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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

ENVIRONMENTAL CONSTRAINTS REGULATING THE DISTRIBUTION
AND ABUNDANCE OF SMALL MAMMALS

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

By

ANTHONY J. STANCAMPIANO

Norman, Oklahoma

1999

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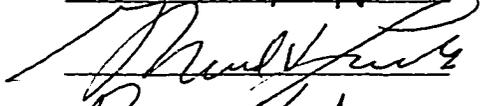
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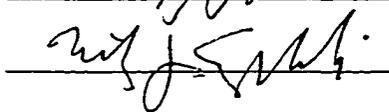
ENVIRONMENTAL CONSTRAINTS REGULATING THE DISTRIBUTION
AND ABUNDANCE OF SMALL MAMMALS

A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY



Victor A. Hutchinson


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PREFACE

This dissertation is presented as two chapters. Each chapter will be submitted to a refereed journal and is formatted accordingly. The first chapter will be submitted to the *Journal of Mammalogy* and the second to *Landscape Ecology*.

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ABSTRACT

I assessed the influence of 19 local-level, 40 landscape-level, and 59 combined variables on the distribution and abundance of small mammals at 60 plots across Fort Sill Military Reservation in Comanche County, Oklahoma. Mammal trapping took place each spring from 1989-1992. I collected 15 small-mammal species and used 10 of these ($n > 10$; *Chaetodipus hispidus*, *Cryptotis parva*, *Microtus ochrogaster*, *Neotoma floridana*, *Peromyscus attwateri*, *P. leucopus*, *P. maniculatus*, *Reithrodontomys fulvescens*, *R. montanus*, and *Sigmodon hispidus*) in my analyses. Variables for each mammal species were evaluated as unweighted measures based on the presence/absence of each mammal species at a plot and as weighted measures based on the abundance of each mammal species at each plot. Both weighted and unweighted data were subjected to cluster analysis, principal-components analysis, and discriminant-function analysis. Similar clusters were produced from unweighted and weighted analyses. General trends of the local, landscape, and combined affinities of species in these clusters were summarized on principal components.

The PCA of local variables showed that four species (*C. hispidus*, *N. floridana*, *P. attwateri*, and *P. leucopus*) occupied barren or rocky areas with a tall herbaceous or woody canopy, while six species (*C. parva*, *M. ochrogaster*, *P. maniculatus*, *R. fulvescens*, *R. montanus*, and *S. hispidus*) preferred open grassy areas. Weighted discriminant analysis of the local variables produced better predictive accuracy (75% correctly classified) than the unweighted data (63% correctly classified). Discriminant analysis using only the two largest clusters produced classification accuracy of 72%

(unweighted) and 83% (weighted). Total number of broadleaf trees and rocky ground cover were the most important factors in discriminating among groups.

I computed 15 landscape variables at four different scales (40 variables total) for each of 60 study plots using a geographic information system and a digitized vegetation map of the 38,000-ha Fort Sill Military Reservation. Results of the PCA of unweighted and weighted data were similar, therefore only weighted data were used in subsequent analyses. Cluster analysis of these weighted data produced three multispecies clusters based on associations of species distributions and abundances to landscape factors.

The landscape predictive models constructed using discriminant function analysis determined which landscape variable or combination of variables were most efficient in classifying species into the appropriate cluster and allowed small-mammal distributions across the landscape to be predicted. Cluster classification accuracy was 59%. When local-level variables were combined with the landscape data, cluster membership remained similar and classification accuracy was 58%.

Since clusters were developed using horizontal elements of a spatially heterogeneous landscape, they consisted of unique species relationships. The two most abundant grassland species, *S. hispidus* and *P. maniculatus*, were not in the same cluster. However, *S. hispidus* did cluster with *P. leucopus*, which is typically considered a woodland/edge species. This suggests that these two species perceive the landscape similarly, preferring areas with a number of contrasting patch types (edge). *Sigmodon hispidus* primarily occupies grassland patches interspersed with shrubby or woody patches, and *P. leucopus* is found in woodlands bordered by grasslands. Conversely, *P. maniculatus* occupies areas dominated by one patch type but made up of several patch

types. One obtains additional insight into habitat preferences of small mammals by evaluating landscape elements, particularly when landscape models are used in combination with local habitat models.

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MICROHABITAT AFFINITIES OF SMALL MAMMALS
IN SOUTHWESTERN OKLAHOMA

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We assessed the influence of 19 microhabitat factors on the distribution and abundance of small mammals at 60 plots across Fort Sill Military Reservation in Comanche County, Oklahoma. Trapping took place each spring from 1989-1992. We collected 15 small-mammal species and used 10 of these ($n > 10$; *Chaetodipus hispidus*, *Cryptotis parva*, *Microtus ochrogaster*, *Neotoma floridana*, *Peromyscus attwateri*, *P. leucopus*, *P. maniculatus*, *Reithrodontomys fulvescens*, *R. montanus*, and *Sigmodon hispidus*) in our analyses. Microhabitat variables for each mammal species were evaluated as unweighted measures based on the presence/absence of each mammal species at a plot and as weighted measures based on the abundance of each mammal species at each plot. Both weighted and unweighted data were subjected to cluster analysis, principal-components analysis, and discriminant-

function analysis. Similar clusters were produced from unweighted and weighted analyses. General trends of the microhabitat affinities of species in these clusters were summarized on principal components. Four species (*C. hispidus*, *N. floridana*, *P. attwateri*, and *P. leucopus*) occupied barren or rocky areas with a tall herbaceous or woody canopy, while six species (*C. parva*, *M. ochrogaster*, *P. maniculatus*, *R. fulvescens*, *R. montanus*, and *S. hispidus*) preferred open grassy areas. Although results were similar, the first two components of the weighted PCA explained more of the variance in the data set than the unweighted analysis. Weighted discriminant analysis also produced better predictive accuracy (75% correctly classified) than the unweighted data (63% correctly classified). Discriminant analysis using only the two largest clusters produced classification accuracy of 72% (unweighted) and 83% (weighted). Total number of broadleaf trees and rocky ground cover were the most important factors in discriminating among groups.

Key words: small mammals, habitat, *Peromyscus*, principal-components analysis, abundance, microhabitat

Small-mammal and bird microhabitat affinities have been used extensively as components of models to determine a range of ecological relationships. Kaufman et al. (1995) assessed temporal abundance of *Peromyscus leucopus* using data for production of seeds, fruits, and nuts by woody plants < 1 m in height. Combinations of a vertical foliage profile, ground cover, and soil

characteristics have been used to differentiate between the microhabitats of forest small-mammal species (Dueser and Shugart, 1978; Seagle, 1985). Others have evaluated the correlation of small-mammal abundance with habitat type (Geir and Best, 1980; Heske et al., 1997; Kirsch, 1997). Overall significant differences in habitat use among sympatric species of small mammals were demonstrated using discriminant-function analysis (Morrison and Anthony, 1988; Seagle, 1985). Small mammals that share microhabitat affinities were grouped into assemblages based on the degree of overlap in microhabitat use (Heske et al., 1997; Seagle, 1985). Similar habitat-characterization studies were performed on avian communities (Pogue and Schnell, 1994).

Van Horne and Wiens (1991:2) stated that the goal of wildlife modeling is “to develop models that can be used to assess wildlife-habitat relations and to predict their sensitivity to perturbations.” Successful wildlife models should be based on biologically realistic (valid) functions that are somewhat general and simple (Van Horne and Wiens, 1991). This leads to accurate, adaptable, and most importantly, usable models. To generate models using these criteria there must be tradeoffs. Most wildlife models meet two of these criteria—validity and simplicity. However, the majority cannot meet the generality criterion. A general model is one which applies to a wide range of situations without major modifications (Van Horne and Wiens, 1991).

Generality may be achieved in three ways: (1) expanding the model coverage from single species to sets of ecologically similar species; (2) increasing the size of the area or geographic region in which a model is used; and (3)

broadening the range of cover types to which a model applies in a given region (Van Horne and Wiens, 1991). Increasing the geographic area in which a model is employed within a landscape has a similar effect to using sets of ecologically similar species in that landscape. As an area increases from ecotope to land facet to land system to landscape, a model becomes more general; concomitantly, a general model should maintain its efficiency at each scale (Naveh and Lieberman, 1994; Zonnveld, 1979). New species are added at each scale and suites of species exist at the landscape level.

After increasing the size of the area modeled or broadening cover types within a region, model efficiency is limited by the size and composition (complexity) of the specific landscape in question. As models are extended in coverage across landscapes, predictions of wildlife-habitat relations are less specific and, therefore, less efficient (Layman and Barrett, 1986).

Models can be efficient and general at large scales by increasing model coverage to include sets of ecologically similar species. This is true as long as the scale of the model does not include several landscapes. These models can then be modified for additional landscapes by including new sets of species based on current landscape variables. Depending on the contrast between landscapes, these modifications may be extreme or minimal. Generalist species may be present in several adjacent landscapes; however, sympatric species with a narrower niche breadth may change from one landscape to another.

Development of single-species models is time and labor intensive (Verner, 1983, 1984). The need to modify single-species models for each new landscape

exacerbates this problem. Our purpose was to contribute to the development of general wildlife-habitat models that predict presence and distribution of small mammals across a landscape. After clustering small-mammal species into ecologically similar assemblages based on microhabitat affinities, we developed predictive models that indicate the composition of the small-mammal fauna in this landscape and forecast the effect of habitat perturbations on the fauna.

METHODS

Study area.—This study took place on the 38,000-ha Fort Sill Military Reservation located in Comanche County in southwestern Oklahoma (Fig. 1). The reservation is bordered on the northwest by the Wichita Mountains Wildlife Refuge and on the south by the city of Lawton. Several small towns are scattered near the reservation boundaries. Fort Sill extends 37 km along an east-west axis and 13 km at its widest point along a north-south axis.

Fort Sill is in the Osage Plains section of the Central Lowlands physiographic province (Hunt, 1974). The eastern, south-central, and western portions of the Reservation are primarily rolling upland plains of low relief. The north-central and northwest sections of the Reservation include the southern portion of the Wichita Mountains. This area contains steep, rocky hills, and moderate relief (Johnson et al., 1990). Many streams are interspersed throughout Fort Sill with most flowing to the south or southeast and draining into Cache Creek.

The following land-cover types are typical on Fort Sill: (1) bottomland forest, located close to perennial drainages on deep soils and dominated by

sugarberry (*Celtis laevigata*) or American elm (*Ulmus americana*); (2) cross timbers, a somewhat open-canopied low forest in uplands and along intermittent streams composed primarily of post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*); (3) mesquite savanna, composed of mixed grasses and mesquite trees (*Prosopis glandulosa*); (4) grasslands, consisting of short, mixed, and tall grasses; (5) oak savanna, composed of scattered trees (*Q. marilandica* and *Q. stellata*) in mixed grasses; and (6) riparian vegetation, located close to ponds and drainages and influenced by saturated soils (Fig. 2; Johnson et al., 1992).

Sampling techniques.—We sampled 60 plots on Fort Sill in late May and early June of each year from 1989-1992 for small mammals (a total of 24,000 trap-nights). To ensure objectivity and representativeness in the placement of these plots, we used a stratified-random procedure to select the sites. This procedure incorporated SPOT (System Probatoire pour l' Observation de la Terra) satellite imagery, digital soil surveys, and the geographic information system GRASS (Geographic Resource Analysis Support System; CERL 1989). Sampling was stratified on the basis of soils and land-cover types as estimated from satellite imagery; within strata, appropriate numbers of sites were randomly selected based on the area of the stratum. Warren et al. (1990) gave a detailed description of this procedure.

The standard length of each permanent plot was 100 m. We surveyed small mammals by setting a line of 20 Museum Special and 5 rat-snap traps 15 m to each side of and parallel to the long axis of each plot for a total of 50 traps at each site (Tazik et al., 1992). We spaced trap stations 7.5 m apart in each line and

baited them with a mixture of rolled oats and peanut butter. Animals that were collected were skinned and prepared as museum specimens then placed in the Oklahoma Museum of Natural History at the University of Oklahoma.

Vegetative, soil, and topographical data were collected at each plot by Army LCTA (Land Condition Trend Analysis) crews. Ground cover was sampled at 100 points along a line transect through the center of each plot beginning at the 0.5-m point and continuing at 1-m intervals. Microhabitat variables indicating vertical structure and vegetation type (annual or perennial grasses and broadleaf trees) were recorded at 500 locations at 0.25-m intervals along this line transect (for details, see Tazik et al., 1992). We used mammal-survey data and microhabitat data collected at each plot in various statistical analyses to provide general descriptive associations between mammal species and the habitats they used.

We calculated species richness and average abundance at each plot and plotted the results as contours, generated by kriging, on a boundary map of Fort Sill. Kriging is a geostatistical gridding method that uses information on patterns of spatial correlation among sampled locations to estimate interpolated points (Maurer, 1994). Kriging was done using a linear-variogram procedure (Surfer for Windows software; Keckler, 1994), and contour maps were produced.

Initially, we included 29 microhabitat variables in a multivariate analysis (Table 1). These variables are primarily indicators of vertical structure, cover type, and cover extent for each plot (Tazic et al., 1991). As indicated in the results, 10 of these microhabitat variables were dropped from subsequent analyses

because they did not have significant loadings in the first principal-components analysis.

We calculated an unweighted average and an abundance-weighted average for each mammal species for each microhabitat variable. The unweighted microhabitat value for a mammal species was obtained by taking the average of the values for the plots where the species occurred, irrespective of the number that were captured. The abundance-weighted variable average (W) for mammal species was calculated as:

$$W_{kj} = \frac{\sum_{i=1}^{60} n_{ik} v_{ij}}{\sum_{i=1}^{60} n_{ik}},$$

where n_{ik} is the number of individuals of mammal species k captured on plot i and v_{ij} is the value of microhabitat variable j on plot i . The purpose of employing both unweighted and weighted averages was to determine whether weighting based on the abundance of individuals of each mammal species would increase the predictive accuracy of our models over the use of presence/absence data.

Principal-components analysis.—Initially we used the 29 microhabitat variables in a principal-components analysis (PCA) to characterize general trends along vegetation gradients based on a rectangular data matrix of 60 sample plots by habitat variables. We mean-centered this raw data set and calculated correlations among variables (Morrison et al., 1992). Standardized data (variables

with a mean of 0 and a standard deviation of 1) were then projected onto eigenvectors extracted from the correlation matrix. In such an analysis, the first principal component explains the maximum character variance, while each subsequent orthogonal component explains the maximum remaining character variance.

We performed parallel analysis (Franklin et al., 1995) to determine the number of significant principal components and the significance level of their loadings in order to reduce the number of variables. Using these results (which reduced the number of variables from 29 to 19 in all subsequent analyses; Table 1), we created two rectangular matrices of mammal species by weighted and unweighted microhabitat-variable averages to be used in two separate PCAs (Appendix I). Projections of species onto principal-component axes provides a way of representing microhabitat affinities of each species. All PCAs were performed using the ordination programs in NTSYS-pc (Rohlf, 1993).

Cluster analysis.—We subjected the resulting data sets (10 mammal species by 19 microhabitat variables) to UPGMA cluster analysis (Rohlf, 1963; Sneath and Sokal, 1973) to create taxonomic assemblages (TAs; Jaksić, 1981; Van Horne and Wiens, 1991), containing species with similar microhabitat affinities. We clustered both weighted and unweighted matrices. A distance matrix (average taxonomic distance) was calculated to determine similarities among the species. The UPGMA algorithm computes the average dissimilarity of a candidate species or cluster to an extant cluster, weighting each species equally (Sneath and Sokal, 1973). The cophenetic correlation coefficient was calculated

for the resulting dendrograms, providing an index as to how well the diagram summarizes the pairwise distances among species.

Niche overlap and breadth.—We evaluated niche overlap and niche breadth relative to a local habitat gradient represented by principal component I. This habitat gradient was subdivided into 10 equal intervals, and we determined the number of plots with projections in each interval: (1) -1.938 to -1.6916; (2) -1.6915 to -1.4452; (3) -1.4451 to -1.1988; (4) -1.1987 to -0.9524; (5) -0.9523 to -0.7060; (6) -0.7059 to -0.4596; (7) -0.4595 to -0.2132; (8) -0.2131 to 0.0332; (9) 0.0333 to 0.2796; (10) 0.2797 to 0.5260.

Niche overlap was evaluated using the simplified Morisita index (Krebs, 1989) as proposed by Horn (1966):

$$M = \frac{2 \sum_{i=1}^n p_{ij} \sum_{i=1}^n p_{ik}}{\sum_{i=1}^n p_{ij}^2 + \sum_{i=1}^n p_{ik}^2},$$

where p_{ij} is the proportion that resource (i.e. projection) i constitutes of the total resources used by species j , and p_{ik} is the proportion that resource i constitutes among the total used by species k . This measure of overlap ranges from 0.0 (no resources in common) to 1.0 (complete overlap).

We evaluated niche breadth using Smith's index (Krebs, 1989):

$$B = \sum_{i=1}^n (p_i a_i)^{0.5},$$

where p_i is the proportion of individuals found in or using resource state (i.e. projection interval) i , a_i is the proportion that resource i is of the total resources, and n is the total number of possible resource states. Smith's measure of niche breadth varies from 0.0 (minimal breadth) to 1.0 (maximum breadth).

We employed a Monte Carlo simulation to evaluate the degree to which the resulting coefficients (M and B) differed statistically from values expected by chance alone (Pogue and Schnell, 1994). We distributed the 60 sample plots among the 10 resource states with the same frequencies of the actual plots and randomly drew (without replacement) the number of plots for species j and the number of plots for species k . We then calculated the simplified Morisita index for the randomly drawn plots. This simulated value of the index was compared to the actual value calculated from the sample plots to determine if the simulated value was less than or greater than/equal to the actual value. The simulation was repeated 1,000 times, and we calculated the two-tailed probability that the sample value deviated from what would be expected by chance alone based on the number of index values less than or greater than/equal to the actual sample value.

Discriminant analysis.—We used stepwise discriminant analysis (Morrison et al., 1992) to derive linear combinations of the habitat variables that would maximally discriminate among the taxonomic assemblages (TAs). Stepwise discriminant analysis selects habitat variables that exhibit high variation among TAs and low variation within TAs. We used forward-stepping discriminant analysis with the F -to-enter set at 4.0. Discriminant-function analysis assigns a weighted score to each observation based on the set of

independent variables for that observation. We derived classification functions to assign each individual observation to a specific TA. Each individual had an equal probability of being assigned to any TA (i.e. we did not, *a priori*, bias the possibility of a particular plot being assigned to or categorized as a particular TA).

The discriminant analysis was calculated for all TA members, and each individual was assigned to the appropriate TA depending on the resulting classification-function value. We also used a jackknifed classification, which leaves out the individual plot being considered when calculating the coefficients of the discriminant functions, and then evaluates the plot (see SPSS, 1997).

We performed discriminant analysis on both abundance weighted and unweighted data for clusters containing the two most abundant taxonomic assemblages and for clusters of all taxonomic assemblages (4 total). Sample plots using canonical scores derived from discriminant analysis were projected onto the resulting canonical axes. Discriminant analyses were performed using SYSTAT 7.0 (SPSS, 1997).

RESULTS

We captured 1,146 small mammals representing 15 species during the study (Table 2), with the three most abundant species being *Sigmodon hispidus* (hispid cotton rat, 39.0%), *Peromyscus leucopus* (white-footed mouse, 21.7%), and *P. maniculatus* (deer mouse, 16.9%). The remaining 13 species, in order of abundance, made up 22.4% of the total captures (with no single species accounting for greater than 8.0% of the total): *P. attwateri* (Texas mouse), *Reithrodontomys fulvescens* (fulvous harvest mouse), *R. montanus* (plains harvest

mouse), *Neotoma floridana* (eastern woodrat), *Chaetodipus hispidus* (hispid pocket mouse), *Cryptotis parva* (least shrew), *Microtus ochrogaster* (prairie vole), *M. pinetorum* (woodland vole), *Mus musculus* (house mouse), *Sylvilagus floridanus* (eastern cottontail), *N. micropus* (southern plains woodrat), and *Spermophilus tridecemlineatus* (thirteen-lined ground squirrel). Our analyses included only those species in which 10 or more individuals were collected; therefore, *M. pinetorum*, *M. musculus*, *N. micropus*, *S. tridecemlineatus*, and *S. floridanus* were not analyzed (Table 2).

Species richness (Fig. 3a) and average number of individuals for all species (Fig. 3b) varied widely across Fort Sill. Species distributions interpolated by kriging are shown as contours of number of individuals for two of the most abundant species, *P. leucopus* and *P. maniculatus* (Figs. 3c and 3d).

Principal-components analysis.—The first three components in the PCA of sample plots explained 53.9% of the total variance in microhabitat variables (Table 3). Parallel analysis of this PCA yields three significant components (I-III) and a significant loading level of > 0.52 . Ten habitat variables did not have significant loadings on any of the three significant components and were dropped from further analysis (19 variables were retained; Table 1).

Projections and character loadings (Table 3, Fig. 4a) indicate that component I represents a gradient from tall broadleaf trees (areas with a canopy) to open areas (no canopy). Component II is a gradient of sites that are barren and rocky with steep slopes, to relatively flat plots with deeper soils and heavy cover. Component III is a gradient of plots with a high density of perennial grasses to

those with mixed perennial and annual grasses (Fig. 4b).

Principal-components analysis of the data matrix of 19 variables for unweighted species averages produced two significant components (i.e. loadings > 0.58). The first component explained 65.7% of the variance in the data set and the second component 26.1% (Table 4). Component I represents a gradient of steeply sloped, barren or rocky areas with intermediate to tall woody and herbaceous plants (low canopy) to areas containing perennial and annual grasses (open, no canopy). Character loadings and projections on component II indicate a gradient from plots with perennial cover to those with annual cover (Fig. 5a).

Species projections onto component I (Fig. 5a) show that six species (*C. parva*, *M. ochrogaster*, *P. maniculatus*, *R. fulvescens*, *R. montanus*, and *S. hispidus*) are found in relatively open areas (i.e. positive loadings) and four species (*C. hispidus*, *N. floridana*, *P. attwateri*, and *P. leucopus*) frequented bare areas with a canopy (i.e. negative loadings). Projections of six species (*C. hispidus*, *C. parva*, *P. leucopus*, *P. maniculatus*, *R. fulvescens*, and *S. hispidus*) onto component II are near the middle of the axis (-0.183 to 0.125). Two species are found on opposite ends of the axis, suggesting an affinity for annual cover (i.e. positive loading; *P. attwateri*) or perennial cover (i.e. negative loading; *N. floridana*).

Principal-components analysis of the weighted microhabitat variables by mammal species produced similar results to the unweighted analysis. We retained the first two components and significant character loadings were > 0.58. Component I explained 70.3% of the variance, while component II explained

19.8% (Table 4). Component I represents a gradient of steep-sloped, barren, and rocky areas with intermediate to tall (> 1.5 m) woody and/or herbaceous cover (canopy) to sites that are open (no canopy) and have deeper soils. Component II represents a gradient of plots from those with annual cover to those with heavy perennial cover. Projections of species onto these two components (Fig. 5b) yielded results similar to the unweighted species projections (Fig. 5a).

Cluster analysis.—Cluster analysis of the standardized unweighted data matrix produced a UPGMA phenogram depicting species similarity based on 19 microhabitat variables. Four clusters (TAs) are defined at a distance of 0.9 (Fig. 6a). The first TA consists of *C. parva*, *M. ochrogaster*, *P. maniculatus*, *R. fulvescens*, and *S. hispidus*, while the second included *C. hispidus*, *P. leucopus*, and *R. montanus*. TAs 3 and 4 have only one species each—*P. attwateri* and *N. floridana*, respectively.

Cluster analysis of the weighted data matrix produced four TAs (Fig. 6b). They have the same group membership as obtained with the unweighted clustering; however, distances differ somewhat.

Niche overlap and breadth.—Niche overlap values using the simplified Morisita's index ranged from 0.310 for overlap between *N. floridana* and *M. ochrogaster* to 0.997 between *C. parva* and *P. maniculatus* (Table 5). When sampling without replacement, the expected overlap values are higher for species where one or both were captured at a relatively large number of plots (Pogue and Schnell, 1994). Expected niche overlap values range from 0.847 for *C. parvus* and *N. floridana* to 0.970 for *S. hispidus* and *P. maniculatus*.

