AN ABSTRACT OF THE THESIS OF

Barry Faye Smart for the Degree of Master of Science in Biological Sciences presented on 21 April 2006.

Title:

ECOLOGICAL NEIGHBORHOODS OF SMALL MAMMAL COMMUNITIES AT FLINT HILLS NATIONAL WILDLIFE REFUGE, KANSAS: A MULTI-SCALE COMPARISON OF COMMUNITY AND HABITAT STRUCTURE

Abstract approved: ______________________
(Thesis Advisor Signature)

ABSTRACT

A multi-scale investigation was conducted to examine patterns of similarity among small mammal communities at the Flint Hills National Wildlife Refuge, Kansas, and determine at what scales these patterns of similarity correlated with habitat and landscape characteristics. Application of the ecological neighborhood concept requires scaling an investigation to a particular ecological process over an appropriate time period, and to the response or influence of the organism during that time. Although multiple processes determine small mammal community structure it is possible to infer the extent of the ecological neighborhoods by evaluating patterns of similarity of small mammal community structure and their environmental correlates. Monthly small mammal and vegetation surveys were conducted from June 2004 to August 2005 at nine sites representing three series of successional grasslands. A total of 5302 individuals consisting of 11 small mammal species was captured over 22,860 potential trapnights. Multi-scale spatial analysis was conducted at station, site, and landscape levels and temporal analysis by season and duration of the study (15 months). Ordination (non-

metric multidimensional scaling) and subsequent correlation analyses demonstrated a relationship between small mammal community structure and vegetation structure. Although small mammal community structure correlated with vegetation at site level, these correlations also existed at the station level, with more corresponding axes between the two ordinations. Thus, station-level vegetation was a better predictor of small mammal community structure than successional type, suggesting that the processes relating small mammal communities to vegetation operate at a scale finer than the patch. The general lack of association between landscape characteristics and small mammal community structure suggests differential access was not a determining factor in this system, except during the April-June season. During that time, it appears that larger scale processes influence small mammal communities than are acting during other times of the year.

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by

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PREFACE

My thesis will be submitted to *Ecological Applications* and is formatted for that journal.

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INTRODUCTION

The fact that scale affects the interpretation of ecological patterns has long been an important topic in the plant ecology literature (Watt 1947, Greig-Smith 1952), but it was not until the latter part of the 20th century that the concept of scale came to the forefront of zoological research (Addicott et al. 1987, Morris 1987, Turner 1989, Wiens 1989, Wiens and Milne 1989, Kotliar and Wiens 1990, Levin 1992). Ambiguous application of the term (scale) occurs extensively throughout the scientific community, often without a clear definition. A dictionary (Agnes 2002) definition of scale as "a system of grouping or classifying in a series of steps or degrees according to a standard of relative size, amount, rank, etc." alludes to the hierarchical nature of scale, but working definitions of scale vary among investigations. Wiens (1989) refers to scale as the extent (the overall area studied) relative to the grain (the individual units being studied) of an investigation indexed by time or space. Spatial scales can range from organs to hosts for parasite infracommunities (Zelmer and Seed 2004) to landscapes of hundreds of km^2 (Turner 1989), and temporal scales range from hours or days in microbial time to geological time scales of million of years. Scale within an ecological investigation can best be explained as the arbitrary spatial and temporal boundaries of the study (Addicott et al. 1987), but should be dependent on the question or processes being investigated.

Scaling investigations to processes is essential because patterns should be evident at the same scale as the observed processes (Addicott et al. 1987, Levin 1992). Scaling to an organism's response to, or influence on a particular process over an appropriate time period is a concept that has been formalized as an ecological neighborhood (Addicott et al. 1987). Application of the ecological neighborhood concept requires evaluation of the grain-response of organisms to environmental heterogeneity (Addicott et al. 1987). The response of an organism to a landscape level distribution of neighborhoods is coarse-grained, whereas the response of the organism within a neighborhood should be relatively fine-grained (Addicott et al. 1987). Given that the ability to detect patterns is a function of the extent and the grain of the investigation (Wiens 1989), investigations at multiple scales are essential for delineating the ecological neighborhood of a particular ecological process (Kotliar and Wiens 1990) because the perception of heterogeneity by the organism of interest might differ from that of the investigator.

Investigations focusing specifically on delineation of ecological neighborhoods are few (but see Ball 2002, DeAngelis and Peterson 2001), and many investigations matching spatial scales of patterns to processes have failed to evaluate the appropriate time scale, even though the importance of temporal scale was discussed. Temporal changes in environmental patterns might affect the mobility of organisms or life history, which could cause variation in the size of the ecological neighborhood (Addicott et al. 1987).

A variety of processes, occurring over different spatial and temporal scales, act together to determine community structure (Wiens 1989, Levin 1992). Small mammal communities are assemblages of generalist and specialist species that can be structured according to habitat characteristics (Morris 1996, 2005), with small mammal species richness and abundances reflecting the habitat structure within different ages of successional grassland (Swihart and Slade 1990, Churchfield et al. 1997, Fox and Fox 2000, Fox et al. 2003). Alternatively, spatial heterogeneity of the landscape could be a determining factor in movement and dispersal of organisms to preferred habitats (Wiens

1976, Johnson et al. 1992). In anthropogenically fragmented landscapes, differential access to patches by members of the regional species pool might be more pronounced than in contiguous landscapes (Wiens 1989, Diffendorfer et al. 1996, Fahrig 2003).

The present investigation is an examination of small mammal communities within three stages of successional grassland embedded in differing landscapes in an effort to detect the scale of small mammal response to habitat. A multi-scale approach, both spatially and temporally, was used to examine patterns of similarity among small mammal communities, and to determine at what scales these patterns of similarities correlated with habitat and landscape characteristics at the Flint Hills National Wildlife Refuge, Kansas.

