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UNIVERSITY OF OKLAHOMA
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THE EFFECTS OF WOODY PATCHES OF HABITAT ON GRASSLAND
SMALL MAMMALS

A Dissertation
SUBMITTED TO THE GRADUATE FACULTY
in partial fulfillment of the requirements for the
degree of
Doctor of Philosophy

By
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Norman, Oklahoma
2002

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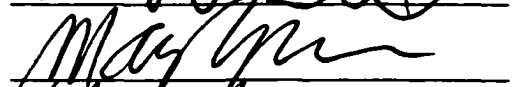
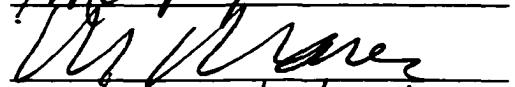
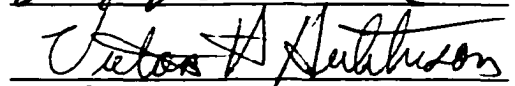
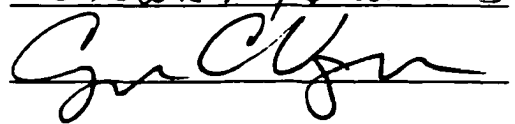
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**THE EFFECTS OF WOODY PATCHES OF HABITAT ON GRASSLAND
SMALL MAMMALS**

**A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY**

BY

PREFACE

This dissertation is presented in three chapters to be submitted for publication to referred journals. Chapters 1 and 3 are formatted for submission to the *Journal of Mammalogy*. Chapter 2 is formatted for the journal *Landscape Ecology*.

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I wish to thank family and friends that have supported me throughout my graduate career.

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ABSTRACT

Habitat modifications (i.e., habitat loss, habitat fragmentation, and species invasion) can affect biological communities. To understand better the influence of habitat modifications on grassland ecosystems, I examined the effects of small introduced woody patches on small mammals inhabiting a grassland. Specifically, I examined: the effects of woody patches on the species richness, species diversity, and total density of grassland small mammals; the role of local (e.g., average grass height) and regional (e.g., distance to mixed-grass prairie) environmental variables in determining abundance of grassland small mammals associated with woody patches; and the effects of edge on small mammals associated with a grassland-woody patch interface. To evaluate the effects of woody patches, I live-trapped a series of sites grouped by treatment (control sites, grassland only; experimental sites, woody patches surrounded by grassland) on Fort Sill Military Reservation in southwestern Oklahoma, primarily during summer months from 1994 to 1997. Total density of small mammals was higher at sites with woody patches than at grassland sites without woody patches, in part because Peromyscus leucopus benefitted the most from woody patches, while numbers of Microtus ochrogaster were lower. Species richness and species diversity did not differ. More animals (all species combined) inhabited sites surrounded by relatively uniform landscapes, which also were farthest from bottomland forest and tallgrass prairie. Numbers and change in abundance of Sigmodon hispidus, the most frequently encountered mammal, did not follow the same pattern as that for all species combined; higher numbers and greater change through time typically occurred at sites with taller grasses located within landscapes having cover types with more complex edges. For P.

leucopus, numbers were higher during two trapping sessions at sites surrounded by relatively uniform landscapes and more distant from bottomland forest and tallgrass prairie; increases over time in its numbers were greater at these sites. Overall, regional environmental variables accounted for more variation in abundance and changes in abundance in small mammals associated with woody patches than did local factors. Edge associated with woody patches varied in its effect on grassland small mammals. Captures of all species combined were more frequent (i.e., a positive effect) within and closer to woody patches than at control sites, in part because S. hispidus, P. leucopus, and Neotoma floridana benefitted from woody patches and/or edge. Numbers of M. ochrogaster were lower (i.e., a negative effect), likely due to interactions with S. hispidus. All species combined, S. hispidus, and M. ochrogaster exhibited ecotonal effects (i.e., unique responses due to presence of edge habitat) that extended at least 10 m but not 25 m into the surrounding grassland, while N. floridana and P. leucopus showed matrix effects (i.e., attribute changes at edge due to different habitats) that ended near the patch edge. Although edge often is discernable to an investigator through structural characteristics of vegetation, my findings suggest that for small mammals it may be more useful to employ a functional description based on attributes of those species, such as abundance. Overall, the addition of woody patches of habitat to grasslands had a significant influence on the small-mammal community. In particular woody-habitat species (e.g., P. leucopus) and habitat generalists (e.g., S. hispidus) benefitted markedly, while grassland species (e.g., M. ochrogaster) were negatively affected.

Running head: Effects of Woody Patches on Small Mammals

HABITAT MODIFICATION: THE EFFECTS OF WOODY PATCHES ON
SMALL MAMMALS OF A FRAGMENTED GRASSLAND

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Habitat modifications (i.e., habitat loss, habitat fragmentation, and species invasion) can affect biological communities. To understand better the influence of habitat modifications on grassland ecosystems, we examined the effects of introduced woody patches on small mammals inhabiting a grassland. We sampled 18 sites grouped by treatment (6 control sites, grassland only; 12 experimental sites, woody patches surrounded by grassland) on Fort Sill Military Reservation in southwestern Oklahoma. Three small-mammal community properties (using mark-recapture techniques), plant composition (based on surveys), and 9 vegetation characteristics (using quadrat sampling) were estimated at all sites. Total density of small mammals was higher at sites with woody patches than at grassland sites without woody patches; species richness and species diversity did not differ. Percent grass cover was lower at sites with woody patches than at sites without; the other 8 vegetation characteristics did not differ. Grassland sites without woody patches had lower plant composition than sites with woody patches, and daily temperature and daily temperature variation were lower within woody patches than in grassland habitat. Sigmodon hispidus, the hispid cotton rat, was the most common small mammal at all sites and gained an advantage from the presence of woody patches in grassland habitat; Microtus ochrogaster, the prairie vole, was captured at sites with woody patches, but only in surrounding grassland; Peromyscus maniculatus, the deer mouse, was common to grassland habitat, but rarely occurred within woody patches; and P. leucopus, the white-footed mouse, was captured in woody patches and surrounding grassland, but was not found at sites without woody patches. Five other species of small mammals were captured in low numbers at our sites. Our

results indicate that woody patches of habitat vary in their effect on the species and community properties of small mammals associated with grasslands. Total density was higher, in part because *P. leucopus* benefitted the most from woody patches, while numbers of *M. ochrogaster* were lower. Modifying grassland habitat with the addition of woody vegetation had a definite influence on the small-mammal community.

Key words: Fort Sill Military Reservation, grassland, habitat modification, Oklahoma, small mammals, species diversity, species richness

Ecological communities are subject to a diverse array of disturbances, both physical and biological, that provide ecological opportunities for species evolution (Whittaker and Levin 1977). Such disturbances accentuate both temporal and spatial heterogeneity, thus having an influence on community properties, including the relative abundance of species (Sousa 1984). North American grasslands are no exception. In the past, large-scale disturbances such as wild fires and grazing by native herbivores inhibited the invasion of woody species and contributed to the evolution of the ecological communities of these grasslands. Concomitantly, woody vegetation often invaded areas where disturbances were less influential (e.g., rocky slopes and riparian zones; Albertson 1937; Anderson 1982; Axelrod 1985; Bragg and Hulbert 1976; Glenn et al. 1992).

During much of the 20th century, grassland management typically included suppression of wild fires (Bragg and Hulbert 1976; Collins 1990; Leach and Givnish

1996). This alteration in the natural disturbance regime, which had been important in developing and maintaining grasslands for centuries, resulted in an increase in forbs and woody species scattered across the landscape (Bragg and Hulbert 1976; Collins and Adams 1983) and the subsequent loss of grassland habitat. In addition, grazing intensities of domestic cattle (Bos taurus), which replaced native bison (Bos bison), often were greater than the prairies could sustain (Weaver and Albertson 1936), thus decreasing the fuel for any fires that did occur. This further allowed woody species to become established at sites where historically they had been excluded (Bragg and Hulbert 1976). This type of vegetative invasion, as well as recent trends in land use, including road construction, urbanization, and agriculture, have modified and fragmented native grasslands, leading to a decline in areal coverage and biological diversity (Bragg and Hulbert 1976; Brown and Lomolino 1998; Leach and Givnish 1996; Nupp and Swihart 1998; Primack 1995; Samson and Knopf 1994).

Hobbs and Mooney (1998) emphasized that factors such as habitat loss, habitat fragmentation, and species invasion contributed to population declines (a precursor to extinction) for a number of plant and animal species present in California and Western Australia. These findings suggest that as habitat modification continues in North American grasslands, ecological communities are at risk of degradation. The purpose of our study was to examine the effects of habitat modification in a grassland ecosystem.

Like other fragmented ecosystems (Saunders et al. 1991), grasslands that do remain often comprise a mosaic of scattered remnants across the landscape. These remnants are separated by a variety of other habitats (e.g., agricultural and urban) that

may be unsuitable for native-grassland species (Leach and Givnish 1996; Pogue 1998). Even within such grasslands, there may be habitat modification (i.e., habitat loss, habitat fragmentation, and species invasion) on a smaller, more local scale. Several studies have evaluated the influence of habitat modification on native species of grassland birds (Herkert 1995; Igl and Johnson 1997; Johnson and Schwartz 1993; Klute et al. 1997), but the phenomenon has been less studied for grassland mammals. We examined small-mammal communities in a locally modified grassland. In our study, local modification refers to the presence of isolated woody patches within otherwise continuous grassland habitat. We address the null hypothesis that, within a grassland, no differences in small-mammal community properties will be evident in remnants that are locally modified versus remnants of continuous grassland.

MATERIALS AND METHODS

Study site.—We conducted our study on Fort Sill Military Reservation (FSMR) in southwestern Oklahoma. FSMR is a 38,300-ha installation situated within Comanche County (Fig. 1) near Lawton, Oklahoma. Mean precipitation for this region of the state is highest in May, while July and August are the hottest months (Johnson et al. 1990). This portion of Oklahoma includes a transition zone between mixed-grass prairie and uplands dominated by post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*). FSMR lies south of the Wichita Mountains Wildlife Refuge, extends eastward, and encompasses a variety of habitats. All sampling was conducted on the East Range of FSMR, where upland plains prevail. The East Range is approximately 14,000 ha and

dominated by mixed-grass prairie (42.0%), rangeland (25.1%), and tallgrass prairie (17.0%), with woody vegetation comprising 5.5%.

Eighteen sampling sites (6 control and 12 experimental) were established on the East Range. Control sites were located in remnants of continuous grassland, and experimental sites consisted of grassland surrounding a woody patch of habitat. One-half of the sites (3 control and 6 experimental) were located in the central portion of the East Range, with the others being in the northern portion (Fig. 1). Central and northern sites were separated by a distance of 8–10 km. Grassland associated with all sampling sites consisted of typical bluestem prairie, as described by Johnson et al. (1990), characterized by little bluestem (Schizachyrium scoparium), Scribner dichanthelium (Dichanthelium oligosanthos), big bluestem (Andropogon gerardii), and Indian grass (Sorghastrum nutans).

At experimental sites, introduced woody patches—encircled by plowed firebreaks—consisted of ornamental and native vegetation. Russian olives (Elaeagnus angustifolia) were planted by FSMR fish-and-wildlife personnel in the early to mid-1970s and were most common on the patches; naturally occurring species such as smooth sumac (Rhus glabra), black locust (Robinia pseudoacacia), Chickasaw plum (Prunus angustifolia), and Osage-orange (Maclura pomifera) typically were present but in lower numbers. Grasses and forbs were common in the woody patches. Experimental sites were selected based on criteria relating to presence of a woody patch of habitat, size of the woody patch, and isolation of the woody patch. The areal coverage of woody patches used in our study averaged 0.18 ha (range 0.15–0.26 ha).

The distance between any 1 of the woody patches and the nearest of the other 11 patches averaged 364 m (range 178–622 m). Other planted woody patches existed but were never closer than 107 m to patches used in our study.

Small-mammal assessment.—Sherman traps (7.6 by 8.9 by 22.9 cm) were used to assess the small-mammal communities. Sampling stations were established on a 12 by 12 grid with 10-m spacing. One trap was placed at each sampling station for a total of 144 traps at each site and an areal coverage of 1.21 ha. Control sites were established in grassland near (i.e. within 500 m) experimental sites, but were not closely associated with woody patches or any other type of habitat (e.g., riparian and agricultural). Sampling grids at experimental sites were centered on woody patches of habitat and extended into the surrounding grassland. None of the grids at any of the sites overlapped with grids from other sites.

We sampled small mammals at each site for 7 consecutive nights from 24 May through 18 June 1996 for a total of 18,144 trap-nights. Traps were baited with rolled oats in the evening and checked the following morning. Because of high temperatures throughout much of the sampling period, traps were set as late in the day, and checked as early in the morning as possible, contingent on the amount of daylight. Captured specimens were marked (i.e., ear-tagged with metal tags, toe-clipped, or both) and released. Due to high temperatures, some mortality did occur. When practical, these specimens were prepared and deposited in the Sam Noble Oklahoma Museum of Natural History.

Vegetation assessment.—We conducted vegetation sampling (i.e., general plant surveys and quadrat sampling) to establish the degree of similarity in vegetative characteristics within and among sites. All vegetation sampling was done in conjunction with small-mammal sampling to reveal site characteristics that may have directly contributed to differences in small-mammal data among sites. General plant surveys were completed at each sampling site on 23 and 24 June 1996. Surveys were conducted by walking through each study site and recording the relative abundance of each taxonomic group listed in Appendix I. We then tabulated presence-absence of each taxon for data analysis.

Quadrat sampling was conducted to examine vegetation characteristics of each site, including: average height of grasses and forbs; litter depth; percent coverage of grasses, forbs, litter, bareground, and sedges and rushes; and a relative estimate of vegetation biomass based on visual-obstruction measurements (Robel et al. 1970). We conducted quadrat sampling from 15–24 June 1996. For each of the 18 sites, vegetation data were collected at 20 sampling stations independent of the 144 small-mammal sampling stations. These 20 stations were uniformly spaced throughout each sampling site. Uniform sampling was used to assure that vegetative characteristics were sampled throughout the study site. At each sampling station, a 0.5 by 0.5-m quadrat was randomly dropped, and measurements on the vegetation within the quadrat were recorded.

Microclimate assessment.—To characterize microclimate at our research sites, we collected temperature data at 4 of the 12 experimental sites from 17 May through 26

September 1997. Two microclimate-sampling stations were established at each of the 4 sites, 1 station within a woody patch and the other positioned outside of the patch.

Stations within a patch were located near the center of the wooded microhabitat. Those located outside of the patches were placed in grassland microhabitat 50 m from the outside edge of the patch. Temperatures were recorded every 30 min with external-temperature data-loggers (Onset Computer Corporation, Pocasset, Massachusetts), and the stored data were downloaded every few weeks. These data were used to calculate a mean daily temperature and daily standard deviation for each day at each sampling station. On any particular day, if data from either the grassland or woody patch of a site were not at least 90% complete, data from all sites were excluded from analysis.

Data analysis.—We used a 2-way ANOVA (Sokal and Rohlf 1995; Zar 1999) to examine the effects of 2 factors, treatment (control or experimental) versus location (central or northern), and their interaction. Tests were used to compare the means of density for each of 9 species of small mammals captured, means for 9 vegetation characteristics measured, and means for 3 small-mammal properties: total density, species richness, and species diversity. The Dunn-Šidák method (Sokal and Rohlf 1995) for experimentwise error rate was used to adjust P-values.

The Jaccard coefficient of community similarity (Brower et al. 1998) was used to estimate the degree of similarity, based on the taxonomic composition of plants, between all possible pairings of sites. Each coefficient was converted to a dissimilarity value by subtracting it from 1 (possible range = 0–1, 0 = sites having identical taxonomic composition, 1 = sites having no taxa in common), and values were placed in

a matrix. We then constructed a 2nd hypothesis matrix comprised of only 0's and 1's based on predicted dissimilarity. 0's were used for all within-group pairings (i.e., we predicted relatively low values for control versus control sites and experimental versus experimental sites) and 1's for all among-group pairings (i.e., control versus experimental sites). We used the Mantel test to calculate the association between the 2 matrices and determined the significance ($P \leq 0.05$) using 100,000 Monte Carlo permutations (Sokal and Rohlf 1995).

We used Wilcoxon's signed-rank test, a nonparametric randomized-blocks design (Sokal and Rohlf 1995; Zar 1999), to examine temperature data. This method allowed paired comparisons at each of the four sites to test for significant differences of mean daily temperature and of daily standard deviation within woody patches versus those in grassland habitat. We analyzed temperature data at the 4 sites separately. BIOMstat (Rohlf and Slice 1996), SigmaStat (Fox et al. 1995), and SYSTAT (SPSS 2000) computer programs were used in data analyses.

RESULTS

We captured 736 small mammals at the 18 sites. The most abundant species found at all sites, at control sites, and at experimental sites was Sigmodon hispidus, the hispid cotton rat, followed by (in order of abundance at all sites): Peromyscus maniculatus, deer mouse; Microtus ochrogaster, prairie vole; P. leucopus, white-footed mouse; Chaetodipus hispidus, hispid pocket mouse; Reithrodontomys fulvescens, fulvous harvest mouse; Neotoma floridana, eastern woodrat; Spermophilus tridecemlineatus, thirteen-lined ground squirrel; and R. montanus, plains harvest mouse

(Table 1). The following small-mammal community properties for all sites are summarized in Table 2: density (individuals/ha) of each species, total density, species richness (no. species), and species diversity (H').

The number of taxa in the plant communities averaged 21.83 ± 2.14 SD (range 18–24, $\underline{n} = 6$) at control sites and 28.17 ± 1.85 (range 25–31, $\underline{n} = 12$) at experimental sites. Jaccard coefficients of similarity between any 2 plant communities averaged 0.75 ± 0.11 (range 0.58–0.96, $\underline{n} = 15$) within control sites, 0.80 ± 0.06 (range 0.66–0.97, $\underline{n} = 66$) within experimental sites, and 0.66 ± 0.06 (range 0.53–0.82, $\underline{n} = 72$) among control versus experimental sites. The matrices of observed and predicted dissimilarity values were significantly correlated (matrix correlation = 0.685, $\underline{P} \leq 0.05$, Mantel test), indicating that plant communities differed more among sites of different treatment than they did among sites of similar treatment.

Table 3 lists vegetative characteristics measured in quadrat sampling and the results of 2-way ANOVA for the equality of their means. For characteristics 1–3, values of 0.0 were excluded from data analysis because the characteristics are more a measure of habitat quality than of presence or absence, which is better revealed in characteristics 4–9. Of the 9 characteristics, only percent grass cover showed a significant difference between sites with woody patches and those without. Two characteristics showed significant differences for location, and none exhibited a significant interaction effect for treatment and location.

Small-mammal properties for all sites ($\underline{n} = 18$), control sites ($\underline{n} = 6$), and experimental sites ($\underline{n} = 12$), respectively, averaged: total density, 33.78 ± 15.51 , $22.98 \pm$

7.21, and 39.18 ± 15.89 individuals/ha; species richness, 4.28 ± 1.23 , 3.50 ± 0.84 , and 4.67 ± 1.23 species; and species diversity, 0.404 ± 0.130 , 0.392 ± 0.076 , and 0.410 ± 0.153 . A 2-way ANOVA revealed significant effects for total density due to treatment and location, and for species diversity due to the interaction of treatment and location (Table 4).

