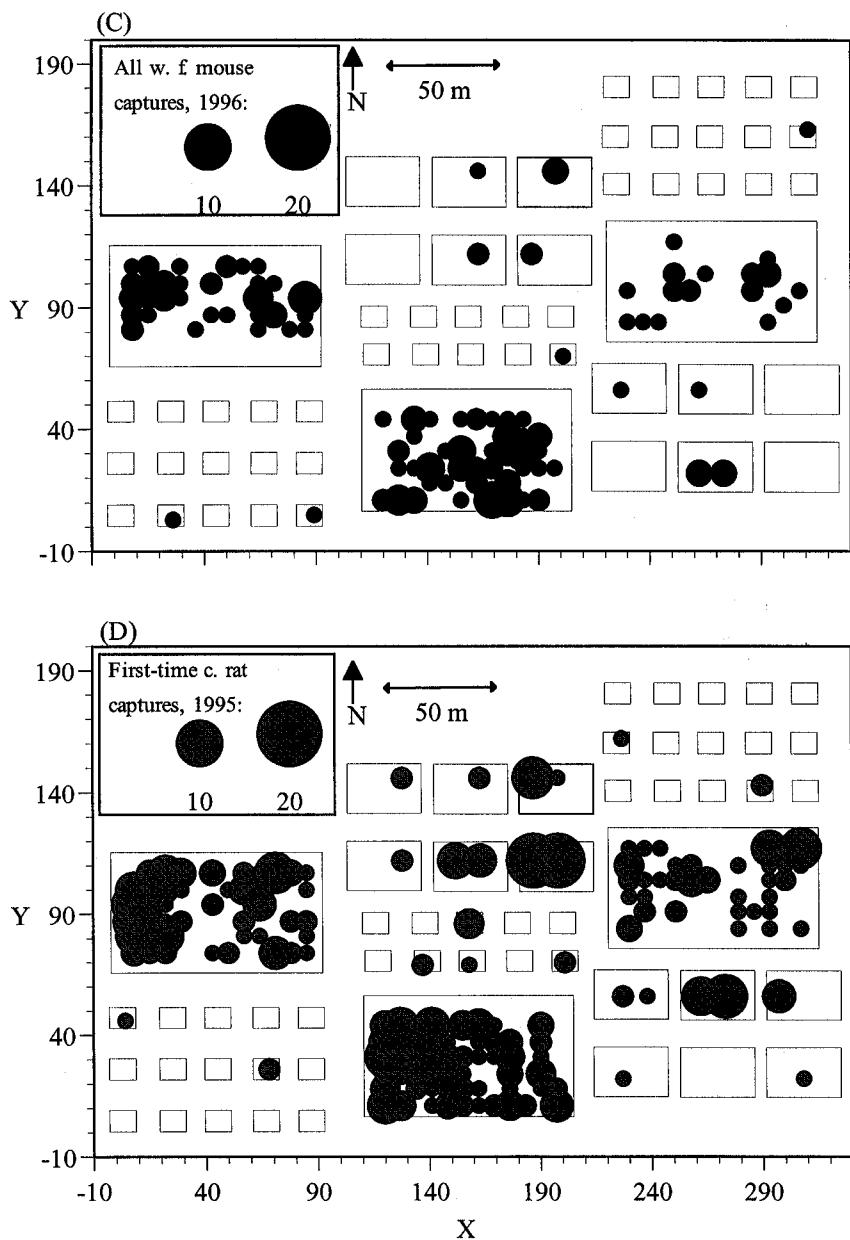


FIGURE 9.5. (continued).

captures were negatively associated with the southwest corner of the study area (axis Bu4), and the edges of all blocks (Bu2). Finally deer mice were negatively associated with traps that were greater than 75 m from brome fields (Bu5). Axes Bu4, Bu5, and Bu2 all had marginal *P* values and must be interpreted with caution.

Deer mouse captures within blocks on the eastern and northern edge of our site (M1, L3, M2 and S3, see Figs. 9.1 and 9.5B) were higher in both 1995 and 1996, which suggests that the location of these blocks had consistent positive effects on deer mouse distribution. M1, L3, and S3 are the most removed blocks from dense forest on the western and southern edge of our grid. Blocks M1 and S3 are also close to open brome field on the north edge of our grid (see Fig. 9.1). Deer mice prefer more open habitat, especially in areas of sympatry with white-footed mice (Kaufman and Fleharty 1974, Hansen and Warnock 1978, Johnson and Gaines 1987, Kamler et al. 1998). In the all-capture deer mouse models (see Schweiger 1998), two content variables had negative effects on deer mouse distributions: woody canopy and the number of captures of white-footed mice. When only first-captures are used, however, the number of captures at each trap station was smaller and any effect of competitive exclusion by white-footed mice or avoidance of dense woody canopy by deer mice was unmeasurable. This suggests that the effect of content on deer mouse distributions may have been an artifact of the nonindependence in the all-captures-dependent variable.