Relatively low significant overlap values (Table 5) indicate less overlap than predicted based on chance alone, and relatively high significant overlap values indicate more overlap. *Neotoma floridana* shows significant deviations, or low overlap, when compared to all other species. In addition, the overlap of *R. fulvescens* and *P. attwateri* was less than expected by chance. All five species in TA1 (*C. parva*, *M. ochrogaster*, *P. maniculatus*, *R. fulvescens*, and *S. hispidus*) have significant positive overlap with each other. *Chaetodipus hispidus* (TA2) has significant positive overlap with *M. ochrogaster*, *R. fulvescens*, and *S. hispidus*, all of which are in TA1.

Calculated values for Smith's index of niche breadth (B) range from 0.3485 for *N. floridana* to 0.7360 for *R. montanus* (Table 6). The species in Table 6 are ordered based on the number of plots where they were captured. The mean simulated values (B_s) increase as the samples increase, since sampling is done without replacement. Negative deviations from the expected values for all species were statistically significant (Table 6), indicating that niche breadth of each species is less than expected simply by chance.

Discriminant analysis.—In the unweighted discriminant analysis, 83% of TA1 species were correctly classified, while only 28% of TA2 species were correctly placed using the classification functions. For TA3, 64% were correctly classified, while 43% of TA4 were assigned correctly (Table 7, Fig. 7a). Correct jackknifed classifications were lower for TA3 and TA4.

The weighted analysis produced better classification results, although it did require more predictive variables (Table 7). For TA1, 86% were correctly

classified, as were 53% of the TA2 species (Table 7, Fig. 7b). We also had slightly better classification success for TA3 and TA4 using the weighted data (67 and 45%, respectively). Corrected jackknifed classifications were lower for TA4.

We then eliminated TA3 and TA4, which had relatively small sample size and included only a single species each, to increase the accuracy of our model. Individual TA and total classification accuracy increased in both the unweighted and weighted analysis (Table 7). In addition, the number of variables entered into the classification decreased in both models (Table 8).

DISCUSSION

Our study indicates the presence of two distinct taxonomic assemblages of small mammals on Fort Sill based on microhabitat variables. These TAs represent 8 of the 10 species considered in the analyses. Canopy cover, or vertical openness, and ground cover are the main microhabitat factors contributing to the separation of these groups. Microhabitat affinities of the constituent species of each assemblage are well supported in the literature (Baker, 1968; Barry and Franq, 1980; Blair, 1954; Choate, 1970; Davis and Joeris, 1945; Glass and Halloran, 1961; Goertz, 1962 and 1963; Kaufman and Fleharty, 1974; Kaufman et al., 1983; Kaufman et al., 1995; Schnell et al., 1980). In Oklahoma, the species in TA1 are found in open areas with moderate to heavy grass cover (Caire et al., 1989; Schnell et al., 1980). Member species of TA2 prefer some type of woody canopy and less dense or barren ground cover (Caire et al., 1989; Kaufman et al., 1983; Kaufman et al., 1995; Schnell et al., 1980).

These microhabitat affinities are not necessarily represented across the

entire range of broadly distributed species, such as *P. maniculatus* (TA1). In the eastern portion of its range (Hall, 1981), two distinct subspecies of *P. maniculatus* are found. One inhabits grassy areas, while the other frequents coniferous and mixed evergreen-deciduous forests (Choate et al., 1994; Garman et al., 1994; Graves et al., 1988). This represents a change in microhabitat affinity for this species. However, *P. leucopus*, the most abundant species in TA2, prefers canopied areas in all portions of its range, including insular situations (Barry and Franq, 1980; Bendell, 1961; Garman et al., 1994; Kirsch, 1997; M'Closkey, 1975).

All members of TA1 have significant intra-assemblage niche overlap values (Table 5), indicating a strong microhabitat relationship among these species. Inter-assemblage significant niche overlap (positive) occurs between TA2 member *C. hispidus* and TA1 members *M. ochrogaster*, *R. fulvescens*, and *S. hispidus*. This overlap may be due to the preference of *C. hispidus* for sites with more ground cover than is the case for the other two members of TA2. In the weighted cluster analysis, these three TA1 members are the last to enter the TA1 cluster (Fig. 6b). For weighted and unweighted data sets, clustering produced identical TA membership. Individual relationships within the assemblages differ somewhat. These differences are made apparent by discriminant analysis. The unweighted discriminant analysis model is very accurate when classifying TA1 membership (83%), but is not satisfactory (28%) when assigning TA2 membership (Table 7). This is due to the high number of shared plots between TA2 and TA1 members (38 shared plots). The overall correct classification is

63%. Abundance weighting increases the accuracy of the classification of TA1 to 86% and TA2 to 53%. Total classification accuracy improves to 75% with abundance weighting.

Elimination of TA3 and TA4 (single-species TAs) increases both weighted and unweighted model accuracy and decreases the number of variables necessary to be entered into the model. The unweighted two-TA model uses two variables and attains an overall accuracy of 72% (82% for TA1 and 53% for TA2; Table 7). The weighted two-TA model uses six variables and correctly classifies species 83% of the time (87% for TA1 and 73% for TA2; Table 7). Of the four separate models, three use the variables Tctb (total count broadleaf trees) and Grck (number of points with rocks) as the top two predictive variables. These variables are indicators of aerial and ground cover. In addition to Tctb, the unweighted two-TA model uses Gcltr (number of points with litter), which also is an indicator of ground cover.

Although the unweighted analysis produced similar results to the weighted analysis, it was less efficient in correctly classifying TA membership. Unweighted data indicate only the presence or absence of a species in a particular plot. Many of the plots occur in or near habitat transitions. Habitat adjacent to these sites may act as either a source or a sink for species captured at these transitional plots (Heske et al. 1997). These data may include captures of many individuals from population sinks, particularly for those plots where a small number of individuals were collected over the course of the study (Dunning et al. 1992). The abundance-weighted data are informative because they more

accurately indicate species preferences and perhaps sources of species dispersal.

Transitional plots also negatively influence a model due to the number of inter-assemblage shared plots. *Peromyscus maniculatus* and *P. leucopus* co-occur in 31 plots, and 27 plots are shared by *P. leucopus* and *S. hispidus*. These common occurrences may represent an affinity for edge by *P. leucopus* (Iverson et al., 1967; Van Deusen and Kaufman, 1977). In almost all instances (29 of 32), *P. leucopus* is found in grassland habitat. Grasslands may represent foraging areas (Stancampiano and Caire, 1995), dispersal routes, or sinks for *P. leucopus*. Abundance weighting increases model accuracy and helps to compensate for this large amount of habitat overlap among TAs. Researchers could develop and use either model (presence/absence or abundance) depending on the level of accuracy desired in their predictions and/or time and funding limitations.

These models indicate the potential for one or many species to be found in a given area based on microhabitat. They also extend model coverage from species to sets of ecologically similar species and use a broad range of applicable cover types, which expands model generality and makes them more useful (Van Horne and Wiens, 1991). Factors such as trapability, source-sink dynamics, and recent climactic conditions influence capture rates and can account for temporary vacancies of certain species from certain predicted areas.

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LITERATURE CITED

- Baker, R. H. 1968. Habitats and distribution. Pp. 99-126, *in* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Special Publication No.2, The American Society of Mammalogists, Stillwater, Oklahoma, 593 pp.
- Barry, R. E., Jr., and Franq, E. N. 1980. Orientation to landmarks within the preferred habitat by *Peromyscus leucopus*. *Journal of Mammalogy*, 61:292-303.
- Bendell, J. F. 1961. Some factors affecting the habitat selection of the white-footed mouse. *The Canadian Field-Naturalist*, 75:244-255.
- Blair, W. F. 1954. Mammals of the mesquite plains biotic district in Texas and Oklahoma, and speciation in the central grasslands. *The Texas Journal of Science*, 3:235-264.
- Caire, W., J. D. Tyler, B. P. Glass, and M. A. Mares. 1989. *Mammals of Oklahoma*. University of Oklahoma Press, Norman, Oklahoma, 567 pp.
- CERL. 1989. GRASS, version 4.1. U.S. Army Corps of Engineers, Construction Engineering and Research Laboratories, Champaign, Illinois.
- Choate, J. R. 1970. Systematics and zoogeography of middle American shrews of the genus *Cryptotis*. *University of Kansas Publications of the Museum of Natural History*, 19:195-317.
- Choate, J. R., J. K. Jones, Jr., and C. Jones. 1994. *Handbook of mammals of the south-central states*. Louisiana State University Press, Baton Rouge, Louisiana, 304 pp.
- Davis, W. B., and L. Joeris. 1945. Notes on the life history of the little short-

- tailed shrew. *Journal of Mammalogy*, 26:136-138.
- Dueser, R. D., and H. H. Shugart, Jr. 1978. Microhabitats in a forest-floor small mammal fauna. *Ecology*, 59:89-98.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos*, 65:169-175.
- Franklin, S. B., D. J. Gibson, P. A. Robertson, J. T. Pohlmann, and J. S. Fralish. 1995. Parallel analysis: a method for determining significant principal components. *Journal of Vegetation Science*, 6:99-106.
- Garman, S. L., A. F. O'Connell, Jr., and J. H. Connery. 1994. Habitat use and distribution of the mice *Peromyscus leucopus* and *P. maniculatus* on Mount Desert Island, Maine. *The Canadian Field-Naturalist*, 108:67-71.
- Geir, A. R., and L. B. Best. 1980. Habitat selection by small mammals of riparian communities: evaluating effects of habitat alterations. *The Journal of Wildlife Management*, 44:16-24.
- Glass, B. P., and A. F. Halloran. 1961. The small mammals of the Wichita Mountains Wildlife Refuge, Oklahoma. *Journal of Mammalogy*, 42:234-239.
- Graves, S., J. Maldonado, and J. O. Wolff. 1988. Use of ground and arboreal microhabitats by *Peromyscus leucopus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology*, 66:277-278.
- Goertz, J. W. 1962. A new marginal record for the fulvous harvest mouse. *Proceedings of the Oklahoma Academy of Sciences*, 42:124-127.
- _____. 1963. Some biological notes on the plains harvest mouse.

- Proceedings of the Oklahoma Academy of Sciences, 43:123-125.
- Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 2:601-1190 + 90.
- Heske, E. J., D. L. Rosenblatt, and D. W. Sugg. 1997. Population dynamics of small mammals in an oak woodland-grassland-chaparral habitat mosaic. The Southwestern Naturalist, 42:1-12.
- Horn, H. S. 1966. Measurement of overlap in comparative ecological studies. The American Naturalist, 100:419-424.
- Hunt, C. B. 1974. Natural regions of the United States and Canada. W. H. Freeman Co., San Francisco, 725 pp.
- Iverson, S. L., R. W. Seabloom, and J. M. Hnatiuk. 1967. Small-mammal distributions across the prairie-forest transition of Minnesota and North Dakota. The American Midland Naturalist, 78:188-197.
- Jaksić, F. M. 1981. Abuse and misuse of the term "guild" in ecological studies. Oikos, 37:397-400.
- Johnson, F. L., R. A. Thompson, R. Rudman, J. R. Estes, G. D. Schnell, and K. D. Harris. 1990. Floral inventory of Fort Sill, Oklahoma. Final report to the United States Army Construction Engineering Laboratory, Champaign, Illinois.
- Johnson, F. L., W. O. Keller, M. D. Proctor, and G. D. Schnell. 1992. Fort Sill vegetation map. Final report, Oklahoma Biological Survey, Norman, Oklahoma.
- Kaufman, D. W., and E. D. Fleharty. 1974. Habitat selection by nine species of

- rodents in north-central Kansas. *The Southwestern Naturalist*, 18:443-451.
- _____, S. K. Peterson, R. Fristik, and G. A. Kaufman. 1983. Effect of microhabitat features on habitat use by *Peromyscus leucopus*. *The American Midland Naturalist*, 110:177-185.
- _____, G. A. Kaufman, and E. J. Finck. 1995. Temporal variation in abundance of *Peromyscus leucopus* in wooded habitats of eastern Kansas. *The American Midland Naturalist*, 133:7-17.
- Kirsch, E. M. 1997. Small mammal community composition in cornfields, roadside ditches, and prairies in eastern Nebraska. *Natural Areas Journal*, 17:204-211.
- Keckler, D. 1994. *Surfer for Windows*. Golden Software, Inc., Golden, Colorado.
- Krebs, C. J. 1989. *Ecological methodology*. Harper Collins Publishers, New York, 654 pp.
- Layman, S. A., and R. H. Barrett. 1986. Developing and testing habitat-capability models: pitfalls and recommendations. Pp 87-91, *in* *Wildlife 2000 modelling habitat relationships of terrestrial vertebrates* (J. Verner, M. Morrison, and C. J. Ralph, eds.). The University of Wisconsin Press, Madison, Wisconsin, 470 pp.
- Maurer, B. A. 1994. *Geographical population analysis: tools for the analysis of biodiversity*. Blackwell Scientific Publications, Oxford, 130 pp.
- M'Closkey, R. T. 1975. Habitat dimensions of white-footed mice, *Peromyscus leucopus*. *The American Midland Naturalist*, 93:158-167.

- Morrison, M. L., and R. G. Anthony. 1988. Habitat use by small mammals On early-growth clear-cuttings in Western Oregon. *Canadian Journal of Zoology*, 67:805-811.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships, concepts and applications. The University of Wisconsin Press, Madison, Wisconsin, 343 pp.
- Naveh, Z., and A. S. Lieberman. 1994. Landscape ecology: theory and application. Springer-Verlag, New York, 360 pp.
- Pielou, E. C. 1984. The interpretation of ecological data: a primer on classification and ordination. John Wiley and Sons, New York, 263 pp.
- Pogue, D. W., and G. D. Schnell. 1994. Habitat characterization of secondary cavity-nesting birds in Oklahoma. *The Wilson Bulletin*, 106:203-226.
- Rohlf, F. J. 1963. Classification of *Aedes* by numerical taxonomic methods (Diptera: Culicidae). *Annual Review of the Entomological Society of America*, 56:798-804.
- _____. 1993. NTSYS-pc Numerical taxonomy and multivariate analysis system. Exeter Software, Setauket, New York.
- Schnell, G. D., R. D. Owen, R. K. Chesser, and P. G. Risser. 1980. Populations of small mammals in north-central Oklahoma. *The Southwestern Naturalist*, 25:67-80.
- Seagle, S. W. 1985. Patterns of small mammal microhabitat utilization in cedar glade and deciduous forest habitats. *Ecology*, 66:22-35.
- Sneath, P. H., and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and

- Company, San Francisco, 573 pp.
- SPSS Inc. 1997. SYSTAT version 7.0 for Windows. SPSS Inc., Chicago, Illinois.
- Stancampiano, A. J., and W. Caire. 1995. Food habits of *Peromyscus* and *Reithrodontomys* in the Wichita Mountains Wildlife Refuge, Oklahoma. *Proceedings of the Oklahoma Academy of Science*, 75:45-49.
- Tazik, D. J., S. D. Warren, V. E. Diersing, R. B. Shaw, R. J. Brozka, C. F. Bagley, W. R. Whitworth. 1992. U. S. Army land condition-trend analysis (LCTA) plot inventory field methods. United States Army Construction Engineering Research Laboratory, Technical Report, TR N-92/03.
- Van Deusen, M., and D. W. Kaufman. 1977. Habitat distribution of *Peromyscus leucopus* within prairie woods. *Transactions of the Kansas Academy of Science*, 80:151-154.
- Van Horne, B., and J. A. Wiens. 1991. Forest bird habitat suitability models and the development of general habitat models. United States Department of the Interior, Fish and Wildlife Service, Fish and Wildlife Research 8, Washington D.C., 31 pp.
- Verner, J. 1983. An integrated system for monitoring wildlife on the Sierra National Forest. *Transactions of the North American Wildlife and Natural Resources Conference*, 48:355-366.
- _____. 1984. The guild concept applied to management of bird populations. *Environmental Management*, 8:1-4.

- Warren, S. D., M. O. Johnson, W. D. Goran, and V. E. Diersing. 1990. An automated, objective procedure for selecting representative field sample sites. *Photogrammetric Engineering and Remote Sensing*, 56:333-335.
- Zonnveld, I. S. 1979. Land evaluation and land(scape) science. International Training Center, Enschede, The Netherlands, 134 pp.

APPENDIX I

Habitat-variable means for unweighted and weighted microhabitat variables (units for individual variables given in Table 1).

Variable	Species ^a									
	CHHI	CRPA	MIOC	NEFL	PEAT	PELE	PEMA	REFU	REMO	SIHI
	Unweighted									
Sldp	2.33	4.00	3.55	2.14	4.33	4.36	3.54	3.97	3.60	4.14
Avslp	0.22	0.20	0.19	0.31	0.37	0.28	0.22	0.25	0.28	0.20
Cnone	12.83	4.27	3.18	14.29	23.88	11.09	7.63	6.87	11.05	4.80
Can	5.00	5.64	1.73	2.29	8.75	5.66	6.29	5.13	6.70	5.23
Cper	70.25	73.82	77.64	78.14	63.88	69.50	69.14	69.07	66.95	69.00
Canpr	11.92	16.27	17.45	5.29	3.50	13.75	16.94	18.93	15.30	20.97
C4m	9.08	0.00	0.00	43.71	17.38	13.31	0.37	1.53	0.65	0.37
H00-15	196.33	329.09	313.64	150.14	117.75	222.09	275.91	253.57	202.15	265.31
H16-40	12.33	0.09	0.09	47.43	35.75	14.56	1.71	3.37	2.00	1.71
H41-85	11.42	0.00	0.00	56.14	32.88	18.00	0.86	2.83	1.50	0.86
Hgt85	3.67	0.00	0.00	16.00	0.13	3.91	0.00	1.13	0.00	0.00
B16-40	5.17	0.00	0.00	28.00	6.63	8.78	0.40	0.40	0.60	0.40
B41-85	6.83	0.00	0.00	34.86	8.75	9.75	0.34	0.40	0.60	0.34
Bgt85	1.50	0.00	0.00	12.86	0.25	3.47	0.00	0.00	0.00	0.00
Tcga	15.92	27.27	21.45	7.71	4.50	18.97	28.00	28.33	24.05	33.06
Tcgp	160.92	253.45	290.73	114.43	88.88	171.97	223.69	206.63	174.40	226.91
Tctb	42.00	0.00	1.73	215.43	101.13	63.16	5.51	9.27	7.35	4.91
Gcltr	51.50	75.91	84.09	63.43	42.63	57.94	66.94	67.57	55.95	74.11
Gcrck	13.50	3.91	21.43	34.63	13.50	18.41	9.11	11.13	16.85	3.09

APPENDIX I.—Continued.

Variable	Species ^a									
	CHHI	CRPA	MIOC	NEFL	PEAT	PELE	PEMA	REFU	REMO	SIHI
	Weighted									
Sldp	4.71	4.45	4.89	3.50	3.23	4.39	4.72	4.76	4.34	4.83
Avslp	0.24	0.20	0.19	0.33	0.43	0.29	0.20	0.24	0.35	0.19
Cnone	14.43	4.15	4.77	14.20	26.67	10.60	8.32	5.57	10.03	2.99
Can	6.21	7.08	1.62	1.65	6.90	5.06	8.16	4.24	6.00	6.72
Cper	67.36	70.46	77.92	81.35	63.91	71.00	64.16	71.81	68.97	63.91
Canpr	12.00	18.31	15.69	2.80	2.52	13.33	19.36	18.38	15.00	26.38
C4m	7.79	0.00	0.00	49.80	22.36	24.19	0.35	1.03	1.23	0.25
H00-15	191.71	327.77	304.92	111.70	104.34	197.89	254.47	250.90	211.10	280.29
H16-40	10.64	0.08	0.08	52.60	42.27	28.08	2.31	1.97	3.54	1.34
H41-85	9.79	0.00	0.00	64.40	36.71	33.03	0.78	2.05	2.95	0.58
Hgt85	3.14	0.00	0.00	13.55	0.36	7.95	0.00	0.59	0.00	0.00
B16-40	4.43	0.00	0.00	37.35	19.10	15.17	0.24	0.62	1.85	0.41
B41-85	5.86	0.00	0.00	47.10	25.23	16.86	0.13	0.62	1.85	0.29
Bgt85	1.29	0.00	0.00	13.80	0.72	5.67	0.00	0.00	0.00	0.00
Tcga	14.29	35.00	19.23	3.75	3.63	18.91	35.15	28.36	25.41	42.68
Tcgp	152.93	241.85	290.23	78.75	58.33	167.38	199.69	210.66	177.05	225.48
Tctb	36.00	0.00	1.46	256.50	152.21	113.32	6.16	6.79	12.21	3.71
Gcltr	48.57	73.77	84.69	64.45	42.83	60.63	66.29	70.90	50.54	79.68
Gcrck	3.92	0.23	19.10	37.14	16.79	16.93	7.68	7.16	18.67	1.48

^a Species names: CHHI, *Chaetodipus hispidus*; CRPA, *Cryptotis parva*; MIOC, *Microtus ochrogaster*; NEFL, *Neotoma floridana*; PEAT, *Peromyscus attwateri*; PELE, *P. leucopus*; PEMA, *P. maniculatus*; REFU, *Reithrodontomys fulvescens*; REMO, *R. montanus*; SIHI, *Sigmodon hispidus*.

TABLE 1.—*Microhabitat variables used in principal-components analysis, cluster analysis, and discriminant function analysis.*

Variable	Variable description
Sldp	Average plot soil depth (dm)
Avslp	Average slope gradient (percent) ^a
SDslp ^b	Standard deviation of slope
Cnone	No. locations with no cover ^c
Can	No. locations with only annual cover ^c
Cper	No. locations with only perennial cover ^c
Canper	No. locations with annual and perennial cover ^c
C4m	No. points with cover above 4 m ^c
H00-15	No. locations with herbaceous cover in 0-15 dm
H16-40	No. locations with herbaceous cover in 16-40 dm
H41-85	No. locations with herbaceous cover in 41-85 dm
Hgt85	No. locations with herbaceous cover greater than 85 dm
B00-15 ^b	No. locations with broadleaf trees in 00-15 dm
B16-40	No. locations with broadleaf trees in 16- 40 dm
B41-85	No. locations with broadleaf trees in 41-85 dm
Bgt85	No. locations with broadleaf trees greater than 85 dm
Tcga	Total count annual grasses
Tcgp	Total count perennial grasses
Tcfa ^b	Total count annual forbs
Tcfp ^b	Total count perennial forbs
Tch ^b	Total count half shrubs
Tcsb ^b	Total count broadleaf shrubs
Tcsc ^b	Total count conifer shrubs
Tctb	Total count broadleaf trees

TABLE 1.—*Continued.*

Variable	Variable description
Tctc ^b	Total count conifer trees
Gcbre ^b	No. bare ground points
Gcltr	No. points with litter ^c
Gcplnt ^b	No. points with plant cover
Gcrck	No. points with rocks ^c

^a Arcsine transformation (Sokal and Rohlf 1981) employed on percentage values.

^b Microhabitat variables dropped after initial analysis.

^c Out of 100 possible points per plot.

TABLE 2.—*Summary of mammal species captured at Ft. Sill Military Reservation from 1989-1993.*

Species	Average number per year ^b	Percent relative abundance
<i>Chaetodipus hispidus</i>	3.25	1.13
<i>Cryptotis parva</i>	3.25	1.13
<i>Microtus ochrogaster</i>	3.25	1.13
<i>Microtus pinetorum</i> ^a	1.00	0.35
<i>Mus musculus</i> ^a	0.75	0.26
<i>Neotoma floridana</i>	5.00	1.75
<i>Neotoma micropus</i> ^a	0.25	0.09
<i>Peromyscus attwateri</i>	22.25	7.77
<i>Peromyscus leucopus</i>	62.25	21.73
<i>Peromyscus maniculatus</i>	48.50	16.93
<i>Reithrodontomys fulvescens</i>	14.50	5.06
<i>Reithrodontomys montanus</i>	9.75	3.40
<i>Sigmodon hispidus</i>	111.75	39.00
<i>Spermophilus tridecemlineatus</i> ^a	0.25	0.09
<i>Sylvilagus floridanus</i> ^a	0.50	0.17

^a Indicates infrequently captured species not included in further analyses.