Mean daily temperature averaged 23.24 to 24.06°C ($\bar{n} = 4$) and 25.89 to 28.57°C ($\bar{n} = 4$) in woody patches and grassland habitat, respectively. Daily standard deviation averaged 2.86 to 3.77 ($\bar{n} = 4$) and 5.72 to 8.89 ($\bar{n} = 4$) for woody patches and grassland habitat, respectively. In all cases, Wilcoxon's signed-rank test indicated that mean daily temperature and daily SD in woody patches was significantly lower than that in surrounding grassland (Table 5).

DISCUSSION

Habitat modifications (i.e., habitat loss, habitat fragmentation, and species invasion) may lead to isolated populations of organisms. These isolated populations are in turn subject to local extinctions and are of concern to conservation biologists (Hobbs and Mooney 1998; Saunders et al. 1991; Wilcox and Murphy 1985). Saunders et al. (1991) reviewed the effects of habitat modification, including changes in microclimate and alterations of processes concerning nutrient cycling, wind damage, evapotranspiration, erosion, and run-off. Andrén (1994) explained that biological diversity (number of species) should increase due to habitat fragmentation and habitat loss if examined across the entire landscape. Based on these findings, and given that the adding of woody patches of habitat in a grassland represents a form of habitat

modification, we would expect the introduced woody patches to have similar effects on small-mammal species associated with grasslands at FSMR.

At FSMR, between-site comparisons revealed, not surprisingly, that sites differing in treatment (i.e., sites with a woody patch versus purely grassland sites) shared a lower percentage of plant species than sites subject to the same treatment. This difference is accounted for by the addition of woody species and other invasive species associated with woody patches to the grassland habitat. This addition of non-native species is similar to expectations for modified ecosystems described by Saunders et al. (1991) and Andrén (1994). Of the vegetation characteristics measured during quadrat sampling, only the means for percent grass cover differed significantly between control and experimental sites. A lower mean value on experimental sites resulted from areal loss of native grassland vegetation as introduced and invasive species became established.

The presence of woody patches in grassland habitat resulted in a higher total density of small mammals than grassland sites without woody patches. This may be attributed to increased habitat heterogeneity and resource availability brought on by the presence of woody patches at experimental sites. Changes in habitat heterogeneity may have significant effects on population dynamics of small mammals (e.g., Adler 1987; Anderson 1970; Birney et al. 1976; Cockburn and Lidicker 1983; Wilcox and Murphy 1985). Species richness and species diversity were not significantly affected by the presence of woody patches, however, our data indicate that small-mammal species vary in their response to woody patches of habitat.

We expected to capture more species of small mammals at locally modified sites than in continuous remnants of grassland (Andrén 1994). We did not find a statistically significant difference in species richness due to treatment. However, N. floridana, P. leucopus, and S. tridecemlineatus were encountered at locally modified sites only, while all other species were captured at both experimental and control sites. Also, the density of M. ochrogaster was lower on sites with woody patches relative to those without, while the density of S. hispidus was higher (but not significantly so). Further evidence of habitat modification, as predicted by Saunders et al. (1991), was seen in microclimate changes as mean daily temperatures and daily SD of temperatures were lower within woody patches of habitat. Woody patches may serve as more predictable, less stressful habitat than grassland, attracting opportunistic small-mammal species or those common to woody habitat and serving as a buffer to environmental conditions (e.g. high ambient temperature) experienced in surrounding grassland. This may account, in part, for higher density estimates of small mammals at sites associated with woody patches.

Sigmodon hispidus occurs throughout Oklahoma (Caire et al. 1989), is common to the Wichita Mountains Wildlife Refuge (Glass and Halloran 1961) adjacent to FSMR, and is found in a variety of habitats, especially those associated with dense grass cover. It often frequents low-growing woody habitat (Caire et al. 1989; Cameron and Spencer 1981), but S. hispidus typically does not frequent dense, woody vegetation (Goertz 1964). Sigmodon hispidus was captured at all but 3 of our 18 sites (4 of 6 control sites and 11 of 12 experimental sites). At experimental sites, we found it both within woody patches of habitat and in surrounding grassland. Sigmodon hispidus

exhibits population declines due to extreme weather conditions, including summer drought (Langley and Shure 1988). Eifler and Slade (1999) found that S. hispidus was negatively affected by high summer temperatures. As summer temperatures increase, growth rates decrease in adults. They also reported that daily activity (e.g. foraging) may decrease as summer temperatures increase. At FSMR, S. hispidus was 3 times more common at experimental than control sites and clearly benefitted from the presence of woody patches, possibly due to a buffering effect against high summer temperatures.

Microtus ochrogaster was the 3rd most common small mammal at all our sites. It was the 2nd most common at control sites (6 of 6 sites) but only 6th at experimental sites (6 of 12 sites). At experimental sites, we found it only in surrounding grassland. The range of M. ochrogaster extends south into Oklahoma (Blair 1939; Caire et al. 1989; Smith 1992; Stangl et al. 1992) including Comanche County (Choate 1989; Stancampiano 1999; Stanka 1997). Microtus ochrogaster has an affinity with grassland habitats, and its presence may be restricted by minimum requirements of cover for building runways (Birney et al. 1976; Caire et al. 1989; Kaufman and Fleharty 1974; Stalling 1990). Considerable research has been done on interspecific interactions involving M. ochrogaster. Microtus ochrogaster competes with S. hispidus for space but not food (Fleharty and Olson 1969), and the 2 often coexist due to habitat partitioning (Stokes 1995). However, increased interactions with S. hispidus will lead to declines in M. ochrogaster populations (Foster and Gaines 1991; Glass and Slade 1980; Prochaska and Slade 1981; Slade et al. 1997; Terman 1974, 1978). Microtus

ochrogaster and S. hispidus overlap in habitat requirements and, since both prefer dense vegetation cover, some minimum threshold must be met before residents of either species become established at a site (Birney et al. 1976; Fleharty and Mares 1973; Foster and Gaines 1991; Goertz 1964).

Our measurements of vegetation characteristics indicate that only percent grass cover differed between treatments. Lower densities of M. ochrogaster at experimental sites may be attributed to the replacement of grassland habitat with woody patches. However, it appears that interactions with S. hispidus, which were 3 times more common at experimental sites, also contributed to lower densities of M. ochrogaster at sites where woody patches of habitat were found. Martin (1956) reported declines in daytime summer-activity for M. ochrogaster, which may be attributable to high daytime temperatures (Madison 1985). At FSMR, M. ochrogaster did not utilize woody patches to the same degree as S. hispidus and, apparently, used other adaptive mechanisms (Wunder 1985) to deal with high summer-temperatures in grassland habitat.

Peromyscus maniculatus was the 2nd most common small mammal at all our sites, being 3rd at control sites (5 of 6 sites) and 2nd at experimental sites (9 of 12 sites). At experimental sites, it was common in surrounding grassland and rare in woody patches. It is found throughout most of Oklahoma, occurring in a wide variety of habitats, and is especially common in grasslands with moderate basal cover (Caire et al. 1989; Clark and Kaufman 1991; Clark et al. 1989; Hansen and Fleharty 1974; Hays 1958; Kaufman and Fleharty 1974; Kaufman et al. 1988; Martin 1960; Schnell et al. 1980). Kaufman and Fleharty (1974) found some overlap in habitat preference with S.

hispidus. Microtus ochrogaster and P. maniculatus are strong competitors, with P. maniculatus showing negative effects from the interaction (Abramsky et al. 1979). Whitaker (1967) found that P. maniculatus and P. leucopus exhibited both ecological and competitive exclusion. Cameron and Spencer (1981) reported that S. hispidus competes and interacts with several small-mammal species; however, they made no mention of P. maniculatus.

Our results indicate that P. maniculatus was most common on sites when densities of M. ochrogaster and S. hispidus were relatively low. Peromyscus maniculatus is most active at intermediate temperatures (Falls 1968), but due to habitat preferences, would not have benefitted from the temperature-buffering effects of woody patches at FSMR. Instead, they may have relied on adaptive mechanisms such as reduced daytime activity (Falls 1968), increased evaporative water loss, and onset of torpor (Hill 1983; MacMillen 1983; MacMillen and Garland 1989) to avoid heat stress from high summer temperatures in grassland habitat.

Peromyscus leucopus was the 4th most frequently captured small mammal on all of our sites at FSMR. It did not occur at any of our control sites, but was present at 11 of 12 experimental sites, where it was the 3rd most common species. We usually found P. leucopus in the woody patches, but also in the surrounding grassland as well. It occurs throughout Oklahoma and is most commonly associated with brushy or wooded habitat (Barry and Francq 1980; Caire et al. 1989; Hays 1958; Kaufman et al. 1985; Kaufman et al. 1983; Lackey et al. 1985). However, Clark et al. (1987) found 9.1% of all small mammals captured on transects through a Kansas prairie to be P. leucopus.

They often captured it in lowland sites associated with ravines that may have served as dispersal corridors. Based on recaptures, they felt that P. leucopus persisted in prairie habitat. Schnell et al. (1980) found P. leucopus in grassland closely associated with woody habitat in north-central Oklahoma.

Peromyscus leucopus, like P. maniculatus, elevates evaporative water loss and may rely on torpor during periods of high daytime temperatures (MacMillen 1983). However, unlike the latter, P. leucopus shows a preference for woody habitats and most likely benefitted from the temperature-buffering characteristic of woody patches. Our results indicate that P. leucopus gained a strong advantage from the presence of woody patches in grassland habitat. They likely spend most of their time within the woody vegetation of a patch, with only infrequent treks into the surrounding grassland.

The remaining 5 species of small mammals were present in low numbers. Neotoma floridana is a species that most likely benefitted from the woody patches of habitat (see Caire et al. 1989), but all others do not typically favor woody vegetation. We are unable to draw conclusions about the effects of woody patches of habitat on these species.

Woody patches of habitat were established at FSMR to enhance game species such as white-tailed deer (Odocoileus virginianus), northern bobwhites (Colinus virginianus), and wild turkeys (Meleagris gallopavo). These patches increase the complexity of habitat for wildlife, including small mammals. They also represent habitat modifications, equivalent to the invasion of woody species, loss of grassland habitat, and to an extent, fragmentation of grassland habitat. Total density was higher,

in part because P. leucopus benefitted the most from the presence of woody patches in grassland, while numbers of M. ochrogaster were lower. In accordance with Saunders et al. (1991) and Andrén (1994), we found a definite effect due to the presence of woody patches; however, our results indicate that effects of such patches varied, depending on the community property and small-mammal species.

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LITERATURE CITED

- ABRAMSKY, Z., M. I. DYER, AND P. D. HARRISON. 1979. Competition among small mammals in experimentally perturbed areas of the shortgrass prairie. *Ecology* 60:530–536.
- ADLER, G. H. 1987. Influence of habitat structure on demography of two rodent species in eastern Massachusetts. *Canadian Journal of Zoology* 65:903–911.

HANER AND SCHNELL—EFFECTS OF WOODY PATCHES ON SMALL MAMMALS

- ALBERTSON, F. W. 1937. Ecology of mixed prairie in west central Kansas. *Ecological Monographs* 7:481–547.
- ANDERSON, P. K. 1970. Ecological structure and gene flow in small mammals. *Symposium of the Zoological Society of London* 26:299–325.
- ANDERSON, R. C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands: an end paper. Pp. 297–308 in *Grasses and grasslands: systematics and ecology* (J. R. Estes, R. J. Tyrl, and J. N. Brunken, eds.). The University of Oklahoma Press, Norman, Oklahoma.
- ANDRÉN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366.
- AXELROD, D. I. 1985. Rise of the grassland biome, central North America. *The Botanical Review* 51:163–201.
- BARRY, R. E., JR., AND E. N. FRANCO. 1980. Orientation to landmarks within the preferred habitat by Peromyscus leucopus. *Journal of Mammalogy* 61:292–303.
- BIRNEY, E. C., W. E. GRANT, AND D. D. BAIRD. 1976. Importance of vegetative cover to cycles of Microtus populations. *Ecology* 57:1043–1051.
- BLAIR, W. F. 1939. Faunal relationships and geographic distribution of mammals in Oklahoma. *The American Midland Naturalist* 22:85–133.
- BRAGG, T. B., AND L. C. HULBERT. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *Journal of Range Management* 29:19–24.

HANER AND SCHNELL—EFFECTS OF WOODY PATCHES ON SMALL MAMMALS

- BROWER, J. E., J. H. ZAR, AND C. N. VON ENDE. 1998. Field and laboratory methods for general ecology. 4th ed. WCB/McGraw-Hill, Boston, Massachusetts.
- BROWN, J. H., AND M. V. LOMOLINO. 1998. Biogeography. 2nd ed. Sinauer Associates, Sunderland, Massachusetts.
- CAIRE, W., J. D. TYLER, B. P. GLASS, AND M. A. MARES. 1989. Mammals of Oklahoma. The University of Oklahoma Press, Norman, Oklahoma.
- CAMERON, G. N., AND S. R. SPENCER. 1981. Sigmodon hispidus. Mammalian Species 158:1–9.
- CHOATE, L. L. 1989. Natural history of a relictual population of the prairie vole, Microtus ochrogaster, in southwestern Oklahoma. Occasional Papers, The Museum, Texas Tech University 129:1–20.
- CLARK, B. K., AND D. W. KAUFMAN. 1991. Effects of plant litter on foraging and nesting behavior of prairie rodents. Journal of Mammalogy 72:502–512.
- CLARK, B. K., D. W. KAUFMAN, E. J. FINCK, AND G. A. KAUFMAN. 1989. Small mammals in tall-grass prairie: patterns associated with grazing and burning. The Prairie Naturalist 21:177–184.
- CLARK, B. K., D. W. KAUFMAN, G. A. KAUFMAN, AND E. J. FINCK. 1987. Use of tallgrass prairie by Peromyscus leucopus. Journal of Mammalogy 68:158–160.
- COCKBURN, A., AND W. Z. LIDICKER, JR. 1983. Microhabitat heterogeneity and population ecology of an herbivorous rodent, Microtus californicus. Oecologia 59:167–177.

HANER AND SCHNELL—EFFECTS OF WOODY PATCHES ON SMALL MAMMALS

- COLLINS, S. L. 1990. Introduction: fire as a natural disturbance in tallgrass prairie ecosystems. Pp. 3–7 in Fire in North American tallgrass prairies (S. L. Collins and L. L. Wallace, eds.). The University of Oklahoma Press, Norman, Oklahoma.
- COLLINS, S. L., AND D. E. ADAMS. 1983. Succession in grasslands: thirty-two years of change in a central Oklahoma tallgrass prairie. *Vegetatio* 51:181–190.
- EIFLER, M. A., AND N. A. SLADE. 1999. Effect of weather on individual growth rates in cotton rats, Sigmodon hispidus. *Journal of Mammalogy* 80:1277–1287.
- FALLS, J. B. 1968. Activity. Pp. 543–570 in Biology of Peromyscus (Rodentia) (J. A. King, ed.). Special Publication, The American Society of Mammalogists 2:1–593.
- FLEHARTY, E. D., AND M. A. MARES. 1973. Habitat preference and spatial relations of Sigmodon hispidus on a remnant prairie in west-central Kansas. *The Southwestern Naturalist* 18:21–29.
- FLEHARTY, E. D., AND L. E. OLSON. 1969. Summer food habits of Microtus ochrogaster and Sigmodon hispidus. *Journal of Mammalogy* 50:475–486.
- FOSTER, J., AND M. S. GAINES. 1991. The effects of a successional habitat mosaic on a small mammal community. *Ecology* 72:1358–1373.
- FOX, E., K. SHOTTON, AND C. ULRICH. 1995. SigmaStat user's manual. Jandel Corporation, San Rafael, California.
- GLASS, B. P., AND A. F. HALLORAN. 1961. The small mammals of the Wichita Mountains Wildlife Refuge, Oklahoma. *Journal of Mammalogy* 42:234–239.

HANER AND SCHNELL—EFFECTS OF WOODY PATCHES ON SMALL MAMMALS

- GLASS, G. E., AND N. A. SLADE. 1980. The effect of Sigmodon hispidus on spatial and temporal activity of Microtus ochrogaster: evidence for competition. *Ecology* 61:358–370.
- GLENN, S. M., S. L. COLLINS, AND D. J. GIBSON. 1992. Disturbances in tallgrass prairie: local and regional effects on community heterogeneity. *Landscape Ecology* 7:243–251.
- GOERTZ, J. W. 1964. The influence of habitat quality upon density of cotton rat populations. *Ecological Monographs* 34:359–381.
- HANSEN, C. M., AND E. D. FLEHARTY. 1974. Structural ecological parameters of a population of Peromyscus maniculatus in west-central Kansas. *The Southwestern Naturalist* 19:293–303.
- HAYS, H. A. 1958. The distribution and movement of small mammals in central Oklahoma. *Journal of Mammalogy* 39:235–244.
- HERKERT, J. R. 1995. An analysis of midwestern breeding bird population trends: 1966–1993. *The American Midland Naturalist* 134:41–50.
- HILL, R. W. 1983. Thermal physiology and energetics of Peromyscus; ontogeny, body temperature, metabolism, insulation, and microclimatology. *Journal of Mammalogy* 64:19–37.
- HOBBS, R. J., AND H. A. MOONEY. 1998. Broadening the extinction debate: population deletions and additions in California and western Australia. *Conservation Biology* 12:271–283.

- IGL, L. D., AND D. H. JOHNSON. 1997. Changes in breeding bird populations in North Dakota: 1967 to 1992–93. *The Auk* 114:74–92.
- JOHNSON, D. H., AND M. D. SCHWARTZ. 1993. The conservation reserve program and grassland birds. *Conservation Biology* 7:934–937.
- 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 U. S. Army Construction Engineering Research Laboratory, Champaign, Illinois. 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* 18:443–452.
- KAUFMAN, D. W., M. E. PEAK, AND G. A. KAUFMAN. 1985. Peromyscus leucopus in riparian woodlands: use of trees and shrubs. *Journal of Mammalogy* 66:139–143.
- KAUFMAN, D. W., 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.
- KAUFMAN, G. A., D. W. KAUFMAN, AND E. J. FINCK. 1988. Influence of fire and topography on habitat selection by Peromyscus maniculatus and Reithrodontomys megalotis in ungrazed tallgrass prairie. *Journal of Mammalogy* 69:342–352.

- KLUTE, D. S., R. J. ROBEL, AND K. E. KEMP. 1997. Will conversion of conservation reserve program (CRP) lands to pasture be detrimental for grassland birds in Kansas? *The American Midland Naturalist* 137:206–212.
- LACKEY, J. A., D. G. HUCKABY, AND B. G. ORMISTON. 1985. Peromyscus leucopus. *Mammalian Species* 247:1–10.
- LANGLEY, A. K., JR., AND D. J. SHURE. 1988. The impact of climate extremes on cotton rat (Sigmodon hispidus) populations. *The American Midland Naturalist* 120:136–143.
- LEACH, M. K., AND T. J. GIVNISH. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273:1555–1558.
- MACMILLEN, R. E. 1983. Water regulation in Peromyscus. *Journal of Mammalogy* 64:38–47.
- MACMILLEN, R. E., AND T. GARLAND, JR. 1989. Adaptive physiology. Pp. 143–168 in *Advances in the study of Peromyscus (Rodentia)* (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock, Texas.
- MADISON, D. M. 1985. Activity rhythms and spacing. Pp. 373–419 in *Biology of New World Microtus* (R. H. Tamarin, ed.). Special Publication, The American Society of Mammalogists 8:1–893.
- MARTIN, E. P. 1956. A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas. University of Kansas Publications, Museum of Natural History 8:361–416.