White-Footed Mice

White-footed mice were not abundant enough to have reasonable sample sizes using only first-captures; however, we were able to generate an adequate model using all captures in 1996. White-footed mouse individuals were recaptured more than any other species, with roughly one third of all individuals captured more than twice.

Roughly 25% of the variance in the distribution of captures of white-footed mice per trap station in 1996 was explained by six predictor variables (final model $r^2 = 0.23$; Fig. 9.5C). Of the explained variance, 62.5% was due to context features. White-footed mouse captures were (marginally) positively affected by blocks L1 and L2 (relative to the small number in reference block S1). Captures were more frequent closer to patch edges (DP) and (marginally) within large wooded patches close to forest on the southern and western edge of the grid (axis Bu1). In addition, captures were positively associated with a dense woody canopy (axis V1), and negatively associated with deer mouse captures (both content features).

The majority of white-footed mouse captures occurred in large blocks L1 and L2, immediately adjacent to the continuous forest surrounding the western and southern portions of our study area (see Figs. 9.1 and 9.5C). These blocks have the highest density of woody stems and the most extensive, continuous woody canopy in our system. Captures were less frequent on large

block L3, which is further from the continuous forests and has the lowest level of woody plant cover and stem counts. White-footed mice in eastern Kansas are a woodland specialist (Kaufman and Fleharty 1974, Batzli 1977, Hamilton and Whitaker 1979, Swihart and Slade 1990) that has only appeared on our site since 1993 (Schweiger et al. unpubl. manuscript). It is not surprising, therefore, that white-footed mice show a distinct preference for those content features that most resemble the forest habitat from which this species has dispersed.

The distribution of white-footed mice appears to be driven by complex interactions between context (block size and adjacency to the forest) and content features (woody canopy). Trapping of the oak-hickory forest to the west of our study area over the last 2 years (C. Welch, unpublished data, see Fig. 9.1) suggest that our site may be arrayed along a larger-scale gradient in white-footed mouse densities running approximately 1 km west to east [in 1996, there were 17.6 (forest), 9.5 (L1), 6.7 (L2), and 3.1 (L3) animals per hectare]. The rank order of woody stems per quadrat was identical to the rank order of white footed mouse density in the three large blocks. Small block S1, however, as close to the forest as large blocks L1 and L2, only had a density of 3.2 white-footed mice per hectare. Finally, there was a higher density of woody stems in large block L3 (on average 33.4 per quadrat) than in small block S1 (on average 25.5 per quadrat), mirroring the pattern in white-footed mouse densities. These data all indicate that suitable habitat for white-footed mice may only be available in sufficient quantity on extensively wooded large blocks adjacent to continuous forest. It is this interaction of landscape context and local habitat content that largely drives patterns in white footed mouse distribution.

Cotton Rats

The 1995 first-capture and all-capture cotton-rat models were essentially the same, with identical final predictor variables, equivalent r^2 values, and similar proportions of the total explained variance accounted for by context variables. Like prairie voles, cotton-rat populations on our site are characterized by high rates of turnover (Foster and Gaines 1991, Diffendorfer et al. 1995b), and most animals are only caught once (59%).

Approximately 30% of the variance in the distribution of first-time cotton-rat captures in 1995 was explained by nine predictor variables (final model $r^2 = 0.28$, Fig. 9.5D). Context features accounted for the majority of the explained variance (77.6%). There were more cotton-rat captures in blocks L1, L2, L3, M1, and M2 than there were in reference block S1. Cotton rats were also captured (marginally) more frequently in traps closer to patch edges (DP). Cotton rat captures were higher in areas with a dense woody canopy (axis V1), and in areas with high vole captures. Finally, cotton rat captures were negatively associated with high cover of perennial grass (axis V2).