^b Total number captured divided by four.

TABLE 3.—*Summary of PCA of 29 microhabitat variables for 60 plots on Fort Sill Military Reservation. Bold indicates significant loadings (P < 0.05) based on parallel analysis.*

Variable	Component		
	I	II	III
Sldp	0.023	0.620	0.221
Avslp	0.006	-0.641	-0.170
SDslp	-0.033	-0.252	-0.029
Cnone	0.081	-0.881	-0.022
Can	0.317	-0.423	0.699
Cper	-0.428	0.372	-0.784
Canper	0.373	0.382	0.751
C4M	-0.966	0.023	0.158
H00-15	0.451	0.562	-0.025
H16-40	-0.672	-0.050	0.089
H41-85	-0.887	-0.010	0.143
Hgt85	-0.767	0.117	0.158
B00-15	-0.180	0.106	-0.003
B16-40	-0.867	0.002	0.236
B41-85	-0.902	-0.005	0.174
Bgt85	-0.820	0.062	0.138
Tcga	0.266	0.264	0.827
Tcgp	0.341	0.683	-0.346
Tcfa	0.324	-0.199	0.271
Tcfp	0.407	0.362	0.071
Tch	0.015	-0.064	0.197

TABLE 3.—Continued.

Variable	Component		
	I	II	III
Tcsb	-0.090	0.235	-0.204
Tcsc	0.114	-0.523	0.160
Tctb	-0.957	-0.014	0.167
Tctc	-0.447	-0.021	0.001
Gcbre	0.072	-0.363	0.190
Gcltr	-0.126	0.901	0.090
Gcplnt	-0.073	-0.188	-0.350
Gcrck	0.134	-0.849	-0.156
Percent of total variance	25.18	17.88	10.82
Cumulative percent of variance	25.18	43.07	53.88

TABLE 4.—*Summary of two PCAs based on 10 mammal species captured on Fort Sill Military Reservation and (1) unweighted and (2) weighted data for 19 microhabitat variables. Weighting based on number of each mammal species caught at each plot. Bold indicates significant loadings (P < 0.05) based on parallel analysis.*

Variable	Unweighted component		Weighted component	
	I	II	I	II
Sldp	0.444	0.572	0.896	0.219
Avslp	-0.830	0.471	-0.798	-0.434
Cnone	-0.823	0.544	-0.799	-0.546
Can	-0.018	0.946	0.328	-0.784
Cper	-0.036	-0.958	-0.323	0.845
Canpr	0.929	-0.167	0.928	0.086
C4M	-0.946	-0.304	-0.942	0.286
H00-15	0.887	-0.374	0.935	0.256
H16-40	-0.980	-0.047	-0.981	0.048
H41-85	-0.974	-0.162	-0.964	0.205
Hgt85	-0.779	-0.584	-0.751	0.537
B16-40	-0.893	-0.420	-0.957	0.241
B41-85	-0.900	-0.415	-0.961	0.221
Bgt85	-0.785	-0.575	-0.779	0.555
Tcga	0.896	-0.105	0.882	0.009
Tcgp	0.899	-0.391	0.909	0.349
Tctb	-0.959	-0.252	-0.969	0.187
Gcltr	0.645	-0.683	0.584	0.715
Gcrck	-0.832	0.539	-0.810	-0.569
Percent of total variance	65.71	26.06	70.30	19.77
Cumulative variance	65.71	91.77	70.30	90.07

TABLE 5.—Niche overlap between species pairs as indicated by simplified Morisita's index based on numbers of each species captured at each of 60 plots. Bold indicates significant overlap ($P < 0.05$) based on Monte Carlo simulation.^a

Species	1	2	3	4	5	6	7	8	9	10
1 <i>Chaetodipus hispidus</i>	1.000									
2 <i>Cryptotis parva</i>	0.974	1.000								
3 <i>Microtus ochrogaster</i>	0.974	0.986	1.000							
4 <i>Neotoma floridana</i>	0.363	0.310	0.345	1.000						
5 <i>Peromyscus attwateri</i>	0.875	0.863	0.883	0.512	1.000					
6 <i>Peromyscus leucopus</i>	0.974	0.968	0.953	0.432	0.917	1.000				
7 <i>Peromyscus maniculatus</i>	0.978	0.997	0.984	0.348	0.883	0.983	1.000			
8 <i>Reithrodontomys fulvescens</i>	0.984	0.997	0.992	0.330	0.389	0.968	0.995	1.000		
9 <i>Reithrodontomys montanus</i>	0.960	0.975	0.982	0.296	0.812	0.916	0.962	0.983	1.000	
10 <i>Sigmodon hispidus</i>	0.982	0.995	0.984	0.346	0.887	0.983	0.999	0.995	0.961	1.000

^aRelatively high significant niche-overlap values indicate more overlap than expected by chance, while relatively low values indicate less overlap than expected.

TABLE 6.—Niche breadth as indicated by Smith's index, with species in ascending order based on the numbers of plots at which they occurred. All deviations are significant ($P < 0.001$) based on Monte Carlo simulation.

Species	No. plots where present	Smith's coefficient ^a		
		Calculated (B)	Random (\bar{B}_s)	Deviation $B - \bar{B}_s$
<i>Neotoma floridana</i>	7	0.3485	0.8534	-0.5049
<i>Peromyscus attwateri</i>	11	0.5630	0.8890	-0.3260
<i>Microtus ochrogaster</i>	11	0.6930	0.8893	-0.1963
<i>Cryptotis parva</i>	11	0.6962	0.8907	-0.1945
<i>Chaetodipus hispidus</i>	12	0.6605	0.8954	-0.2349
<i>Reithrodontomys montanus</i>	20	0.7360	0.9273	-0.1913
<i>Reithrodontomys fulvescens</i>	30	0.6950	0.9481	-0.2531
<i>Peromyscus leucopus</i>	38	0.6273	0.9581	-0.3308
<i>Sigmodon hispidus</i>	46	0.6739	0.9656	-0.2917
<i>Peromyscus maniculatus</i>	50	0.6765	0.9682	-0.2917

^a Actual value (B), mean value (\bar{B}_s) for 1,000 simulations, and deviation of simulated from actual ($B - \bar{B}_s$).

TABLE 7.—*Classification of species into TAs using stepwise discriminant analysis.^a*

Group	Percent correctly classified	Classified as			
		TA1	TA2	TA3	TA4
Unweighted four-TA analysis					
TA1	83	101	17	3	1
TA2	28	32	18	8	6
TA3	63 (38)	1	2 (3)	5 (3)	0 (1)
TA4	43 (29)	0	1 (2)	3	3 (2)
Total	63 (62)	134	38 (40)	19 (17)	10
Weighted four-TA analysis					
TA1	86	587	97	1	0
TA2	53	76	157	17	46
TA3	67	2	20	58	6
TA4	45 (30)	0	1 (4)	10	9 (6)
Total	75 (74)	665	275 (278)	86	61 (58)
Unweighted two-TA analysis					
TA1	82	100	22		
TA2	53	30	34		
Total	72	130	56		
Weighted two-TA analysis					
TA1	87 (86)	597 (587)	88 (98)		
TA2	73	79	217		
Total	83 (82)	676 (666)	305 (315)		

^a Parentheses indicate jackknifed classification results.

TABLE 8.—*Statistics for stepwise discriminant analysis of TAs based on microhabitat variables.*

Variable	F-value to enter	Order of entry	Standardized canonical discriminant function			Classification function ^a			
			1	2	3	TA1	TA2	TA3	TA4
Unweighted four-TA analysis									
Tctb	26.65	1	-1.072	-0.501	-0.800	0.003	0.014	0.052	0.052
Gcrck	13.94	2	-0.653	-0.352	0.734	0.019	0.056	0.116	0.108
Hgt85	4.906	3	0.169	1.171	0.751	-0.003	-0.005	-0.298	-0.065
Weighted four-TA analysis									
Tctb	169.88	1	3.535	-6.569	3.561	-0.257	-0.297	-0.031	-0.023
Gcrck	238.10	2	0.673	0.157	-0.255	0.047	0.116	0.213	0.184
C4m	71.132	3	-1.606	3.216	-2.817	-0.331	-0.230	-0.776	0.910
Cnone	13.12	4	0.254	-0.441	-0.059	0.650	0.634	0.785	0.732
Gcltr	8.90	5	0.082	-0.496	0.243	0.463	0.442	0.490	0.491
Bgt85	9.71	6	-0.274	0.866	1.502	1.457	1.536	1.117	1.689
B16-40	7.16	7	-1.325	3.765	-1.753	0.186	0.367	-0.318	-0.312
B41-85	38.28	8	0.809	-2.041	0.404	0.365	0.292	0.624	0.562
H16-40	15.27	9	-0.730	2.666	-0.574	0.701	0.801	0.480	0.542
Avslp	4.13	10	0.062	0.242	0.021	27.589	30.124	28.025	29.715

TABLE 8.—Continued.

Variable	F-value to enter	Order of entry	Standardized canonical discriminant function			Classification function ^a			
			1	2	3	TA1	TA2	TA3	TA4
Unweighted two-TA analysis									
Tctb	17.063	1	0.797			-0.006	-3.017		
Gcltr	18.343	2	-0.746			0.104	0.078		
Weighted two-TA analysis									
Tctb	293.930	1	1.052			-0.002	0.024		
Gcrck	258.269	2	0.596			0.246	0.313		
Gcltr	10.833	3	-0.246			0.235	0.217		
Bgt85	10.740	4	-0.559			-0.063	-0.216		
B41-85	5.234	5	0.372			0.010	0.051		

^a Used with original variables. Add products of measurements and corresponding function values to constant; classify as TA1, TA2, TA3, or TA4, depending on which has the highest function for its classification.

FIGURE LEGENDS

Fig. 1.—Detailed map of study area including Fort Sill Military Reservation, Wichita Mountains Wildlife Refuge, and surrounding communities. Thin lines indicate county lines and heavy solid lines indicate major highways.

Fig. 2.—Land-cover classification of Fort Sill Military Reservation showing 16 land-cover types (based on Johnson et al., 1992)

Fig. 3.—Contour lines generated by kriging (using a linear variogram) of (a) species richness, (b) average number of individuals of all species, (c) average number of *P. leucopus*, and (d) average number of *P. maniculatus*. Legend indicates number of species in panel *a* and average number of individuals in panels *b*, *c*, and *d*.

Fig. 4.—Projections of 60 plots based on 29 microhabitat variables onto principal components: (a) I and II; and (b) I and III.

Fig. 5.—Projections of small-mammal species based on 19 microhabitat variables onto principal components I and II using (a) unweighted variables and (b) weighted variables. Ovals indicate species taxonomic assemblages (TAs). Species abbreviations found in Appendix I.

Fig. 6.—UPGMA dendrogram depicting taxonomic assemblages (TAs) and their relationships based on (a) unweighted variables and (b) weighted variables. Membership in TAs based on species associated at an average taxonomic distance of 0.9. Cophenetic correlation coefficients were (a) 0.93 and (b) 0.90.

Fig. 7.—Projections of canonical scores of taxonomic assemblages (TAs) on discriminant factors determined using (a) unweighted variables and (b) weighted variables in stepwise discriminant analysis. Solid lines indicate 95% confidence ellipses.