HANER AND SCHNELL—EFFECTS OF WOODY PATCHES ON SMALL MAMMALS

- MARTIN, E. P. 1960. Distribution of native mammals among the communities of the mixed prairie. Fort Hays Studies (n.s.), Science Series 1:1–26.
- NUPP, T. E., AND R. K. SWIHART. 1998. Effects of forest fragmentation on population attributes of white-footed mice and eastern chipmunks. Journal of Mammalogy 79:1234–1243.
- 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.
- PRIMACK, R. B. 1995. A primer of conservation biology. Sinauer Associates, Sunderland, Massachusetts.
- PROCHASKA, M. L., AND N. A. SLADE. 1981. The effect of Sigmodon hispidus on summer diel activity patterns of Microtus ochrogaster in Kansas. Transactions of the Kansas Academy of Sciences 84:134–138.
- ROBEL, R. J., J. N. BRIGGS, A. D. DAYTON, AND L. C. HULBERT. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 33:295–297.
- ROHLF, F. J., AND D. E. SLICE. 1996. BIOMstat for Windows. Exeter Software, Setauket, New York.
- SAMSON, F., AND F. KNOPF. 1994. Prairie conservation in North America. BioScience 44:418–421.
- SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18–32.

HANER AND SCHNELL—EFFECTS OF WOODY PATCHES ON SMALL MAMMALS

- SCHNELL, G. D., R. D. OWEN, R. K. CHESSER, AND P. G. RISSE. 1980. Populations of small mammals in north-central Oklahoma. *The Southwestern Naturalist* 25:67–80.
- SLADE, N. A., L. A. RUSSELL, AND T. J. DOONAN. 1997. The impact of supplemental food on movements of prairie voles (Microtus ochrogaster). *Journal of Mammalogy* 78:1149–1155.
- SMITH, K. S. 1992. The prairie vole, Microtus ochrogaster, in Caddo County, Oklahoma. *The Texas Journal of Science* 44:116–117.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. W. H. Freeman and Company, New York, New York.
- SOUSA, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353–391.
- SPSS INC. 2000. *SYSTAT for windows*. Version 10. SPSS Inc., Chicago, Illinois.
- STALLING, D. T. 1990. Microtus ochrogaster. *Mammalian Species* 355:1–9.
- STANCAMPIANO, A. J. 1999. Environmental constraints regulating the distribution and abundance of small mammals. Ph.D. dissertation, University of Oklahoma, Norman.
- STANGL, F. B., JR., W. W. DALQUEST, AND R. J. BAKER. 1992. Mammals of southwestern Oklahoma. *Occasional Papers, The Museum, Texas Tech University* 151:1–47.

- STANKA, L. N. 1997. Factors influencing small-mammal distributions in a native grassland containing introduced woody-vegetation patches. M.S. thesis, University of Oklahoma, Norman.
- STOKES, M. K. 1995. Selection of refuge sites by sympatric Microtus ochrogaster and Sigmodon hispidus. *Journal of Mammalogy* 76:83–87.
- TERMAN, M. R. 1974. Behavioral interactions between Microtus and Sigmodon: a model for competitive exclusion. *Journal of Mammalogy* 55:705–719.
- TERMAN, M. R. 1978. Population dynamics of Microtus and Sigmodon in central Kansas. *Transactions of the Kansas Academy of Science* 81:337–351.
- WEAVER, J. E., AND F. W. ALBERTSON. 1936. Effects of the great drought on the prairies of Iowa, Nebraska, and Kansas. *Ecology* 17:567–639.
- WHITAKER, J. O., JR. 1967. Habitat relationships of four species of mice in Vigo County, Indiana. *Ecology* 48:867–872.
- WHITTAKER, R. H., AND S. A. LEVIN. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* 12:117–139.
- WILCOX, B. A., AND D. D. MURPHY. 1985. Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist* 125:879–887.
- WUNDER, B. A. 1985. Energetics and thermoregulation. Pp. 812–844 in *Biology of New World Microtus* (R. H. Tamarin, ed.). Special Publication, The American Society of Mammalogists 8:1–893.
- ZAR, J. H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Upper Saddle River, New Jersey.

FIG. 1.—Map showing enlarged Comanche County, Oklahoma and relative position of central and northern sampling sites. Boundary of Fort Sill Military Reservation (FSMR) in Comanche County is indicated.

FIGURE 1

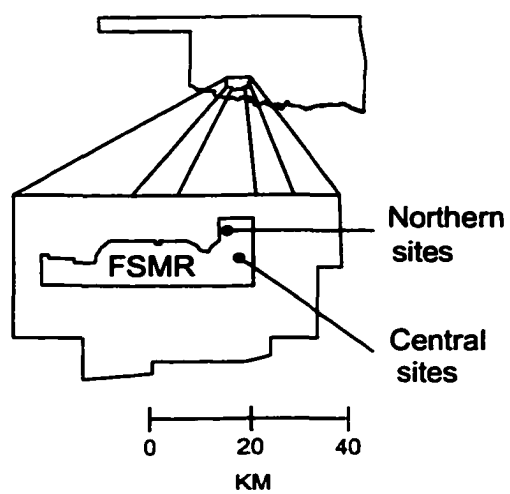


TABLE 1.—Average density \pm SD (individuals/ha) for small mammals captured at FSMR on all sites ($n = 18$), by treatment (control, $n = 6$; experimental, $n = 12$), and by location (central, $n = 9$; northern, $n = 9$), and results of 2-way ANOVA for equality of means among sites. Dunn-Šidák method was used to adjust P -values.

Species	Total	Treatment		Location		F-ratio		
		Control	Experimental	Central	Northern	Treatment	Location	Interaction
<u>Chaetodipus hispidus</u>	1.47 \pm 2.02	0.97 \pm 1.33	1.72 \pm 2.30	0.09 \pm 0.27	2.84 \pm 2.08	1.01	11.63 *	0.68
<u>Microtus ochrogaster</u>	2.99 \pm 3.58	6.07 \pm 4.49	1.46 \pm 1.71	4.14 \pm 3.17	1.84 \pm 3.77	10.94 *	2.99	0.05
<u>Neotoma floridana</u>	0.18 \pm 0.34	0.00 \pm 0.00	0.27 \pm 0.39	0.27 \pm 0.40	0.09 \pm 0.27	2.67	0.67	0.67
<u>Peromyscus leucopus</u>	2.29 \pm 2.44	0.00 \pm 0.00	3.44 \pm 2.22	1.29 \pm 1.44	3.30 \pm 2.89	24.80 **	4.76	4.76
<u>Peromyscus maniculatus</u>	4.77 \pm 4.92	5.37 \pm 5.66	4.47 \pm 4.74	1.09 \pm 1.54	8.44 \pm 4.31	0.29	17.11 **	0.48
<u>Reithrodontomys fulvescens</u>	1.38 \pm 1.66	1.10 \pm 1.70	1.53 \pm 1.69	2.49 \pm 1.55	0.28 \pm 0.83	0.42	11.35 *	0.00
<u>Reithrodontomys montanus</u>	0.09 \pm 0.26	0.13 \pm 0.33	0.07 \pm 0.23	0.18 \pm 0.35	0.00 \pm 0.00	0.26	2.33	0.26
<u>Sigmodon hispidus</u>	20.53 \pm 19.23	9.38 \pm 8.24	26.10 \pm 20.96	33.07 \pm 18.44	7.99 \pm 9.61	7.84	13.56 *	2.42
<u>Spermophilus tridecemlineatus</u>	0.09 \pm 0.40	0.00 \pm 0.00	0.14 \pm 0.49	0.19 \pm 0.57	0.00 \pm 0.00	0.47	0.47	0.47

* $P \leq 0.05$, ** $P \leq 0.01$

TABLE 2.—Density (individuals/ha), species richness (no. species), and species diversity (H') for small mammals captured at FSMR on central and northern sites. Control sites designated with a "C" and experimental sites with an "E".

	Central										Northern								
Property	C1	C2	C3	E1	E2	E3	E4	E5	E6	C4	C5	C6	E7	E8	E9	E10	E11	E12	
Density																			
<u>Chaetodipus hispidus</u>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	1.7	3.3	0.8	5.0	4.1	4.1	0.0	0.8	5.8	
<u>Microtus ochrogaster</u>	9.9	8.3	4.1	2.5	1.7	3.3	2.5	5.0	0.0	0.8	1.7	11.6	0.0	0.0	0.0	2.5	0.0	0.0	
<u>Neotoma floridana</u>	0.0	0.0	0.0	0.0	0.0	0.8	0.8	0.8	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	
<u>Peromyscus leucopus</u>	0.0	0.0	0.0	3.3	0.8	3.3	2.5	1.7	0.0	0.0	0.0	0.0	6.6	7.4	3.3	3.3	3.3	5.8	
<u>Peromyscus maniculatus</u>	4.1	0.0	3.3	0.0	0.8	0.0	0.8	0.8	0.0	9.1	14.9	0.8	9.1	7.4	10.7	5.0	13.2	5.8	
<u>Reithrodontomys fulvescens</u>	0.0	3.3	3.3	1.7	3.3	5.0	0.8	1.7	3.3	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	
<u>Reithrodontomys montanus</u>	0.0	0.0	0.8	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<u>Sigmodon hispidus</u>	14.9	11.6	20.7	43.0	55.4	28.9	32.2	24.8	66.1	0.0	0.0	9.1	1.7	2.5	0.0	19.8	25.6	13.2	
<u>Spermophilus tridecemlineatus</u>	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Total	28.9	23.1	32.2	50.4	62.0	42.1	41.3	34.7	70.2	11.6	19.8	22.3	22.3	22.3	18.2	33.1	43.0	30.6	
Species richness	3	3	5	4	5	6	7	6	3	3	3	4	4	5	3	5	4	4	
Species diversity	0.429	0.431	0.482	0.250	0.204	0.462	0.389	0.428	0.110	0.285	0.313	0.413	0.544	0.613	0.416	0.525	0.410	0.568	

TABLE 3.—Means \pm SD of vegetation characteristics measured during quadrat sampling and results of 2-way ANOVA for equality of means among sites. Sites are grouped as total ($n = 18$), treatment (control, $n = 6$; experimental, $n = 12$), and location (central, $n = 9$; northern, $n = 9$). Dunn-Šidák method was used to adjust P -values.

Characteristic	Total	Treatment		Location		F-ratio		
		Control	Experimental	Central	Northern	Treatment	Location	Interaction
Grass height (cm)	28.57 \pm 5.75	29.88 \pm 3.05	27.91 \pm 6.75	32.06 \pm 5.66	25.08 \pm 3.31	0.69	7.28	0.48
Forb height (cm)	23.51 \pm 4.17	24.01 \pm 2.54	23.26 \pm 4.88	26.00 \pm 3.74	21.02 \pm 3.01	0.18	6.36	1.06
Litter depth (cm)	3.42 \pm 2.50	3.74 \pm 2.68	3.27 \pm 2.51	5.24 \pm 1.72	1.61 \pm 1.71	0.27	16.68 **	0.07
Visual obstruction value	2.35 \pm 0.77	2.55 \pm 0.34	2.25 \pm 0.91	2.78 \pm 0.73	1.92 \pm 0.56	0.86	5.26	1.25
Grass cover (%)	48.46 \pm 12.48	59.14 \pm 6.98	43.12 \pm 11.19	53.07 \pm 7.96	43.85 \pm 14.82	11.95 *	3.16	0.41
Forb cover (%)	13.52 \pm 4.54	11.34 \pm 3.42	14.61 \pm 4.76	11.78 \pm 5.38	15.26 \pm 2.84	2.37	2.81	0.01
Litter cover (%)	22.62 \pm 14.26	21.27 \pm 14.95	23.29 \pm 14.53	32.01 \pm 6.73	13.23 \pm 13.72	0.13	9.72	0.30
Bare ground (%)	14.49 \pm 18.05	8.35 \pm 12.82	17.56 \pm 19.95	1.94 \pm 2.97	27.05 \pm 18.14	2.17	13.41 *	1.12
Sedge and rush cover (%)	0.08 \pm 0.14	0.12 \pm 0.22	0.05 \pm 0.09	0.14 \pm 0.18	0.01 \pm 0.02	1.00	5.96	1.59

* $P \leq 0.05$, ** $P \leq 0.01$

TABLE 4.—Means \pm SD of small-mammal properties and results of 2-way ANOVA for equality of means among sites. Sites are grouped as total (n = 18), treatment (control, n = 6; experimental, n = 12), and location (central, n = 9; northern, n = 9). Total density, species richness, and species diversity are based on small-mammal data collected at all sites. Dunn-Šidák method was used to adjust P-values.

Property	Total	Treatment		Location		<u>F</u> -ratio		
		Control	Experimental	Central	Northern	Treatment	Location	Interaction
Total density (individuals/ha)	33.78 \pm 15.51	22.98 \pm 7.21	39.18 \pm 15.89	42.77 \pm 15.57	24.80 \pm 9.32	10.15 *	9.92 *	1.32
Species richness (no. species)	4.28 \pm 1.23	3.50 \pm 0.84	4.67 \pm 1.23	4.67 \pm 1.50	3.89 \pm 0.78	4.48	1.46	0.37
Species diversity (H')	0.404 \pm 0.130	0.392 \pm 0.076	0.410 \pm 0.153	0.354 \pm 0.132	0.454 \pm 0.115	0.12	0.89	9.76 *

* P \leq 0.05

TABLE 5.—Means (\bar{n} = 86 days for each of 4 sites) of mean daily temperature and daily standard deviation and results of Wilcoxon's signed-rank test (paired-comparisons design) for equality of means between woody patch and grassland habitat.

Site	Mean daily temperature (°C)			Daily standard deviation		
	Woody patch	Grassland	\underline{Z}	Woody patch	Grassland	\underline{Z}
E1	23.24	28.57	-8.05 ***	2.86	8.89	-8.05 ***
E2	23.96	26.77	-8.05 ***	3.67	6.85	-8.02 ***
E8	24.06	25.89	-7.40 ***	3.77	5.72	-6.78 ***
E10	23.85	27.00	-8.05 ***	3.47	6.94	-7.56 ***

*** $P \leq 0.001$

APPENDIX I

List of plants used to calculate Jaccard coefficients.

Yarrow (Achillea millefolium), ragweed (Ambrosia spp.), lead plant (Amorpha canescens), big bluestem (Andropogon gerardii), three awn (Aristida spp.), milkweed (Asclepias spp.), silver bluestem (Bothriochloa saccharoides), grama (Bouteloua spp.), Indian paintbrush (Castilleja coccinea), windmill grass (Chloris verticillata), thistles (Cirsium spp.), unknown aster (Compositae), plains coreopsis (Coreopsis tinctoria), bermuda grass (Cynodon dactylon), sedges (Cyperaceae), Scribner dichanthelium (Dichanthelium oligosanthes), crabgrass (Digitaria spp.), echinacea (Echinacea angustifolia), Russian olive (Elaeagnus angustifolia), gumweed (Grindelia squarrosa), sunflower (Helianthus spp.), rushes (Juncus spp.), Osage orange (Maclura pomifera), common evening primrose (Oenothera biennis), eastern prickly pear (Opuntia humifusa), switchgrass (Panicum virgatum), unknown grasses (Poaceae), Chickasaw plum (Prunus angustifolia), scurf pea (Psoralea spp.), post oak (Quercus stellata), prairie coneflower (Ratibida columnifera), smooth sumac (Rhus glabra), black locust (Robinia pseudoacacia), little bluestem (Schizachyrium scoparium), sensitive briar (Schrankia uncinata), green foxtail (Setaria viridis), Indian grass (Sorghastrum nutans).

Local and regional variables affecting small mammals

**The role of local and regional variables in determining abundance of
grassland small mammals associated with woody patches**

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Key words: abundance, Fort Sill Military Reservation, grassland, local environmental variables, Oklahoma, regional environmental variables, scale, small mammals

Abstract

Both local- and regional-scale environmental factors potentially can affect small-mammal populations. At Fort Sill Military Reservation (southwestern Oklahoma) we studied a series of introduced, small woody habitat patches in an extensive mixed-grass prairie to evaluate the role of local and regional environmental variables in determining small-mammal abundance and changes in abundance. For four sessions small mammals were live-trapped at 12 sites, where we also evaluated 10 local (e.g., average grass height) and 19 regional (e.g., distance to mixed-grass prairie) environmental variables that were then summarized using principal-components analysis. Multiple regression was used to determine the relationship of environmental components to small-mammal abundance and changes in abundance. Hispid cotton rats (Sigmodon hispidus) and white-footed mice (Peromyscus leucopus) were the most common of seven species captured. More animals (all species combined) were at sites surrounded by relatively uniform landscapes, which also were farthest from bottomland forest and tallgrass prairie. Numbers and change in abundance of S. hispidus, the most frequently encountered mammal, did not follow the same pattern as that for all species combined; higher numbers and greater change typically occurred at sites with taller grasses in surrounding landscapes having cover types with more complex edges. For P. leucopus, during two trapping sessions, numbers were higher at sites surrounded by relatively

uniform landscapes and more distant from bottomland forest and tallgrass prairie; increases in its numbers were greater at these sites. Overall, regional environmental variables accounted for more variation in abundance and changes in abundance in small mammals associated with woody patches than did local factors.

1. Introduction

For biological communities, properties such as species composition may remain relatively constant over long periods of time (Vance 1984). However, ecologists realize that the distributions and abundances of individuals are dynamic, exhibiting both spatial and temporal variation. Variables ranging from those on a local scale (e.g., vegetative characters; Dueser and Shugart 1978; Cockburn and Lidicker 1983; Swihart and Slade 1990) to a regional scale (e.g., landscape features; Johnson et al. 1992; With and Crist 1995; Delattre et al. 1996) have important roles in determining the distribution and abundance of individuals throughout the range of a species. In some cases, local-scale patterns (e.g., abundance or species richness) may not reflect local variables due to the influence of regional factors (Abramsky and Tracy 1979; Hansson 1979; Wiens 1989; Cornell and Lawton 1992; Holt 1993; Schweiger et al. 2000). Local variables may affect the demographics of populations through alteration of birth and death rates at least in part by affecting food and habitat resources, while regional variables can influence emigration and immigration rates, and tend to stabilize a population or community as births and deaths fluctuate.

Anthropogenic land-uses (e.g. urbanization and agriculture) alter the natural landscape and promote patchiness. As a result, the availability and connectivity of patches of an organism's preferred habitat, in addition to the abundance of individuals, may be altered. Studies that examine the influence of local and regional variables on natural populations are needed to understand the effect of habitat modifications that promote patchiness (Pulliam 1988; Pulliam and Danielson 1991; Danielson 1992; O'Neill et al. 1997; Wolff et al. 1997; Dooley and Bowers 1998; Bowers and Dooley 1999), and models that incorporate both local and regional variables can assist in predicting population attributes (Schweiger et al. 1999; Fauth et al. 2000). Although small mammals are an ideal group for examining the role of local and regional variables (Barrett and Peles 1999), small-mammal studies that examine the corresponding influence of within-patch processes (i.e., local) and between-patch processes (i.e., regional) are generally lacking (Bowers and Dooley 1999).