If differential access to patches is a primary determining factor of community structure, patterns of community similarity should be associated with surrounding landscapes. If, however, patch-level processes are the primary determinants, similar community structure should be found within patches of similar habitat independent of the surrounding landscape. Processes governing community structure also might be operating at finer scales within a patch, which would produce patterns of similarity of community structure associated with patches of habitat within a larger, contiguous patch. During succession, vegetation structure becomes increasingly complex (Southwood 1996) but over the course of a growing season, grassland vegetation can change from cool or early season grasses and forbs to warm or late season grasses and forbs. If small mammal community structure does respond to habitat, small mammal assemblages should reflect seasonal changes of habitat with similar assemblages on similar patches. If competition is a dominant force, assemblages might differ among patches or vary at a smaller scale than the patch such that within-patch differences or similarities occur that cannot be explained by vegetation. Patterns of assemblage similarities then will reveal at what scale determining forces are acting, and provide clues to what the structuring forces are.

Vegetation community and small mammal community structures were analyzed at station, site, and landscape scale by season and overall time of investigation (15 months). Delineation of small mammal communities and vegetation communities, at station and site scales, was performed using non-metric multidimensional scaling (Kruskal 1964), in conjunction with "analysis of similarity" (Minchin 2005) to examine patterns of similarity of small mammal and vegetation communities. Multivariate analysis of landscape characteristics was performed using principal component analysis. Ordination axes of small mammal communities, vegetation, and landscape variables then were evaluated for covariance using Spearman rank correlation to determine an appropriate temporal and spatial scale to detect patterns of similarity.

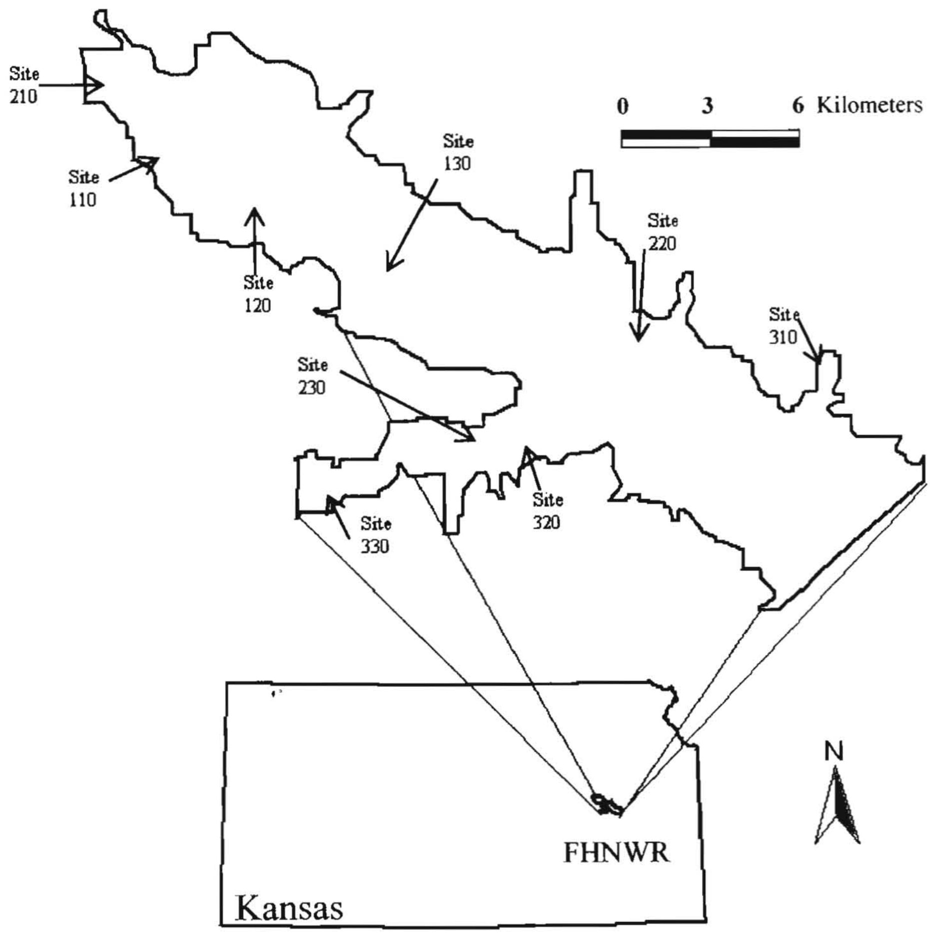
METHODS

Site description

The present investigation was conducted at the Flint Hills National Wildlife Refuge (FHNWR), Hartford, Kansas (Figure 1). The FHNWR is located within an ecotone region of tallgrass prairie to the west and eastern deciduous forest to the east. The refuge consists of 7487 hectares of annual crop fields, moist soil units, riparian areas, and restored and native grasslands bordering the Neosho River, within the floodplain of John Redmond Reservoir. Management by the U. S. Fish and Wildlife Service is for migratory waterfowl and native wildlife. Restoration of agricultural fields to grassland within the past decade provided the opportunity to study small mammal communities in varying stages of grassland succession. Management techniques used to restore desired grasslands included prescribed burning, mowing, and over-seeding. Short-term disturbances from flooding occur at least annually.

Three different grassland communities were selected for treatments: 1) newly restored fields planted in May 2004, 2) restored grasslands planted eight years (1986) prior to this investigation, and 3) native prairie. Newly restored sites were planted with warm season grasses including big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and western wheatgrass (*Elymus smithii*) and forbs including Illinois bundleflower (*Desmanthus illinoensis*), daisy fleabane (*Erigeron strigosus*), and showy partridge pea (*Cassia chamaecrista*). Previously restored grasslands were dominated by warm-season grasses such as big bluestem, Indian grass, and switchgrass, interspersed

FIGURE 1. Site locations at Flint Hills National Wildlife Refuge (FHNWR), Hartford, Kansas. Sites 110, 120, and 130 are newly restored sites. Sites 210, 220, and 230 are 8-yr restored sites. Sites 310, 320, and 330 are native sites.