Fig. 1

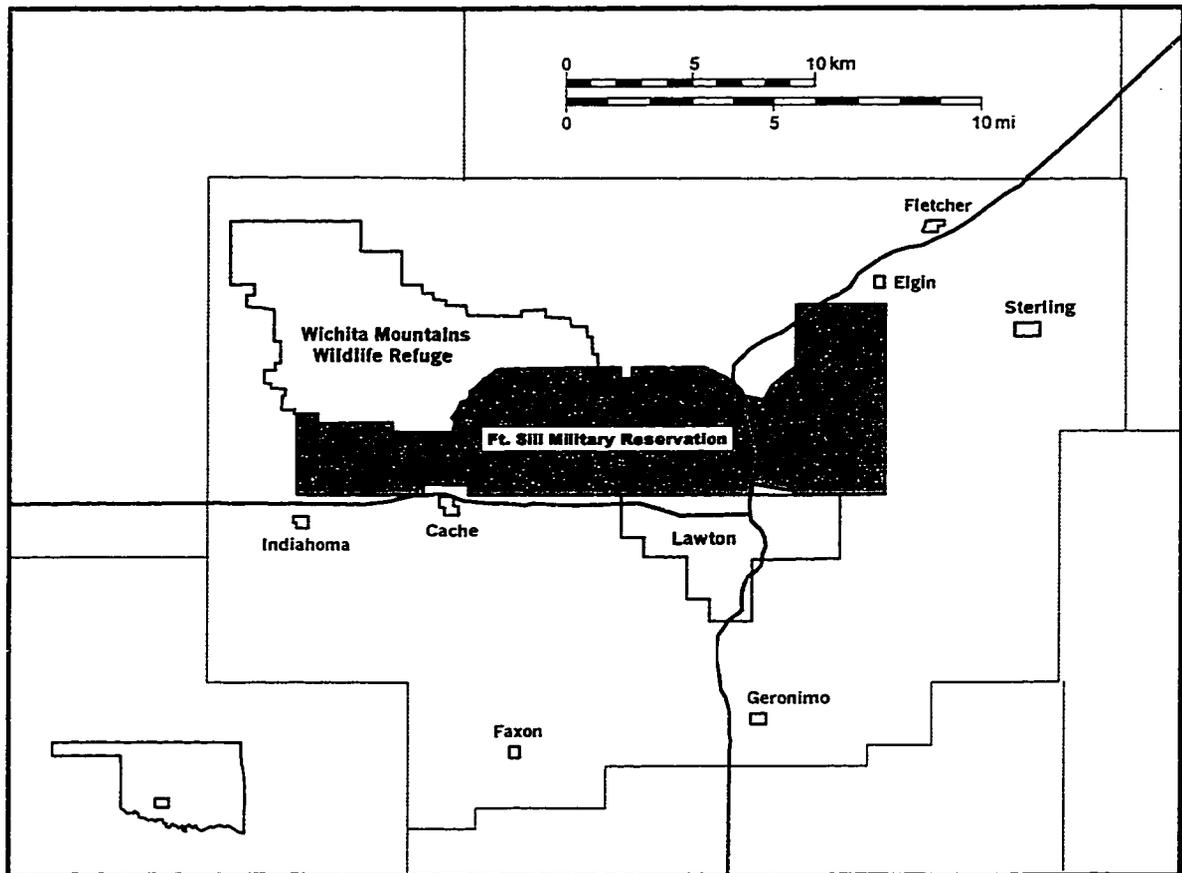


Fig. 2



44

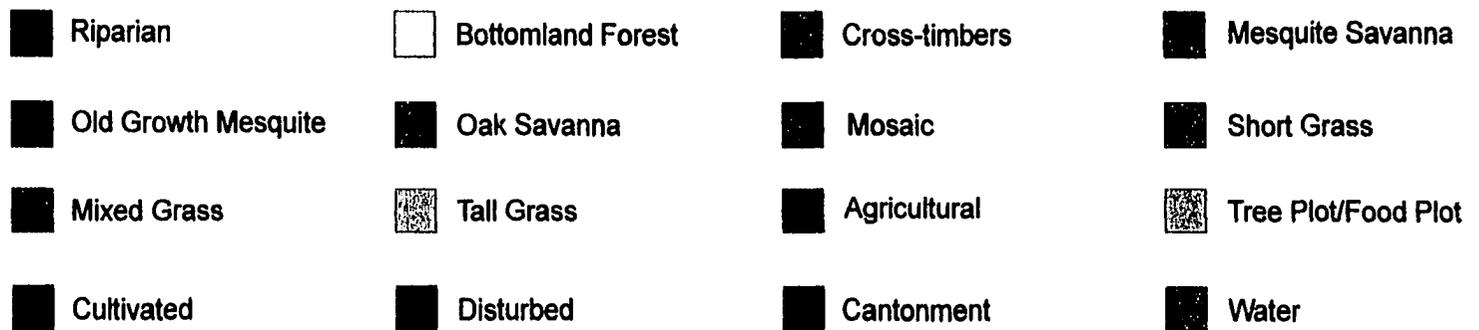


Fig. 3

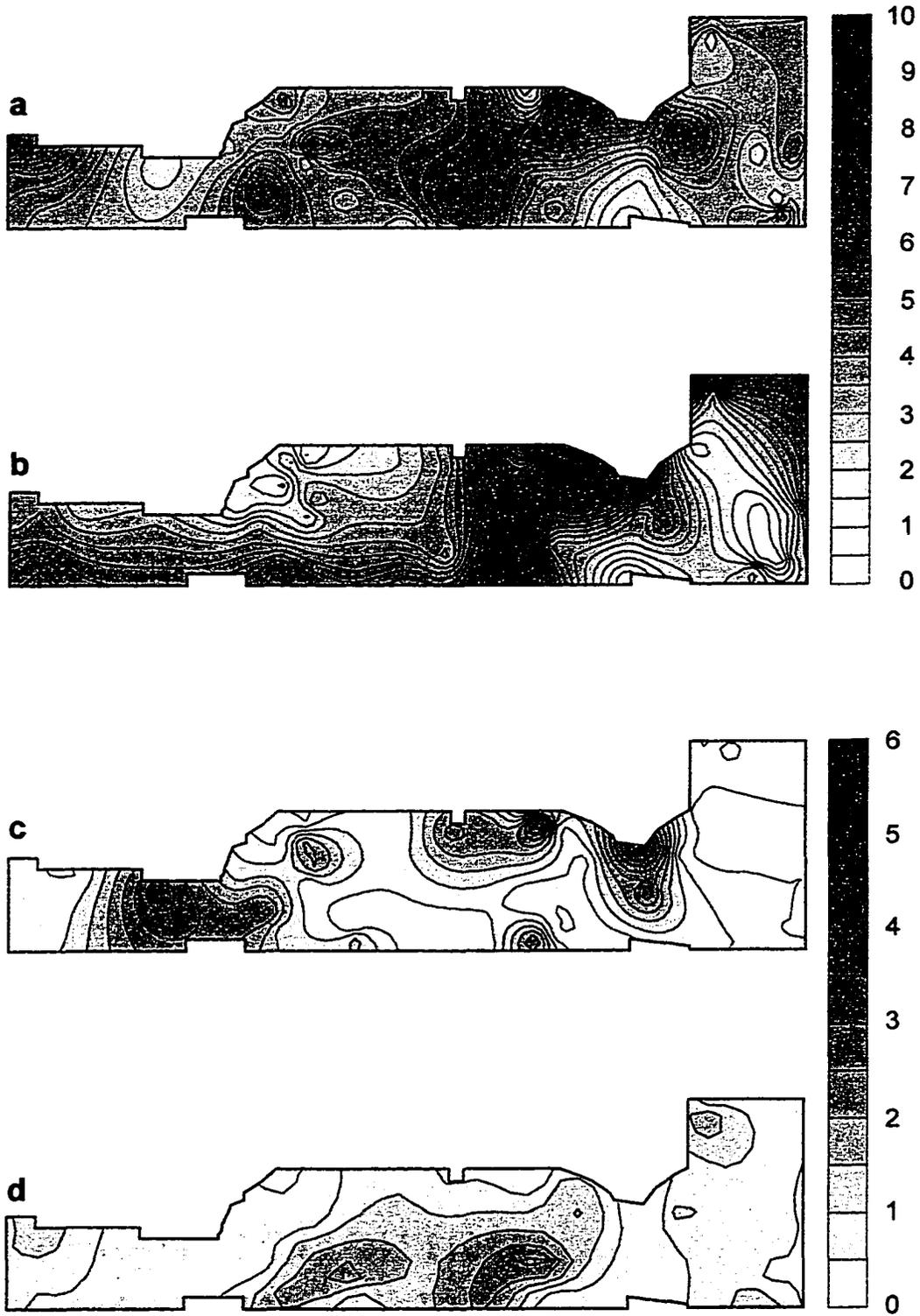


Fig. 4

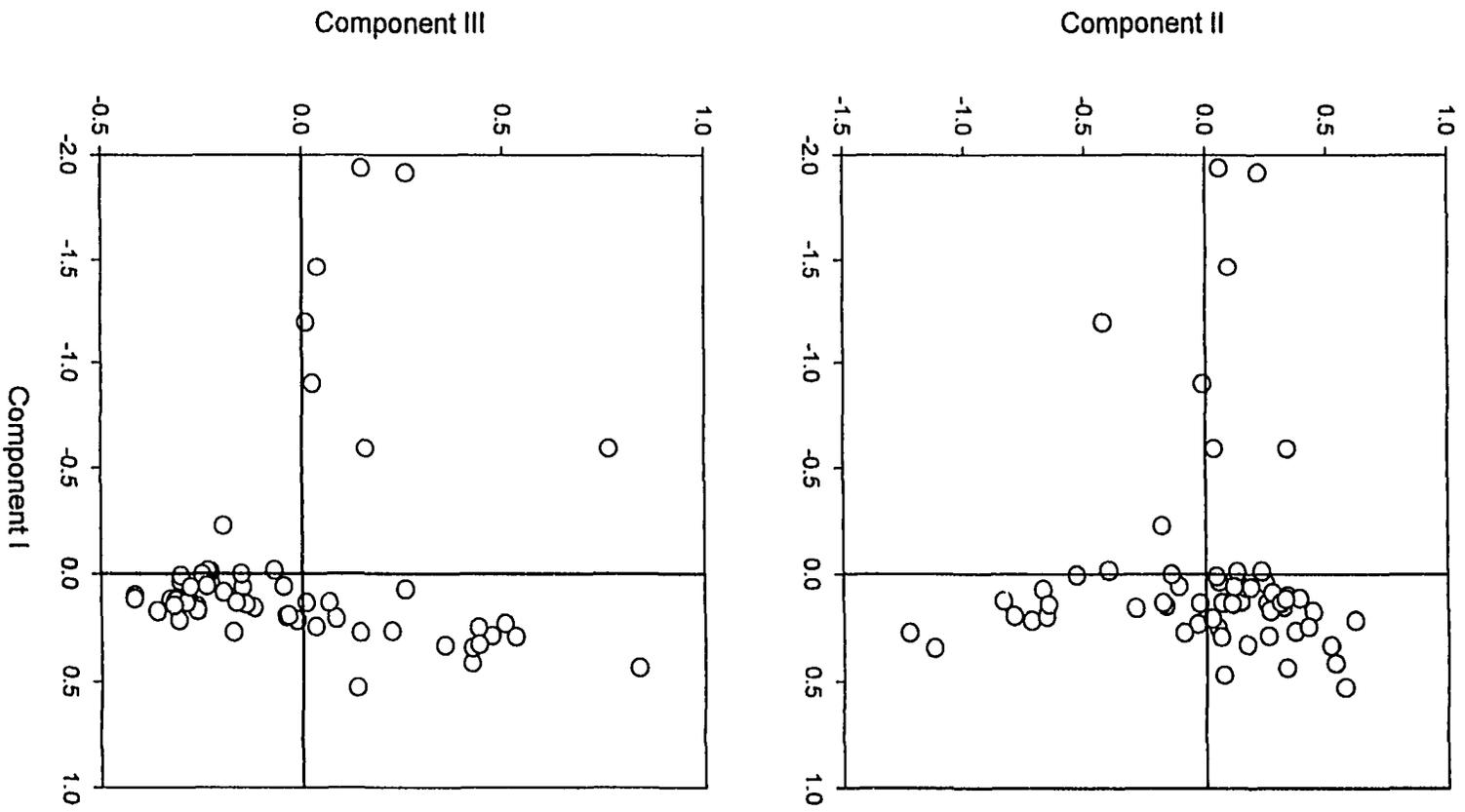


Fig. 5

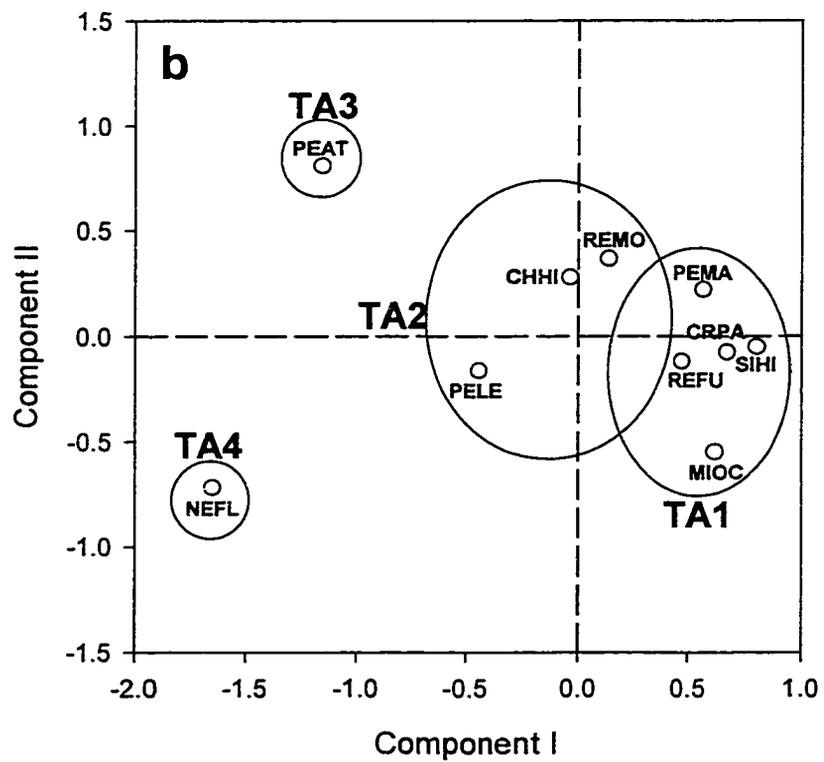
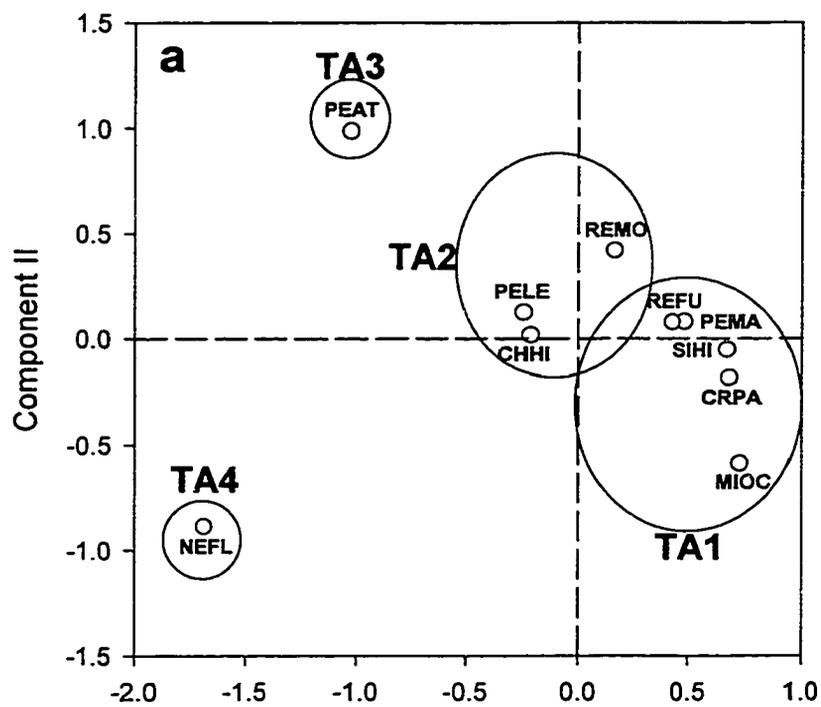
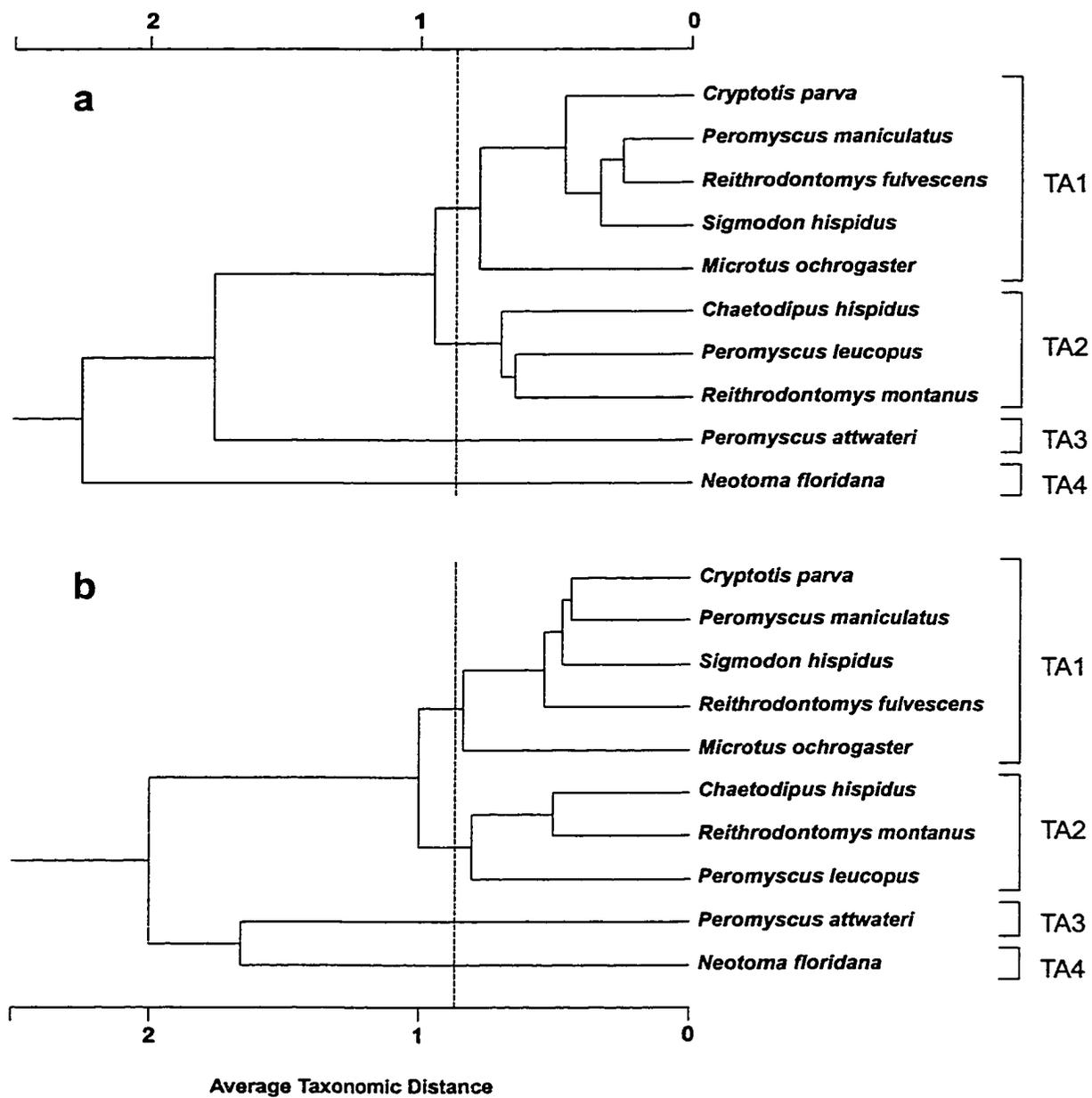


Fig. 6



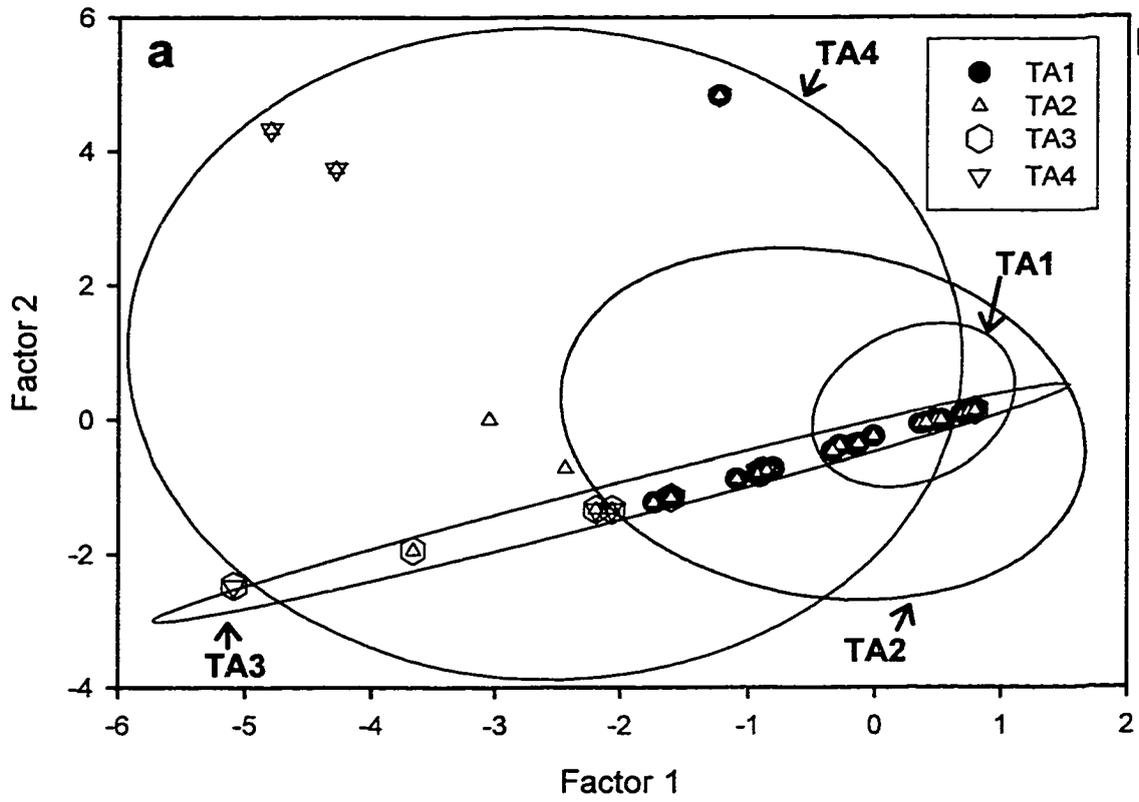
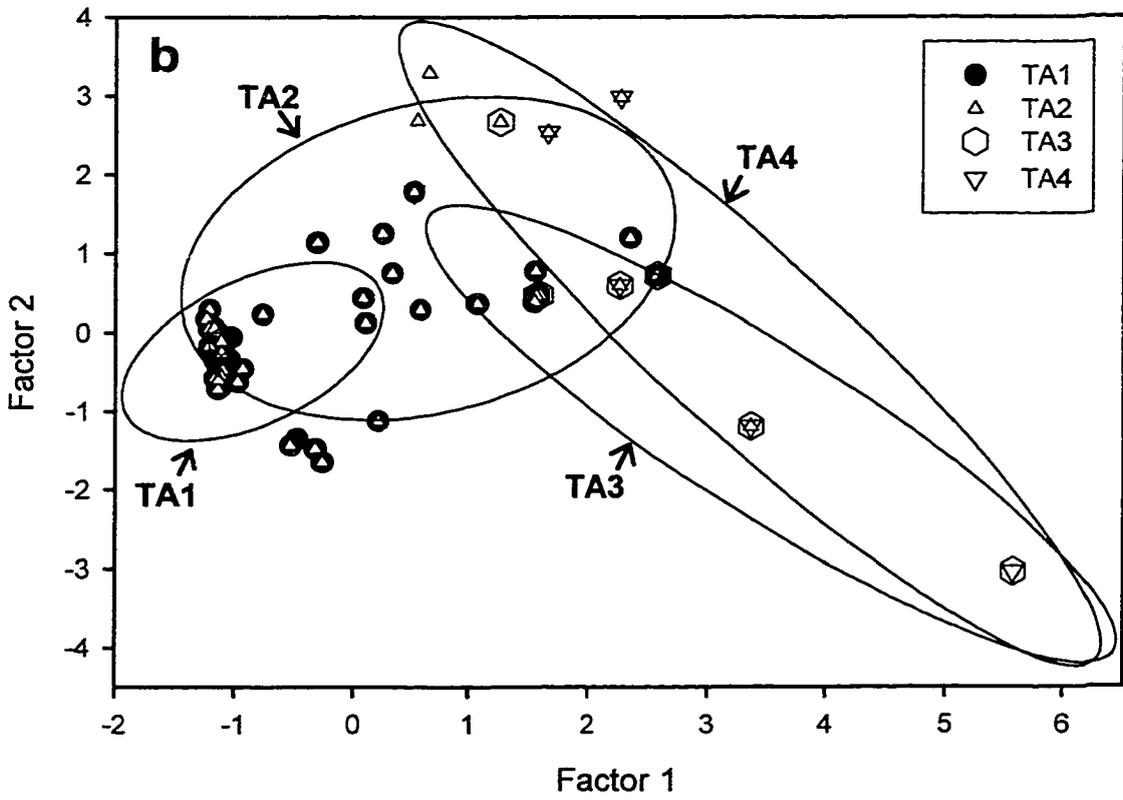


Fig. 7



Local- and landscape-level influences on distributions of small mammals in Southwestern Oklahoma

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Abstract

I studied the influence of landscape-level and a combined data set consisting of local- and landscape-level factors on small-mammal communities in the southern Great Plains, USA. I computed 15 landscape variables at four different scales (40 variables total) for each of 60 study plots using a geographic information system and a digitized vegetation map of the 38,000-ha Fort Sill Military Reservation in Oklahoma. The small-mammal fauna was surveyed at each plot in the spring for four consecutive years and 15 species were caught. The 10 most common species (*Chaetodipus hispidus*, *Cryptotis parva*, *Microtus ochrogaster*, *Neotoma floridana*, *Peromyscus attwateri*, *P. leucopus*, *P. maniculatus*, *Reithrodontomys fulvescens*, *R. montanus*, and *Sigmodon hispidus*) were used in multivariate analyses. I calculated a weighted average of the 40 landscape variables for each mammal species based on the abundance of each species. Cluster analysis of these weighted data produced three multispecies clusters based on associations of species distributions and abundances to landscape factors. General trends of the landscape affinities of these clusters were summarized on principal components. Landscape predictive models were constructed using discriminant function analysis. These models determined which landscape variable or combination of variables was most effective in classifying species into the appropriate cluster and allowed small-mammal distributions across the landscape to be predicted. Cluster classification accuracy was 59%. When local-level variables were combined with the landscape data, cluster membership remained similar and classification accuracy was 58%. Since clusters were developed using horizontal elements of a

spatially heterogeneous landscape, they consisted of unique species relationships. The two most abundant grassland species, *S. hispidus* and *P. maniculatus*, were not in the same cluster. However, *S. hispidus* did cluster with *P. leucopus*, which is typically considered a woodland/edge species. This suggests that these two species perceive the landscape similarly, preferring areas with a number of contrasting patch types (edge). *Sigmodon hispidus* primarily occupies grassland patches interspersed with shrubby or woody patches, and *P. leucopus* is found in woodlands bordered by grasslands. Conversely, *P. maniculatus* occupies areas dominated by one patch type but made up of several patch types. One obtains additional insight into habitat preferences of small mammals by evaluating landscape elements, particularly when landscape models are used in combination with local habitat models.

Keywords: landscape-level, mammal distributions, multiscale analysis, landscape suitability models, principal components

1. Introduction

A fundamental rule of species distribution states that species are more abundant in some habitats than in others (Morris 1987). Habitats and their patterns of spatial distribution within a landscape can influence the abundance, distribution, and other dynamics of vertebrate populations found in those landscapes (Wiens 1976, 1989, McGarigal and McComb 1995). Each habitat contributing to this spatial heterogeneity is considered a patch. The structure of patches in the environment is important if it is recognized by or relevant to the organisms under consideration. That is to say that the patchiness of a landscape is organism defined (Wiens 1976).

Organisms respond to environmental patchiness at different scales and in different ways (Johnson *et al.* 1992). Zonnveld (1979) defined a patch (ecotope) as the smallest holistic land unit, characterized by homogeneity of at least one land attribute of the geosphere, and with non-excessive variation in other attributes. The spatial configuration of these patches in a landscape may affect populations by influencing movement patterns of individuals, interactions among individuals, and exposure to factors associated with adjacent patches of contrasting types (*i.e.*, juxtaposition; McGarigal and McComb 1995).

Potentially, animals can perceive habitat vertically and horizontally at different scales. Populations may be affected by the structure of the local environment (Stancampiano and Schnell 1999) and the surrounding landscape at a variety of spatial scales (Pearson 1993, Turner *et al.* 1995, Pogue 1998). Perception of these spatial scales may be influenced by different behavioral

strategies and temporal scales. Pearson (1993) examined the relative influence of local- and landscape-level factors on wintering bird populations. Pogue and Schnell (1994, 1998) evaluated local- and landscape-level factors influencing the distribution of breeding birds. Similar studies involving small mammals have been conducted by Nupp and Swihart (1996), Songer *et al.* (1997), and Bayne and Hobson (1998).

By determining the affinities of species for landscape elements at the appropriate scale(s), models can be constructed that allow us to predict species presence and abundance among habitats in a landscape. Similar distribution patterns should occur among species with comparable foraging strategies (Morris 1987). These similarities can be used to increase model generality by expanding coverage from single species to sets of ecologically similar species (Van Horne and Wiens 1991, Stancampiano and Schnell 1999).

In this study I examined the distribution and abundance of small mammals relative to various elements of landscape heterogeneity at four spatial scales. I evaluated these landscape-level affinities to construct predictive models of species presence. I also used these landscape-level factors in combination with local-level factors in an attempt to increase the efficiency of these predictive models.

2. Methods

2.1. Study Area

This study took place on the 38,000-ha Fort Sill Military Reservation located in Comanche County in southwestern Oklahoma (Fig. 1). The reservation is bordered on the northwest by the Wichita Mountains Wildlife Refuge and on the

south by the city of Lawton. Fort Sill extends 37 km along an east-west axis and is 13 km at its widest point along a north-south axis.

Fort Sill is in the Osage Plains section of the Central Lowlands physiographic province (Hunt 1974). The eastern, south-central, and western portions of the Reservation are primarily rolling upland plains of low relief. The Wichita Mountains extend south into the north-central and northwest sections of the Reservation. This area contains granitic hills of steep to moderate relief. Many streams are interspersed throughout Fort Sill. These streams flow to the south or southeast and drain into Cache Creek. Appendix A gives descriptions of habitat types on Fort Sill.

2.2. *Sampling techniques*

I sampled 60 plots (30 m x 100 m) on Fort Sill to survey the small-mammal fauna and measure various landscape elements. To ensure objectivity and representativeness in the placement of these plots, I employed a stratified-random procedure for site selection. This procedure incorporated SPOT (System Probatoire pour l' Observation de la Terra) satellite imagery, digital soil surveys, and the geographic information system GRASS (Geographic Resource Analysis Support System; CERL 1989). An unsupervised classification of satellite imagery of Fort Sill was performed to select land-cover categories based on reflectance values. The resulting land-cover type layer was superimposed on a digital soils layer. Each unique landcover/soil combination indicated a separate land-cover category. Plots were allocated to each category in proportion to the percent of the land area it covered. Warren *et al.* (1990) gave a complete

description of this procedure.

2.2.1. Mammal sampling

Small mammals were trapped on the sample plots in late May and early June of each year from 1989-1992 (24,000 trap-nights). The standard length of a transect through each permanent plot was 100 m. I set two rows of 20 Museum Special snap-traps and 5 rat snap-traps 15 m to each side of and parallel to the transect, for a total of 50 traps at each site per night (Tazik *et al.* 1992). Traps in each line were 7.5 m apart, and baited with a mixture of rolled oats and peanut butter.

Trapped animals were skinned and placed in the Oklahoma Museum of Natural History at the University of Oklahoma.

2.2.2. Landscape sampling

I used the “r.le” programs (Baker 1997) within GRASS and a digital vegetation/land-cover map produced by Johnson *et al.* (1992) to analyze the landscape structure of Fort Sill at four different spatial scales (1, 5, 10, and 25 ha) around each of the 60 permanent plots. This map was produced from 1990 National High Altitude Photography panchromatic aerial photographs. Johnson *et al.* (1992) identified 17 land-cover categories from the aerial photographs and ground-level observations that are used in the analyses (Appendix A).

I used GRASS to define the sampling areas around each of the 60 plots. A digital vector transect was created for each plot using UTM coordinates and a random azimuth assigned to each plot. I converted each vector based transect into a raster format and defined four buffers around each one (Fig. 2). The first buffer occupied an area of 1 ha around and including the transect. The second buffer had

an area of 5 ha, including the first buffer. Buffer 3 was a 10-ha area around and including the first two buffers, and buffer 4 was a 25-ha area including the first three buffers.

The following ten measures of landscape structure were computed at each of the four areal extents for each plot (total of 40 landscape variables): (1) total number of patches; (2) standard deviation of patch size; (3) standard deviation of patch shape; (4) standard deviation of perimeter; (5) habitat richness; (6) Shannon index; (7) dominance; (8) contagion; (9) standard deviation of juxtaposition; (10) sum of edges by type (see Appendix B for detailed descriptions). I defined a patch as a unit of the landscape characterized by homogeneity of a dominant vegetation type.

2.3. Statistical analysis

I calculated an unweighted average and an abundance-weighted average for each mammal species for each landscape variable. The unweighted landscape value for a mammal species was obtained by taking the average of the values for the plots where the species occurred, irrespective of the number captured on each plot. The abundance-weighted variable average (W) for mammal species was calculated as:

$$W_{kj} = \frac{\sum_{i=1}^{60} n_{ik} v_{ij}}{\sum_{i=1}^{60} n_{ik}},$$

where n_{ik} is the number of individuals of mammal species k captured on plot i , and v_{ij} is the value of landscape variable j on plot i . The purpose of employing both unweighted and weighted averages was to determine whether weighting based on

the abundance of individuals of each mammal species would increase the predictive accuracy of our models over the use of presence/absence data.

2.3.1. Principal-components analysis

I used these variables (weighted and unweighted) in a principal-components analysis (PCA) to characterize general trends along orthogonal gradients based on a rectangular data matrix of the 60 sample plots and 40 landscape variables. I mean-centered this raw data set and calculated correlations among variables (Morrison *et al.* 1992). Standardized data (variables with a mean of 0 and a standard deviation of 1) were then projected onto eigenvectors extracted from the correlation matrix. In such an analysis, the first component explains the maximum character variance, while each subsequent orthogonal component is in the direction of greatest variance perpendicular to the previous component (Morrison *et al.* 1992).

Parallel analysis (Franklin *et al.* 1995) was used to determine the number of significant principal components and the significance level of their loadings to reduce the number of variables. I created two rectangular matrices of mammal species by unweighted and weighted landscape-variable averages for use in separate PCAs as indicated by the results of parallel analysis.

To determine the importance of local versus landscape effects, I combined these landscape data with local habitat variables (hereafter referred to as combined variables) previously collected from the same plots (Stancampiano and Schnell 1999). I subjected these combined variables, weighted and unweighted, to PCA following the same procedure as above. The points where species occur along the

principal-component axes are representative of the habitats used by those species. All PCAs were performed using the ordination programs in NTSYS-pc (Rohlf 1993). Results of the weighted and unweighted PCAs were similar, so subsequent analyses involved only abundance-weighted data.

2.3.2. Cluster analysis

I subjected these data sets (10 mammal species by 40 landscape and 59 combined variables) to UPGMA cluster analysis (Sneath and Sokal 1973), creating taxonomic assemblages (TAs; Jaksić 1981) containing species with similar landscape and local-landscape affinities. A distance matrix (average taxonomic distance; Sneath and Sokal 1973) was calculated to determine similarities among the species. The UPGMA algorithm computes the average similarity (dissimilarity) of a candidate species or cluster to an extant cluster, weighting all species in that cluster equally (Sneath and Sokal 1973). Cophenetic correlation coefficients for the resulting dendrograms provide indices of how well the dendrograms summarize the pairwise distances among species.