Habitat patches are of particular concern in ecological studies (e.g., Foster and Gaines 1991; Harper et al. 1993; Bowers et al. 1996; Wolff et al. 1997) because current land-use trends often result in isolated patches due to habitat loss, habitat fragmentation, and species invasion. Subsequently, patches of habitat may be isolated, surrounded by a matrix of potentially unsuitable cover types. Further examination of how small mammals are affected by habitat patches and the surrounding matrix will help us to focus on the ramifications of habitat modification. Small mammals associated with habitat patches have been studied under conditions where a relatively homogeneous area is divided into patches of specific areal coverage (e.g., Foster and Gaines 1991; Bowers

and Dooley 1999). However, relatively few studies have been conducted on habitat patches under more natural, field conditions.

At Fort Sill Military Reservation in southwestern Oklahoma, small woody patches of habitat were established within an extensive grassland in the early to mid-1970s. These woody patches are maintained as wildlife habitat, thus providing the opportunity to examine small mammals in isolated habitat patches. We examined the role of 29 local and regional variables in determining abundance of small mammals associated with woody patches in this grassland. Our goal was to evaluate statistical associations and form predictions as to whether local and regional variables act independently or in concert with one another to determine small-mammal abundance. We used ordination to summarize the original habitat variables into a few interpretable composites that best explained the abundance of small mammals, thus allowing us to examine the contributions of the more important variables to small-mammal abundance in this grassland system.

2. Methods

2.1. Study area

The study was conducted on Fort Sill Military Reservation, a 38,300-ha installation in Comanche County (Figure 1), southwestern Oklahoma. Mean precipitation for this region is highest in May, while July and August are the hottest months (Johnson et al. 1990). This portion of Oklahoma includes a transition zone between mixed-grass prairie and uplands dominated by post oak (*Quercus stellata*) and blackjack oak (*Q.*

marilandica). Fort Sill lies south of the Wichita Mountains Wildlife Refuge, extends eastward, and encompasses a variety of habitats. We conducted all sampling on the East Range (ca. 14,000 ha) of Fort Sill, where upland plains prevail. The most prevalent cover types on the East Range are mixed-grass prairie (42.0%), rangeland (25.1%), and tallgrass prairie (17.0%). Woody vegetation is found on 5.5% of the area.

We established 12 sampling sites on the East Range (Figure 1) based on criteria relating to presence, size, and isolation of woody habitat patches. Sampling sites consisted of woody patches of habitat surrounded by grassland. The areal coverage of woody patches averaged 1834 m² (range 1469–2552 m²). Nearest-neighbor distance between woody patches used in our study averaged 364 m (range 178–622 m). Other planted woody patches existed, but were never closer than 107 m to patches used in our study.

Woody patches of habitat were encircled by firebreaks and contained ornamental and native woody-vegetation, grasses, forbs, and bare ground. Planted Russian olives (Elaeagnus angustifolia) were most common on the patches, while naturally occurring species such as smooth sumac (Rhus glabra), black locust (Robinia pseudoacacia), Chickasaw plum (Prunus angustifolia), and Osage-orange (Maclura pomifera) typically were present in lower numbers. Grasses and forbs were common to the woody patches and surrounding grassland. Grassland surrounding woody patches at sampling sites consisted of typical bluestem prairie, characterized by little bluestem (Schizachyrium scoparium), Scribner dichanthelium (Dichanthelium oligosanthes), and other species

including big bluestem (Andropogon gerardii) and Indian grass (Sorghastrum nutans; Johnson et al. 1990).

2.2. Small-mammal sampling

We used Sherman traps (7.6 by 8.9 by 22.9 cm) to assess the small-mammal communities. Two patterns of trap placement were used at each site. We established a large grid with 10-m spacing that was centered on the woody patch. Traps were placed at each grid point that fell within the woody patch and the surrounding firebreak. In addition, we established a transect of traps with 10-m spacing in the surrounding grassland at each site. This transect was 15 m from the outer edge of the firebreak and followed the contour of the patch edge, thus encircling the woody patch. The number of traps within a woody patch ranged from 16 to 33, depending on the areal coverage of the patch. Each grassland transect associated with a particular woody patch had the same number of traps as placed in the respective woody patch of habitat.

Traps were opened in the late afternoon or early evening, baited with rolled oats, and checked the following morning. We sampled small mammals four times (sampling sessions A–D) at each site from 16 May to 27 September 1997: (SS-A) 16–19 May; (SS-B) 27–30 May; (SS-C) 17 July–5 August; and (SS-D) 11–27 September. Within a sampling session, each site was sampled for three consecutive nights. Captured specimens were marked (i.e., ear-tagged with metal tags, toe clipped, or both) and released. Due to high temperatures, some mortality did occur. When practical, these

specimens were prepared and deposited in the Sam Noble Oklahoma Museum of Natural History.

2.3. Local-variable sampling

Variables 1–10 (Appendix) are local variables based on vegetation characteristics and patch size. We used vegetation sampling (i.e., quadrat and point-quarter sampling) to measure local variables at sampling sites. Quadrat sampling was conducted on two separate occasions: 29–30 June; and 3–9 October 1997. We sampled each site twice and used mean values of vegetation characteristics based on these sampling periods in data analyses. We collected vegetation data at 12 sampling stations uniformly spaced throughout each of the 12 sampling sites. At each sampling station, a 0.5-by-0.5-m quadrat was randomly dropped, and we recorded measurements within the quadrat of the following vegetation characteristics: average height of grasses and forbs; litter depth; a relative estimation of vegetation biomass based on visual-obstruction measurements (Robel et al. 1970); and percent cover of grasses, forbs, litter, bareground, and sedges and rushes (see Appendix for abbreviations and descriptions).

We conducted point-quarter sampling of the woody patches from 27 October–6 November 1997. Five points were systematically located in each woody patch, one at the center of each site and four positioned 14.1 m to the northeast, northwest, southeast, and southwest, respectively, of the center point. At each point, we measured the distance to the nearest tree (single individual or clump of stems > 2.5 cm in diameter

and 1.0 m in height) in each of four quadrants, and we estimated total tree density from these data (Brower et al. 1998).

2.4. Regional-variable sampling

Variables 11–29 are regional variables that we measured for the East Range of Fort Sill. Variables 11–20 are distance measures, and variables 21–29 are landscape indices that were assessed within 1000 m of each woody patch. We used a land-cover map of Fort Sill and the surrounding area to evaluate regional variables. The map was produced from panchromatic National High Altitude Photography (NHAP; scale 1:7920) taken from 24 November–9 December 1990 and georeferenced with 7.5-min topographic maps (scale 1:24000) from the U.S. Geological Survey. Fifteen cover types were categorized on the map (for land-cover map, see Pogue and Schnell 2001: figure 2).

The Geographical Resource Analysis Support System (GRASS; CERL 1989) was used to produce a digitized vector map with labeled polygons for each cover type and roads. The vector map was converted to a 10-m resolution raster map and final cover type classifications were checked for accuracy by ground-truthing (Pogue and Schnell 2001). We used the *r.le* programs (Baker and Cai 1992) of GRASS 4.1 to calculate regional variables on the East Range. The *r.le.dist* program was used to determine distances from the center of woody patches at sampling sites to the nearest edge of 10 cover types (including roads) found in and around the East Range of Fort Sill. Distances greater than 5677 m were recorded as 5677 m due to limitations of the digitized map; this occurred infrequently. We calculated other regional variables (i.e.,

richness and dominance of cover types, edge, fractal dimension, mean perimeter/area, mean corrected perimeter/area, mean related circumscribing circle, contagion, and angular second moment; see Appendix for abbreviations and descriptions) with the *r.le.patch* and *r.le.tex* programs.

2.5. Data analysis

We used the Jolly-Seber method for population estimation (Krebs 1999) to determine the number of small-mammal individuals associated with woody patches of habitat at Fort Sill. The method estimates the size of the trappable population in the area being surveyed. These estimates were employed to determine rate of change in small-mammal abundance and abundance during each of the four sampling sessions for all sites. Due to limitations of the Jolly-Seber method, we used the mean of estimates from the second and third nights ($\underline{n} = 2$) of trapping at each site to determine the number of individuals for the first sampling session (16–19 May). For the second (27–30 May) and third (17 July–5 August) sampling sessions, we used estimates from all three nights ($\underline{n} = 3$) at each site. For the fourth sampling session (11–27 September), we used estimates from the first and second nights ($\underline{n} = 2$) at each site. Rate of change from 16 May to 27 September is reflected in the slope of the linear regression equation for all population estimates ($\underline{n} = 10$) and is indicative of the dynamic nature of small mammals at the respective sites. We used Friedman's method for randomized blocks (Sokal and Rohlf 1995) to test for variation in small-mammal abundance among the 12 sites for the four sampling sessions (SigmaStat; Fox et al. 1995).

We subjected local and regional environmental variables to principal components analysis (Pielou 1984; Dunteman 1989; Legendre and Legendre 1998) using a correlation matrix and standardized variables (mean across sites of 0 and standard deviation of 1; NTSYSpc; Rohlf 2000). Loadings and projections were calculated.

Projections of the 12 sites onto the first four principal components based on environmental variables were employed as independent variables in backward, stepwise multiple regression (Sokal and Rohlf 1995). Dependent variables (abundance attributes)—analyzed for all species combined, for S. hispidus, and for P. leucopus—include the rate of change (i.e., slope) over the four sampling periods, as well as the estimates of abundance for each of those periods. We used a P-to-enter of 0.071 and a P-to-remove of 0.074 so as to add and remove variables in search of the best combination of independent variables to statistically explain the dependent variable. These P-values allowed for variables close to statistically significant to be retained throughout the procedure, thus leaving the interpretation of any statistically marginal variables to the discretion of the investigator. To reveal the influence of the local- and regional-variable composites on small-mammal abundance, we determined the amount of variation associated with each of the retained components (partial R²) for the rate of change in mammal numbers, as well as for abundance estimates for each of the sampling periods.

3. Results

3.1. Mammal abundance and rate of change

We captured 708 individuals of seven small-mammal species at our 12 sampling sites. The most abundant species found at all sites was Sigmodon hispidus, the hispid cotton rat (466 individuals), followed by (in order of abundance): Peromyscus leucopus, white-footed mouse (112); Chaetodipus hispidus, hispid pocket mouse (57); P. maniculatus, deer mouse (40); Microtus ochrogaster, prairie vole (16); Neotoma floridana, eastern woodrat (13); and Reithrodontomys fulvescens, fulvous harvest mouse (4).

Estimates (Jolly-Seber method) of abundance and the rate of change in abundance for all species combined and the two most abundant species, S. hispidus and P. leucopus, at each site are shown in Figure 2. Rate of change for all species of small mammals and for S. hispidus increased at all sites (10 of 12 and 11 of 12, respectively, were statistically significant; Table 2). Concomitantly, the rate of change for P. leucopus increased at one-half of the sites (2 of 6 increased and 1 of 6 decreased significantly). Friedman's method for randomized blocks revealed significant variation among sites for the rate of change in abundance over time and the number of individuals associated with each site over time for all species, for S. hispidus, and for P. leucopus.

3.2. Analysis of environmental variables

Principal-components analysis condensed the 29 local and regional variables into eight components (based on eigenvalues > 1.0) that explained 94.2% of the total variance in the original variables. However, upon examination it was evident that components 5–8

were not particularly helpful in interpretation and that they accounted for relatively little variation in the total numbers of all species, of S. hispidus, and of P. leucopus at our sites. We therefore excluded components 5–8 from further analysis.

Character loadings for components I–IV are listed in Table 3, and projections of sites onto the first four components are shown in Figure 3. Component I (30.5% of total variance), with the highest loadings being for regional variables (Table 3), represents a gradient from sites shown to the left in Figure 3 that are more closely associated with bottomland forest and tallgrass prairie to those found to the right in the figure that are more isolated from these cover types (high positive loadings for BLFD and TGD). In addition, a high positive loading for angular second moment (t2) and a high negative loading for richness of cover types (d1) indicates a generally south-to-north gradient (left to right in Figure 3) from woody patches encompassed by a heterogeneous landscape with many cover types to those situated in a relatively homogeneous landscape with fewer cover types. The regional aspect of this component is further reflected by the fact that the six southern sites are positioned to the left in Figure 3, while the six northern sites are to the right.

Component II (18.2% of variance; Table 3) represents a gradient of sites from those (near bottom of Figure 3A) that have shorter grasses (high positive loading for AGH) and landscapes comprised of small, relatively circular cover-type patches (high positive loading for m1 and high negative loading for m3) to sites (near top of Figure 3A) with taller grasses and landscapes with relatively long, thin patches or with complex, convoluted perimeters. Component II is a composite of both local (AGH) and

regional (m1 and m3) variables. It can be thought of as representing a contrast between site 6 (and to some extent site 7) and the other sites (see Figure 3).

Component III (15.7% of variance) is also a composite of local and regional variables, with high loadings for one local variable and three that are regional (Table 3). Sites near the bottom of Figure 3B tend to have less litter depth (high positive loading for ALD), are relatively far from water (high negative loading for H2OD), and occur in landscapes with a clearly dominant cover type that shows clumping (high negative loading for t1 and d3, respectively). Those sites near the top of Figure 3B have more litter depth, are closer to water, and are in landscapes where cover types are relatively even (in area covered) and more uniformly dispersed.

Component IV (8.7% of variance) represents a gradient from sites relatively far from agricultural land-use and close to disturbed areas (high negative loading for AGD and high positive loading for DAD, respectively; near bottom of Figure 3C) to those closer to agriculture and farther from disturbed areas. Both of the variables with high loadings are regional variables.

3.3. Relation of mammal numbers to environmental variation

Based on multiple-regression analyses, change in total numbers (i.e., slope) for all species over the four sampling periods was not strongly related to environmental components (Table 4). However, when analyzing abundance of all small mammals as the dependent variable for each sampling period and considering the first four environmental principal components as independent variables, the best composite

variable for statistically explaining intersite differences in abundance was environmental component I; it accounted for from 32 to 54% of the variance in numbers of all small mammals over the 12 sites (Table 4). This component, which contrasts southern and northern sites (1–6 versus 7–12, respectively), reflects the fact that sites in the north are surrounded by relatively uniform landscapes, as well as being farther from bottomland forest and tallgrass prairie. As indicated by the positive regression coefficients listed for component I under all species in Table 4, these northern woody plots tended to have higher total numbers of small mammals (see Table 1). Each of the other three principal components enters one or more of the multiple-regression equations for analyses of numbers of all species, but the explanatory power of these components is much less than that for component I.

For S. hispidus, the associations of abundance or change in abundance with environmental components are different from that of all small mammals (Table 4). In only one case (i.e., for sampling session A) did component I enter into the regression equation; this was only at a marginal level (see Table 4). For two of the sessions, SS-A and SS-D, the statistically most important component was II, which explained 69% and 48%, respectively, of the variation in S. hispidus numbers. Environmental component II contrasts sites 6 and 7 (which have taller grasses and surrounding landscapes comprised of cover types having more complex edges) with the other sites. For the first trapping session (SS-A), the high percentage explained by component II reflects the fact that sites 6 and 7 had by far the highest numbers of S. hispidus (see Table 1). In the third trapping period (SS-C), component III explained the greatest amount of variation,

indicating that the sites with higher numbers had more litter, were closer to water, and were in landscapes with cover types that were more uniformly dispersed. For the fourth session (SS-D), the number of S. hispidus was highest for site 6—the site with the highest projection on component II (Figure 3A)—but a number of other sites have relatively high S. hispidus numbers as well (Table 1). The regression equation for SS-D also incorporates component IV, which explains an additional 24% of the intersite variance, with the sites tending to have relatively high numbers of S. hispidus being closer to agricultural fields and farther from disturbed areas. The intersite differences in degree of change in S. hispidus abundance (i.e., slope; Table 4) also are best predicted by a combination of components II and IV.

When analyzing P. leucopus numbers with environmental components, we found no relationship for the first two trapping sessions (SS-A and SS-B; Table 4). For the last two sessions (SS-C and SS-D), environmental component I statistically explained a significant portion (35%) of the variation among sites; there is a tendency for northern sites to have higher numbers, although the pattern is not nearly as clear-cut as found for all species. Marginally, for these two trapping sessions (SS-C and SS-D), component II enters the equations with a negative coefficient, reflecting the fact that numbers of P. leucopus were quite low at site 6 for SS-C, and that the species was not encountered at the site during SS-D (see Table 1). Intersite differences in slope (rate of change over the four trapping sessions) is partly explained (35%) by environmental component I, reflecting the fact that sites with the largest projections on component I

(sites 8, 9, and 11; see Figure 3) showed the greatest positive change in numbers over the course of our study (see Table 2).

4. Discussion

4.1 All species

Most of the estimates at our sites for abundance of all species of small mammals varied substantially over time (Table 2). Component I, with its contrast between environmental conditions of southern and northern sites, was the most important composite of original variables associated with the abundance of all species collectively (Table 4), although components II–IV also entered into one or more of the multiple-regression equations. Of all the species captured at our sites, only P. leucopus and N. floridana are considered non-grassland species (Lackey et al. 1985; Caire et al. 1989). These two species comprised just 17.7% of the small mammals captured at our sites; therefore, variables relating to the isolation of patches from bottomland forest and tallgrass prairie habitats may not influence the general abundance of small mammals, as they did for P. leucopus when that species was considered alone.

Instead, the variables relating to richness and homogeneity of cover types may be the portion of component I that associate it best with the abundance of all species. In general, the highest combined abundances for all sampling sessions were obtained for the northern sites. These results indicate that sites with relatively low cover-type richness (d1) and high homogeneity (t2; see Figure 3), have higher numbers of small mammals associated with them. Likewise, increasing cover-type complexity can

increase the relative length of edge in a landscape and may increase the number of individuals for all species at those sites, as indicated by the influence of component II (i.e., variables m1 and m3) during sampling session D for all species. All of the species included in “all species” are non-predators and may benefit from a reduction in predation risk afforded them by this apparent increase in the complexity of edge habitat (Yahner 1988), whereas simply increasing edge length may increase predation risk.

4.2. Sigmodon hispidus

Populations of S. hispidus tend to exhibit annual fluctuations in size. Populations in Oklahoma and Kansas are near the northern extent of the species' range and are limited, in part, by weather conditions and energy reserves (Goertz 1964; Fleharty et al. 1972). However, the species typically exhibits substantial population growth during the summer months. Estimates for abundance of S. hispidus increased at all sites during the course of our study from 16 May to 27 September (Table 2). Intersite differences in S. hispidus numbers and in rate of change were most closely associated with environmental component II, which set apart site 6 (with its taller grass and surrounding landscapes with more convoluted edges) from the other sites. Site 6 had higher numbers and exhibited the greatest change in numbers of S. hispidus.