Context, by influencing the character of succession in small and large blocks, may have indirectly affected the distribution of cotton rats in 1995 by

changing the content of patches. Cotton rats are at the extreme northern limit of their geographic range in northeastern Kansas, and winters can severely stress individuals (Frydenhall 1969, Slade et al. 1984, Swihart and Slade 1990, Stokes 1994). In the early years of our study cotton rats may have only been able to find enough resources to fulfill metabolic demands and adequate refugia to avoid predation on large blocks (Foster and Gaines 1991, Diffendorfer et al. 1995b). Succession within medium and perhaps small blocks increased vegetative cover to the point that cotton rats may have been able to find adequate refugia and forage to allow the use of these smaller patches (see Schweiger et al. unpubl. data). Moreover, succession within large blocks has actually reduced the cover of preferred cotton rat forage species (Fleaharty and Olson 1969, Carnes 1980). Anecdotal support of this pattern was seen with the habitat selection of the first spring cotton rat recruits in 1995, 1996, and 1997. These animals appeared on medium block M1 where they persisted for several months (E. W. Schweiger, unpubl. data).

Conclusions

In this chapter, we examined the relative ability of variance in content (local vegetation structure) and context (landscape structure) to account for patterns in the distributions of four small mammal species inhabiting a fragmented old field. Even though it is difficult to extend our conclusions to the daily activity of individual animals, examining the annual number of captures per trap station reveals patterns that reflect the effects of relatively persistent environmental features on small mammal births, deaths, dispersal, and aggregate habitat use. Our results suggest three general conclusions.

First, the landscape context of habitat fragments appears to have strong, species-specific effects on spatial distributions. Several other authors have suggested that the spatial patterning of relatively vagile, small-bodied animals responds to large-scale landscape features (Morris 1987, Pearson 1993, Kelt et al. 1994, Bowers 1995, G. Anderson and B. Danielson, unpubl. data). General statements of this nature must be made with caution, given that it is not possible to include all potentially important variables in these analyses (Morris 1987, Wolff 1995, Pedlar et al. 1997). Nevertheless, features of the landscape evident at a scale larger than a single home range, patch, or block of patches accounted for most of the explained variation in the distribution of captures for each species in our system—even in the face of substantial heterogeneity in vegetation within patches.

Second, superimposed upon these landscape effects, select measures of local vegetative composition clearly influence small mammal distributions. There is a long-standing tradition of describing small-mammal community structure in terms of microhabitat selection along gradients or niche axes of local vegetation structure (e.g., Pearson 1959, M'Closkey and Fieldwick 1975, Dueser and Shugart 1978, Carnes 1980, Vickery 1981, Cockburn and Lidicker

1984, McMurry et al. 1994). Select results from our models concur with this body of work. Moreover, responses to content measures varied with species.

Finally, small mammal distributions appear to be strongly influenced by interactions between context and content habitat features. Such interactions are probably common over long time scales, and understanding these interactions may be key to predicting long-term responses of small mammals to changes in landscapes. Analyses (E.W. Schweiger, unpubl. data) show that the rate of plant succession on our site has varied with patch size. This dynamic process partially explains the habitat heterogeneity, both within and among patches on our site, to which the single-year regression models reveal small mammal distributions respond. Select examples of this content-context interaction include (1) increased use of medium patches by cotton rats once the culmination of woody stems made these smaller patches suitable habitat, and (2) that the nonrandom colonization of the site by white-footed mice was affected by the proximity of the patches to the surrounding forest. Patches closer to the forest (context) have more woody stems (content) and higher numbers of white-footed mice.

Other interactions between context and content may occur over a shorter time frame. For example, large vertebrate predators move across our entire study area, yet they adjust their local foraging behavior as a function of patch size and proportion of edge habitat (P. Wilson and R. Pierotti, unpubl. data). From the perspective of a small-mammal prey species, this variance in predation pressure would be an impact of context. Certain blocks on our site may be more dangerous than others simply because predators can move more efficiently within them or they are closer to large scale features on the periphery of our site that offer cover for the predators (e.g., Andr n and Angelstam 1988). The perceived threat of predation on each small mammal species, however, is likely to be a complex function of several content measures, including local cover, quality of habitat, interactions with competitors and species-specific attributes such as body size and social structure (e.g., Holt 1984, Kotler et al. 1991). Hence, context and content may interact in long-term and dynamic short-term processes that might influence the distribution and habitat use of the small mammal species on our site.

Our models left a sizable proportion of the total variance in the number of captures unexplained. This may be due to a variety of factors. It is difficult to include all important biological phenomena in regression models (Ruggiero et al. 1988, Wolff 1995, MacNally 1996). Spatial patterns in species density vary by sex, age class, and season (Foster and Gaines 1991, Diffendorfer et al. 1995a,b, 1996). Abundance estimates or numbers of captures per trap are several steps removed from the fundamental processes of births and deaths that generate patterns within populations across space and time (van Horne 1983), and measures of abundance may not be the most appropriate way to characterize how species perceive habitat heterogeneity. Finally, differences across years in our models suggest that even at a coarse temporal scale (year), species vary through time in their responses to habitat and the landscape template perhaps

because of density-dependent responses to varying abundances or to climatically driven shifts in habitat use.