2.3.3. Discriminant analysis

I used stepwise discriminant analysis (Morrison *et al.* 1992) to derive linear combinations of the landscape and combined variables that would maximally discriminate among the TAs. Discriminant analysis selects variables that exhibit high variation among TAs and low variation within TAs. I used forward-stepping discriminant analysis with an F -to-enter set at 4.0. Discriminant analysis assigns a weighted score to each observation based on the set of independent variables for that observation. Using discriminant analysis I derived classification functions to

assign each individual observation to a specific TA. Each individual had an equal probability of being assigned to any TA (*i.e.*, I did not bias the possibility of a particular plot being assigned to or categorized as a particular TA *a priori*).

A discriminant analysis was calculated for all TA members, and each individual was assigned to the appropriate TA depending on the resulting classification-function value. I also used a jackknifed classification, which leaves out the individual plot being considered when calculating the coefficients of the discriminant functions, and then evaluates the plot (see SPSS, 1997).

Discriminant analyses were performed using SYSTAT 7.0 (SPSS 1997).

3. Results

I captured 1,146 small mammals representing 15 species during the study (Table 1). The three most abundant species were *Sigmodon hispidus* (hispid cotton rat, 39.0%), *Peromyscus leucopus* (white-footed mouse, 21.7%), and *P. maniculatus* (deer mouse, 16.9%). The remaining 12 species made up 22.4% of the total captures (with no single species accounting for greater than 8.0% of the total). They are, in order of abundance: *P. attwateri* (Texas mouse), *Reithrodontomys fulvescens* (fulvous harvest mouse), *R. montanus* (plains harvest mouse), *Neotoma floridana* (eastern woodrat), *Chaetodipus hispidus* (hispid pocket mouse), *Cryptotis parva* (least shrew), *Microtus ochrogaster* (prairie vole), *M. pinetorum* (woodland vole), *Mus musculus* (house mouse), *Sylvilagus floridanus* (eastern cottontail), *N. micropus* (southern plains woodrat), and *Spermophilus tridecemlineatus* (thirteen-lined ground squirrel). Analyses included only those 10 species for which 10 or more individuals were collected (*i.e.*, *M. pinetorum*, *M.*

musculus, *N. micropus*, *S. floridanus*, and *S. tridecimlineatus* were not analyzed).

3.1. *Principal-components analysis*

Parallel analysis of the PCA of 60 plots and 40 landscape variables yielded four significant components (I-IV) and a significant loading level of > 0.35 . All landscape variables had significant loadings; therefore, no variables were dropped from further analysis. These four components explain 78.4% of the total variance.

Projections and character loadings (Table 2, Fig. 3a) indicate that component I represents a gradient from areas of low patch diversity and richness, but with larger patch sizes, to areas with many smaller patches of different landscape types (high patch diversity and patch number) at the 5- and 10-ha scale. Component II is a gradient of areas dominated by one or a few clumped landscape types at the 5- and 10-ha scale (high dominance) to those with more patches of different landscape types (high diversity) at the 1-ha scale (Fig. 3a). Component III represents a gradient from areas with non-contiguous patches of the same landscape type at the 5-ha scale to areas of larger contiguous patches of the same landscape type at the largest scale (Fig. 3b). The fourth component is a gradient of areas with contrasting landscape types at the three larger scales to those that are dominated by one landscape type at the 1-ha scale.

Principal-components analysis of the 40 landscape variables and 10 mammal species produced three significant components, explaining 86.7% of the character variance (Table 3). Component I represents a gradient of areas containing many different patch types that are dominated by one or a few patch types at the 1-ha scale to areas of many different patch types and different sizes

due to clumping at the 5-ha scale. These areas also exhibited contrasting patch types and patch shapes at the 10-ha scale and high diversity at the 25-ha scale. The second component shows a trend of areas that are dominated by large clumps of patches at the 25-ha scale to areas that have many different patch types of various sizes at the 1-ha scale. Component III shows a gradient from areas with contrasting patch types and sizes that are dominated by one or a few patch types at the 5-ha scale to those with many different patch types that are dominated by clumps of like patch types at the 10- and 25-ha scales (Table 3).

Species projections onto component I (Fig. 4a) show that four species (*N. floridana*, *P. leucopus*, *R. fulvescens*, and *S. hispidus*) were found in areas with many contrasting patch types at intermediate scales. Two species (*C. hispidus* and *C. parva*) are found near the midpoint of the axis, and four species (*M. ochrogaster*, *P. attwateri*, *P. maniculatus*, and *R. montanus*) occur in areas with a diversity of similar patch types dominated by contiguous areas of one patch type at the 1-ha scale. Projections of species onto component II (Fig. 4a) show five species (*C. hispidus*, *N. floridana*, *P. attwateri*, *R. fulvescens*, and *S. hispidus*) occupying areas at or near the midpoint of the axis. Two species (*C. parva*, and *M. ochrogaster*) are found in areas dominated by contiguous patches of one landscape type at the 25-ha scale, while three species (*P. leucopus*, *P. maniculatus*, and *R. montanus*) occur in areas with a richness of clumped patch types at the 1-ha scale (Fig 4a). Species projections onto component III find *P. attwateri* and *N. floridana* in areas of contrasting patch type, varying patch shape, and varying patch perimeter that are dominated by one or a few patch types, all at

the 5-ha scale (Fig. 4b). Five species (*C. hispidus*, *C. parva*, *P. leucopus*, *P. maniculatus*, and *S. hispidus*) occur near the middle of the axis, and three species (*M. ochrogaster*, *R. montanus*, and *R. fulvescens*) are found in areas that are dominated by one or a few patch types, but contain many contrasting patch types at the 10- and 25-ha scales.

Principal-components analysis of the 59 combined variables yielded two significant components (I-II). These two components explain 77% of the variance in the data (Table 4). Component I represents a gradient from areas with a high diversity of patch types and shapes at the 1- and 5-ha scale to areas with many different and contrasting patches dominated by one or more patch types at the 10- and 25-ha scale. The second component is a gradient from areas that are diverse in patch type, but dominated by broadleaf trees, at the 5-ha scale to areas of deep soils, and short, perennial grasses.

Species projections onto component I show two species (*P. maniculatus* and *R. montanus*) occupying areas composed of many patch types, but dominated by one or a few patch types at the 10- and 25-ha scale (Fig. 5). Five species (*C. hispidus*, *C. parva*, *P. leucopus*, *R. fulvescens*, and *S. hispidus*) are found near the middle of the axis. The remaining three (*M. ochrogaster*, *N. floridana*, and *P. attwateri*) are found where patch size varies greatly at the 1-ha scale. This condition is found, for example, where most of the transect extends through a grassland, but then passes into a small stream (riparian) and ends just inside an area of cross-timbers. Projections of species onto component II reveal four species (*C. parva*, *M. ochrogaster*, *R. fulvescens*, and *S. hispidus*) in areas of deep

soils and short, perennial grasses with many contrasting patch types at the 1-ha scale. Three species (*C. hispidus*, *P. leucopus*, and *P. maniculatus*) are found near the middle of the axis and three (*N. floridana*, *P. attwateri*, and *R. montanus*) are in rocky areas with broadleaf cover that are dominated by one patch type, but possess many contrasting patches at the 5-ha scale (Fig. 5). These areas are typically along bluffs or in boulders dominated by oaks, but interspersed with small barren areas (boulder fields) and small areas with grasses and forbs.

3.2. Cluster analysis

Cluster analysis of the landscape data produced a phenogram based on the weighted averages of 40 variables. Six TAs are defined at a distance of 1.0 (Figs. 4 and 6a). The first is composed of *C. parva* and *M. ochrogaster*, while the second consists of *P. maniculatus* and *R. montanus*. TA3 is made up of *P. leucopus*, *R. fulvescens*, and *S. hispidus*. The fourth, fifth, and sixth TAs are composed of single species—*Chaetodipus hispidus*, *N. floridana*, and *P. attwateri*, respectively.

The phenogram produced from cluster analysis of the combined data matrix included five clusters defined at a distance of 0.9. These five TAs are the same as those produced by the landscape clustering, except for the addition of *C. hispidus* into TA3 with *P. leucopus*, *S. hispidus*, and *R. fulvescens*.

3.3. Discriminant analysis

Discriminant analysis of the six TAs formed using the landscape data resulted in an overall correct classification of 38% based on seven variables. When the single species TAs were dropped from the analysis the correct classification

percentage of the remaining three TAs increased to 59% based on six landscape variables (Tables 5 and 6). Discriminant analysis of the two largest TAs (TA2 and TA3) resulted in an overall classification accuracy of 64%.

Discriminant analysis of five TAs using the combined variables resulted in an overall classification efficiency of 52% (51% jackknifed). This classification efficiency increases to 58% when the single-species TAs are removed.

Discriminant analysis of the two largest TAs (2 and 3) results in an overall correct classification of 64% (Table 5).

4. Discussion

The appropriate scale for evaluating the relationship of an organism with its environment may vary not only with the type of organism but, in the case of small mammals, with how each organism interacts with patch and boundary features in landscape mosaics (Johnson *et al.* 1992). In terrestrial ecosystems, an obvious framework of spatial patchiness is that produced by vegetation patterns (Wiens 1976). In this analysis I have defined a patch as a unit of land characterized by a homogeneous dominant vegetation type.

Organisms may have habitat preferences across many scales (Wiens 1989, Pogue 1998). Morris (1987) asked whether species select habitat based on micro- or macrohabitat characteristics, and indicated that similar patterns should occur among species with similar foraging strategies. Many studies indicate species habitat affinities at a local scale (Dueser and Shugart 1978, Pogue and Schnell 1994, Heske *et al.* 1997, Stancampiano and Schnell 1999). Other investigators use landscape factors to interpret habitat preferences (Wiens and Milne 1989,

Delattre et al. 1996, Nupp and Swihart 1996, Bayne and Hobson 1998), but only a few studies have combined small-scale factors with large-scale factors in an attempt to better understand how organisms perceive their environment (Pearson 1993, Songer *et al.* 1997, Pogue 1998).

4.1. *Landscape-level analysis*

Stancampiano and Schnell (1999) clustered the small-mammal fauna at Fort Sill based on local (microhabitat) factors. Cluster membership consisted of species related by conventional microhabitat affinities. Examples include *P. leucopus* in the woodlands and edges of woodlands (Bendell 1961, Barry and Franq 1980), *S. hispidus* and *P. maniculatus* in grasslands (Caire *et al.* 1989, Garman *et al.* 1994), and *P. attwateri* in rocky habitat (Baker 1968, Hall 1981). Clustering of these same species based on landscape factors resulted in non-conventional relationships in the small-mammal fauna, indicating that species are influenced by spatial patterns at different scales in the landscape. For example, some species typically found in woodlands are clustered with grassland species, and grassland species may not be grouped.

The most pronounced differences in TA membership between analyses based on local variables and those of landscape-level variables were the presence of *P. leucopus* with *S. hispidus* in the same TA, and the exclusion of *P. maniculatus* (Stancampiano and Schnell 1999). In the landscape analysis, this relationship is based primarily on a preference by *P. maniculatus* for areas dominated by one patch type (grass), but with a number of different patch types present, while *P. leucopus* and *S. hispidus* occupy a portion of the landscape with

more edge at a larger scale (10-25 ha). For example, *P. maniculatus* occurs primarily in areas with large patches of tall grass, which include smaller patches of other vegetation types such as short grass, mixed grass, wildlife plots, riparian (intermittent streams), and agricultural strips. In contrast, *C. parva* and *M. ochrogaster* cluster together based on local affinities (Stancampiano and Schnell 1999) and landscape factors. These two species maintain this unique cluster in all analyses.

The landscape analysis produced six distinct taxonomic assemblages; however, three of these were single-species TAs involving species infrequently caught. By eliminating the single-species TAs, the overall classification accuracy of the discriminant analysis increases from 38% to 59 % (Table 5).

Discriminant analysis of the two-TA landscape data (TA2 and TA3) produced a function with six variables. As indicated in Table 6, the best variable for separating TA2 and TA3 was the standard deviation of the landscape juxtaposition (JuxtaSD) at the 10-ha scale. This variable represents areas within the landscape consisting of a large number of similar patches (*e.g.*, short, mixed, and tall grasses) interspersed with patches of contrasting vegetation types (*e.g.*, tall grass and bottomland forest). These attributes are preferred by members of TA2.

Researchers can develop landscape models using satellite imagery and/or aerial photography without having to conduct intense microhabitat sampling. These data are informative because they accurately indicate species preferences and perhaps sources of species dispersal. Although some measures of

heterogeneity (*e.g.*, the number of patch types present) are not spatially explicit, they do have important spatial effects (Gustafson 1998). Models based on spatial heterogeneity may also improve model generality by increasing the area or regions in which a model may be employed. Wildlife-habitat models that are general in their applications, but specific in their predictions, are more useful to modelers and wildlife managers (Van Horne and Wiens 1991). These landscape models, however, are not as accurate as those produced using local variables alone (Stancampiano and Schnell 1999).

4.2. *Combined analysis*

The combined analyses indicated the same TA membership as the landscape analysis, except for the addition of *C. hispidus* to TA3. Separation of these clusters along PC I was due primarily to landscape factors. Members of TA2 (*P. maniculatus* and *R. montanus*) show a preference for areas rich in diversity of patch types, but dominated by large contiguous areas of one or a few patch types (grassland) at the 25-ha scale. This is in contrast to the landscape analysis, where species in TA2 show a preference for these same measures at the 1-ha scale. Pearson (1993) stated that, if spatial patterns in the landscape are very coarse (*i.e.*, large patches) relative to the ecological neighborhood of the study species, the landscape influence may not extend beyond adjacent patches. Alternatively, if landscape variation is fine (*i.e.*, small patches), more distant patches may have an effect. When sampling at increasing areal extent, particularly when including the area of previous samples in each successive sample extent, the landscape may appear to be coarse at smaller scales and fine at larger scales. Members of TA2

are apparently influenced by both small-scale (1-ha) and large scale (10- and 25-ha) spatial patterns, depending on the scale being analyzed. Principal component II represents a combination of local and landscape variables. Species of TA2 are found in areas dominated at the 5-ha scale by tall grass, but with a high diversity of patch types and shapes. Members of TA3 occur near the middle of PC II, while species in TA1 (*C. parva* and *M. ochrogaster*) prefer areas of deep soils with short, dense, perennial grasses, and a diversity of patch types at the 1-ha scale. This is consistent with the results of the landscape-level analysis.

Discriminant analysis combining local and landscape data does not result in an increase in accuracy over landscape data alone in the classification of species into their prospective TAs. As expected, however, classification accuracy improves as single-species TAs are eliminated (Table 5). Separation of the two largest TAs (TA2 and TA3) is based on nine variables (Table 6). Six of these are landscape-level factors. The standard deviation of patch shape at the 25-ha scale and tall herbaceous cover are important factors for correctly classifying these two TAs (Table 6). These variables represent 25-ha (or larger) areas of the landscape, which are dominated by large patches of grasses interspersed with riparian and other differently shaped patches of vegetation. Large areas of grass are preferred by *P. maniculatus*, the most abundant species in TA2 (Stancampiano and Schnell 1999). *Peromyscus leucopus* typically is perceived as a woodland/edge species (Van Deusen and Kaufman 1977; Kaufman *et al.* 1995). This view is supported by my findings. Conversely, *S. hispidus* is considered a grassland species, but clusters with *P. leucopus*. My study indicates that, while *S. hispidus* may be

found in grasslands, it can also be considered an edge species. *Peromyscus leucopus* and *S. hispidus* occupy more heterogeneous areas made up of many patches but not dominated by one patch type. Kincaid and Cameron (1985) indicated that, although grass makes up 74.3% of the diet in *S. hispidus*, individuals may prefer a more patchy habitat, particularly one where shrubby patches and grassy patches are contiguous.

In a study of wintering bird communities, Pearson (1993) concluded that the distribution of some species may depend not only on the local characteristics, but also on those of surrounding patches. This appears to be the case with *S. hispidus*. A study in southern Texas determined that *S. hispidus* occurred most frequently in monocot habitat (42%), but was found in mixed monocot/dicot (shrubby) habitat 38% of the time (Kincaid and Cameron 1985). Goertz (1964) also indicated that *S. hispidus* is not supported by large expanses of short grass.

It appears that *P. leucopus* and *S. hispidus* perceive the landscape at similar scales, but from different perspectives. *Peromyscus leucopus* occurs in the woodland areas and ventures into grassland borders, while *S. hispidus* occurs mainly in grassland areas bordered by shrubby or perhaps riparian habitat (Stancampiano and Schnell 1999).

Classification of mammal species into TAs using either landscape or combined data was not as accurate as when local data alone were used (Stancampiano and Schnell 1999). Both landscape and combined variables do indicate how species or groups of species are distributed horizontally across a landscape. These horizontal elements also offer researchers and wildlife

managers a different perspective from which to view species under investigation. Models constructed using landscape elements could be used in combination with models using local variables to improve the forecasting of species distributions across landscapes.

Researchers should continue to look for new avenues to reach their goals when studying the ecology of organisms. Revealing the spatial arrangement of a landscape is one means to achieve this pursuit.

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References

- Baker, W. L. and Cai, Y. 1997. The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. *Landscape Ecol.* 7:291-302.
- Baker, R. H. 1968. Habitats and distribution. Pp. 99-126, *in* *Biology of Peromyscus (Rodentia)* (J. A. King, ed.). Special Publication No. 2, American Society of Mammalogists, Stillwater, OK. 593 pp.
- Barry, R. E., Jr. and Franq, E. N. 1980. Orientation to landmarks within the preferred habitat by *Peromyscus leucopus*. *J. Mammal.* 61:292-303.
- Bayne, E. M. and Hobson, K. A. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. *Can. J. Zool.* 76:62-69.
- Bendell, J. F. 1961. Some factors affecting the habitat selection of the white-footed mouse. *Can. Field-Nat.* 75:244-255.
- Caire, W., Tyler, J. D., Glass, B. P. and Mares, M. A.. 1989. *Mammals of Oklahoma*. University of Oklahoma Press, Norman, OK. 567 pp.
- CERL. 1989. GRASS, version 4.1. U.S. Army Corps of Engineers, Construction Engineering and Research Laboratories, Champaign, IL.
- Delattre, P., Giraudoux, P., Baudry, J., Quéré, J. P. and Fichet, E. 1996. Effect of landscape structure on common vole (*Microtus arvalis*) distribution and abundance at several spatial scales. *Landscape Ecol.* 11:279-288.
- Dueser, R. D. and Shugart, H. H. Jr. 1978. Microhabitats in a forest-floor small mammal fauna. *Ecology* 59:89-98.

- Dunning, J. B., Danielson, B. J. and Pulliam, H. R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169-175.
- Franklin, S. B., Gibson, D. J., Robertson, P. A., Pohlmann, J. T. and Fralish, J. S. 1995. Parallel analysis: a method for determining significant principal components. *J. Veg. Sci.* 6:99-106.
- Garman, S. L., O'Connell, A. F. Jr. and Connery, J. H. 1994. Habitat use and distribution of the mice *Peromyscus leucopus* and *P. maniculatus* on Mount Desert Island, Maine. *Can. Field-Nat.* 108:67-71.
- Goertz, J. W. 1964. The influence of habitat quality upon the density of cotton rat populations. *Ecol. Monogr.* 34:359-381.
- Gustafson, E. J. 1998. Quantifying landscape spatial pattern: what is state of the art? *Ecosystems* 1:143-156.
- Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, NY. 2:601-1190 + 90.
- Heske, E. J., Rosenblatt, D. L. and Sugg, D. W. 1997. Population dynamics of small mammals in an oak woodland-grassland-chaparral habitat mosaic. *Southwest. Nat.* 42:1-12.
- Hunt, C. B. 1974. Natural regions of the United States and Canada. W. H. Freeman Co., San Francisco, CA. 725 pp.
- Jaksić, F. M. 1981. Abuse and misuse of the term "guild" in ecological studies. *Oikos* 37:397-400.
- Johnson, A. R., Wiens, J. A., Milne, B. T. and Crist, T. O. 1992. Animal movements and population dynamics in heterogeneous landscapes.

Landscape Ecol. 7:63-75.

- Johnson, F. L., Keller, W. O., Proctor, M. D. and Schnell, G. D. 1992. Fort Sill vegetation map. Final report, Oklahoma Biological Survey, Norman, OK.
- Kaufman, D. W., Kaufman, G. A. and Finck, E. J. 1995. Temporal variation in abundance of *Peromyscus leucopus* in wooded habitats of eastern Kansas. Am. Midl. Nat. 133:7-17.
- Kincaid, W. B. and Cameron, G. N. 1985. Interactions of cotton rats with a patchy environment: dietary responses and habitat selection. Ecology 66:1769-1783.
- McGarigal, K. and McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. 65:235-260.
- Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362-369.
- Morrison, M. L., Marcot, B. G. and Mannan, R. W. 1992. Wildlife-habitat relationships, concepts and applications. University of Wisconsin Press, Madison, WI. 343 pp.
- Nupp, T. E. and Swihart, R. K. 1996. Effect of forest patch area on population attributes of white-footed mice (*Peromyscus leucopus*) in fragmented landscapes. Can. J. Zool. 74:467-472.
- Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecol. 8:3-18.
- Pogue, D. W. 1998. A multiscale analysis of factors influencing the distributions of birds in the southern Great Plains. Ph.D. Dissertation. University of

- Oklahoma, Norman, OK. 130 pp.
- Pogue, D. W. and Schnell, G. D. 1994. Habitat characterization of secondary cavity-nesting birds in Oklahoma. *Wilson Bull.* 106:203-226.
- Rohlf, F. J. 1993. NTSYS-pc: numerical taxonomy and multivariate analysis system. Exeter Software, Setauket, NY.
- Sneath, P. H., and Sokal, R. R. 1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco, CA. 573 pp.
- Songer, M. A., Lomolino, M. V. and Perault, D. R. 1997. Niche dynamics of deer mice in a fragmented, old-growth-forest landscape. *J. Mammal.* 78:1027-1039.
- SPSS Inc. 1997. SYSTAT version 7.0 for Windows. SPSS Inc., Chicago, IL.
- Stancampiano, A. J. and Schnell, G. D. 1999. Microhabitat affinities of small mammals in the southern Great Plains. *J. Mammal.* Submitted for publication.
- Tazik, D. J., Warren, S. D., Diersing, V. E., Shaw, R. B., Brozka, R. J., Bagley, C. F. and Whitworth, W. R. 1992. U.S. Army land condition-trend analysis (LCTA) plot inventory field methods. U.S. Army Construction Engineering Research Laboratory, Technical Report, TR N-92/03.
- Turner, M. G., Gardner, R. H. and O'Neill, R. V. 1995. Ecological dynamics at broad scales: ecosystems and landscapes. *BioScience* 45:S29-S35.
- Van Deusen, M. and Kaufman, D. W. 1977. Habitat distribution of *Peromyscus leucopus* within prairie woods. *Trans. Kansas Acad. Sci.* 80:151-154.
- Van Horne, B. and Wiens, J. A. 1991. Forest bird habitat suitability models and

the development of general habitat models. U.S. Department of the Interior, Fish and Wildlife Service, Fish and Wildlife Research 8, Washington, D.C. 31 pp.

- Warren, S. D., Johnson, M. O., Goran, W. D. and Diersing, V. E. 1990. An automated, objective procedure for selecting representative field sample sites. *Photogrammetric Engineering and Remote Sensing*, 56:333-335.
- Wiens, J. A. 1976. Population response to patchy environments. *Annu. Rev. Ecol. Syst.* 7:81-129.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3:385-397.
- Wiens, J. A. and Milne, B. T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecol.* 3:87-96.
- Zonnveld, I. S. 1979. Land evaluation and land(scape) science. International Training Center, Enschede, The Netherlands. 134 pp.

Appendix A: Description of land-cover types

Following are descriptions of the land-cover types at Fort Sill Military Reservation (based on Johnson *et al.* 1992).