Sigmodon hispidus is a habitat generalist found in a variety of habitats, including those associated with dense grass cover and low-growing woody vegetation (Goertz 1964; Cameron and Spencer 1981; Caire et al. 1989). The association of component II with abundance of S. hispidus suggests that this species is sensitive to grass height and

patch shape of cover types within the landscape. Taller grasses may afford S. hispidus protection from both weather and predators (Schnell 1968; Fleharty et al. 1972; Fleharty and Mares 1973). At Fort Sill, Haner and Schnell (submitted for publication) found S. hispidus in woody patches, in grassland surrounding woody patches, and in continuous grassland void of woody patches. For S. hispidus, sites 6, 7, 10, and 11 (near the top in Figure 3A) are among the sites with the highest combined abundance estimates for the four sampling sessions (A–D). Our results support the species' preference for increased grass cover and suggest an association with edge habitat, as S. hispidus was more common to sites in landscapes comprised of cover-type patches with long, convoluted shapes that increase perimeter length and complexity.

4.3. Peromyscus leucopus

Most estimates for abundance of P. leucopus showed little variation over the course of our study (Table 2), and environmental component I was the composite of original variables that most associated with the species, statistically explaining a significant portion of intersite variability in numbers for two of the trapping sessions (Table 4). In Oklahoma, P. leucopus is typically a woodland species (Hays 1958; Caire et al. 1989), but may frequent grassland habitat (Schnell et al. 1980; Lackey et al. 1985; Clark et al. 1987). At Fort Sill, Haner and Schnell (submitted for publication) found P. leucopus in woody patches and grassland surrounding woody patches, but not in continuous grassland that lacked woody patches.

In north-central Oklahoma, Schnell et al. (1980) found high numbers of P. leucopus in lowland and upland forests, but relatively few in grasslands immediately adjacent to forest habitats. In the Flint Hills of Kansas, Clark et al. (1987) found P. leucopus to frequent lowland prairie sites when associated with ravines. Ravines may have acted as corridors—connecting woody habitat for dispersing individuals. Adler et al. (1984) and Adler (1987) found that grasslands acted as dispersal sinks to P. leucopus in Massachusetts, and density of the species in grasslands was affected by woody vegetation.

The abundance-environmental relationships for P. leucopus were opposite of what we expected, given that abundance of mice was higher at northern sites, farthest from what we considered might be important—bottomland forest, a cover type that supports substantial numbers of P. leucopus (personal observation). The landscape around the northern sites also was more homogeneous. The effect of a landscape relies on the dispersal ability of the organism (Dooley and Bowers 1996; Danielson and Anderson 1999), and a less complex landscape may increase a species' ability to find preferred habitat (Danielson 1991). Peromyscus leucopus may have been more abundant at northern sites because woody patches are easier for a few dispersing individuals to find in homogeneous landscapes, even grasslands which typically act as sinks for the species, rather than heterogeneous landscapes associated with southern sites. Concomitantly, heterogeneous landscapes surrounding southern sites may attract predators more than homogenous landscapes to the north, thus limiting dispersal of P. leucopus and successful colonization of woody patches due to predation risks (Bowers

and Dooley 1993). In general, we suspect that P. leucopus is not an efficient disperser in grassland landscape (heterogeneous or not) unless suitable corridors of woody vegetation (e.g., riparian habitat) exist close by. The general idea of differential dispersal could be evaluated in future comparative studies.

4.4. Relative influence of regional and local environmental variables

In general, when we looked for trends in environmental variation across study sites using principal-components analysis, the resulting components subsumed primarily regional variables. Furthermore, the composite environmental variable most predictive of small-mammal numbers was component I, for which all of the high loadings were for regional variables. For components II and III, a single local variable each had a high correlation, but the components also had two and three regional variables (respectively) with high loadings as well. While it is obvious that local variables are important at some level in determining whether a species is present at a site, they proved relatively unimportant in explaining intersite differences in small-mammal abundance at Fort Sill. This is further revealed by examining the environmental components associated with numbers for all species and for S. hispidus.

Sigmodon hispidus was the dominant small-mammal species at our sites. While numerically dominant species are thought to strongly influence community properties, Brady and Slade (2001) reported that S. hispidus affected the relative abundance of other grassland species in Kansas only during years that it exhibited high density. At Fort Sill, we initially expected the same environmental variables to associate with the

abundance of all species and the numerically dominant S. hispidus, as numbers of S. hispidus appeared to dictate the numbers of all small mammals (see Figure 2). Instead, the abundance of all species was strongly associated with the exclusively regional component I and to a lesser extent with the predominantly regional components II and III; component IV, an exclusively regional composite, also showed some association with abundance of all species combined. In contrast, S. hispidus was most associated with component II and to a lesser extent III and IV. It may be that in years when S. hispidus is less abundant, other small mammals would not be subject to the same environmental variables affecting S. hispidus abundance, and other species would benefit due to decreased competition with the dominant species.

The scale (i.e., temporal and spatial) at which ecological patterns (e.g., abundance) and environmental variables (i.e., local and regional variables) are examined can have a marked effect on the conclusions drawn from ecological research (Wiens 1989). In our study, local variables involved measures taken in the immediate vicinity of the site, while landscape indices (i.e., variables 21–29; Appendix) were assessed within a 1000-m-radius sampling area centered over woody patches so as to include the home ranges and typical dispersal abilities of grassland small mammals, without exceeding the spatial extent of landscape that we felt actually influenced small mammals. It is clear in our study that the differences in regional environmental variables, rather than those for local measures, were much more closely linked to intersite small-mammal abundance differences. While the small-mammal species present were basically the same in each of the relatively isolated woody patches

(personal observation), the characteristics of the surrounding landscape appears to be important in determining how many of the various species were present.

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References

- Abramsky, Z. and Tracy, C.R. 1979. Population biology of a "noncycling" population of prairie voles and a hypothesis on the role of migration in regulating microtine cycles. *Ecology* 60: 349–361.
- Adler, G.H. 1987. Influence of habitat structure on demography of two rodent species in eastern Massachusetts. *Canadian Journal of Zoology* 65: 903–912.

- Adler, G.H., Reich, L.M. and Tamarin, R.H. 1984. Characteristics of white-footed mice in woodland and grassland in eastern Massachusetts. *Acta Theriologica* 29: 57–62.
- Baker, W.L. and Cai, Y. 1992. The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. *Landscape Ecology* 7: 291–302.
- Barrett, G.W. and Peles, J.D. 1999. Small mammal ecology: a landscape perspective. In *Landscape Ecology of Small Mammals*, pp. 1–8. Edited by G.W. Barrett and J.D. Peles. Springer-Verlag: New York.
- Bowers, M.A. and Dooley, J.L., Jr. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. *Oecologia* 94: 247–254.
- Bowers, M.A. and Dooley, J.L., Jr. 1999. EMS studies at the individual, patch, and landscape scale: designing landscapes to measure scale-specific responses to habitat fragmentation. In *Landscape Ecology of Small Mammals*, pp. 147–174. Edited by G.W. Barrett and J.D. Peles. Springer-Verlag: New York.
- Bowers, M.A., Gregario, K., Brame, C.J., Matter, S.F. and Dooley, J.L., Jr. 1996. Use of space and habitats by meadow voles at the home range, patch and landscape scales. *Oecologia* 105: 107–115.
- Brady, M.J. and Slade, N.A. 2001. Diversity of a grassland rodent community at varying temporal scale: the role of ecologically dominant species. *Journal of Mammalogy* 82: 974–983.

- Brower, J.E., Zar, J.H. and von Ende, C.N. 1998. Field and Laboratory Methods for General Ecology. Fourth edition. WCB/McGraw-Hill: Boston.
- Caire, W., Tyler, J.D., Glass, B.P. and Mares, M.A. 1989. Mammals of Oklahoma. University of Oklahoma Press: Norman.
- Cameron, G.N. and Spencer, S.R. 1981. Sigmodon hispidus. Mammalian Species 158: 1–9.
- CERL. 1989. GRASS-GRID, Version 4.1. U.S. Army Corps of Engineers, Construction Engineering and Research Laboratory, Champaign, IL.
- Clark, B.K., Kaufman, D.W., Kaufman, G.A. and Finck, E.J. 1987. Use of tallgrass prairie by Peromyscus leucopus. Journal of Mammalogy 68: 158–160.
- Cockburn, A. and Lidicker, W.Z., Jr. 1983. Microhabitat heterogeneity and population ecology of an herbivorous rodent, Microtus californicus. Oecologia 59: 167–177.
- Cornell, H.V. and Lawton, J.H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology 61: 1–12.
- Danielson, B.J. 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. American Naturalist 138: 1105–1120.
- Danielson, B.J. 1992. Habitat selection, interspecific interactions and landscape composition. Evolutionary Ecology 6: 399–411.

- Danielson, B.J. and Anderson, G.S. 1999. Habitat selection in geographically complex landscapes. In Landscape Ecology of Small Mammals, pp. 89–103. Edited by G.W. Barrett and J.D. Peles. Springer-Verlag: New York.
- 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 space scales. Landscape Ecology 11: 279–288.
- Dooley, J.L., Jr. and Bowers, M.A. 1996. Influences of patch size and microhabitat on the demography of two old-field rodents. Oikos 75: 453–462.
- Dooley, J.L., Jr. and Bowers, M.A. 1998. Demographic responses to habitat fragmentation: experimental tests at the landscape and patch scale. Ecology 79: 969–980.
- Dueser, R.D. and Shugart, H.H., Jr. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59: 89–98.
- Dunteman, G.H. 1989. Principal components analysis. Sage University Paper Series on Quantitative Applications in the Social Sciences. Sage Publications: Beverly Hills, CA.
- Fauth, P.T., Gustafson, E.J. and Rabenold, K.N. 2000. Using landscape metrics to model source habitat for Neotropical migrants in the midwestern U.S. Landscape Ecology 15: 621–631.
- Fleharty, E.D., Choate, J.R. and Mares, M.A. 1972. Fluctuations in population density of the hispid cotton rat: factors influencing a “crash.” Bulletin of the Southern California Academy of Sciences 71: 132–138.

- Fleharty, E.D. and Mares, M.A. 1973. Habitat preference and spatial relations of Sigmodon hispidus on a remnant prairie in west-central Kansas. *Southwestern Naturalist* 18: 21–29.
- Foster, J. and Gaines, M.S. 1991. The effects of a successional habitat mosaic on a small mammal community. *Ecology* 72: 1358–1373.
- Fox, E., Shotton, K. and Ulrich, C. 1995. *SigmaStat User's Manual*. Jandel Corporation: San Rafael, CA.
- Goertz, J.W. 1964. The influence of habitat quality upon density of cotton rat populations. *Ecological Monographs* 34: 359–381.
- Hansson, L. 1979. On the importance of landscape heterogeneity in northern regions for the breeding population densities of homeotherms: a general hypothesis. *Oikos* 33: 182–189.
- Harper, S.J., Bollinger, E.K. and Barrett, G.W. 1993. Effects of habitat patch shape on population dynamics of meadow voles (Microtus pennsylvanicus). *Journal of Mammalogy* 74: 1045–1055.
- Hays, H.A. 1958. The distribution and movement of small mammals in central Oklahoma. *Journal of Mammalogy* 39: 235–244.
- Holt, R.D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. *In* *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, pp. 77–88. Edited by R.E. Ricklefs and D. Schluter. University of Chicago Press: Chicago.

- Johnson, A.R., Wiens, J.A., Milne, B.T. and Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* 7: 63–75.
- Johnson, F.L., Thompson, R.A., Rudman, R., Estes, J.R., Schnell, G.D. and Harris, K.D. 1990. Floral inventory of Fort Sill, Oklahoma. Final Report to U.S. Army Construction Engineering Research Laboratory, Champaign, Illinois. Oklahoma Biological Survey: Norman.
- Krebs, C.J. 1999. *Ecological Methodology*. Second edition. Benjamin/Cummings: Menlo Park, CA.
- Lackey, J.A., Huckaby, D.G. and Ormiston, B.G. 1985. Peromyscus leucopus. *Mammalian Species* 247: 1–10.
- Legendre, P. and Legendre, L. 1998. *Numerical ecology*. Second edition. *Developments in Environmental Modeling* 20: 1–853. Elsevier Science B.V.: Amsterdam, The Netherlands.
- O'Neill, R.V., Hunsaker, C.T., Jones, K.B., Riitters, K.H., Wickham, J.D., Schwartz, P.M., Goodman, L.A., Jackson, B.L. and Baillargeon, W.S. 1997. Monitoring environmental quality at the landscape scale. *BioScience* 47: 513–519.
- Pielou, E.C. 1984. *The Interpretation of Ecological Data: a Primer on Classification and Ordination*. John Wiley and Sons: New York.
- Pogue, D.W. and Schnell, G.D. 2001. Effects of agriculture on habitat complexity in a prairie-forest ecotone in the southern Great Plains of North America. *Agriculture, Ecosystems, and Environment* 87: 278–298.

- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132: 652–661.
- Pulliam, H.R. and Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137: S50–S66.
- Robel, R.J., Briggs, J.N., Dayton, A.D. and Hulbert, L.C. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 33: 295–297.
- Rohlf, F.J. 2000. NTSYS: Numerical Taxonomy and Multivariate Analysis System Version 2.1 User Guide. Exeter Software: New York.
- Schnell, G.D., Owen, R.D., Chesser, R.K. and Risser, P.G. 1980. Populations of small mammals in north-central Oklahoma. *Southwestern Naturalist* 25: 67–80.
- Schnell, J.H. 1968. The limiting effects of natural predation on experimental cotton rat populations. *Journal of Wildlife Management* 32: 698–711.
- Schweiger, E.W., Diffendorfer, J.E., Holt, R.D., Pierotti, R. and Gaines, M.S. 2000. The interaction of habitat fragmentation, plant, and small mammal succession in an old field. *Ecological Monographs* 70: 383–400.
- Schweiger, E.W., Diffendorfer, J.E., Pierotti, R. and Holt, R.D. 1999. The relative importance of small-scale and landscape-level heterogeneity in structuring small mammal distributions. *In* *Landscape Ecology of Small Mammals*, pp. 175–207. Edited by G.W. Barrett and J.D. Peles. Springer-Verlag: New York.
- Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: the Principles and Practice of Statistics in Biological Research*. Third edition. W.H. Freeman and Company: New York.

Swihart, R.K. and Slade, N.A. 1990. Long-term dynamics of an early successional small mammal community. *American Midland Naturalist* 123: 372–382.

Vance, R.R. 1984. The effect of dispersal on population stability in one-species, discrete-space population growth models. *American Naturalist* 123: 230–254.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.

With, K.A. and Crist, T.O. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76: 2446–2459.

Wolff, J.O., Schaubert, E.M. and Edge, W.D. 1997. Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. *Conservation Biology* 11: 945–956.

Yahner, R.H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2: 333–339.

Figure 1. Map showing (1) Oklahoma; (2) enlarged Comanche County with boundary of Fort Sill Military Reservation; and (3) enlarged East Range with locations of sampling sites. Sites are numbered from south to north.

Figure 2. Number of individuals calculated using Jolly-Seber method and linear regression line based on 10 estimates from May to September for each of the 12 sites at Fort Sill Military Reservation.

Figure 3. Projections of all 12 sites at Fort Sill Military Reservation onto principal components based on 29 local and regional variables: (A) components I and II; (B) components I and III; (C) components I and IV. Variables with high positive and negative loadings on particular axes are listed.

Figure 1

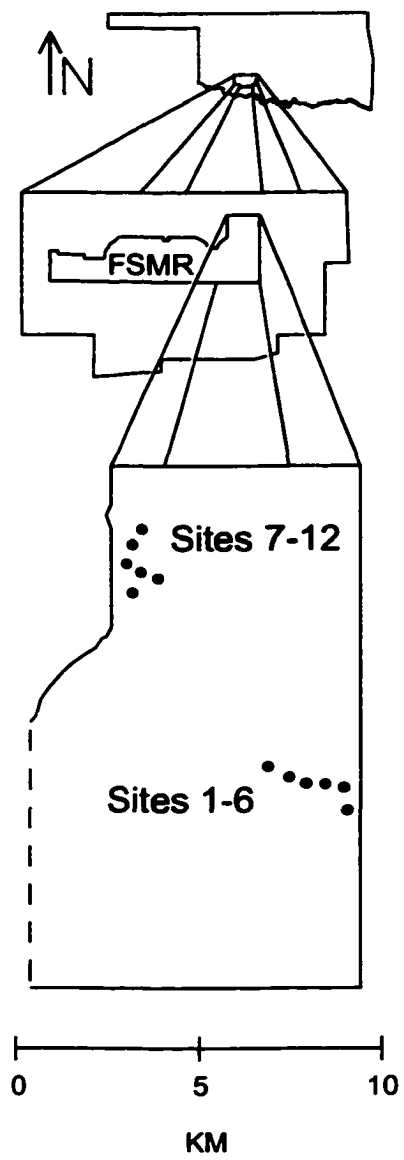


Figure 2

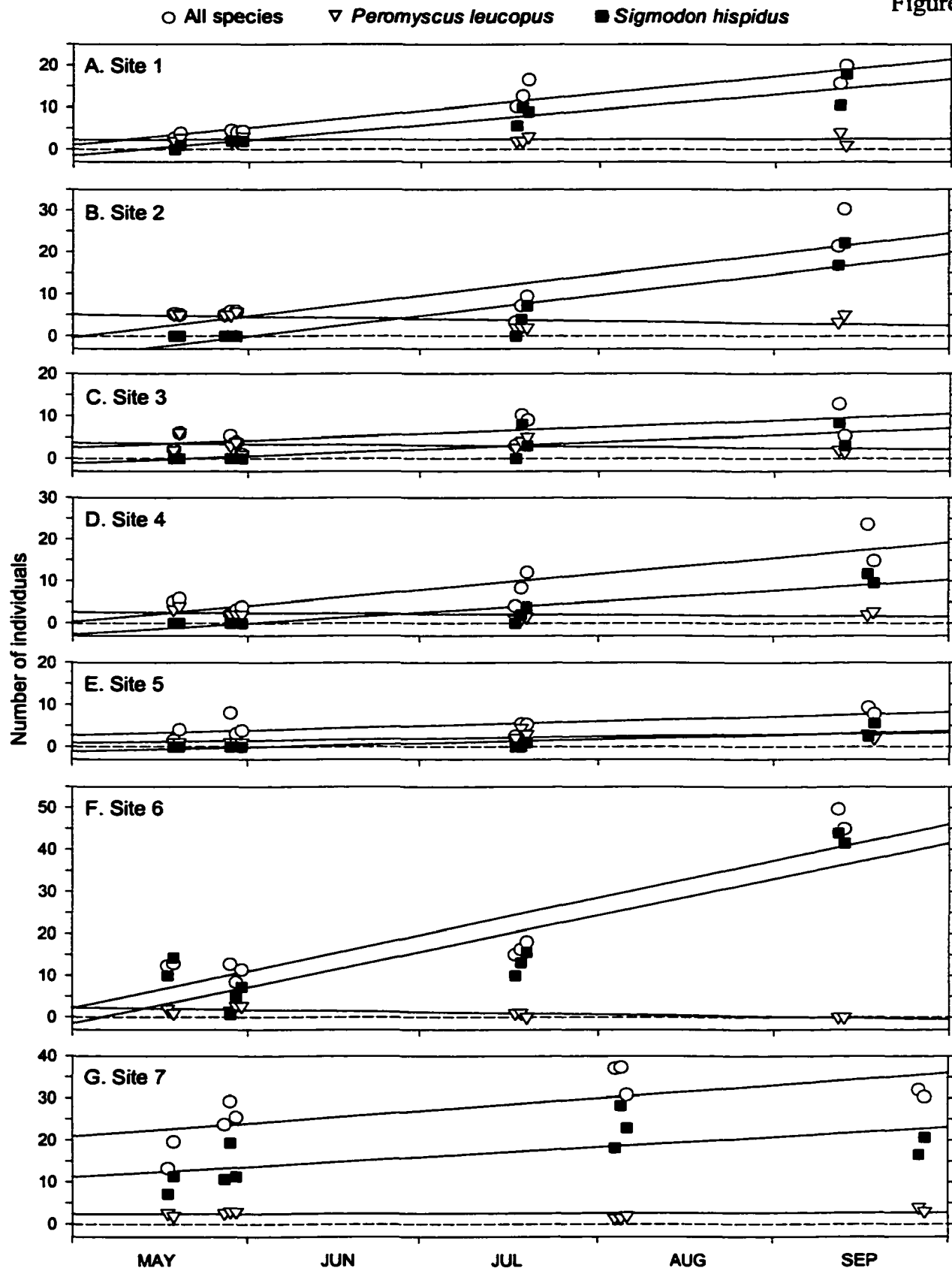


Figure 2 (cont.)