Even though stepwise regression may be inappropriate for direct tests of theory (e.g., Studenmund and Cassidy 1987), the technique was well suited to our general, exploratory goals (Menard 1995), even in the face of the potential problems noted earlier. The general set of methods we used has proven to be a valuable method for addressing the relative explanatory utility of factors that influence species distributions and habitat selection (Morris 1987, Pearson 1993, but see Wolff 1995, Seamon and Adler 1996, Pedlar et al. 1997). Future work should include alternate dependent variables and experimental techniques designed to isolate species specific behavioral responses to habitat heterogeneity at multiple scales.

Applications for Management at the Landscape Scale

Anthropogenic habitat fragmentation often generates mosaics of habitat patches that are nonrandomly distributed across landscapes, typically have abrupt edges, and are often characterized by radical shifts in habitat composition and quality across fragment boundaries. Experimental landscapes such as ours incorporate random placement in their design (e.g., the location of experimental patches does not follow gradients in altitude or soil type like many anthropogenic-fragments do), but in other respects may mirror many key features of anthropogenically fragmented landscapes. Studies such as ours explicitly address many of the features of this type of spatial heterogeneity.

We hesitate to draw specific applied implications from the results of our study. Similar analyses need to be applied to these taxa (and others) across a wider range of landscapes to assess the robustness of our general procedures and conclusions. The analyses reported here are primarily exploratory. Nevertheless, given the experimental nature of the study, our conclusions likely have more weight than similar studies done in unmanipulated habitats. The main applied implication of our work may be methodological and already well ingrained in the management literature (e.g., Morrison et al. 1992). In managing natural populations either for conservation, harvesting, or pest control, the relationship of wildlife to habitat is paramount. Our findings suggest that landscape structure influences the nature of habitat-wildlife relationships and should continue to be considered explicitly in management. Our results also suggest that models that do not incorporate context may not reveal the complexity behind species distributions.

Spatial distributions of species reflect processes occurring at multiple spatial scales. Spatially mediated, indirect interactions between patch size, landscape context, and vegetation composition influenced species-specific small-mammal distributions within our system. It is safe to assume that individual small mammals are fairly accurate habitat selectors and typically select areas of habitat in which they can establish a home range and successfully

reproduce (Morris 1989). At this smallest scale, individual choices are vital components of habitat use patterns. The large amount of variation explained by context variables, however, shows that larger-scale features of a landscape can interact with habitat selection at small scales to create observed spatial distributions. Context can limit the ability of organisms to find suitable habitat, (e.g., by disrupting patterns of dispersal). It can also make animals in certain areas within a landscape more prone to predation by organisms operating at larger scales. Context can also directly affect the local habitat type by changing patterns of plant community composition (e.g., by altering rates of succession). Changes in content, caused by context, feed back on annual spatial distributions by affecting habitat selection and local birth and death rates. This complex and exciting dynamic of processes interacting across scales should continue to be a major focus of study in landscape ecology because we will never successfully predict species responses to changes in landscape structure without it.

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APPENDIX 9.1. Results from stepwise regressions of the number of captures on a suite of content and context predictor variables.*

Prairie voles, 1995

$F(8, 271) = 29.77$, $P < 0.0001$, $SE = 0.67$, Multiple $R = 0.68$, $r^2 = 0.47$, % due to context variables: 85.8%
 Number of first-time captures = 688

Beta(Var.):	$-(.171)DP$	$-(.142)Bu4$	$-(.614)L1$	$(.180)Bu5$	$-(.440)L3$	$-(.365)L2$	$(.169)Crats$	$-(.147)V1$
P:	0.003	0.010	0.000	0.024	0.000	0.000	0.000	0.010
Partial r^2 :	0.032	0.024	0.265	0.019	0.114	0.054	0.046	0.024
Df^2 :	0.253	0.029	0.221	0.071	0.031	0.026	0.021	0.013

Prairie voles, 1996

$F(6, 273) = 30.98$, $P < 0.0001$, $SE = 0.75$, Multiple $R = 0.64$, $r^2 = 0.41$, % due to context variables: 84.9%
 Number of first-time captures = 521

Beta(Var.):	$-(.220)DP$	$-(.181)V1$	$-(.497)L1$	$-(.461)L2$	$-(.389)L3$	$(.098)V5$
P:	0.000	0.001	0.000	0.000	0.000	0.041
Partial r^2 :	0.041	0.055	0.089	0.065	0.053	0.055
Df^2 :	0.047	0.039	0.152	0.126	0.099	0.015