Riparian.—Vegetation close to ponds and drainages. Strongly influenced by water saturated soil and/or mechanical action of floodwater.

Bottomland Forest.—Tall forest with closed, coarse-textured canopy located close to perennial drainages on deep soils. May have as many as 15 tree species, but usually dominated by sugarberry (*Celtis laevigata*) or American elm (*Ulmus americana*). Other important species include bur oak (*Quercus macrocarpa*), soapberry (*Sapindus saponaria*), and box elder (*Acer negundo*). Often a dense understory of shrubs, vines, and herbaceous plants present.

Cross-timbers.—Closed-canopy or somewhat open, low forest composed mostly of post oak (*Q. stellata*) and blackjack oak (*Q. marilandica*) in uplands and along intermittent streams. Understory sparse in closed-canopy sites and moderately dense in more open sites.

Mesquite savanna.—Mixed grass with scattered individuals of mesquite (*Prosopis glandulosa*). Occurs on level areas with deep soils.

Old growth mesquite.—Mesquite savanna visible on 1957 photographs having larger trees than those found in younger stands.

Oak savanna.—Scattered trees in mixed grass. Transitional between cross timbers and mixed grass in most cases.

Mosaic.—Intermingling of oak savanna and short grass usually occurring on shallow soils on hillsides.

Short grass.—Occurs on shallow, rocky soils on hillsides and ridges, usually with bare rock. Dominated by grama grasses (*Bouteloua gracilis* and *B. hirsuta*).

Mixed grass.—Grasses dominated by little bluestem (*Schizachyrium scoparium*) that usually reach a height of 0.5-1.0 m. Big bluestem (*Andropogon gerardi*), sideoats grama (*B. curtipendula*), and switchgrass (*Panicum virgatum*) often important.

Tall grass.—Grasses dominated by big bluestem that grows to height of 2 m or more. Switchgrass and little bluestem also important.

Leased/agricultural.—Agricultural areas that have distinct boundaries.

Tree plot/food plot.—Areas planted to provide food for wildlife. Typically contained both trees and shrubs.

Disturbed areas.—Areas regularly maintained or where disturbance was clearly distinguishable on aerial photographs. Includes buildings, ranges, parade fields, airfields, and firing points for the military.

Old landfill/grass.—Areas that once were landfills, but now covered with tall grass.

Old field.—Areas disturbed sometime in past, but reverting to native vegetation.

Cantonment.—Areas covered by paved roads, houses, and other man-made buildings.

Water.—Any stream, creek, pond, or lake.

Appendix B: Description of landscape indices

Variables and indices used in evaluation of landscape features. Descriptions of variables taken in part from Baker (1992, 1994), O'Neill *et al.* (1988), and Ritters *et al.* (1995).

No.Patches.—Total number of patches.

PatchSizeSD.—Standard deviation of patch size. Standard deviation of sizes (in pixels) of all patches, ignoring group of each patch.

PatchShapeSD.—Standard deviation of patch shape. Standard deviation of shapes of all patches, ignoring group of each patch.

PatchPerSD.—Standard deviation of perimeter. Standard deviation of perimeter length for all patches, ignoring group of each patch.

Richness.—Richness. Number of different patch attributes.

Shannon.—Shannon index (H').

$$H' = - \sum_{i=1}^n P_i \ln(P_i),$$

where P_i is fraction of sampling area occupied by land-cover type i and n is number of land-cover types in sampling area.

Dominance.—Dominance (D). Related to Shannon index, but emphasizes deviation from evenness. Measures extent to which one or more cover types dominate the landscape. At large values landscape is dominated by one or a few cover types.

$$D = \ln(n) - H',$$

where n is number of land-cover types in sampling area and H' is Shannon index.

Contagion.—Contagion (C). Quantifies degree of clumping. Measures extent to which cover types are aggregated. At high values, contiguous patches found. At low

values, the landscape dissected into many small patches.

$$C = 2 \ln(n) \sum_{i=1}^n \sum_{j=1}^n P_{ij} \ln(P_{ij}),$$

where n is number of land-cover types and P_{ij} refers to proportion of times where pixel of land-cover type i occurs next to pixel of land-cover type j .

JuxtaSD.—Standard deviation of juxtaposition (s). Juxtaposition is measure of the weighted length edges surrounding a central pixel. Diagonal edges assigned value of 1 and vertical and horizontal assigned value of 2. Weighting factors range from 0-1 and are assigned to represent quality of different land-cover junctions.

$$s = \sqrt{\left(\frac{\sum_{i=1}^n (x_i - \bar{x})^2}{n} \right)},$$

where x_i is juxtaposition for cell i , \bar{x} is mean juxtaposition of all pixels, and n is total number of pixels. Patches of similar habitat types (e.g. mixed grass and tall grass) given weighting of zero, while contrasting habitat patches (e.g. short grass and bottomland forest) given weight of 0.75.

SumEdge.—Sum of edges by type. Length (in pixels) of all edges of particular type. Edges consisting of two contrasting land-cover types given value of 1 and counted. Edges consisting of two similar land-cover types not counted.

Appendix C: Local habitat variables used in principal-components analysis

Variable	Variable description
Sldp	Average plot soil depth (dm)
Avslp	Average slope gradient (percent) ^a
Cnone	No. locations with no cover ^b
Can	No. locations with only annual cover ^b
Cper	No. locations with only perennial cover ^b
Canper	No. locations with annual and perennial cover ^b
C4m	No. points with cover above 4 meters ^b
H00-15	No. locations with herbaceous cover in 0-15 dm
H16-40	No. locations with herbaceous cover in 16-40 dm
H41-85	No. locations with herbaceous cover in 41-85 dm
Hgt85	No. locations with herbaceous cover greater than 85 dm
B16-40	No. locations with broadleaf trees in 16- 40 dm
B41-85	No. locations with broadleaf trees in 41-85 dm
Bgt85	No. locations with broadleaf trees greater than 85 dm
Tcga	Total count annual grasses
Tcgp	Total count perennial grasses
Tctb	Total count broadleaf trees
Gcltr	No. points with litter ^b
Gcrck	No. points with rocks ^b

^a Arcsine transformation (Sokal and Rohlf 1981) employed on percentage values.

^b Out of 100 possible points per plot.

Table 1. Summary of mammal species used in analyses and their abundances.

Species	<i>n</i>	Average abundance per year ^a	Percent relative abundance
<i>Chaetodipus hispidus</i>	13	3.25	1.13
<i>Cryptotis parva</i>	13	3.25	1.13
<i>Microtus ochrogaster</i>	13	3.25	1.13
<i>Neotoma floridana</i>	20	5.00	1.75
<i>Peromyscus attwateri</i>	89	22.25	7.77
<i>P. leucopus</i>	249	62.25	21.73
<i>P. maniculatus</i>	194	48.50	16.93
<i>Reithrodontomys fulvescens</i>	58	14.50	5.06
<i>R. montanus</i>	39	9.75	3.40
<i>Sigmodon hispidus</i>	447	111.75	39.00

^aTotal number captured divided by four.

Table 2. Loadings for PCA of 40 landscape-level variables for 60 plots on Fort Sill Military Reservation. All landscape variables have significant loadings.

Variable	Component			
	I	II	III	IV
No.Patches[1]	0.705	0.554	0.115	0.139
No.Patches[5ha]	0.842	-0.028	-0.026	-0.216
No.Patches[10ha]	0.771	-0.237	0.013	0.017
No.Patches[25ha]	0.575	-0.367	0.463	-0.242
PatchSizeSD[1ha]	0.593	0.464	-0.046	0.543
PatchSizeSD[5ha]	0.400	-0.664	-0.416	0.328
PatchSizeSD[10ha]	0.323	-0.643	-0.282	0.406
PatchSizeSD[25ha]	-0.422	-0.208	0.434	0.455
PatchShapeSD[1ha]	0.629	0.510	-0.012	0.162
PatchShapeSD[5ha]	0.623	-0.177	-0.245	-0.151
PatchShapeSD[10ha]	0.695	-0.345	-0.116	-0.181
PatchShapeSD[25ha]	0.466	-0.151	0.591	-0.209
PatchPerSD[1ha]	0.587	0.511	-0.057	0.549
PatchPerSD[5ha]	0.579	-0.573	-0.319	0.224
PatchPerSD[10ha]	0.643	-0.478	-0.131	0.342
PatchPerSD[25ha]	0.289	-0.293	0.597	0.391
Richness[1ha]	0.722	0.574	0.093	0.205
Richness[5ha]	0.883	-0.090	-0.129	-0.133
Richness[10ha]	0.846	-0.266	0.022	-0.162
Richness[25ha]	0.695	-0.324	0.437	-0.135
Shannon[1ha]	0.677	0.522	0.093	-0.067
Shannon[5ha]	0.856	0.418	0.013	-0.106
Shannon[10ha]	0.920	0.150	-0.127	-0.136

Table 2. Continued.

Variable	Component			
	I	II	III	IV
Shannon[25ha]	0.869	-0.082	-0.053	-0.191
Dominance[1ha]	0.523	0.449	-0.025	0.592
Dominance[5ha]	0.413	-0.736	-0.382	0.172
Dominance[10ha]	0.435	-0.761	0.013	0.140
Dominance[25ha]	-0.099	-0.439	0.787	0.262
Contagion[1ha]	0.699	0.573	0.028	0.390
Contagion[5ha]	0.779	-0.430	-0.324	0.094
Contagion[10ha]	0.766	-0.529	-0.050	0.047
Contagion[25ha]	0.417	-0.463	0.710	0.136
JuxtaSD[1ha]	0.692	0.503	0.095	0.020
JuxtaSD[5ha]	0.796	0.204	-0.071	-0.141
JuxtaSD[10ha]	0.827	-0.064	-0.067	-0.141
JuxtaSD[25ha]	0.717	-0.150	0.254	-0.158
SumEdge[1ha]	0.657	0.540	0.070	-0.058
SumEdge[5ha]	0.800	0.295	-0.021	-0.227
SumEdge[10ha]	0.852	0.058	-0.045	-0.265
SumEdge[25ha]	0.819	-0.124	0.158	-0.249
Percent variance explained	45.39	17.95	8.28	6.81
Cumulative variance	45.39	63.34	71.62	78.43

Table 3. Summary of PCA based on 10 mammal species and 40 landscape variables for 60 plots on Fort Sill Military Reservation. Bold indicates significant loadings ($P < 0.05$).

Variable	Component		
	I	II	III
No.Patches[1]	0.354	0.737	0.458
No.Patches[5ha]	0.624	0.751	-0.079
No.Patches[10ha]	0.678	0.331	0.609
No.Patches[25ha]	0.431	-0.113	0.875
PatchSizeSD[1ha]	0.100	0.732	0.524
PatchSizeSD[5ha]	0.275	0.621	-0.353
PatchSizeSD[10ha]	-0.050	-0.143	-0.206
PatchSizeSD[25ha]	-0.347	-0.606	0.414
PatchShapeSD[1ha]	-0.374	0.575	0.320
PatchShapeSD[5ha]	0.708	0.145	-0.620
PatchShapeSD[10ha]	0.906	-0.039	0.315
PatchShapeSD[25ha]	0.744	-0.443	0.425
PatchPerSD[1ha]	0.903	-0.173	0.021
PatchPerSD[5ha]	0.853	-0.079	-0.483
PatchPerSD[10ha]	0.884	-0.356	-0.041
PatchPerSD[25ha]	0.757	-0.612	-0.100
Richness[1ha]	-0.687	0.609	0.367
Richness[5ha]	0.927	0.336	-0.028
Richness[10ha]	0.850	0.134	0.497
Richness[25ha]	0.704	-0.390	0.578
Shannon[1ha]	-0.650	0.650	0.370
Shannon[5ha]	0.725	0.595	0.047

Table 3. Continued.

Variable	Component		
	I	II	III
Shannon[10ha]	0.769	0.611	-0.007
Shannon[25ha]	0.908	0.254	0.203
Dominance[1ha]	-0.573	0.661	0.465
Dominance[5ha]	0.849	0.001	-0.403
Dominance[10ha]	0.354	-0.364	0.718
Dominance[25ha]	0.360	-0.702	0.593
Contagion[1ha]	0.099	0.787	0.513
Contagion[5ha]	0.922	0.219	-0.285
Contagion[10ha]	0.722	0.004	0.603
Contagion[25ha]	0.604	-0.534	0.574
JuxtaSD[1ha]	-0.684	0.612	0.366
JuxtaSD[5ha]	0.608	0.581	-0.479
JuxtaSD[10ha]	0.752	0.387	-0.391
JuxtaSD[25ha]	0.914	-0.113	0.039
SumEdge[1ha]	0.786	0.139	-0.304
SumEdge[5ha]	0.839	0.177	-0.275
SumEdge[10ha]	0.935	0.177	-0.194
SumEdge[25ha]	0.737	-0.103	0.319
Percent variance explained	48.06	21.18	17.45
Cumulative variance	48.06	69.24	86.69

Table 4. Summary of PCA of 10 mammal species and 59 combined variables for 60 plots on Fort Sill Military Reservation. Bold indicates significant loadings ($P < 0.05$). Variables are defined in Appendices B and C.

Variable	Component	
	I	II
Sldp	0.521	0.787
Avslp	-0.229	-0.821
Cnone	-0.416	-0.726
Can	0.483	-0.048
Cper	-0.445	0.025
Canper	0.610	0.693
C4m	-0.609	-0.681
H00-15	0.378	0.870
H16-40	-0.633	-0.744
H41-85	-0.619	-0.711
Hgt85	-0.465	-0.487
B16-40	-0.615	-0.715
B41-85	-0.630	-0.718
Bgt85	-0.484	-0.539
Tcga	0.652	0.574
Tcgp	0.375	0.875
Tctb	-0.626	-0.726
Gcltr	-0.005	0.716
Gcrck	-0.289	-0.805
No.Patches[1]	0.307	-0.510
No.Patches[5ha]	0.278	-0.637
No.Patches[10ha]	0.641	-0.091
No.Patches[25ha]	0.732	0.492

Table 4. Continued.

Variable	Component	
	I	II
PatchSizeSD[1ha]	0.664	-0.292
PatchSizeSD[5ha]	0.860	-0.380
PatchSizeSD[10ha]	0.787	-0.486
PatchSizeSD[25ha]	0.841	-0.327
PatchShapeSD[1ha]	-0.802	0.504
PatchShapeSD[5ha]	0.860	-0.477
PatchShapeSD[10ha]	0.201	-0.770
PatchShapeSD[25ha]	0.881	-0.377
PatchPerSD[1ha]	0.860	-0.379
PatchPerSD[5ha]	0.878	-0.390
PatchPerSD[10ha]	0.702	-0.574
PatchPerSD[25ha]	0.976	0.087
Richness[1ha]	-0.459	0.753
Richness[5ha]	-0.638	-0.696
Richness[10ha]	0.914	-0.110
Richness[25ha]	0.978	-0.083
Shannon[1ha]	-0.636	0.620
Shannon[5ha]	-0.578	-0.760
Shannon[10ha]	0.773	-0.407
Shannon[25ha]	0.844	-0.346
Dominance[1ha]	-0.534	0.442
Dominance[5ha]	-0.123	-0.916
Dominance[10ha]	0.818	0.406
Dominance[25ha]	0.730	0.103

Table 4. Continued.

Variable	Component	
	I	II
Contagion[1ha]	0.127	0.850
Contagion[5ha]	0.843	-0.517
Contagion[10ha]	0.899	0.140
Contagion[25ha]	0.928	-0.077
JuxtaSD[1ha]	-0.571	0.701
JuxtaSD[5ha]	-0.641	-0.707
JuxtaSD[10ha]	0.535	-0.589
JuxtaSD[25ha]	0.450	-0.566
SumEdge[1ha]	0.855	-0.367
SumEdge[5ha]	0.939	-0.303
SumEdge[10ha]	0.941	-0.226
SumEdge[25ha]	0.962	-0.261
Percent variance explained	45.17	31.86
Cumulative variance	45.17	77.03

Table 5. Classification of species into TAs using stepwise discriminant analysis.^a

Group	Percent correctly classified	Classified as					
		TA1	TA2	TA3	TA4	TA5	TA6
Six-TA landscape analysis							
TA1	46(23)	12(6)	1	4(9)	7(8)	0	2
TA2	21	49	45	50	55	0	14
TA3	43	171	65	317	102	62	21
TA4	50(21)	2	1(5)	4	7(3)	0	0
TA5	75	2	0	1	0	15	2
TA6	30	4	10	0	10	37	26
Total	38	240(234)	122(126)	376(381)	181(178)	114	65
Three-TA landscape analysis							
TA1	35	9	11	6	—	—	—
TA2	65	14	139	60	—	—	—
TA3	58	61	249	428	—	—	—
Total	59	84	399	494	—	—	—
Two-TA landscape analysis							
TA2	63	137	80	—	—	—	—
TA3	64	261	461	—	—	—	—
Total	64	398	541	—	—	—	—
Five-TA combined analysis							
TA1	65	17	4	5	0	0	—
TA2	47(44)	50	101(96)	59(64)	0	7	—
TA3	50	114	183	358	46	21	—
TA4	45(30)	0	0	3(6)	9(6)	8	—
TA5	79	0	0	12	6	68	—
Total	52(51)	181(179)	288(285)	437(445)	61(58)	104	—

Table 5. Continued.

Group	Percent correctly classified	Classified as					
		TA1	TA2	TA3	TA4	TA5	TA6
Three-TA combined analysis							
TA1	38(31)	10(8)	10	6(8)	—	—	—
TA2	62(60)	21	135(130)	61(66)	—	—	—
TA3	57	49	262	411	—	—	—
Total	58(57)	80(78)	407(402)	478(485)	—	—	—
Two-TA combined analysis							
TA2	63	—	137	80	—	—	—
TA3	64	—	261	461	—	—	—
Total	64	—	398	541	—	—	—

^a Parentheses indicate jackknifed classification results.

Table 6. Statistics for stepwise discriminant analysis of TAs based on landscape and local-landscape variables. Variables are in order of entry.

Variable	Standardized canonical discriminant function					Classification function ^a					
	1	2	3	4	5	TA1	TA2	TA3	TA4	TA5	TA6
Six-TA landscape analysis											
Contagion[25ha]	1.050	0.005	-0.615	-0.092	0.172	5.124	4.469	4.485	4.187	1.773	0.595
JuxtaSD[10ha]	-0.731	-0.978	-0.805	0.784	0.115	-36.866	-30.718	4.561	-15.647	196.049	104.390
PatchSizeSD[1ha]	0.751	0.303	0.388	0.645	0.250	0.001	0.001	0.001	0.001	0.000	0.000
SumEdge[25ha]	1.023	0.206	1.256	-0.026	0.034	0.003	0.004	0.004	0.004	0.001	0.001
PatchPerSD[25ha]	-1.442	-0.282	0.076	-0.597	-1.441	-0.012	-0.013	-0.012	-0.011	-0.003	-0.001
PatchSizeSD[25ha]	1.127	0.421	-0.158	1.073	0.475	0.000	0.000	0.000	0.000	0.000	0.000
PatchShapeSD[10ha]	0.408	-0.042	-0.202	-0.289	0.326	8.470	7.182	7.420	6.007	2.972	1.588
Constant	-2.792	0.715	0.685	-1.325	1.980	-10.537	-10.236	-10.532	-10.702	-7.974	-6.168
Three-TA landscape analysis											
JuxtaSD[10ha]	-0.788	-0.250	—	—	—	-23.005	-23.258	22.027	—	—	—
PatchPerSD[5ha]	-1.550	-0.725	—	—	—	-0.002	-0.004	0.002	—	—	—
PatchSizeSD[10ha]	0.783	-0.946	—	—	—	0.000	0.000	0.000	—	—	—
Shannon[5ha]	0.583	1.484	—	—	—	-2.681	1.414	-0.418	—	—	—
PatchSizeSD[5ha]	0.777	2.209	—	—	—	0.000	0.000	0.000	—	—	—
Shannon[25ha]	-0.018	-1.002	—	—	—	6.112	3.198	3.750	—	—	—

Table 6. Continued.

Variable	Standardized canonical discriminant function					Classification function ^a					
	1	2	3	4	5	TA1	TA2	TA3	TA4	TA5	TA6
Constant	0.728	0.084	—	—	—	-3.853	-3.314	-3.681	—	—	—
Two-TA landscape analysis											
JuxtaSD[10ha]	-0.739	—	—	—	—	—	-138.560	-97.925	—	—	—
PatchPerSD[5ha]	-1.911	—	—	—	—	—	-0.036	-0.029	—	—	—
PatchSizeSD[5ha]	1.715	—	—	—	—	—	0.001	0.001	—	—	—
Shannon[5ha]	0.796	—	—	—	—	—	8.786	7.355	—	—	—
PatchPerSD[25ha]	0.458	—	—	—	—	—	0.015	0.014	—	—	—
PatchShapeSD[25ha]	-0.306	—	—	—	—	—	8.894	9.911	—	—	—
Constant	0.001	—	—	—	—	—	-9.644	-9.516	—	—	—
Five-TA combined analysis											
Cnone	0.543	0.225	0.104	0.199	—	0.501	0.484	0.468	0.604	0.688	—
Tctb	2.570	-0.966	1.724	0.308	—	0.180	0.174	0.180	0.305	0.294	—
C4m	-2.089	-0.030	-2.377	-0.450	—	-0.811	-0.766	-0.743	-1.219	-1.168	—
Gcrck	0.597	-0.372	-0.261	-0.204	—	0.237	0.259	0.279	0.379	0.409	—
Gcltr	0.534	-0.121	0.281	0.642	—	0.363	0.334	0.340	0.415	0.422	—
SumEdge[10ha]	-0.445	-0.153	-0.347	0.025	—	0.000	0.000	0.001	-0.004	-0.004	—
Dominance[25ha]	-0.107	0.389	0.138	-0.076	—	7.049	7.228	5.936	4.144	4.916	—
PatchShapeSD[10ha]	0.254	-0.210	0.114	0.580	—	10.635	5.879	7.596	14.543	14.217	—

Table 6. Continued.

Variable	Standardized canonical discriminant function					Classification function ^a					
	1	2	3	4	5	TA1	TA2	TA3	TA4	TA5	TA6
SumEdge[1ha]	1.246	0.378	-0.714	0.208	—	0.027	0.029	0.028	0.067	0.127	—
JuxtaSD[1ha]	-1.305	-0.426	0.704	0.365	—	-122.315	-187.787	-170.307	-363.223	-626.290	—
JuxtaSD[5ha]	0.715	0.463	-0.197	-0.549	—	-153.430	-81.473	-117.656	6.062	161.259	—
Bgt85	-0.269	-0.666	1.293	-0.123	—	0.630	0.593	0.627	0.888	0.398	—
Shannon[5ha]	-0.351	0.300	0.416	-0.914	—	11.099	13.852	12.374	10.702	8.228	—
PatchPerSD[5ha]	-0.427	-1.602	-0.744	0.100	—	-0.047	-0.047	-0.039	-0.042	-0.052	—
PatchSizeSD[5ha]	0.175	1.428	0.767	-0.708	—	0.001	0.001	0.001	0.001	0.001	—
PatchShapeSD[25ha]	-0.117	-0.499	-0.105	0.033	—	10.998	10.762	13.188	13.423	9.472	—
Canper	0.078	-0.367	-0.385	-0.305	—	0.090	0.120	0.142	0.151	0.156	—
B16-40	-1.819	0.815	-0.047	-0.136	—	-0.368	-0.371	-0.417	-0.798	-0.858	—
B41-85	2.036	-0.053	-0.116	0.380	—	0.159	0.152	0.162	0.459	0.599	—
Constant	-1.972	1.654	-0.142	-0.203	—	-23.848	-23.075	-24.352	-37.649	-39.755	—
Three-TA combined analysis											
H41-85	0.741	0.182	—	—	—	0.017	0.008	0.034	—	—	—
PatchShapeSD[25ha]	0.499	0.113	—	—	—	5.395	4.706	6.942	—	—	—
PatchPerSD[5ha]	1.792	0.248	—	—	—	-0.016	-0.017	-0.009	—	—	—
PatchSizeSD[10ha]	-0.086	1.201	—	—	—	0.000	0.000	0.000	—	—	—
Shannon[5ha]	-0.616	-1.267	—	—	—	2.302	6.755	4.825	—	—	—

Table 6. Continued.