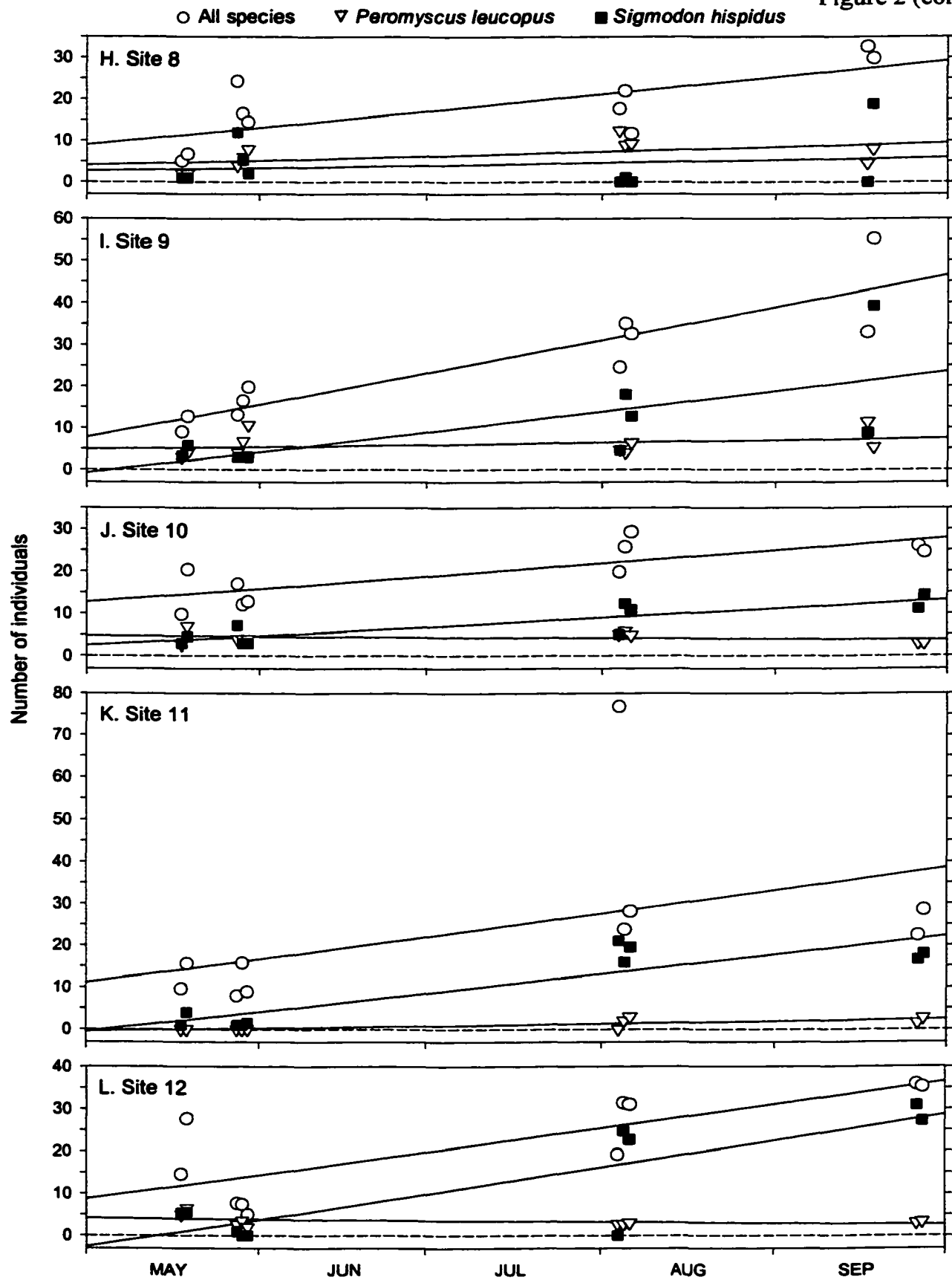


Figure 3

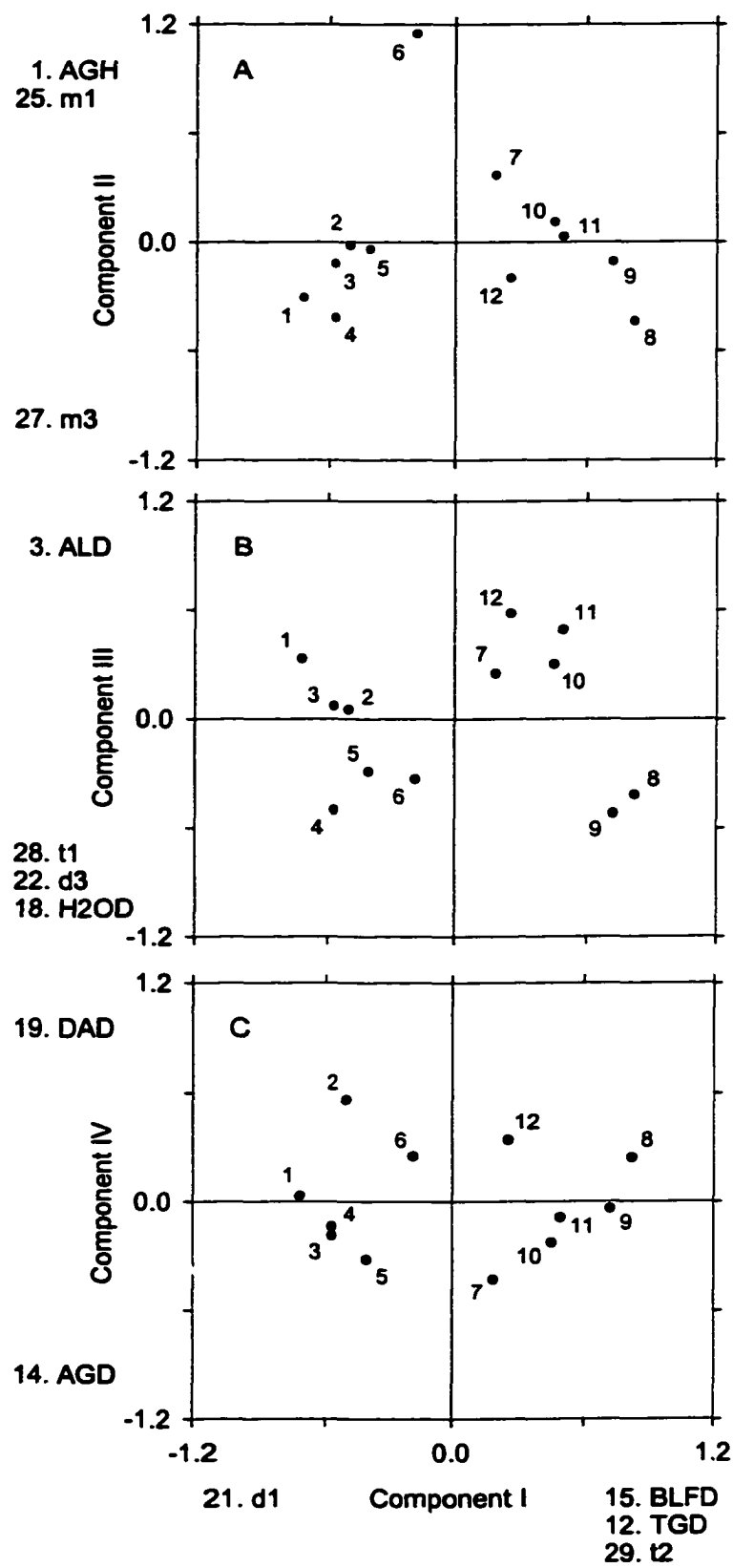


Table 1. Number of individuals (Jolly-Seber method) associated with sampling sites during sampling sessions (SS). Sampling sessions were: (SS-A) 16–19 May; (SS-B) 27–30 May; (SS-C) 17 July–5 August; and (SS-D) 11–27 September.

Site	All species				<u>Sigmodon hispidus</u>				<u>Peromyscus leucopus</u>			
	SS-A	SS-B	SS-C	SS-D	SS-A	SS-B	SS-C	SS-D	SS-A	SS-B	SS-C	SS-D
1	3.2	4.3	13.1	17.7	0.5	2.0	8.2	14.2	2.3	2.3	2.3	2.5
2	5.2	5.6	6.7	25.9	0.0	0.0	3.7	19.5	5.2	5.3	2.0	4.2
3	4.0	3.4	7.4	9.0	0.0	0.0	3.7	5.7	4.0	2.6	3.8	1.8
4	5.4	2.9	8.1	19.2	0.0	0.0	1.9	10.6	3.7	2.0	1.2	2.3
5	2.8	4.9	4.4	8.5	0.0	0.0	0.3	4.1	1.0	1.0	3.1	2.5
6	12.6	10.8	16.4	47.2	12.1	4.3	12.9	42.7	1.5	2.3	0.7	0.0
7	16.4	26.1	35.0	31.1	9.3	13.8	23.1	18.7	2.3	2.9	1.7	3.5
8	5.8	18.4	17.1	31.2	1.0	6.4	0.3	9.4	2.0	6.0	10.2	6.3
9	10.8	16.5	30.7	44.1	4.6	3.0	11.8	24.0	3.5	7.1	5.0	8.3
10	15.1	13.9	24.9	25.3	3.8	4.4	9.4	12.8	4.8	4.0	5.2	3.0
11	12.6	10.9	42.9	25.4	2.5	1.2	18.9	17.3	0.0	0.0	1.7	2.1
12	21.2	6.7	27.2	35.6	5.5	0.3	15.9	29.0	5.8	2.7	2.8	3.2

Table 2. Rate of change (i.e., slope) in abundance from 16 May–27 September for small mammals based on slope of linear regression equation. Asterisks indicate slopes statistically different from zero.

Site	All species	<u>Sigmodon hispidus</u>	<u>Peromyscus leucopus</u>
1	0.133***	0.118***	0.001
2	0.162**	0.161***	−0.017
3	0.052	0.053*	−0.010
4	0.124***	0.085***	−0.007
5	0.036*	0.032**	0.016*
6	0.287***	0.281***	−0.018**
7	0.099*	0.078*	0.002
8	0.132*	0.021	0.035
9	0.253***	0.159*	0.017
10	0.099**	0.070**	−0.006
11	0.179	0.149***	0.018**
12	0.182**	0.205**	−0.010

*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

Table 3. Principal-component loadings for local and regional variables based on analysis of 12 sites.^a

Variable	Component			
	I	II	III	IV
<u>Local variables</u>				
1 AGH	0.051	0.939	0.168	0.203
2 AFH	0.580	0.361	0.212	0.168
3 ALD	-0.120	0.526	0.639	-0.206
4 VOV	0.106	0.572	0.147	0.161
5 GC%	-0.544	0.618	0.470	-0.130
6 FC%	0.528	0.154	0.153	-0.085
7 LC%	-0.403	-0.515	-0.376	0.358
8 BG%	0.416	-0.045	-0.377	0.155
9 PTQ	0.606	-0.176	-0.260	-0.054
10 PSZ	-0.539	0.069	-0.373	0.415
<u>Regional variables</u>				
11 MGD	-0.579	-0.425	-0.133	-0.140
12 TGD	0.921	-0.106	0.307	-0.086
13 RLD	0.747	-0.284	-0.343	0.407
14 AGD	0.306	0.038	-0.067	-0.654
15 BLFD	0.925	0.084	-0.145	-0.047
16 RPD	-0.123	0.698	-0.552	0.041
17 TPD	-0.202	0.575	-0.382	0.555
18 H2OD	0.293	0.438	-0.728	-0.095
19 DAD	-0.398	-0.222	0.236	0.710

Table 3. continued.

Variable	Component			
	I	II	III	IV
20 RDD	-0.681	-0.261	0.194	0.321
21 d1	-0.955	-0.039	-0.064	0.064
22 d3	0.462	0.139	-0.766	-0.068
23 e2	0.773	-0.205	0.335	0.405
24 f1	0.782	-0.235	0.438	0.156
25 m1	-0.393	0.727	-0.227	-0.316
26 m2	0.393	0.450	0.436	0.285
27 m3	-0.177	-0.822	-0.076	-0.325
28 t1	-0.312	0.138	-0.774	-0.073
29 t2	0.830	-0.019	-0.496	0.103
Eigenvalue	8.85	5.27	4.55	2.54
Percentage explained	30.5	18.2	15.7	8.7

* Relatively high loadings highlighted in bold as follows: (component I) > |0.800|; (component II) > |0.700|; (components III and IV) > |0.600|.

Table 4. Unstandardized regression coefficients (with partial R^2 in parentheses, indicating proportion explained) for backward, stepwise multiple regression, with independent variables being population attributes and dependent variables being principal-component projections of environmental variables for the 12 sites. Sampling sessions were: (SS-A) 16–19 May; (SS-B) 27–30 May; (SS-C) 17 July–5 August; and (SS-D) 11–27 September.

Dependent variable ^a	Component (independent variable)				Constant
	I	II	III	IV	
All species					
SS-A	6.135 (0.32)*	—	7.410 (0.24) ^b	—	9.592
SS-B	9.564 (0.54)**	—	—	—	10.367
SS-C	16.676 (0.54)**	—	13.851 (0.19)*	—	19.492
SS-D	12.839 (0.34)**	13.986 (0.24)*	—	17.352 (0.18)*	26.683
Slope	—	—	—	0.139 (0.31) ^b	0.145
<u>Sigmodon hispidus</u>					
SS-A	2.327 (0.10) ^b	7.804 (0.69)***	—	—	3.275
SS-B	No variables remained as predictors				
SS-C	—	8.263 (0.22) ^b	10.701 (0.32)*	—	9.175
SS-D	—	17.552 (0.48)**	—	17.859 (0.24)*	17.333
Slope	—	0.106 (0.35)*	—	0.146 (0.32)*	0.118

Table 4. continued.

Dependent variable ^a	Component (independent variable)				Constant
	I	II	III	IV	
<u>Peromyscus leucopus</u>					
SS-A	No variables remained as predictors				
SS-B	No variables remained as predictors				
SS-C	2.786 (0.35)*	−2.686 (0.20) ^b	—	—	3.308
SS-D	2.332 (0.35)*	−2.392 (0.22) ^b	—	—	3.308
Slope	0.018 (0.35)*	—	—	—	0.002

*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

^a Dependent variables that were analyzed separately. SS-A through SS-D indicate mammal abundance in the four sampling periods. Slope is rate of change in abundance over four sampling periods. Values for dependent variables are given in Tables 1 and 2.

^b Indicates a partial R^2 value that was retained as a predictor due to parameters of test, but was not significant.

Appendix. Original variables used in principal component analysis and abbreviations used in Table 3.

No.	Abbreviation	Description
<u>Local variables</u>		
1	AGH	Average height (cm) of all grasses within quadrat.
2	AFH	Average height (cm) of all forbs within quadrat.
3	ALD	Average depth (cm) of vegetative litter within quadrat.
4	VOV	Visual obstruction value (range 0.0–18.0), measure of relative thickness of cover.
5	GC%	Percent cover of all grasses within quadrat.
6	FC%	Percent cover of all forbs within quadrat.
7	LC%	Percent cover of vegetative litter within quadrat.
8	BG%	Percent cover of bare ground within quadrat.
9	PTQ	Point-quarter method to measure the amount (no./100 m ²) of woody vegetation in woody patch.
10	PSZ	Patch size, measure of the areal coverage (m ²) of woody patches.
<u>Regional variables</u>		
11	MGD	Distance (m) to mixed grass prairie from center of woody patch.
12	TGD	Distance (m) to tallgrass prairie from center of woody patch.
13	RLD	Distance (m) to rangeland from center of woody patch.
14	AGD	Distance (m) to agriculture land use from center of woody patch.
15	BLFD	Distance (m) to bottomland forest from center of woody patch.
16	RPD	Distance (m) to riparian habitat from center of woody patch.
17	TPD	Distance (m) to nearest-neighbor woody patch from center of woody patch.
18	H2OD	Distance (m) to water from center of woody patch.

Appendix. continued.

No.	Abbreviation	Description
19	DAD	Distance (m) to disturbed area from center of woody patch.
20	RDD	Distance (m) to road from center of woody patch.
21 ^a	d1	Richness, number of cover types.
22 ^a	d3	Dominance (high values) versus evenness (low values) of cover types based on area.
23 ^a	e2	Sum of edges (m), total length of all edges separating cover types.
24 ^a	f1	Fractal dimension, complexity (high values) or lack thereof (low values) of perimeter for patches of all cover types.
25 ^a	m1	Mean perimeter/area, average for all patches of perimeter length divided by area (range from low values for small circular patches to high values for large circular patches, long, thin patches, or patches with extensive convolutions).
26 ^a	m2	Mean corrected perimeter/area, same as m1, but corrected for size (range 0.0 for circular patch to infinity).
27 ^a	m3	Mean related circumscribing circle, compares area of patch to area of smallest circumscribing circle (range 0.0 for elongated patches and/or patches with convoluted edges to 1.0 for circular patches).
28 ^a	t1	Contagion is the degree of clumping (high values) or lack thereof (low values) for cover types relative to the cover types present.
29 ^a	t2	Angular second moment is the homogeneity (high values) or lack thereof (low values) of the landscape.

^a Based on all cover types and patches within 1000 m of center of woody patches. For more detailed description, see Baker and Cai (1992).