Site
210
Site
110
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120
Site
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0 3 6 Kilometers
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310
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230
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Site
330
N
FHNWR
Kansas

with forbs. Native prairies were dominated by warm-season grasses, interspersed with woody vegetation and forbs. Three sites for each treatment (nine total sites) were chosen, with the proximity of >2 km among adjacent sites.

Small mammals

Small mammal surveys were conducted at all nine sites with three to five trapping stations per site (36 stations total). Permanent trapping stations were placed 100 m apart and no less than 100 m from the field edge. Trapping stations consisted of one chipmunk-sized Tomahawk live-trap (12.7 x 12.7 x 40.8 cm; Tomahawk Live Trap, Tomahawk, Wisconsin) located at the center of the station, surrounded by one large Sherman live-trap (10.2 x 11.4 x 38.1 cm; H. B. Sherman Traps, Tallahassee, Florida), and three small Sherman live-traps (7.6 x 7.6 x 22.9 cm) placed in the cardinal directions at five meters from the center. A 10-meter drift fence with 2-liter pitfalls buried at each end and in the center was placed 10 m from the center of the station. Holes were placed into the bottom of the pitfalls to allow water to drain. Tomahawk traps were baited with cracked corn, a mixture of peanut butter and oats, and mackerel. Sherman traps were baited with a mixture of peanut butter and oats. A small wad of cotton was added to the Sherman traps when temperatures were below 0°C to supply insulation. Pitfalls were baited with mackerel and a mixture of peanut butter and oats.

Simultaneous surveys of small mammals were conducted monthly from June 2004 to August 2005. Traps were locked open and baited for a 3-day pre-bait period, then unlocked, rebaited, and monitored for seven consecutive days. Captures were identified by species and sex, weighed, marked by toe clipping (or ear tags in the case of *Sigmodon hispidus*), location of capture, and the reproductive condition were recorded before release. Voucher specimens were collected for each species of small mammal and deposited at the Richard H. Schmidt Museum of Natural History, Emporia State University, Emporia, Kansas. Animal care and use followed guidelines set forth by the Emporia State University Animal Care and Use Committee (permit # ESU-ACUC-04-004). Relative frequencies of captured species were determined by dividing the number of unique individuals (for each trapping session) of a species by the number of functional trapnights specific to that species. Each trapping session was considered a "snapshot" of the community at a particular time period. Species specific functional trap nights were calculated by determining the type of trap(s) used to capture that species, then subtracting from the potential number of trap nights 1.0 for traps that were not functional, and 0.5 for traps that were disturbed or contained a recaptured individual (Songer et al. 1997).

Vegetation

Monthly local vegetation surveys were conducted at each trapping station and at an alternate sampling transect that was 50 m in the direction of the field edge from each station. The direction of the sampling transect from the station was alternated to obtain a representation of the vegetation of the site. The line-transect method was used, placing a 10 m tape measure on the ground, then recording the presence and coverage of each plant species or litter, bare ground, water, and stem. Height of vegetation at 1 m intervals along the transect was recorded within the following categories: 0-10 cm, 11-25 cm, 26-50 cm, 51-75cm, 76-100 cm, and >100 cm. Relative density of vegetation was calculated as the proportion of coverage of a species along the transect.

No surveys of vegetation or small mammals were conducted in November and December 2004. A flood event in June 2005 resulted in no surveys of vegetation or small mammals, with sites 110, 130, 210, 220, and 230 flooded over varying durations within the month. As a result of the flood, the standing vegetation within these sites was killed and did not recover by the end of the investigation.

Landscape

The habitat surrounding each site was characterized by creating a 1 km buffer around the site using ArcView 3.3 (Environmental Systems Research Institute, Inc. 2002*a*) and ArcView 8.3 (ESRI 2002*b*). Heads-up digitizing of satellite images (USDA-FSA-APFO 2004) was then used to categorize vegetation into land use categories (see Appendices). Land use was verified by on-site inspection. Categories of land use were: agricultural row crop, farmstead, brome grass, brome grass grazed, brome grass hayed, native grass, native grass and timber mix, native grass grazed, native grass hayed, newly restored grass, 8-year restored grass, restored grass, restored grass and timber mix, marsh, pond, riparian, river, road, and urban. Relative frequency of land use types of the surrounding landscape was calculated by proportion of land use area to total area of buffer.

Statistical analysis

Patterns of similarity among small mammal and vegetation communities were delineated by indirect gradient analysis, specifically non-metric multidimensional scaling (NMS) (Minchin 2005). Data were pooled by season and over the duration of the investigation (June 2004 through August 2005), both by station and site, using the relative frequencies of small mammals and relative densities of vegetation. Data were pooled from January-March, April-June, and July-October to evaluate seasonal changes. Given the absence of data for November and December, October was included with the

July-September season. Relative frequencies and relative densities were standardized to unit maxima. The Bray-Curtis measure of dissimilarity was used in the analysis. An analysis of similarity, a Monte Carlo procedure that tests the null hypothesis that dissimilarities between pairs of samples within a group were the same as dissimilarities between pairs of samples among groups, was conducted among treatments for each analysis using ANOSIM in the DECODA software (Minchin 2005). Correlation of three axes of the ordination of small mammal communities and vegetation by seasons and overall was performed using Spearman rank correlation (Systat Software, Inc. 2004).