Variable	Standardized canonical discriminant function					Classification function ^a					
	1	2	3	4	5	TA1	TA2	TA3	TA4	TA5	TA6
PatchSizeSD[5ha]	-1.407	-1.832	—	—	—	0.000	0.000	0.000	—	—	—
Dominance[25ha]	-0.389	-0.768	—	—	—	3.954	7.117	5.703	—	—	—
Richness[25ha]	0.050	0.894	—	—	—	1.066	0.241	0.363	—	—	—
Canper	0.322	0.095	—	—	—	0.064	0.057	0.074	—	—	—
Constant	-1.207	0.146	—	—	—	-7.295	-6.852	-7.663	—	—	—
Two-TA combined analysis											
H41-85	0.030	—	—	—	—	—	0.006	0.032	—	—	—
PatchShapeSD[25ha]	2.077	—	—	—	—	—	5.404	7.198	—	—	—
PatchPerSD[5ha]	0.005	—	—	—	—	—	-0.006	-0.002	—	—	—
Canper	0.068	—	—	—	—	—	-0.025	0.033	—	—	—
Tcga	-0.024	—	—	—	—	—	0.035	0.015	—	—	—
PatchSizeSD[1ha]	-0.000	—	—	—	—	—	0.001	0.000	—	—	—
PatchSizeSD[5ha]	-0.000	—	—	—	—	—	0.000	0.000	—	—	—
Contagion[25ha]	-0.472	—	—	—	—	—	3.992	3.585	—	—	—
PatchShape[10ha]	1.602	—	—	—	—	—	-3.970	-2.587	—	—	—
Constant	-1.265	—	—	—	—	—	-6.169	-7.061	—	—	—

^a Used with original variables. Add products of measurements and corresponding function values to constant; classify as TA1, TA2, TA3, TA4, TA5, or TA6, depending on which has the highest function for its classification.

FIGURE CAPTIONS

Fig. 1. Study area including Fort Sill Military Reservation, Wichita Mountains Wildlife Refuge, and surrounding communities. Dashed lines indicate study area, thin lines indicate county lines and heavy solid lines indicate major highways.

Fig. 2. Sample study plot showing buffered transect consisting of 1-, 5-, 10-, and 25-ha areas.

Fig. 3. Projections of 60 plots based on 40 landscape variables onto principal components: (a) I and II, and (b) I and III.

Fig. 4. Projections of mammal species based on 40 landscape variables onto principal components (a) I and II, and (b) I and III. Ovals indicate species TAs (taxonomic assemblages). Species names abbreviated as follows: CHHI, *Chaetodipus hispidus*; CRPA, *Cryptotis parva*; MIOC, *Microtus ochrogaster*; NEFL, *Neotoma floridana*; PEAT, *Peromyscus attwateri*; PELE, *P. leucopus*; PEMA, *P. maniculatus*; REFU, *Reithrodontomys fulvescens*; REMO, *R. montanus*; SIHI, *Sigmodon hispidus*.

Fig. 5. Projections of small-mammal species based on 59 combined local and landscape variables onto principal components I and II. Ovals indicate species TAs (taxonomic assemblages). Species names abbreviated as follows: CHHI, *Chaetodipus hispidus*; CRPA, *Cryptotis parva*; MIOC, *Microtus ochrogaster*; NEFL, *Neotoma floridana*; PEAT, *Peromyscus attwateri*; PELE, *P. leucopus*; PEMA, *P. maniculatus*; REFU, *Reithrodontomys fulvescens*; REMO, *R. montanus*; SIHI, *Sigmodon hispidus*.

Fig. 6. UPGMA dendrogram depicting taxonomic assemblages and their relationships based on (a) 40 landscape variables and (b) 59 combined variables. Membership in TAs (taxonomic assemblages) based on species associated at an average

taxonomic distance of (a) 1.0 and (b) 0.9. Cophenetic correlation coefficients were (a) 0.80 and (b) 0.88.

Fig. 1

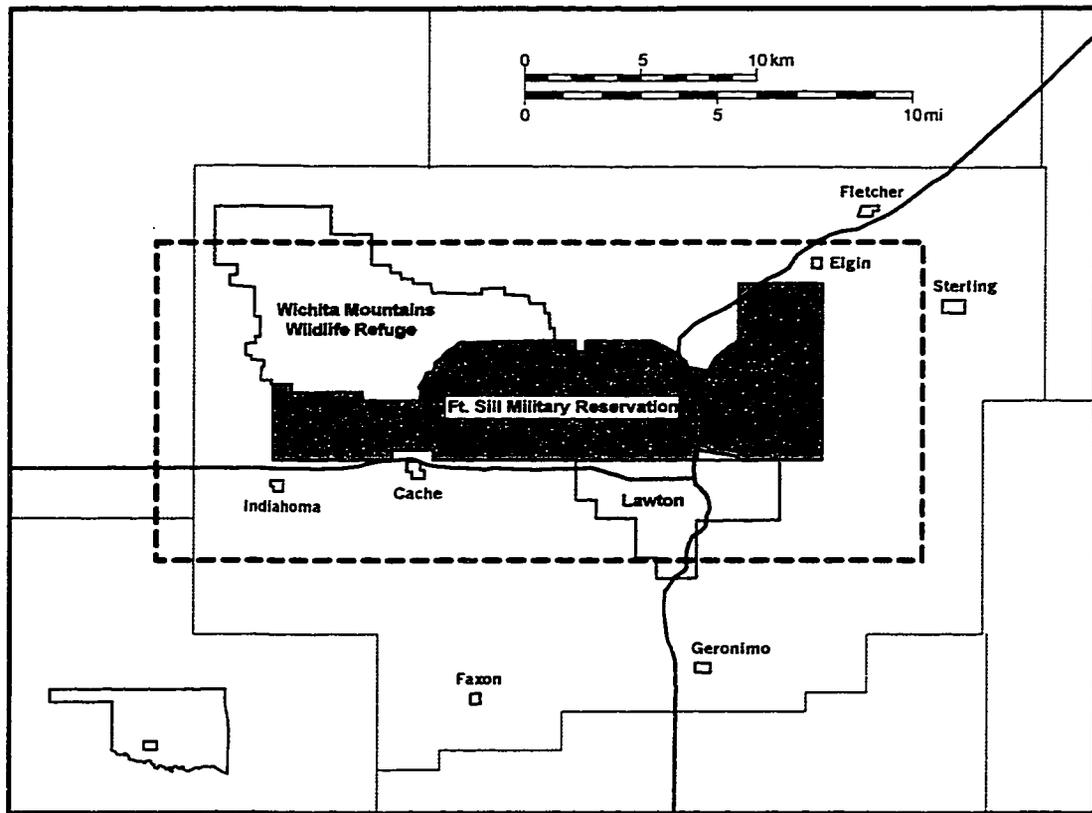


Fig. 2

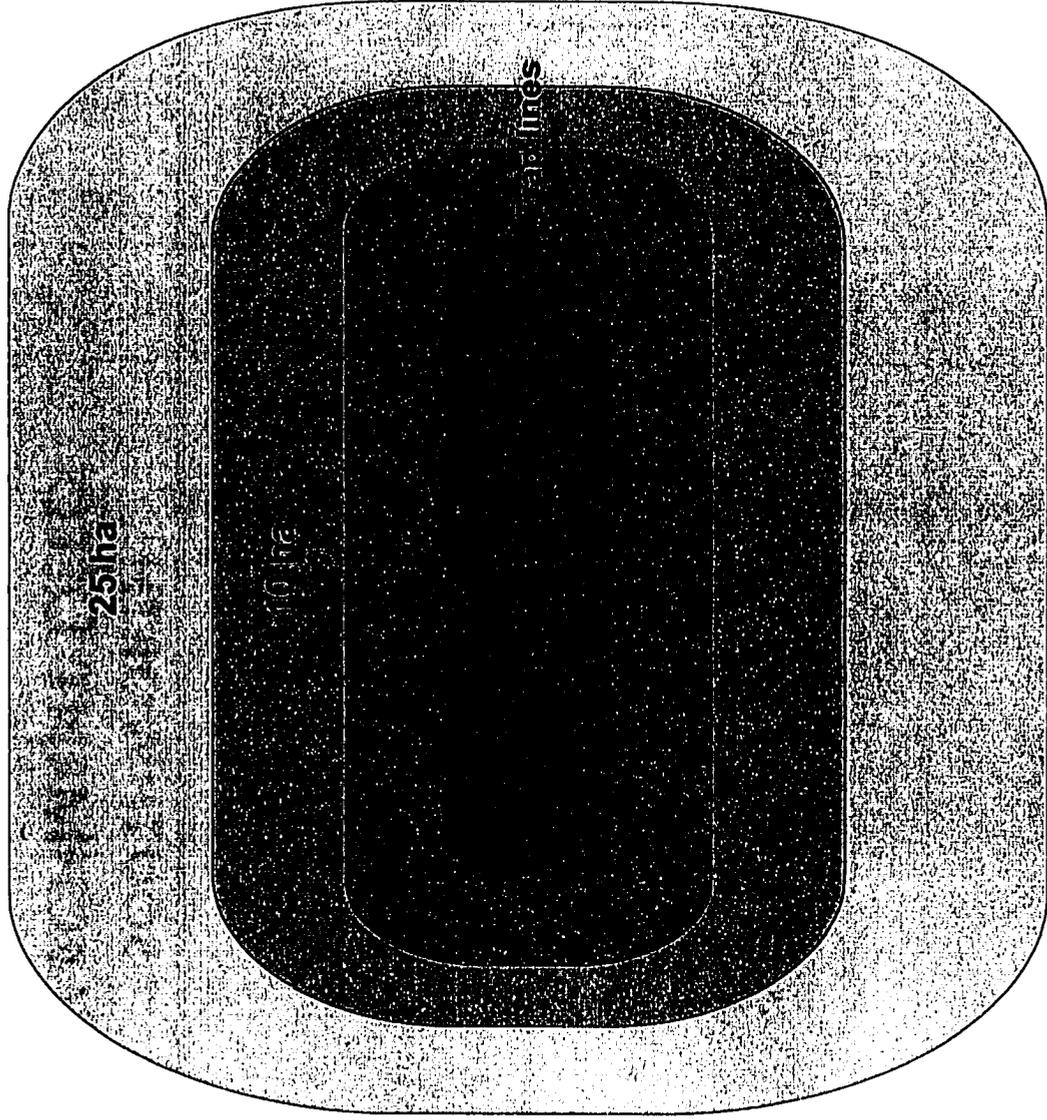


Fig. 3

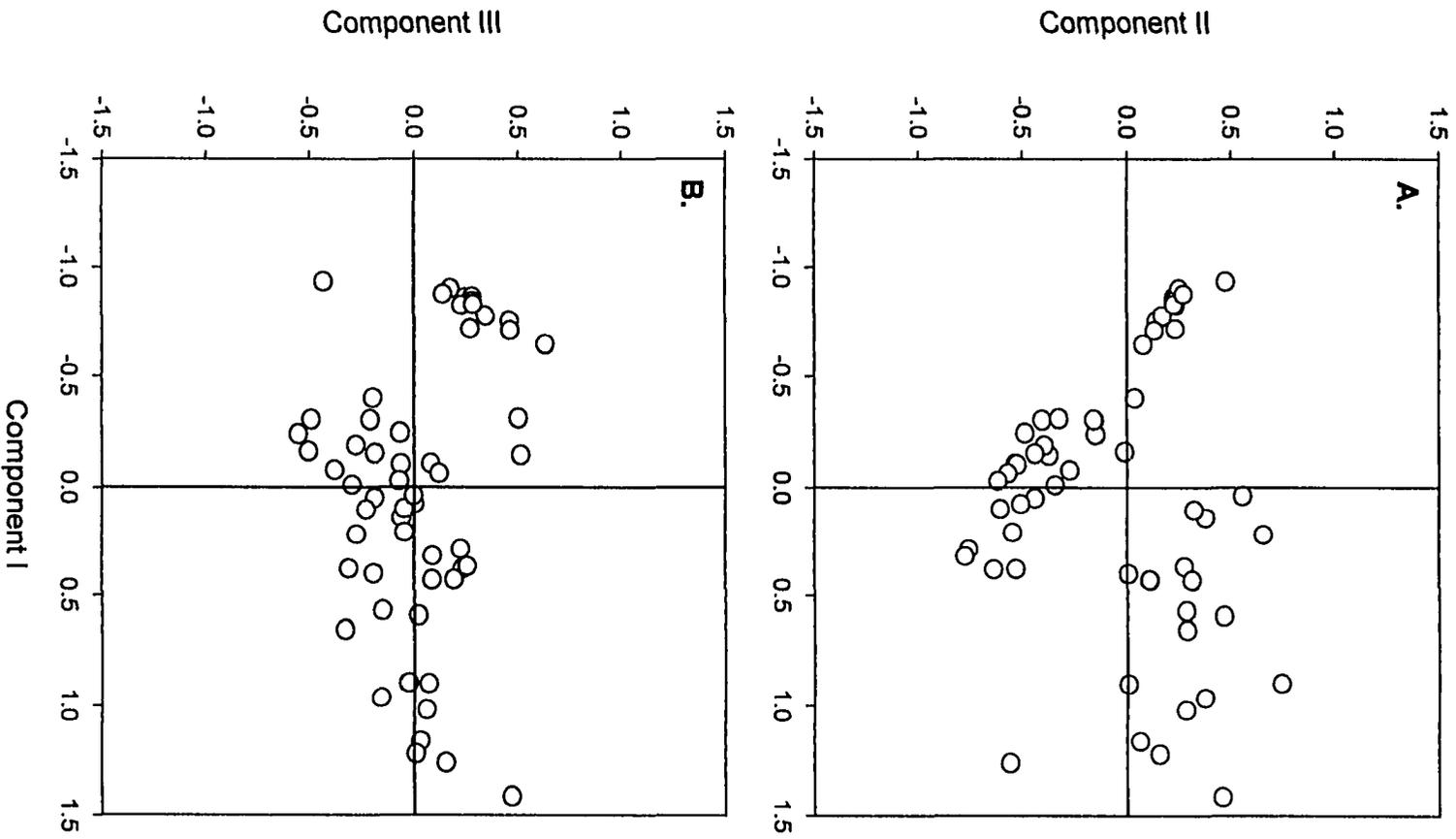


Fig. 4

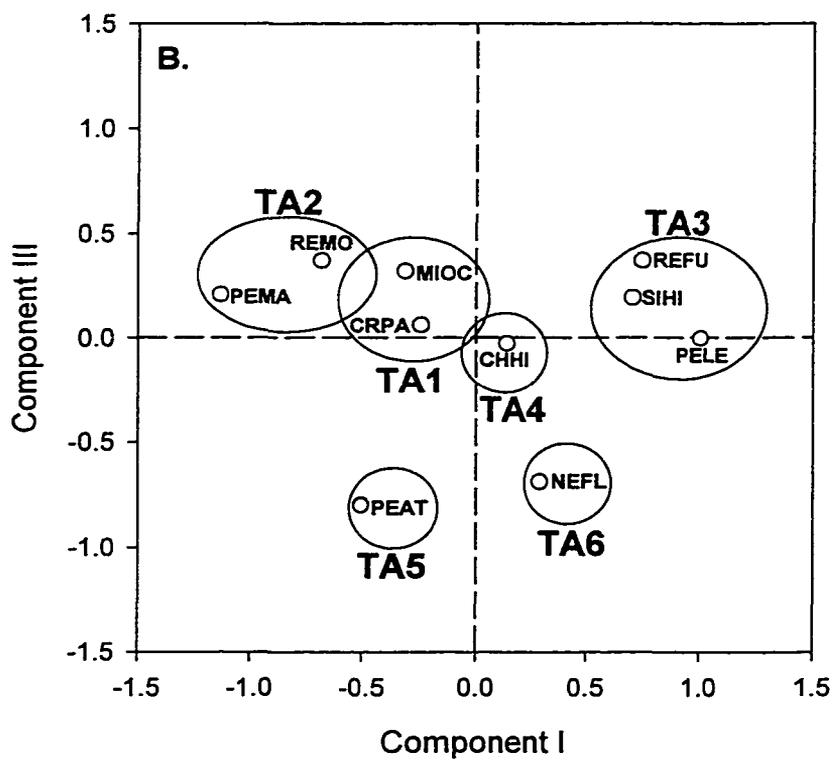
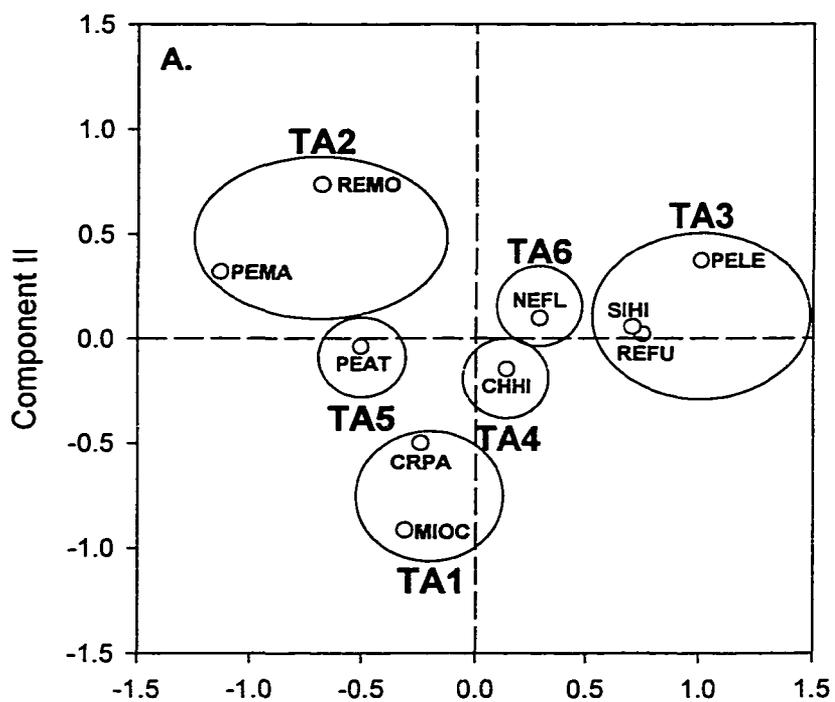


Fig. 5

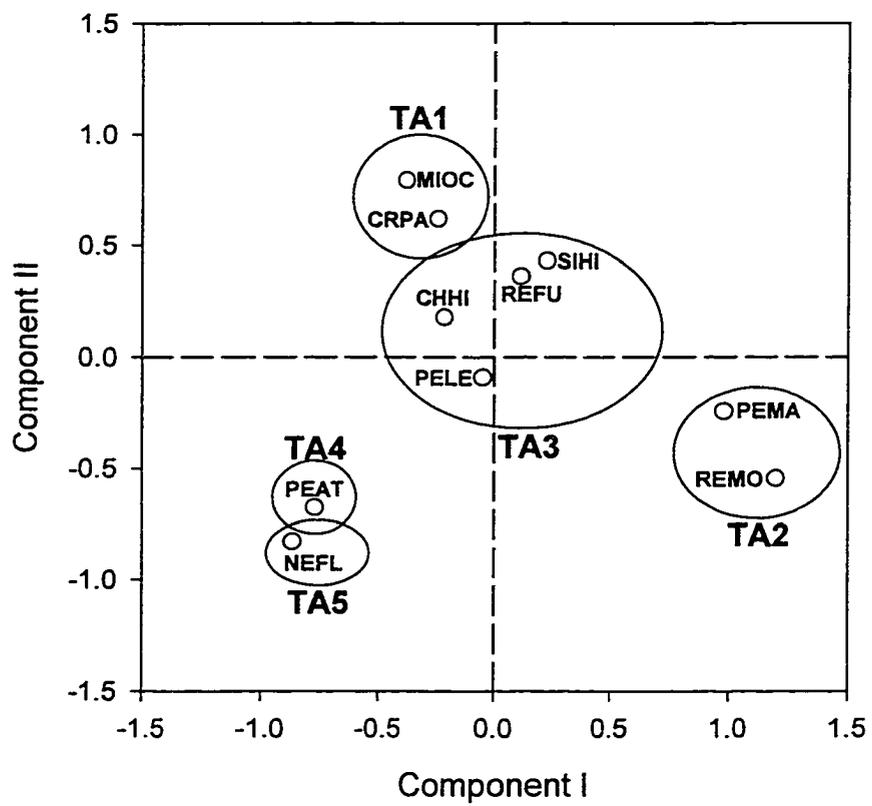
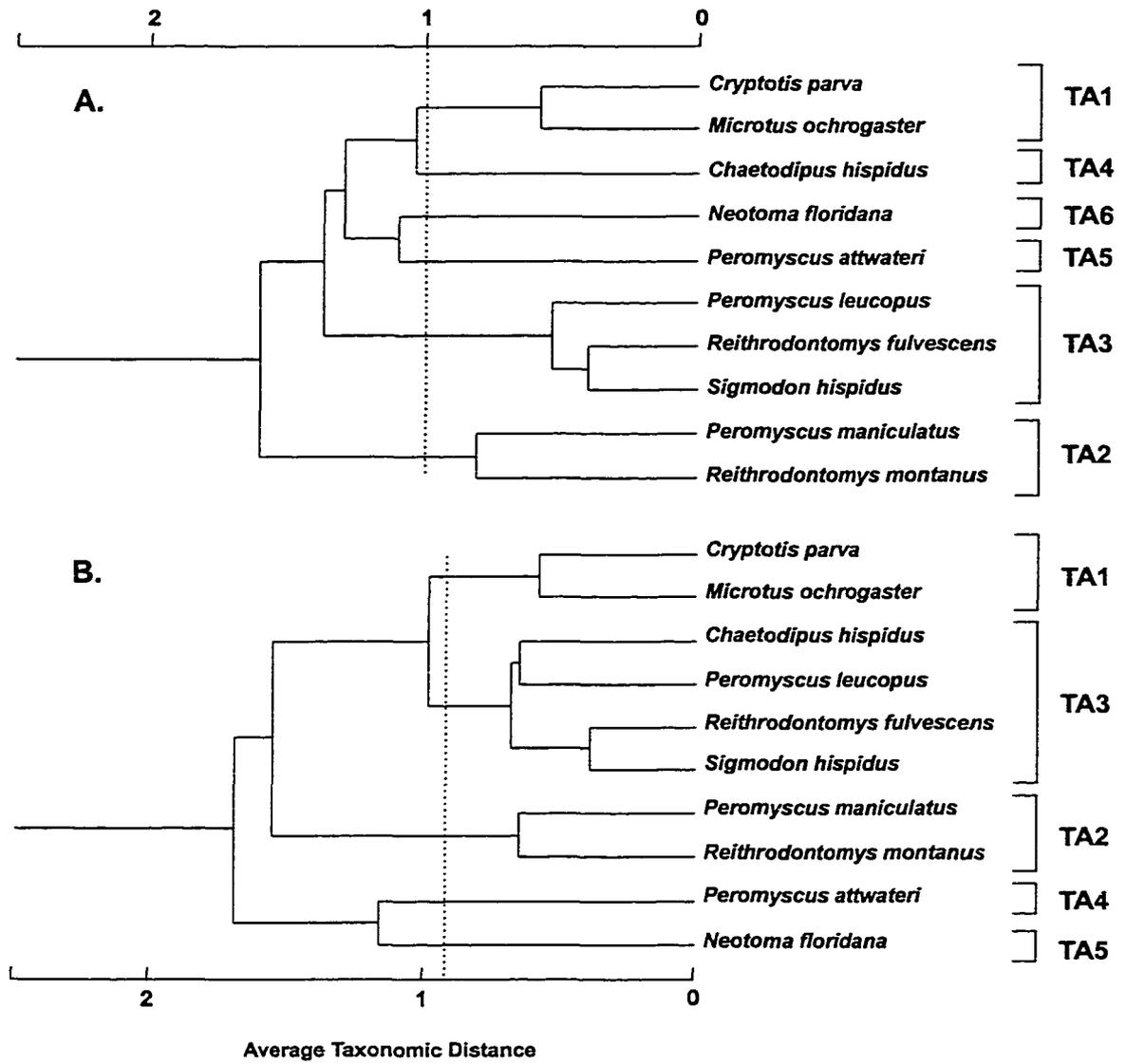


Fig. 6



APPENDIX.— Correlation matrix of combined local and landscape variables.