Running head: Edge Effects on Small Mammals

EDGE EFFECTS ON SMALL MAMMALS ASSOCIATED WITH A
GRASSLAND-WOODY PATCH INTERFACE

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Edge habitat can result from anthropogenic activity and may have a measurable effect on wildlife. Previous authors have categorized edge effect as: (1) positive or negative; and (2) matrix (i.e., an attribute change at edge due to different habitats) or ecotonal (i.e., a unique response due to presence of edge habitat). We examined the influence of small, introduced woody patches in grassland and their associated edge on small mammals on Fort Sill Military Reservation (southwestern Oklahoma), sampling 20 sites grouped by treatment (8 control sites, grassland only; 12 experimental sites, woody patches surrounded by grassland). Except immediately adjacent to woody patches, the surrounding grassland at experimental sites was similar to that of controls. Captures per trap-night were calculated for trap transects located within woody patches, as well as 10, 25, 50, and 100 m away from the patches; similar sampling occurred at control sites. Edge associated with woody patches varied in its effect on grassland small mammals. Captures of all species combined were higher (i.e., a positive effect) within and closer to woody patches than at control sites, in part because Sigmodon hispidus, Peromyscus leucopus, and Neotoma floridana benefitted from woody patches and/or edge. Numbers of Microtus ochrogaster were lower (i.e., a negative effect), likely due to interactions with S. hispidus. All species combined, S. hispidus, and M. ochrogaster exhibited ecotonal effects that extended at least 10 m but not 25 m into the surrounding grassland, while N. floridana and P. leucopus showed matrix effects that ended near the patch edge. Although edge often is discernable to an investigator through structural characteristics of vegetation, our findings support the idea that, relative to small-mammal species, it may

be more useful to employ a functional description based on attributes of those species, such as abundance.

Key words: edge effect, Fort Sill Military Reservation, grassland, Oklahoma, small mammals, woody patch

Yahner (1988) defined edge as the junction of two different elements of a landscape. Changes in edge (e.g., length, width, and shape) may affect the abundance and diversity of wildlife across a landscape (Harris 1988; Heske 1995; Leopold 1933). While edge does occur naturally where two distinct habitats abut, it also may arise or change in both quality and quantity as a result of habitat loss and fragmentation. Therefore, increased understanding of edge effects relative to wildlife can be important when managing biodiversity, particularly as anthropogenic activities continue to create, increase, and alter edge habitat (Lidicker and Peterson 1999).

Delineating the dimensions (i.e., length and width) of edge may prove difficult and subjective for transitional zones between habitat types (Lidicker 1999). In such cases the dimensions of edges may better be described by how wildlife perceive the edge (i.e., a functional description) rather than through the investigator's perception of vegetation (i.e., a structural description; Gates and Mosher 1981; Yahner 1988). For example, induced edges that result from human modification of the landscape (e.g., road construction, power-line clearings, and agriculture) are usually abrupt and easily described structurally but may vary functionally relative to a species' response.

Edge may promote a positive or negative response, depending on the taxon and attribute of concern (Lidicker 1999; Lidicker and Peterson 1999; Mills 1995). At the interface of adjacent habitats, an increase in abundance of some species (i.e. a positive effect) may coincide with or result in displacement of others (i.e. a negative effect). Furthermore, the spatial extent of edge effects vary. For instance, predation on the nests of some birds extends as much as 600 m into forest (Wilcove 1985).

Lidicker and Peterson (1999) proposed that the influences of edge be viewed as either “matrix” or “ecotonal” effects. Matrix effects typically are sharp changes in an attribute brought about by changes in habitat. For example, as a result of a matrix effect, a species common to forests would be absent from grassland adjacent to forested habitat. However, when a transition zone between habitats occurs, the matrix effect also may be transitional. Ecotonal effects occur when a species exhibits a unique attribute due to the juxtaposition of habitat types. This is a response that the species does not exhibit in either habitat type when the habitats are not closely associated with one another. For example, a predator that is rare in grassland and rare in forests may be abundant along edge habitat at the grassland-forest interface due to an ecotonal effect.

Numerous investigators have evaluated edge effects on birds, particularly on their nesting success and risk to predation (e.g. Gates and Gysel 1978; Heske et al. 1999), but the phenomenon has been less well studied for mammals (Heske 1995). Investigations of voles (i.e., Microtus spp.) under experimental conditions (i.e., mowed and unmowed patches of grass) have focused on the effects of edge and patchy conditions (see Lidicker and Peterson 1999), but few researchers have examined responses of small mammals

under more natural settings. Ecological research involving habitat patches is of interest to resource managers and conservation biologists because current trends in land-use often result in isolated patches due to habitat fragmentation and other forms of landscape modification.

At Fort Sill Military Reservation in southwestern Oklahoma, small woody patches are maintained as wildlife habitat for species such as the white-tailed deer (Odocoileus virginianus) and wild turkey (Meleagris gallopavo). These woody patches of habitat were planted within an extensive grassland in the early to mid-1970s and provided us with the opportunity to examine small mammals in isolated habitat patches. We conducted research to examine the response of small mammals to a grassland-woody patch interface. Our goal was to determine the nature (i.e., positive or negative), type (i.e., matrix or ecotonal), and extent (i.e., distance from patch) of edge effect brought on by the juxtaposition of grassland and woody habitat patches. These woody patches were useful for studying possible edge effects in that the edge between the patch and grassland was well defined, and the spatial configuration was relatively simple, thus limiting the number of factors that potentially could be responsible for the abundance patterns observed. We expected that small mammals common to woody habitat would show a positive effect, while those common to grassland habitat would exhibit a negative effect, although this was not always the case. We interpret the edge effects as matrix or ecotonal based on a measure of abundance for small mammals and quantify the extent of edge effect through interpretation of results from data analyses.

MATERIALS AND METHODS

Study site.—We conducted our study on Fort Sill Military Reservation, a 38,300-ha installation situated within Comanche County (Fig. 1) in southwestern Oklahoma. Mean precipitation for this region is highest in May, while July and August are the hottest months (Johnson et al. 1990). This portion of Oklahoma includes a transition zone between mixed-grass prairie and uplands dominated by post oak (Quercus stellata) and blackjack oak (Q. marilandica). Fort Sill lies south of the Wichita Mountains Wildlife Refuge, extends eastward, and encompasses a variety of habitats. All sampling was conducted on the East Range (ca. 14,000 ha) of Fort Sill, where upland plains prevail. The most prevalent cover types on the East Range are mixed-grass prairie (42.0%), rangeland (25.1%), and tallgrass prairie (17.0%), with woody vegetation comprising 5.5%.

We sampled 20 sites (8 control and 12 experimental) on the East Range (Fig. 1). Control sites were located in remnants of continuous grassland and were not closely associated with woody vegetation. Experimental sites, consisting of woody patches of habitat surrounded by grassland, were selected based on criteria related to the presence of a woody patch, as well as its size and isolation. The areal coverage of woody patches used in our study ranged from 0.16 to 0.26 ha, and the distance from any of the patches to the nearest woody vegetation was always greater than 100 m.

Grassland associated with all sampling sites consisted of typical bluestem prairie, characterized by little bluestem (Schizachyrium scoparium), Scribner dichanthelium (Dichanthelium oligosanthos), big bluestem (Andropogon gerardii), and Indian grass

(Sorghastrum nutans; Johnson et al. 1990). At experimental sites, introduced woody patches—encircled by 5-m-wide plowed firebreaks—consisted of ornamental and native vegetation. Russian olives (Elaeagnus angustifolia) were planted by Fort Sill fish-and-wildlife personnel in the early to mid-1970s and were most common on the patches; naturally occurring species such as smooth sumac (Rhus glabra), black locust (Robinia pseudoacacia), Chickasaw plum (Prunus angustifolia), and Osage-orange (Maclura pomifera) typically were present but in lower numbers. Grasses and forbs were common in the woody patches.

Vegetation assessment.—While trapping mammals, we also sampled grassland vegetation to establish the degree of structural similarity in vegetation between control and experimental sites. We evaluated 8 variables: average height of grasses and forbs; average depth of litter; percent coverage of grasses, forbs, litter, and bareground; and a relative estimate of vegetation biomass based on visual-obstruction measurements (Robel et al. 1970). We conducted quadrat sampling twice (17 May–1 June and 18–21 June) in 1994 and twice (18 May–1 June and 18–28 June) in 1995. During each sampling period vegetation data were collected at 3 stations uniformly spaced at each of the trapping transects placed in grassland (i.e., 12 stations at experimental sites and 15 at control sites). At each sampling station a 0.5 by 0.5-m quadrat was randomly dropped and vegetation measurements recorded.

Small-mammal assessment.—Sherman traps (7.6 by 8.9 by 22.9 cm) were used to assess small mammals. We placed 5 transects of traps at each site. Each transect had 10 Sherman traps placed at 5-m intervals. At experimental sites, one transect was placed

within the woody patch, 5 m from the edge and parallel to it (Fig. 2). Four more transects were established in the surrounding grassland at intervals of 10, 25, 50, and 100 m from the edge and parallel to it. Control sites had an identical layout of 5 transects with similar spacing, but all traps were placed in open grassland.

We sampled small mammals during 4 trapping periods (16 May–1 June 1994, 16–21 June 1994, 17 May–2 June 1995, and 18–29 June 1995) for 4 consecutive nights at each site, resulting in 6400 trap-nights (i.e., 800 each at 8 sites) at control sites and 9600 trap-nights (i.e., 800 each at 12 sites) at experimental sites. In 1995, we were unable to reuse one of the experimental sites (E1A) established in 1994; it was replaced with an alternate site (E1B) close by.

Traps were opened in the late afternoon or early evening, baited with rolled oats, and checked the following morning. Captured specimens were marked (i.e., ear-tagged with metal tags, toe-clipped, or both) and released. Due to high temperatures, some mortality occurred. When practical, these specimens were prepared and deposited in the Sam Noble Oklahoma Museum of Natural History.

Data analysis.—We used a paired-comparison design 2-way ANOVA (Sokal and Rohlf 1995) to examine the effect of year (i.e., 1994 and 1995) on captures per trap-night at each site for all small mammals combined. There was no significant effect at sites due to year ($F = 0.12$, $d.f. = 1, 19$, $P > 0.05$), so we were able to combine data from both years for further analyses. We used a single-classification ANOVA (Sokal and Rohlf 1995) to compare control transects and experimental transects with respect to captures per trap-night for each of 8 species of small mammals and for all species combined. For

the ANOVA we combined data from all control transects but considered the 5 experimental transects separately for a total of 6 groups. If results were statistically significant, we proceeded with planned comparisons (Sokal and Rohlf 1995) between control transects ($\underline{n} = 40$) and each of the 5 experimental transects ($\underline{n} = 12$ each) considered separately.

We examined grassland vegetation in a similar manner. We combined data from both years and used a single-classification ANOVA to compare means of variables for control transects ($\underline{n} = 40$) and the 4 grassland transects ($\underline{n} = 12$ each) associated with woody patches. If results were statistically significant, we proceeded with planned comparisons of control transects and each experimental transect individually. The BIOMstat (Rohlf and Slice 1996) computer program was used in data analyses.

RESULTS

Vegetation.—Single-classification ANOVAs comparing vegetation variables indicated that experimental transects did not differ from controls for forb height and percent grass cover (Table 1). Planned comparisons revealed that the structure of grassland at experimental sites was different from controls for the other 6 variables at transects 10 m from the woody patches. Four variables were statistically different at 25 m and 2 at 50 m. Only litter depth deviated significantly at 100 m (Table 1). These results suggest a subtle edge effect in vegetation that may be related to the presence of woody patches and/or animals associated with them.

Mammals.—We captured 992 small mammals of 8 species at 20 sites. The most abundant species was Sigmodon hispidus, the hispid cotton rat (82 and 315 captures at

control sites and experimental sites, respectively), followed by (in order of total captures): Peromyscus leucopus, white-footed mouse (1 and 328); P. maniculatus, deer mouse (35 and 88); Microtus ochrogaster, prairie vole (59 and 32); Neotoma floridana, eastern woodrat (0 and 31); Reithrodontomys fulvescens, fulvous harvest mouse (5 and 10); Chaetodipus hispidus, hispid pocket mouse (0 and 5); and Blarina hylophaga, Elliot's short-tailed shrew (0 and 1). Peromyscus leucopus was the most commonly captured species at transects set within woody patches 5 m from the edge. Sigmodon hispidus was the most common at grassland transects 10 m, 25 m, and 50 m from the woody patch, and P. maniculatus was the most common 100 m from the woody patch (Table 2).

Single-classification ANOVAs revealed that captures per trap-night at experimental transects did not differ from controls for B. hylophaga, C. hispidus, and R. fulvescens. However, statistically significant differences did occur for 5 species and all species combined (Table 2; Fig. 3). Planned comparisons revealed that captures per trap-night at experimental transects located within woody patches and 5 m from the edge were different from those at control transects for 4 species and all species combined. Captures per trap-night at experimental transects set 10 m from the woody patch in surrounding grassland also were different from controls for 2 of those species and all species combined. Planned comparisons showed that captures per trap-night of P. maniculatus were significantly higher in grassland 100 m from the woody patch relative to those at control transects in grasslands isolated from wood patches, a result for which there is no obvious biological explanation.

DISCUSSION

We captured small mammals at transects associated with woody patches nearly three times as often as we did at transects in continuous grassland. Much of this deviation from the grassland controls can be directly attributed to the presence of woody patches (Fig. 3F). In general, woody patches and the edge associated with them have a positive effect on grassland small mammals as reflected by increased numbers. Furthermore, this positive effect appears to extend into the grassland habitat surrounding woody patches. At woody-patch sites, we captured small mammals more often at a distance of 10 m into the grassland than in continuous grasslands (Table 2; Fig. 3F). At distances greater than 10 m from woody patches, captures did not vary between control and experimental transects. Thus, there was a positive effect (i.e., increase in numbers of small mammals, all species combined) due to woody patches and edge that extends at least 10 m but not as much as 25 m into surrounding grassland habitat.

A matrix effect, as described by Lidicker (1999) and Lidicker and Peterson (1999), is present when a response is due solely to the positioning of different landscape elements next to one another. If this were the case for all species of small mammals at Fort Sill, we would have expected to find a similar number of individuals in grassland immediately adjacent to woody patches as that found in continuous grassland. This was not the case. It appears, based on differences between numbers of captures at 10 m from woody patches and control sites, that some emergent property is present, as we found small mammals to be more common in grassland adjacent to woody patches than the control. As indicated by examination of vegetation variables (Table 1), grassland

adjacent to woody patches is not the same as continuous grassland habitat in general structure, the edge being more structurally transitional than initial observations indicated. However, the difference in grassland surrounding woody patches and continuous grassland does not seem as influential as the obvious differences between woody habitat and grassland. Our data suggest that for small mammals an “ecotonal” effect occurs due to the presence of woody patches and concomitant with some transitional variation in grassland characteristics. A positive ecotonal effect exists for all species of small mammals combined that extends 10–25 m into the surrounding grassland. However, not all species of small mammals, when examined individually, exhibit this pattern.

We did not find differences in capture rates at transects associated with woody patches and those in continuous grassland for B. hylophaga, C. hispidus, and R. fulvescens. This reflects: (1) limited or no effect due to the presence of edge and the woody patch; and/or (2) lower statistical power due to the fact that these species were less frequently encountered. Blarina hylophaga is typically associated with woody habitat (Caire et al. 1989); Manson et al. (1999) found that an increase in its numbers was facilitated by predation on the young of other species associated with edge habitat. We would have expected an edge effect associated with this species, but since it was captured only once (i.e., within a woody patch) there was no basis for statistical comparison. Chaetodipus hispidus and R. fulvescens are both found in association with grassland habitat (Caire et al. 1989), but neither was commonly encountered at Fort Sill. Reithrodontomys fulvescens frequents grasslands closely associated with woody habitat

(Spencer and Cameron 1982) including transitional habitat and, as expected, we had more captures of the species 10 m from woody patches than at any other transect at both experimental and control sites.

Peromyscus leucopus is a species typically found in woody habitat throughout much of its range, including Oklahoma (Caire et al. 1989; Hays 1958). It is not common in grassland habitat but may be encountered during movements from one patch of woody habitat to another (Clark et al. 1987; Lackey et al. 1985; Schnell et al. 1980). At Fort Sill P. leucopus benefits directly from the presence of woody patches, but does not frequent the surrounding grassland at a greater rate than continuous grassland. The sharp decrease in captures from transects placed in woody patches to those 10 m away from them indicates a matrix effect. Peromyscus leucopus appeared to perceive the grassland surrounding woody patches in a similar way to that of continuous grassland. Due to the presence of woody patches and edge habitat, P. leucopus shows a positive matrix effect that is abrupt and clearly does not extend 10 m into the grassland.

Neotoma floridana, which shows a preference for woody habitat and grassland-woody habitat associations (Blair 1939; Caire et al. 1989; Goertz 1970; Hays 1958), was captured only in woody patches at Fort Sill. This species also showed a positive matrix effect due to the presence of woody patches.

Sigmodon hispidus is commonly found in habitats dominated by grassy cover (see Cameron and Spencer 1981). It may use grassy habitat in close association with overhead cover from woody species (Goertz 1964), thus gaining protection from climatic elements and predators, especially important over winter months (Fleharty et al. 1972;

Lidicker et al. 1992; Schnell 1968). Our findings suggest that the species gains an advantage both within and in surrounding grassland approaching 25 m from the edge of woody patches of habitat. The positive edge effect likely is ecotonal, as it extends into surrounding grassland.

Several investigators have reported on the influence of S. hispidus relative to other species (Brady and Slade 2001; Cameron and Spencer 1981). These are predominantly cases of direct interaction and interspecific competition between species that result in competitive exclusion and are based on space, not food (Fleharty and Olson 1969). Fleharty and Choate (1973) showed that 0.79 percent of the net primary productivity of a grassland in Kansas was ingested by S. hispidus during summer. This value likely is representative for our control sites as well; however, locally (e.g., adjacent to woody patches) the effect probably is more pronounced. For vegetation and small mammals, a number of the differences between control and experimental transects at 10 and possibly 25 m may be attributable to effects of foraging by this species.

Microtus ochrogaster is common to grasslands as far south as Oklahoma (Caire et al. 1989; Choate 1989; Stangl et al. 1992) and is found in habitat with dense grass cover for building runways and avoiding predators (Birney et al. 1976; Caire et al. 1989; Kaufman and Fleharty 1974; Stalling 1990). Numbers of captures for M. ochrogaster were lower within and adjacent to woody patches than found at control transects. The species exhibited a negative ecotonal effect that included the woody patch and approached 25 m into surrounding grassland from the patch edge. The effect appears to be ecotonal due in part to the influence of the dominant species, S. hispidus (Brady and

Slade 2001; Stalling 1990). At Fort Sill, S. hispidus may influence the abundance of M. ochrogaster indirectly by decreasing the amount of vegetative grass cover near woody patches to a level not suitable for M. ochrogaster (Birney et al. 1976), or directly by interactions (Stalling 1990; Terman 1974). Increased susceptibility to predation near edges (Yahner 1988) also may contribute to decreased abundance of M. ochrogaster closer to the woody-grassland interface.

Peromyscus maniculatus is a near-ubiquitous species commonly found in grassland habitat throughout Oklahoma (Caire et al. 1989). At Fort Sill, it is not commonly found in woody patches but does occur in surrounding habitat (T. W. Haner and G. D. Schnell, in litt.). Our results indicate that P. maniculatus exhibits a neutral response to the presence of woody patches and associated edge habitat. Microtus ochrogaster and P. maniculatus are strong competitors, with the latter showing a negative effect due to the interaction (Abramsky et al. 1979). However, P. maniculatus prefers grassland with less litter and overhead cover than that preferred by M. ochrogaster (Clark and Kaufman 1991; Clark et al. 1989). Interactions of P. maniculatus with S. hispidus are not well documented and, overall, interactions of P. maniculatus, M. ochrogaster, and S. hispidus warrant further ecological investigation, especially when one is locally dominant (Brady and Slade 2000).