The land-uses surrounding each site were constant site-specific characters and thus principal component analysis (PCA) in PCOrd, version 4.32 (McCune and Medford 1999), was used to categorize sites based on the similarity of their landscapes. Ordinations (NMS) of small mammal composition were performed using the sites' seasonal total relative frequencies and sites' overall relative frequencies. Spearman rank correlation (Systat Software, Inc. 2004) was used to examine correlations between seasonal and overall community composition and land use surrounding the sites.

RESULTS

Small mammals

A total of 5302 individual mammals within 11 species was captured over 22,860 potential trapnights. To calculate relative frequencies of small mammal species, 2539 unique individuals over 21,853 functional trapnights were used (Table 1). Ninety-six percent of the unique individuals captured in this study were representatives of the six most abundant species: 48% *S. hispidus* (hispid cotton rat), 24% *Peromyscus maniculatus* (deer mouse), 8% *Reithrodontomys megalotis* (western harvest mouse), 6% *Microtus ochrogaster* (prairie vole), 6% *Cryptotis parva* (least shrew), and 4% *Peromyscus leucopus* (white-footed mouse) (Table 1).

Non-metric multidimensional scaling by stations during the overall time of the investigation did not show clear grouping by treatments in two dimensional space (Figure 2) but there was significant pairwise dissimilarity of small mammal composition between newly restored and 8-yr restored treatments ($R = 0.157$, $p < 0.001$) and newly restored and native treatments ($R = 0.276$, $p < 0.001$). For station-level ordination of small mammal communities by season, the pairwise dissimilarity of small mammal community composition was significant among the three treatments for January-March and April-June periods (Table 2). There were significant pairwise dissimilarities among the community composition at the station level between newly restored and 8-yr restored treatments, and the newly restored and native prairie treatments in the July-October period (Table 2).

Small mammal composition did not show clear grouping by treatment in NMS at the site level, overall (Figure 3). There were significant pairwise dissimilarities of small

TABLE 1. Unique individuals by species captured by site treatment from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. Species abbreviations are: Sihi – *Sigmodon hispidus*, Pema – *Peromyscus maniculatus*, Reme – *Reithrodontomys megalotis*, Mioc – *Microtus ochrogaster*, Crpa – *Cryptotis parva*, Pele – *Peromyscus leucopus*, Mumu – *Mus musculus*, Syco – *Synaptomys cooperi*, Blhy – *Blarina hylophaga*, Nefl – *Neotoma floridana*, Zahu – *Zapus hudsonius*.

Treatment	Species										
	Sihi	Pema	Reme	Mioc	Crpa	Pele	Mumu	Syco	Blhy	Nefl	Zahu
Newly Restored	137	323	97	26	79	14	29	1	5	0	0
8-yr Restored	566	190	78	36	33	25	3	0	7	0	0
Native Prairie	516	89	34	99	47	67	3	19	5	10	1
Totals	1219	602	209	161	159	106	35	20	17	10	1

FIGURE 2. Non-metric multidimensional scaling of small mammal communities at each station from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. (N = 395)