Deer mice, 1995

$F(5, 274) = 32.57$, $P < 0.00001$, $SE = 0.45$, Multiple $R = 0.61$, $r^2 = 0.37$, % due to context variables: 100%
 Number of first-time captures = 115

Beta(Var.):	$(.325)M1$	$(.216)S3$	$(.341)M2$	$-(.249)Bu1$	$-(.190)Bu4$
P:	0.000	0.000	0.000	0.000	0.000
Partial r^2 :	0.120	0.060	0.128	0.059	0.050
Df^2 :	0.178	0.076	0.055	0.032	0.033

Deer mice, 1996

$F(7, 272) = 14.31$, $P < 0.0001$, $SE = 0.03$, Multiple $R = 0.52$, $r^2 = 0.27$, % due to context variables: 100%
 Number of first-time captures = 93

Beta(Var.):	$(.414)M2$	$(.320)M1$	$(.287)L3$	$(.230)S3$	$-(.110)Bu4$	$-(.117)Bu5$	$-(.123)Bu2$
P:	0.000	0.000	0.000	0.000	0.045	0.037	0.049
Partial r^2 :	0.154	0.112	0.094	0.050	0.015	0.016	0.014
Df^2 :	0.084	0.079	0.057	0.020	0.010	0.008	0.010

APPENDIX 9.1. Results from stepwise regressions of the number of captures on a suite of content and context predictor variables.*

White-footed mice, 1996 (all captures)

F(6, 273) = 11.48, $P < 0.0001$, SE = 0.60, Multiple $R = 0.45$, $r^2 = 0.23$, % due to context variables: 62.5%

Number of total captures = 184

Beta(Var.):	(.191)L1	(.159)L2	-(.190)Dmice	(.213)V1	(.164)DP	(.159)Bu1
P:	0.020	0.022	0.002	0.000	0.006	0.015
Partial r^2 :	0.020	0.019	0.035	0.041	0.028	0.021
Dr ² :	0.077	0.034	0.029	0.0246	0.017	0.017

Cotton rats, 1995

F(9, 270) = 7.97, $P < 0.0001$, SE = 0.17, Multiple $R = 0.46$, $r^2 = 0.28$, % due to context variables: 77.6%

Number of first-time captures = 243

Beta(Var.):	(.200)V1	(.256)M1	-(.138)V2	(.542)L2	(.239)Pvoles	(.478)L1	(.386)L3	(.190)M2	-(.147)DP
P:	0.003	0.000	0.024	0.000	0.001	0.000	0.000	0.002	0.045
Partial r^2 :	0.031	0.060	0.018	0.094	0.040	0.077	0.052	0.033	0.015
Dr ² :	0.060	0.027	0.017	0.014	0.017	0.019	0.020	0.022	0.012

*Values reported with each equation include: (1) F-test (Regression Mean Square / Residual Mean Square), (2) standard error of the dispersion of the observed values about the regression line, (3) coefficient of multiple correlation, (4) coefficient of multiple determination, (5) % due to context, calculated as the proportion of the sum of all beta values due to the sum of beta coefficients for context predictors, and (6) the total number of captures used in each model. For each equation, predictor variables are listed in order of entry to the final model, with those on the left of the table entering first. Each significant predictor variable is shown with its beta coefficient, P value, partial r^2 , and the change in the final model r^2 due to the inclusion of the predictor variable. All context predictor variables are given in bold italics. Codes used in the equations: distance to closest patch edge (DP), distance to closest boundary edge (DB), block size dummy variables (S2, S3, M1, M2, L1, L2, L3; see Fig. 9.1), 1995 content axes (see Table 9.1): "Woody canopy" (V1); "Perennial grass" (V2); "Short stems vs. variance in stem heights" (V3); "Annual grass" (V4); "Herbaceous cover and forb height" (V5); "Perennial forb cover" (V6); 1996 content axes (see Table 9.2): "Woody canopy" (V1); "Short woody stems" (V2); "Perennial grass" (V3); "Annual grass" (V4); "Annual grass and -species richness" (V5); Number of first-time captures of small mammals: Prairie voles (Pvoles); Deer mice (Dmice); Cotton rats (Crats); White-footed mice (Wmice); Buffer zone axes (see Table 9.3): "Forest, road, and woody large patch" (Bu1); "Large patch and interstitial" (Bu2); "Medium patch (near)" (Bu3); "Medium patch (far)" (Bu4); "Field" (Bu5).

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