While several attempts have been made to quantify the effects of edge habitat, no set protocol has been developed (Yahner 1988). Gates and Mosher (1981) compared three different methods for quantifying edge habitat. They considered one structural estimate derived from the investigators' perception of vegetation and two functional

approaches based on dispersion of nests of 5 bird species associated with edge habitat, concluding that functional approaches are ecologically more meaningful. While functional descriptions are likely the most ecologically realistic interpretations of edge habitat, a set protocol may not be feasible with the limited amount of information on edge currently available to ecologists. Our study adds to a much needed base of knowledge on the effects of patches and edge habitat on small mammals. Such information is critical to the management and preservation of species diversity as anthropogenic activities continue to reshape landscapes.

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LITERATURE CITED

ABRAMSKY, Z., M. I. DYER, AND P. D. HARRISON. 1979. Competition among small mammals in experimentally perturbed areas of the shortgrass prairie. *Ecology* 60:530–536.

- BIRNEY, E. C., W. E. GRANT, AND D. D. BAIRD. 1976. Importance of vegetative cover to cycles of Microtus populations. *Ecology* 57:1043–1051.
- BLAIR, W. F. 1939. Faunal relationships and geographic distribution of mammals in Oklahoma. *The American Midland Naturalist* 22:85–133.
- BRADY, M. J., AND N. A. SLADE. 2001. Diversity of a grassland rodent community at varying temporal scales: the role of ecologically dominant species. *Journal of Mammalogy* 82:974–983.
- CAIRE, W., J. D. TYLER, B. P. GLASS, AND M. A. MARES. 1989. Mammals of Oklahoma. The University of Oklahoma Press, Norman, Oklahoma.
- CAMERON, G. N., AND S. R. SPENCER. 1981. Sigmodon hispidus. *Mammalian Species* 158:1–9.
- CHOATE, L. L. 1989. Natural history of a relictual population of the prairie vole, Microtus ochrogaster, in southwestern Oklahoma. *Occasional Papers, The Museum, Texas Tech University* 129:1–20.
- CLARK, B. K., AND D. W. KAUFMAN. 1991. Effects of plant litter on foraging and nesting behavior of prairie rodents. *Journal of Mammalogy* 72:502–512.
- CLARK, B. K., D. W. KAUFMAN, E. J. FINCK, AND G. A. KAUFMAN. 1989. Small mammals in tall-grass prairie: patterns associated with grazing and burning. *The Prairie Naturalist* 21:177–184.
- CLARK, B. K., D. W. KAUFMAN, G. A. KAUFMAN, AND E. J. FINCK. 1987. Use of tallgrass prairie by Peromyscus leucopus. *Journal of Mammalogy* 68:158–160.

- FLEHARTY, E. D., AND J. R. CHOATE. 1973. Bioenergetic strategies of the cotton rat, Sigmodon hispidus. *Journal of Mammalogy* 54:680–692.
- FLEHARTY, E. D., J. R. CHOATE, AND M. A. MARES. 1972. Fluctuations in population density of the hispid cotton rat: factors influencing a “crash.” *Bulletin of the Southern California Academy of Sciences* 71:132–138.
- FLEHARTY, E. D., AND L. E. OLSON. 1969. Summer food habits of Microtus ochrogaster and Sigmodon hispidus. *Journal of Mammalogy* 50:475–486.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.
- GATES, J. E., AND J. A. MOSHER. 1981. A functional approach to estimating habitat edge width for birds. *The American Midland Naturalist* 105:189–192.
- GOERTZ, J. W. 1964. The influence of habitat quality upon density of cotton rat populations. *Ecological Monographs* 34:359–381.
- GOERTZ, J. W. 1970. An ecological study of Neotoma floridana in Oklahoma. *Journal of Mammalogy* 51:94–104.
- HARRIS, L. D. 1988. Edge effects and conservation of biotic diversity. *Conservation Biology* 2:330–332.
- HAYS, H. A. 1958. The distribution and movement of small mammals in central Oklahoma. *Journal of Mammalogy* 39:235–244.
- HESKE, E. J. 1995. Mammalian abundances on forest-farm edges versus forest interiors in southern Illinois: is there an edge effect? *Journal of Mammalogy* 76:562–568.

- HESKE, E. J., S. K. ROBINSON, AND J. D. BRAWN. 1999. Predator activity and predation on songbird nests on forest-field edges in east-central Illinois. *Landscape Ecology* 14:345–354.
- 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 U. S. Army Construction Engineering Research Laboratory, Champaign, Illinois. 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* 18:443–452.
- LACKEY, J. A., D. G. HUCKABY, AND B. G. ORMISTON. 1985. Peromyscus leucopus. *Mammalian Species* 247:1–10.
- LEOPOLD, A. 1933. Game management. Charles Scribner Sons, New York, New York.
- LIDICKER, W. Z., JR. 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14:333–343.
- LIDICKER, W. Z., JR., AND J. A. PETERSON. 1999. Responses of small mammals to habitat edges. Pp. 211–227 in *Landscape ecology of small mammals* (G. W. Barrett and J. D. Peles, eds.). Springer-Verlag, New York.
- LIDICKER, W. Z., JR., J. O. WOLFF, L. N. LIDICKER, AND M. H. SMITH. 1992. Utilization of a habitat mosaic by cotton rats during a population decline. *Landscape Ecology* 6:259–268.

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- MANSON, R. H., R. S. OSTFELD, AND C. D. CANHAM. 1999. Responses of a small mammal community to heterogeneity along forest-old-field edges. *Landscape Ecology* 14:355–367.
- MILLS, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. *Conservation Biology* 9:395–403.
- ROBEL, R. J., J. N. BRIGGS, A. D. DAYTON, AND L. C. HULBERT. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 33:295–297.
- ROHLF, F. J., AND D. E. SLICE. 1996. BIOMstat for Windows. Exeter Software, Setauket, New York.
- SCHNELL, G. D., R. D. OWEN, R. K. CHESSEY, AND P. G. RISSER. 1980. Populations of small mammals in north-central Oklahoma. *The Southwestern Naturalist* 25:67–80.
- SCHNELL, J. H. 1968. The limiting effects of natural predation on experimental cotton rat populations. *Journal of Wildlife Management* 32:698–711.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. W. H. Freeman and Company, New York, New York.
- SPENCER, S. R., AND G. N. CAMERON. 1982. Reithrodontomys fulvescens. *Mammalian Species* 174:1–7.
- STALLING, D. T. 1990. Microtus ochrogaster. *Mammalian Species* 355:1–9.

- STANGL, F. B., JR., W. W. DALQUEST, AND R. J. BAKER. 1992. Mammals of southwestern Oklahoma. Occasional Papers, The Museum, Texas Tech University 151:1–47.
- TERMAN, M. R. 1974. Behavioral interactions between Microtus and Sigmodon: a model for competitive exclusion. Journal of Mammalogy 55:705–719.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.
- YAHNER, R. H. 1988. Changes in wildlife communities near edges. Conservation Biology 2:333–339.

FIG. 1.—Map showing (1) Oklahoma; (2) enlarged Comanche County with boundary of Fort Sill Military Reservation; and (3) enlarged East Range with locations of sampling sites. Sites numbered from south to north. Control sites indicated by open circles and experimental sites by filled circles. Site E1A, sampled in 1994, was replaced with site E1B in 1995 due to military activity.

FIG. 2.—Layout of 50 traps in transects at an experimental site, consisting of a woody patch surrounded by grassland. The configuration for control sites was the same except that all transects were placed in grassland.

FIG. 3.—Deviation from control of number of captures per trap-night at experimental transects for: (A) Microtus ochrogaster; (B) Neotoma floridana; (C) Peromyscus leucopus; (D) P. maniculatus; (E) Sigmodon hispidus; and (F) all species combined. Shaded portion represents the woody patch. Symbols with white outer rings indicate statistically significant differences between experimental and control transects. For N. floridana, there were no captures for experimental or control transects at 10, 25, 50, and 100 m from the edge.

FIGURE 1

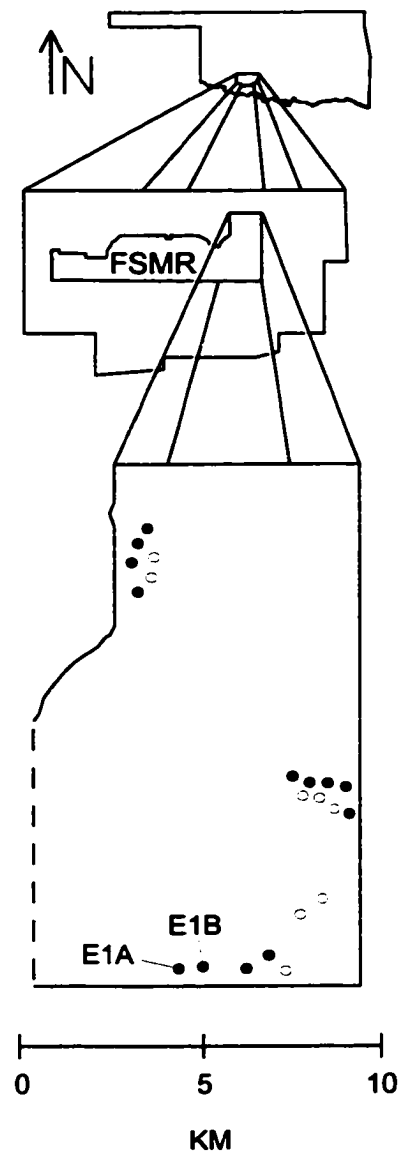


FIGURE 2

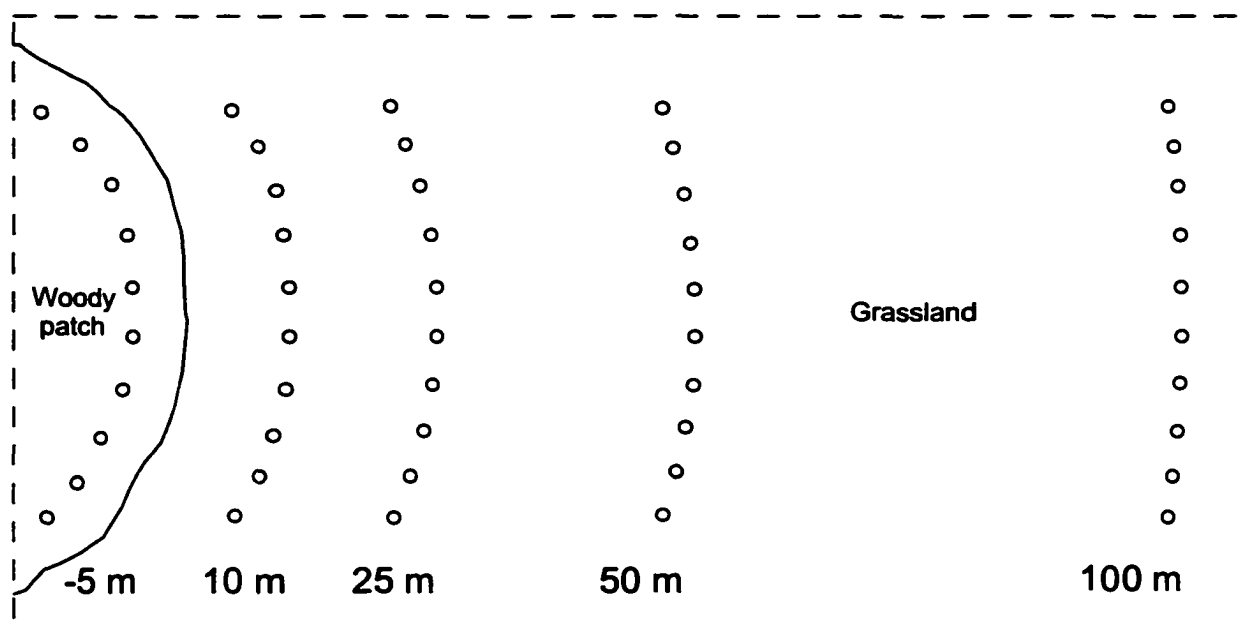


FIGURE 3

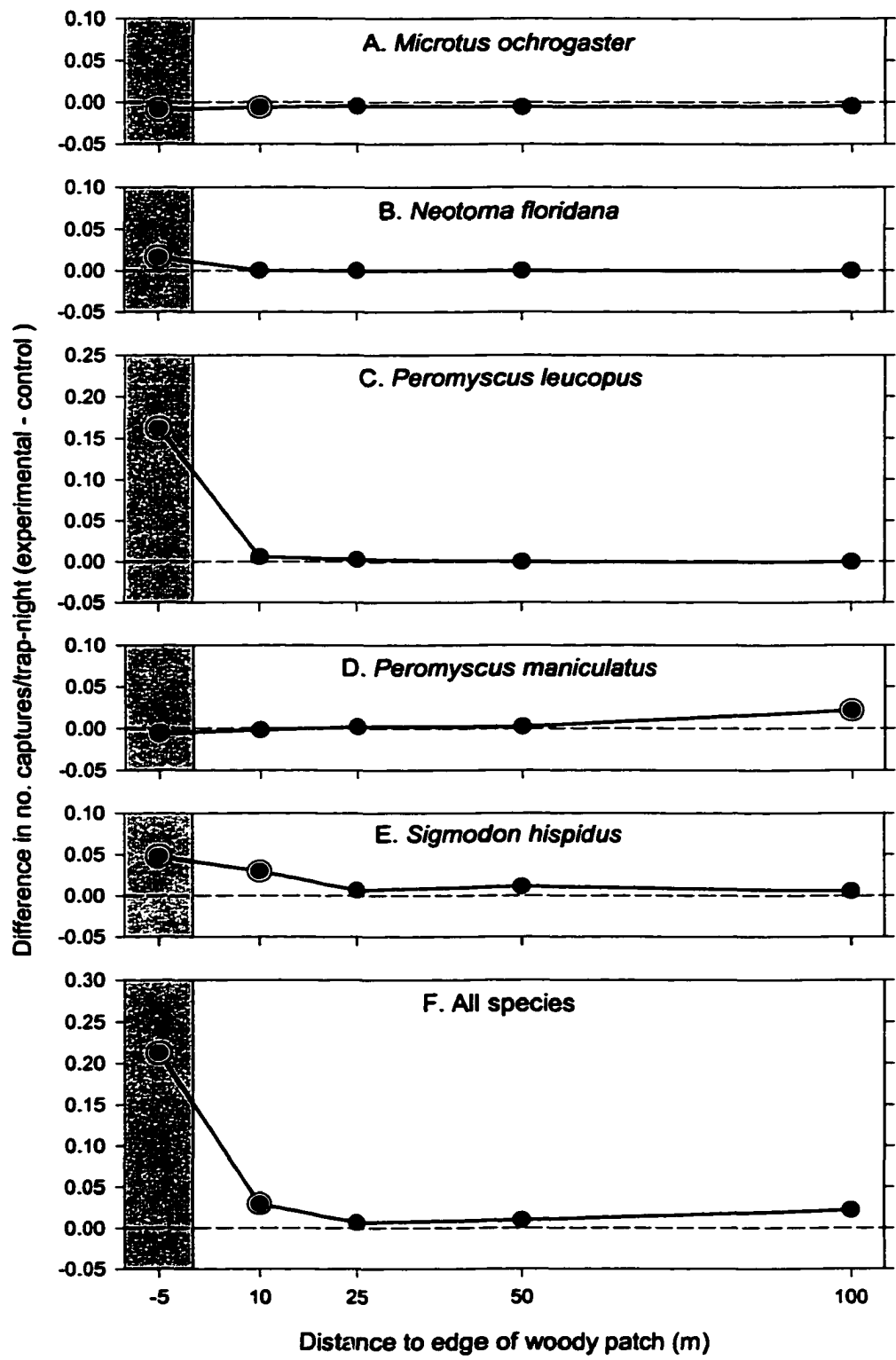


TABLE 1.—Means¹ of characteristics for grassland vegetation at experimental sites (woody patches of habitat surrounded by grassland; \bar{n} = 12) and control sites (continuous grassland; \bar{n} = 8). Values for control transects represent means for 40 control transects (5 at each of the 8 sites).

Vegetation variable ²	Transect ²				Control transects
	2 (10 m)	3 (25 m)	4 (50 m)	5 (100 m)	
Grass height (cm)**	34.4**	36.0*	36.5*	36.9	40.8
Forb height (cm)	29.8	29.6	28.9	29.0	28.3
Litter depth (cm)***	3.7***	3.9***	5.3*	4.7**	7.3
Visual obstruction*	3.0**	3.1	3.2	3.3	3.7
Percent grass cover	48.4	49.3	55.5	52.7	56.1
Percent forb cover***	22.3***	18.0**	13.7	15.5	11.7
Percent litter cover*	23.0**	28.3	27.0	28.4	31.6
Percent bare ground*	5.7**	4.5*	3.6	3.1	0.4

¹Means for experimental transects based on 144 samples (3 samples × 4 sampling periods × 12 sites) per transect, and means for control transects based on 480 samples (3 samples × 4 sampling periods × 8 sites × 5 transects).

²Asterisks following name of vegetation variable indicate statistically significant difference among 5 control and experimental groups in single-classification ANOVA (*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$), while those following transect means are for planned comparisons of specific experimental transects with controls.

TABLE 2.—Number of captures per trap-night¹ of small mammals associated with transects at experimental sites (woody patches of habitat surrounded by grassland; \bar{n} = 12) and control sites (continuous grassland; \bar{n} = 8). Values for control transects represent means for 40 control transects (5 at each of the 8 sites).

Species ²	Experimental transect ²					Control transects
	1 (-5 m)	2 (10 m)	3 (25 m)	4 (50 m)	5 (100 m)	
<u>Blarina hylophaga</u>	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000
<u>Chaetodipus hispidus</u>	0.0000	0.0005	0.0005	0.0016	0.0000	0.0000
<u>Microtus ochrogaster</u> *	0.0005**	0.0031*	0.0047	0.0036	0.0047	0.0092
<u>Neotoma floridana</u> ***	0.0161***	0.0000	0.0000	0.0000	0.0000	0.0000
<u>Peromyscus leucopus</u> ***	0.1625***	0.0057	0.0026	0.0000	0.0000	0.0002
<u>Peromyscus maniculatus</u> ***	0.0000	0.0036	0.0073	0.0078	0.0271***	0.0055
<u>Reithrodontomys fulvescens</u>	0.0005	0.0026	0.0005	0.0010	0.0005	0.0008
<u>Sigmodon hispidus</u> ***	0.0604***	0.0422**	0.0193	0.0240	0.0182	0.0128
All species***	0.2406***	0.0578*	0.0349	0.0380	0.0505	0.0284

¹Numbers for experimental transects based on 1920 trap-nights (10 trap-nights × 4 consecutive nights × 4 sampling periods × 12 sites) per transect, and numbers for control transects based on 6400 trap-nights (10 trap-nights × 4 consecutive nights × 4 sampling periods × 8 sites × 5 transects).

²Asterisks following species name indicate significant differences among 6 control and experimental groups in single-classification ANOVA (*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$), while those following numbers are for planned comparisons of specific experimental transects with controls.