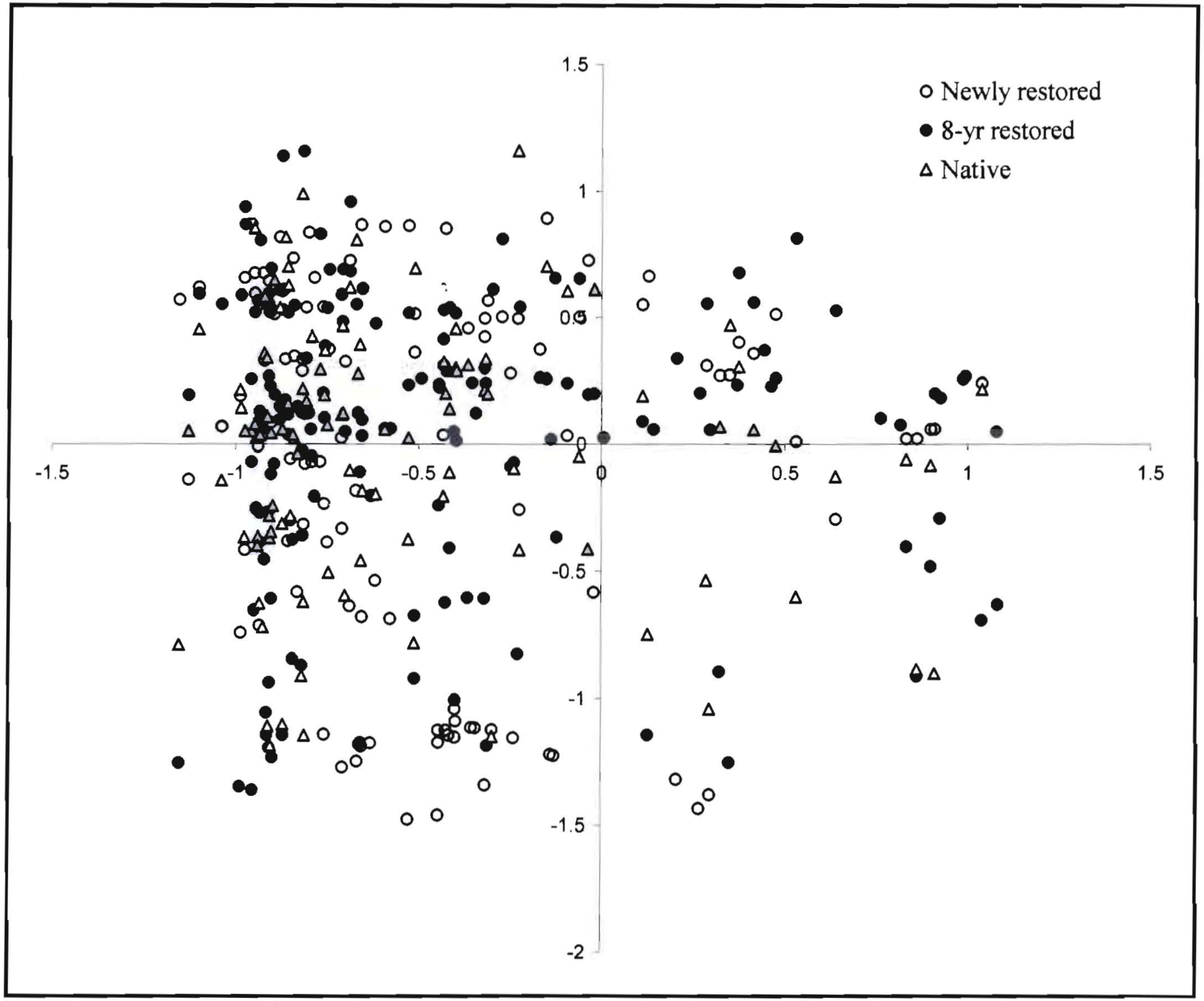
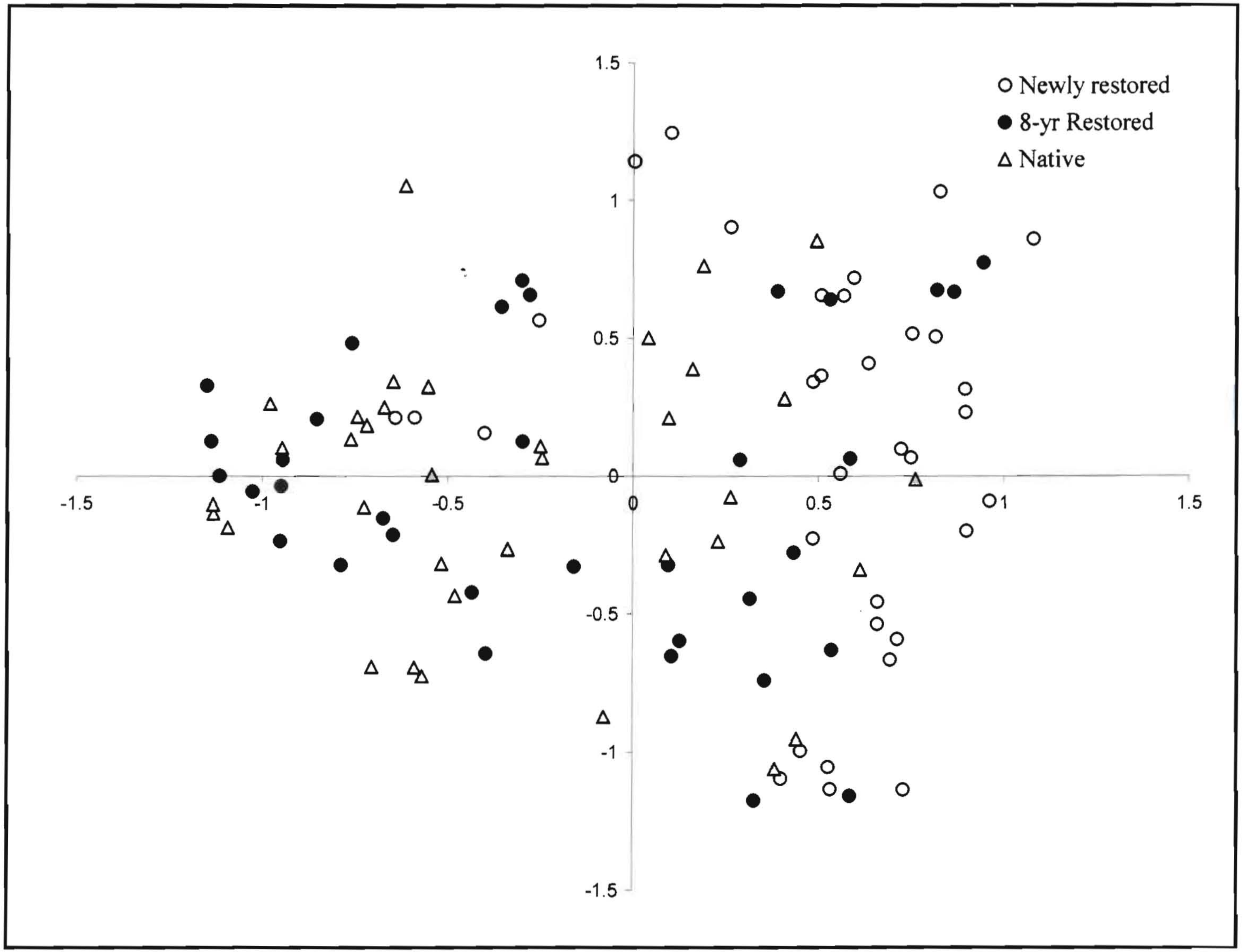

Newly restored
8-yr restored
Native
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5

TABLE 2. Results of analysis of similarity for small mammal communities by treatments of newly restored, 8-yr restored, and native grasslands at different temporal scales from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. Significance indicates pairwise dissimilarity of community composition among treatments is greater than dissimilarities within treatments.