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Sldp	1.00															
2 Avslp	-0.86	1.00														
3 Cnone	-0.82	0.84	1.00													
4 Can	0.10	-0.05	0.10	1.00												
5 Cper	-0.12	-0.01	-0.17	-0.93	1.00											
6 Canper	0.86	-0.79	-0.85	0.35	-0.35	1.00										
7 C4m	-0.78	0.59	0.57	-0.45	0.48	-0.80	1.00									
8 H00-15	0.83	-0.85	-0.88	0.14	-0.06	0.86	-0.81	1.00								
9 H16-40	-0.89	0.73	0.76	-0.31	0.30	-0.87	0.96	-0.89	1.00							
10 H41-85	-0.83	0.65	0.64	-0.41	0.420	-0.83	0.99	-0.84	0.98	1.00						
11 Hgt85	-0.47	0.30	0.25	-0.54	0.61	-0.57	0.91	-0.59	0.76	0.86	1.00					
12 B16-40	-0.83	0.64	0.61	-0.43	0.46	-0.82	0.99	-0.83	0.97	0.99	0.86	1.00				
13 B41-85	-0.85	0.64	0.63	-0.43	0.45	-0.84	0.99	-0.84	0.97	0.99	0.84	0.99	1.00			
14 Bgt85	-0.55	0.33	0.27	-0.57	0.65	-0.60	0.93	-0.60	0.79	0.89	0.98	0.91	0.89	1.00		
15 Tcga	0.74	-0.72	-0.81	0.48	-0.41	0.97	-0.76	0.83	-0.83	-0.79	-0.58	-0.78	-0.79	-0.58	1.00	
16 Tcgp	0.88	-0.84	-0.89	-0.04	0.06	0.82	-0.78	0.97	-0.88	-0.82	-0.54	-0.81	-0.82	-0.56	0.74	1.00

APPENDIX.—Continued.

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
17 Tctb	-0.85	0.67	0.66	-0.40	0.41	-0.84	0.99	-0.85	0.99	0.99	0.84	0.99	0.99	0.88	-0.80	-0.83
18 GcItr	0.58	-0.78	-0.84	-0.35	0.35	0.63	-0.33	0.76	-0.48	-0.39	-0.14	-0.35	-0.36	-0.10	0.57	0.78
19 Gcck	-0.84	0.94	0.96	0.13	-0.18	-0.82	0.58	-0.90	0.76	0.65	0.29	0.62	0.63	0.23	-0.76	-0.91
20 No.Patches[1ha]	-0.29	0.55	0.47	0.54	-0.70	-0.06	0.04	-0.47	0.21	0.11	-0.15	0.06	0.06	-0.18	-0.02	-0.51
21 No.Patches[5ha]	-0.34	0.56	0.34	0.26	-0.36	-0.12	0.32	-0.56	0.38	0.35	0.25	0.32	0.30	0.22	-0.07	-0.57
22 No.Patches[10ha]	0.30	0.03	-0.37	0.05	-0.14	0.45	-0.19	0.09	-0.26	-0.20	-0.04	-0.21	-0.24	-0.08	0.43	0.14
23 No.Patches[25ha]	0.77	-0.42	-0.65	0.25	-0.33	0.81	-0.76	0.62	-0.80	-0.77	-0.56	-0.80	-0.81	-0.63	0.74	0.66
24 PatchSizeSD[1ha]	0.19	0.04	-0.14	0.45	-0.42	0.33	-0.11	-0.09	-0.17	-0.13	0.04	-0.13	-0.15	-0.01	0.38	-0.13
25 PatchSizeSD[5ha]	0.12	0.11	-0.06	0.38	-0.30	0.18	-0.31	0.04	-0.31	-0.31	-0.29	-0.29	-0.29	-0.25	0.28	0.05
26 PatchSizeSD[10ha]	0.06	0.13	-0.14	0.13	-0.05	0.13	-0.06	-0.06	-0.13	-0.08	0.02	-0.05	-0.07	0.06	0.22	-0.03
27 PatchSizeSD[25ha]	0.18	-0.03	-0.15	0.34	-0.24	0.24	-0.29	0.12	-0.32	-0.30	-0.24	-0.28	-0.29	-0.20	0.34	0.117
28 PatchShapeSD[1ha]	-0.01	-0.15	0.04	-0.34	0.24	-0.13	0.14	0.06	0.15	0.143	0.13	0.12	0.13	0.08	-0.25	0.07
29 PatchShapeSD[5ha]	0.04	0.19	-0.00	0.46	-0.38	0.17	-0.22	-0.06	-0.21	-0.22	-0.21	-0.20	-0.21	-0.18	0.28	-0.07
30 PatchShapeSD[10ha]	-0.39	0.41	0.22	-0.05	0.14	-0.31	0.60	-0.59	0.50	0.57	0.67	0.59	0.58	0.68	-0.23	-0.60
31 PatchShapeSD[25ha]	0.17	0.02	-0.22	0.35	-0.26	0.32	-0.21	0.07	-0.26	-0.23	-0.13	-0.21	-0.23	-0.10	0.42	0.06
32 PatchPerSD[1ha]	0.12	0.12	-0.07	0.37	-0.29	0.18	-0.31	0.05	-0.30	-0.31	-0.29	-0.29	-0.29	-0.25	0.28	0.05

APPENDIX.--- Continued.

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
33 PatchPerSD[5ha]	0.12	0.13	-0.07	0.41	-0.33	0.21	-0.31	0.04	-0.30	-0.31	-0.29	-0.29	-0.30	-0.26	0.30	0.03
34 PatchPerSD[10ha]	-0.03	0.26	-0.06	0.06	-0.05	0.08	0.09	-0.23	0.03	0.08	0.17	0.10	0.07	0.19	0.14	-0.18
35 PatchPerSD[25ha]	0.60	-0.32	-0.45	0.45	-0.39	0.61	-0.65	0.45	-0.68	-0.66	-0.48	-0.66	-0.68	-0.51	0.63	0.46
36 Richness[1ha]	0.42	-0.47	-0.36	-0.27	0.18	0.28	-0.15	0.38	-0.21	-0.18	0.01	-0.21	-0.22	-0.09	0.12	0.41
37 Richness[5ha]	-0.94	0.74	0.79	-0.21	0.18	-0.84	0.77	-0.81	0.88	0.82	0.45	0.83	0.86	0.55	-0.76	-0.83
38 Richness[10ha]	0.39	-0.01	-0.23	0.52	-0.54	0.50	-0.47	0.17	-0.46	-0.47	-0.36	-0.49	0.51	-0.42	0.52	0.17
39 Richness[25ha]	0.47	-0.15	-0.39	0.37	-0.36	0.55	-0.49	0.28	-0.53	-0.50	-0.33	-0.50	-0.52	-0.35	0.58	0.30
40 Shannon[1ha]	0.21	-0.33	-0.23	-0.35	0.27	0.12	0.05	0.22	-0.00	0.03	0.15	0.01	0.00	0.08	-0.03	0.24
41 Shannon[5ha]	-0.94	-0.75	0.77	-0.23	0.21	-0.84	0.81	-0.84	0.90	0.85	0.52	0.87	0.89	0.62	-0.75	-0.86
42 Shannon[10ha]	0.08	0.29	0.12	0.58	-0.63	0.21	-0.24	-0.18	-0.17	-0.21	-0.24	-0.24	-0.25	-0.29	0.26	-0.19
43 Shannon[25ha]	0.18	0.18	-0.02	0.56	-0.57	0.30	-0.28	-0.07	-0.24	-0.26	-0.28	-0.29	-0.31	-0.27	0.36	-0.09
44 Dominance[1ha]	0.13	-0.21	-0.16	-0.19	0.11	0.12	0.14	0.08	0.09	0.13	0.24	0.09	0.08	0.15	0.02	0.06
45 Dominance[5ha]	-0.83	0.74	0.64	-0.08	0.11	-0.69	0.66	-0.76	0.72	0.69	0.42	0.72	0.74	0.54	-0.55	-0.78
46 Dominance[10ha]	0.79	-0.46	-0.68	0.25	-0.26	0.79	-0.67	0.61	-0.75	-0.70	-0.40	-0.72	-0.75	-0.49	0.73	0.65
47 Dominance[25ha]	0.52	-0.43	-0.67	-0.11	0.21	0.51	-0.36	0.49	-0.52	-0.42	-0.13	-0.37	-0.39	-0.09	0.53	0.54
48 Contagion[1ha]	0.83	-0.73	-0.76	-0.34	0.31	0.59	-0.55	0.75	-0.69	-0.61	-0.24	-0.60	-0.61	-0.31	0.42	0.84

APPENDIX.— Continued.

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
49 Contagion[5ha]	0.00	0.26	0.04	0.43	-0.38	0.14	-0.20	-0.11	-0.17	-0.19	-0.21	-0.17	-0.18	-0.18	0.24	-0.12
50 Contagion[10ha]	0.61	-0.23	-0.45	0.42	-0.44	0.66	-0.59	0.38	-0.62	-0.59	-0.39	-0.62	-0.65	-0.47	0.64	0.40
51 Contagion[25ha]	0.47	-0.25	-0.51	0.19	-0.13	0.54	-0.40	0.33	-0.50	-0.44	-0.20	-0.41	-0.44	-0.20	0.57	0.36
52 JuxtaSD[1ha]	0.33	-0.44	-0.34	-0.40	0.32	0.19	-0.02	0.32	-0.11	-0.06	0.12	-0.7	-0.08	0.05	0.03	0.35
53 JuxtaSD[5ha]	-0.94	0.72	0.76	-0.26	0.24	-0.84	0.81	-0.81	0.90	0.85	0.52	0.87	0.89	0.62	-0.76	-0.83
54 JuxtaSD[10ha]	-0.08	0.35	0.23	0.36	-0.39	-0.01	0.17	-0.44	0.16	0.17	0.23	0.14	0.12	0.16	0.02	-0.44
55 JuxtaSD[25ha]	-0.07	0.16	-0.05	0.04	-0.01	0.04	0.34	-0.35	0.22	0.30	0.48	0.32	0.29	0.47	0.09	-0.33
56 SumEdge[1ha]	0.14	0.05	-0.08	0.41	-0.32	0.20	-0.31	0.07	-0.31	-0.31	-0.29	-0.29	-0.30	-0.25	0.31	0.06
57 SumEdge[5ha]	0.25	0.03	-0.16	0.45	-0.38	0.32	-0.37	0.11	-0.38	-0.38	-0.29	-0.37	-0.38	-0.29	0.40	0.11
58 SumEdge[10ha]	0.35	-0.01	-0.17	0.53	-0.50	0.40	-0.41	0.10	-0.42	-0.41	-0.29	-0.43	-0.44	-0.34	0.44	0.10
59 SumEdge[25ha]	0.31	-0.02	-0.19	0.47	-0.42	0.38	-0.40	0.13	-0.41	-0.41	-0.30	-0.41	-0.42	-0.32	0.45	0.13

APPENDIX.— Continued.

Variable	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
17 Tctb	1.00															
18 Gcltr	-0.39	1.00														
19 Gcrck	0.66	-0.90	1.00													
20 No.Patches[1ha]	0.10	-0.60	0.58	1.00												
21 No.Patches[5ha]	0.34	-0.50	0.51	0.88	1.00											
22 No.Patches[10ha]	-0.23	0.05	-0.16	0.50	0.68	1.00										
23 No.Patches[25ha]	-0.78	0.28	-0.52	0.22	0.17	0.74	1.00									
24 PatchSizeSD[1ha]	-0.15	-0.31	0.03	0.53	0.67	0.71	0.47	1.00								
25 PatchSizeSD[5ha]	-0.30	-0.27	0.05	0.27	0.25	0.39	0.34	0.53	1.00							
26 PatchSizeSD[10ha]	-0.08	-0.14	0.00	0.24	0.40	0.56	0.28	0.58	0.92	1.00						
27 PatchSizeSD[25ha]	-0.29	-0.12	-0.08	0.15	0.16	0.32	0.28	0.44	0.97	0.92	1.00					
28 PatchShapeSD[1ha]	0.13	0.23	-0.08	-0.31	-0.37	-0.43	-0.23	-0.53	-0.96	-0.96	-0.97	1.00				
29 PatchShapeSD[5ha]	-0.21	-0.35	0.14	0.42	0.43	0.49	0.34	0.66	0.97	0.92	0.93	-0.96	1.00			
30 PatchShapeSD[10ha]	0.56	-0.39	0.36	0.32	0.66	0.42	-0.20	0.66	0.38	0.62	0.36	-0.52	0.50	1.00		
31 PatchShapeSD[25ha]	-0.23	-0.10	-0.08	0.35	0.45	0.62	0.42	0.64	0.91	0.96	0.93	-0.96	0.94	0.53	1.00	
32 PatchPerSD[1ha]	-0.30	-0.25	0.04	0.26	0.25	0.39	0.33	0.51	0.99	0.92	0.97	-0.97	0.97	0.37	0.91	1.00

APPENDIX.— Continued.

Variable	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
33 PatchPerSD[5ha]	-0.30	-0.28	0.06	0.32	0.31	0.45	0.37	0.57	0.99	0.92	0.96	-0.96	0.99	0.40	0.92	0.99
34 PatchPerSD[10ha]	0.07	-0.21	0.11	0.43	0.65	0.73	0.31	0.67	0.78	0.94	0.76	-0.86	0.84	0.75	0.91	0.78
35 PatchPerSD[25ha]	-0.67	0.04	-0.35	0.17	0.12	0.51	0.70	0.55	0.85	0.74	0.85	-0.77	0.81	0.10	0.83	0.85
36 Richness[1ha]	-0.21	0.43	-0.42	-0.33	-0.34	-0.11	0.20	-0.28	-0.81	-0.76	-0.81	0.88	-0.82	-0.53	-0.73	-0.82
37 Richness[5ha]	0.85	-0.43	0.74	0.21	0.23	-0.39	-0.84	-0.32	-0.25	-0.17	-0.76	0.12	-0.20	0.30	-0.29	-0.25
38 Richness[10ha]	-0.49	-0.22	-0.06	0.58	0.56	0.78	0.77	0.78	0.73	0.68	0.65	-0.67	0.79	0.28	0.79	0.72
39 Richness[25ha]	-0.52	-0.03	-0.24	0.37	0.42	0.77	0.74	0.73	0.83	0.83	0.80	-0.80	0.85	0.33	0.90	0.83
40 Shannon[1ha]	0.01	0.41	-0.30	-0.31	-0.28	-0.17	0.01	-0.35	-0.92	-0.86	-0.91	0.94	-0.91	-0.44	-0.82	-0.93
41 Shannon[5ha]	0.88	-0.44	0.74	0.22	0.29	-0.32	-0.82	-0.23	-0.19	-0.07	-0.20	0.04	-0.13	0.41	-0.20	-0.18
42 Shannon[10ha]	-0.22	-0.53	0.29	0.79	0.75	0.69	0.53	0.81	0.70	0.65	0.60	-0.68	0.81	0.44	0.74	0.69
43 Shannon[25ha]	-0.28	-0.41	0.16	0.70	0.71	0.74	0.59	0.83	0.74	0.71	0.66	-0.73	0.84	0.46	0.81	0.74
44 Dominance[1ha]	0.09	0.25	-0.17	-0.05	0.04	0.04	0.07	-0.07	-0.86	-0.75	-0.87	0.84	-0.77	-0.20	-0.67	-0.87
45 Dominance[5ha]	0.72	-0.50	0.67	0.29	0.40	-0.08	-0.63	0.07	0.32	0.43	0.30	-0.46	0.37	0.65	0.28	0.32
46 Dominance[10ha]	-0.74	0.28	-0.55	0.14	0.17	0.72	0.95	0.53	0.46	0.44	0.45	-0.38	0.46	-0.05	0.57	0.46
47 Dominance[25ha]	-0.42	0.45	-0.60	-0.27	-0.09	0.47	0.48	0.30	0.68	0.78	0.77	-0.69	0.60	0.23	0.76	0.69
48 Contagion[1ha]	-0.63	0.64	-0.79	-0.60	-0.57	0.11	0.56	-0.10	-0.18	-0.21	-0.17	0.34	-0.30	-0.48	-0.22	-0.19

APPENDIX.— Continued.

Variable	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
49 Contagion[5ha]	-0.18	-0.38	0.18	0.48	0.50	0.53	0.34	0.67	0.96	0.92	0.90	-0.96	0.99	0.52	0.93	0.96
50 Contagion[10ha]	-0.63	0.01	-0.29	0.41	0.41	0.80	0.90	0.70	0.61	0.57	0.56	-0.54	0.65	0.14	0.70	0.60
51 Contagion[25ha]	-0.44	0.15	-0.37	0.14	0.27	0.70	0.63	0.62	0.83	0.90	0.86	-0.84	0.82	0.38	0.93	0.84
52 JuxtaSD[1ha]	-0.08	0.49	-0.41	-0.42	-0.37	-0.17	0.07	-0.35	-0.87	-0.81	-0.85	0.91	-0.88	-0.47	-0.79	-0.88
53 JuxtaSD[5ha]	0.88	-0.40	0.71	0.16	0.23	-0.38	-0.85	-0.30	-0.25	-0.14	-0.27	0.11	-0.20	0.35	-0.27	-0.25
54 JuxtaSD[10ha]	0.15	-0.57	0.38	0.72	0.86	0.66	0.26	0.88	0.51	0.60	0.44	-0.56	0.67	0.76	0.63	0.50
55 JuxtaSD[25ha]	0.29	-0.18	0.10	0.41	0.73	0.68	0.14	0.78	0.45	0.71	0.47	-0.60	0.58	0.91	0.69	0.46
56 SumEdge[1ha]	-0.30	-0.22	0.01	0.25	0.22	0.35	0.30	0.48	0.99	0.91	0.99	-0.97	0.96	0.36	0.92	0.99
57 SumEdge[5ha]	-0.38	-0.24	-0.03	0.35	0.35	0.53	0.49	0.65	0.97	0.91	0.94	-0.94	0.98	0.39	0.94	0.97
58 SumEdge[10ha]	-0.43	-0.30	-0.02	0.48	0.47	0.64	0.62	0.79	0.86	0.79	0.81	-0.81	0.91	0.39	0.87	0.85
59 SumEdge[25ha]	-0.41	-0.22	-0.06	0.40	0.40	0.61	0.56	0.71	0.94	0.89	0.91	-0.91	0.96	0.39	0.94	0.94

APPENDIX.— Continued.

Variable	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
33 PatchPerSD[5ha]	1.00															
34 PatchPerSD[10ha]	0.80	1.00														
35 PatchPerSD[25ha]	0.85	0.61	1.00													
36 Richness[1ha]	-0.81	-0.70	-0.41	1.00												
37 Richness[5ha]	-0.26	-0.08	-0.71	-0.34	1.00											
38 Richness[10ha]	0.77	0.71	0.85	-0.34	-0.56	1.00										
39 Richness[25ha]	0.86	0.80	0.93	-0.44	-0.60	0.94	1.00									
40 Shannon[1ha]	-0.91	-0.72	-0.62	0.97	-0.10	-0.50	-0.60	1.00								
41 Shannon[5ha]	-0.19	0.03	-0.66	-0.40	0.99	-0.50	-0.52	-0.17	1.00							
42 Shannon[10ha]	0.74	0.73	0.68	-0.49	-0.25	0.93	0.82	-0.59	-0.19	1.00						
43 Shannon[25ha]	0.78	0.78	0.76	-0.48	-0.35	0.96	0.89	-0.60	-0.28	0.99	1.00					
44 Dominance[1ha]	-0.83	-0.54	-0.57	0.89	-0.07	-0.31	-0.47	0.94	-0.11	-0.34	-0.35	1.00				
45 Dominance[5ha]	0.32	0.45	-0.21	-0.78	0.81	-0.13	-0.08	-0.61	0.87	0.14	0.08	-0.52	1.00			
46 Dominance[10ha]	0.49	0.44	0.82	0.09	-0.89	0.82	0.84	-0.12	-0.86	0.56	0.66	-0.05	-0.58	1.00		
47 Dominance[25ha]	0.67	0.65	0.75	-0.38	-0.54	0.48	0.73	-0.50	-0.46	0.24	0.37	-0.54	-0.04	0.62	1.00	
48 Contagion[1ha]	-0.20	-0.28	0.22	0.65	-0.77	0.02	0.11	0.50	-0.78	-0.30	-0.22	0.31	-0.82	0.53	0.35	1.00

APPENDIX.— Continued.

Variable	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
49 Contagion[5ha]	0.98	0.87	0.78	-0.83	-0.15	0.80	0.85	-0.90	-0.07	0.83	0.85	-0.76	-0.41	0.44	0.57	-0.33
50 Contagion[10ha]	0.64	0.60	0.86	-0.13	-0.75	0.96	0.93	-0.31	-0.70	0.80	0.86	-0.17	-0.37	0.95	0.55	0.27
51 Contagion[25ha]	0.85	0.83	0.90	-0.50	-0.56	0.80	0.95	-0.63	-0.47	0.63	0.74	-0.54	-0.00	0.76	0.90	0.16
52 JuxtaSD[1ha]	-0.87	-0.71	-0.53	0.98	-0.21	-0.48	-0.55	0.99	-0.27	-0.61	-0.60	0.89	-0.68	-0.04	-0.38	0.62
53 JuxtaSD[5ha]	-0.26	-0.05	-0.71	-0.34	0.99	-0.57	-0.59	-0.10	-0.99	-0.27	-0.36	-0.07	0.83	-0.89	-0.49	-0.75
54 JuxtaSD[10ha]	0.56	0.76	0.43	-0.42	-0.06	0.74	0.64	-0.45	0.03	0.87	0.86	-0.15	0.29	0.36	0.15	-0.38
55 JuxtaSD[25ha]	0.49	0.85	0.34	-0.44	0.01	0.53	0.58	-0.42	0.13	0.59	0.64	-0.16	0.41	0.28	0.43	-0.30
56 SumEdge[1ha]	0.98	0.76	0.85	-0.83	-0.25	0.70	0.82	-0.94	-0.18	0.67	0.72	-0.88	0.32	0.44	0.70	-0.21
57 SumEdge[5ha]	0.98	0.81	0.92	-0.70	-0.40	0.85	0.93	-0.84	-0.32	0.80	0.86	-0.73	0.18	0.62	0.69	-0.12
58 SumEdge[10ha]	0.88	0.76	0.91	-0.51	-0.51	0.95	0.95	-0.67	-0.43	0.91	0.95	-0.51	0.01	0.72	0.56	-0.05
59 SumEdge[25ha]	0.95	0.82	0.93	-0.64	0.45	0.90	0.96	-0.78	-0.38	0.85	0.90	-0.65	0.11	0.68	0.68	-0.08

APPENDIX.— Continued.

Variable	49	50	51	52	53	54	55	56	57	58	59
49 Contagion[5ha]	1.00										
50 Contagion[10ha]	0.64	1.00									
51 Contagion[25ha]	0.81	0.80	1.00								
52 JuxtaSD[1ha]	-0.89	-0.27	-0.55	1.00							
53 JuxtaSD[5ha]	-0.15	-0.75	-0.53	-0.20	1.00						
54 JuxtaSD[10ha]	0.69	0.60	0.51	-0.49	-0.04	1.00					
55 JuxtaSD[25ha]	0.60	0.44	0.62	-0.42	0.06	0.84	1.00				
56 SumEdge[1ha]	0.94	0.58	0.84	-0.88	-0.25	0.48	0.45	1.00			
57 SumEdge[5ha]	0.96	0.76	0.90	-0.79	-0.39	0.62	0.53	0.96	1.00		
58 SumEdge[10ha]	0.89	0.88	0.85	-0.64	-0.51	0.76	0.57	0.84	0.95	1.00	
59 SumEdge[25ha]	0.94	0.83	0.91	-0.74	-0.45	0.67	0.57	0.93	0.99	0.98	1.00