		Overall		January-March		April-June		July-October	
Treatment		New	8-yr	New	8-yr	New	8-yr	New	8-yr
Stations									
8-yr	*R*	0.157		0.294		0.059		0.264	
	p	***<0.001***		***<0.001***		***0.021***		***<0.001***	
Native	*R*	0.276	-0.009	0.214	0.169	0.356	0.060	0.351	0.018
	p	***<0.001***	*0.772*	***<0.001***	***<0.001***	***<0.001***	***0.035***	***<0.001***	*0.846*
Sites									
8-yr	*R*	0.155		0.274		0.039		0.068	
	p	***<0.001***		***0.010***		*0.267*		*0.079*	
Native	*R*	0.307	0.053	0.184	0.091	0.315	0.107	0.155	0.025
	p	***<0.001***	***0.018***	***0.034***	*0.134*	*0.107*	*0.112*	***0.002***	*0.682*

Note: Significant differences are shown in boldface

FIGURE 3. Non-metric multidimensional scaling of small mammal communities by site from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. (N = 105)


Newly restored
8-yr Restored
Native
1.5
1
0.5
0
-0.5
-1
-1.5
-1.5
-1
-0.5
0
0.5
1
1.5

mammal communities during the overall time period at site level between newly restored and 8-yr restored treatments ($R = 0.155$, $p < 0.001$), newly restored and native treatments ($R = 0.307$, $p < 0.001$), and 8-yr restored and native treatments ($R = 0.053$, $p = 0.018$). Seasonally at site-level, January-March had significant pairwise dissimilarities of community composition between newly restored and 8-yr restored treatments, and between newly restored and native prairie treatments, July-October had a significant pairwise dissimilarity of community composition at the site level between the newly restored and native prairie treatments, while April-June period had no significant pairwise differences among small mammal communities (Table 2).

Vegetation

Ninety-one vegetation species and ground variables were used in the vegetation analysis (Appendix A). Grasses were the most abundant species in the three treatments overall (Table 3). Seasonally, the dominant variables observed during the January-March period were ground variables (litter, bare ground, water, and stem) in each of the three treatments, with grasses species being the dominant variable observed during the April-June and July-October periods (Table 3).

Non-metric multidimensional scaling of vegetation by station during the overall time (Figure 4) and by site during the overall time (Figure 5) showed significant pairwise dissimilarities among the three treatments (Table 4). Seasonally at the station level and site level, significant pairwise dissimilarities were found among all three treatments (Table 4).

Landscape

The first three axes of the PCA ordination of landscape characteristics

TABLE 3. Relative frequency of vegetation types by treatment at different time periods from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. Vegetation variables are grouped by classes and LBWS (litter, bare ground, water, and stem) (see Appendix A).

		Vegetation Variables			
Treatment	Season	LBWS	Woody	Grasses	Forbs
Newly restored					
	Overall	0.33	0.00	0.42	0.24
	January-March	0.66	0.00	0.26	0.07
	April-June	0.18	0.00	0.44	0.38
	July-October	0.24	0.00	0.49	0.26
8-yr restored					
	Overall	0.27	0.00	0.48	0.25
	January-March	0.65	0.00	0.32	0.03
	April-June	0.12	0.00	0.60	0.28
	July-October	0.16	0.00	0.50	0.34
Native prairie					
	Overall	0.18	0.16	0.44	0.22
	January-March	0.61	0.08	0.27	0.04
	April-June	0.08	0.19	0.49	0.24
	July-October	0.02	0.19	0.50	0.29

FIGURE 4. Non-metric multidimensional scaling of vegetation communities at each station from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. (N = 432)

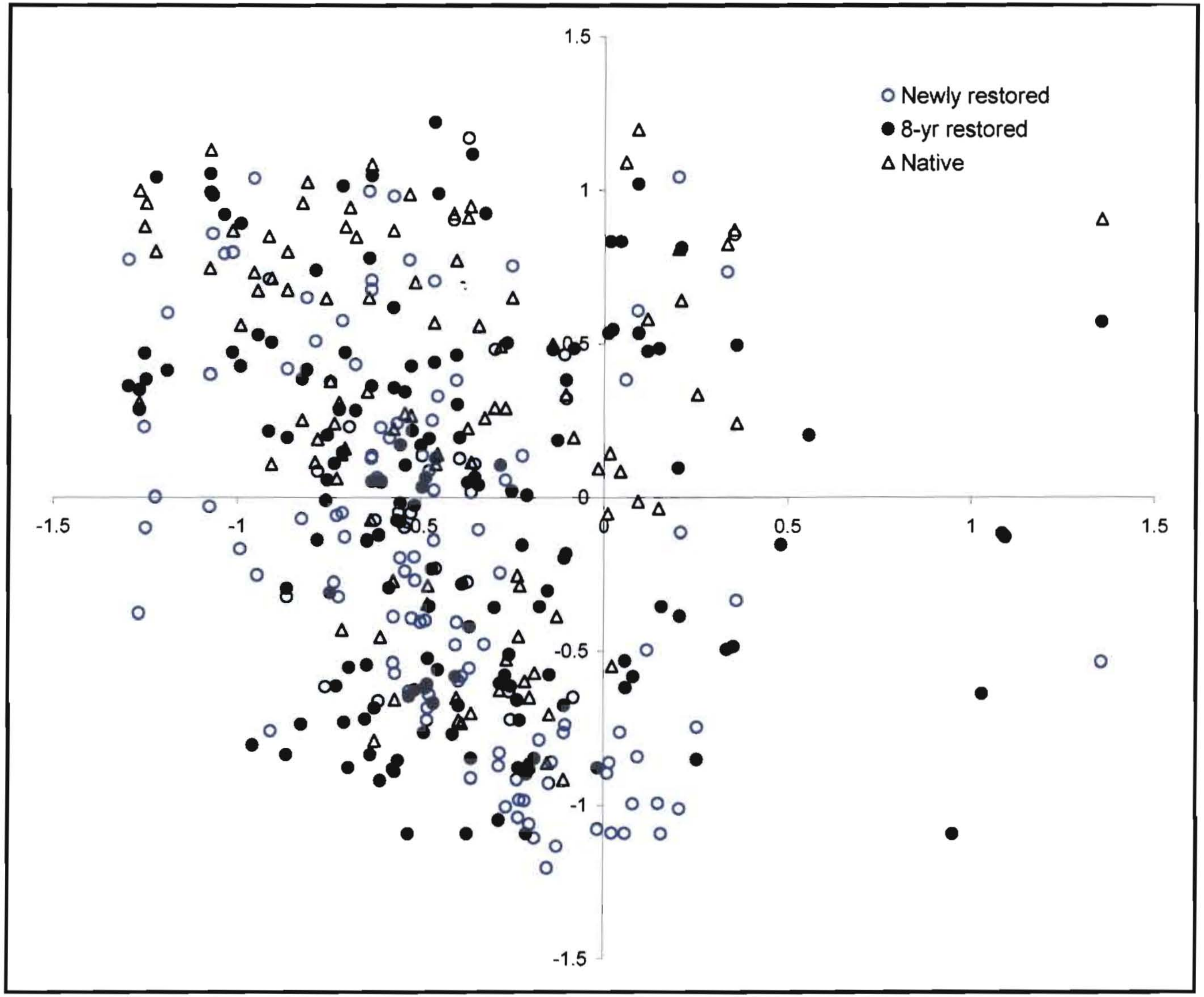
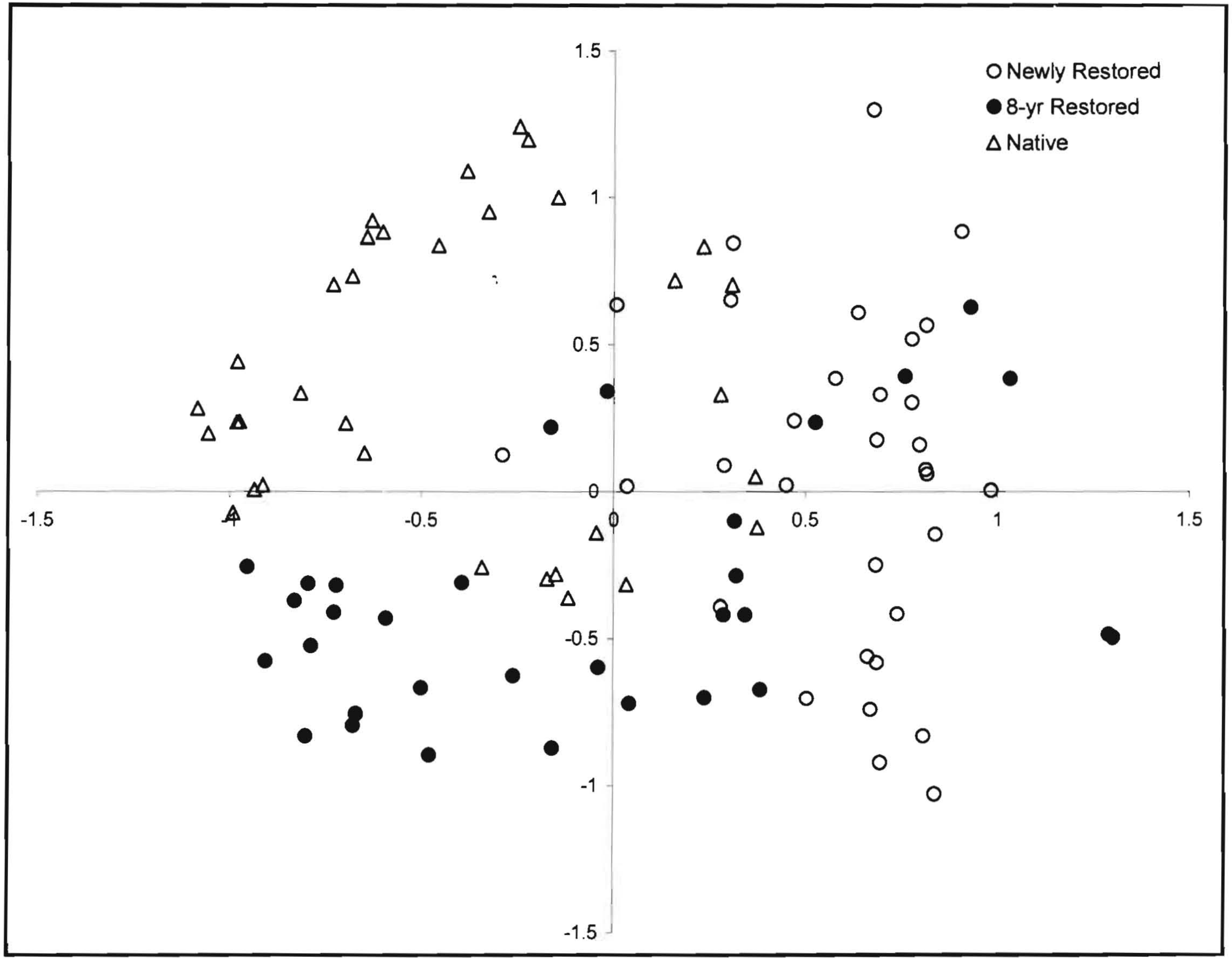

Newly restored
8-yr restored
Native
1.5
1
0.5
0
-0.5
-1
-1.5
-1.5
-1
-0.5
0
0.5
1
1.5

FIGURE 5. Non-metric multidimensional scaling of vegetation communities at each site from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. (N = 105)



Newly Restored
8-yr Restored
Native
1.5
1
0.5
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-1
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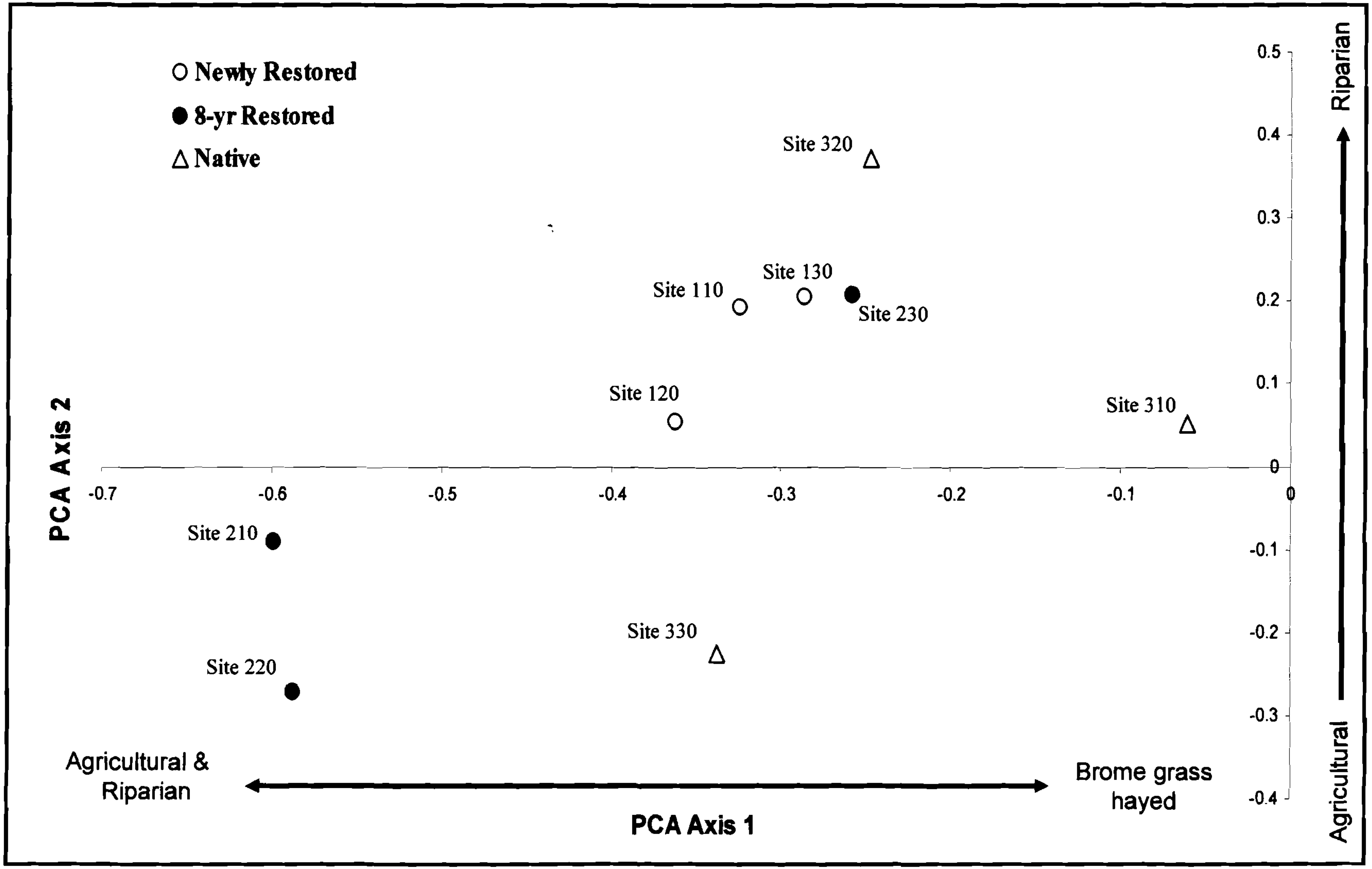
-1.5
-1
-0.5
0
0.5
1
1.5

TABLE 4. Results of analysis of similarity for vegetation communities by treatment of newly restored, 8-yr restored, and native grasslands at different temporal scales from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. Significance indicates pairwise dissimilarity of community composition among treatments is greater than dissimilarities within treatments.

		Overall		January-March		April-June		July-October	
Treatment		New	8-yr	New	8-yr	New	8-yr	New	8-yr
Stations									
8-yr	*r*	0.245		0.144		0.059		0.393	
	P	***<0.001***		***<0.001***		***0.021***		***<0.001***	
Native	*r*	0.338	0.262	0.370	0.255	0.356	0.060	0.644	0.400
	P	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***0.035***	***<0.001***	***<0.001***
Sites									
8-yr	*r*	0.390		0.219		0.282		0.606	
	P	***<0.001***		***<0.001***		***0.005***		***<0.001***	
Native	*r*	0.581	0.469	0.740	0.374	0.575	0.577	0.816	0.675
	P	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***

Note: Significant differences are shown in boldface.

FIGURE 6. Principal component analysis of landscape characteristics surrounding each site from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. (N = 9)


O Newly Restored
● 8-yr Restored
Δ Native
Site 320
Site 130
Site 110
Site 230
Site 120
Site 310
Site 210
Site 330
Site 220
PCA Axis 2
PCA Axis 1
Agricultural &
Riparian
Brome grass
hayed
Riparian
Agricultural
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.7
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
0

surrounding the sites (Figure 6) explained 83% of the variation among the sites. Axis 1 explained 55% of the variation with sites with high values tending to have hayed brome grass and sites with low values tending to have agricultural row crops and riparian areas. For axis 2 (17% of the variation) sites with high values tending to have riparian areas and sites with low values tending to have agricultural row crops. On axis 3 (11% of the variation) sites with high values tending to have newly restored grass and sites with low values tending to have native grass (Table 5). Analysis of similarity of PCA axis scores indicated no significant pairwise differences between land use surrounding a site and the site's treatment type [newly restored and 8-yr restored treatments ($R = 0.148$, $p = 0.399$), newly restored and native treatments ($R = 0.185$, $p = 0.196$), or 8-yr restored and native treatments ($R = 0.037$, $p = 0.518$)].

Comparisons of communities: correlations of ecological distances

Small mammal community structure and vegetation community structure varied within and across sites throughout the study. All three small mammal community NMS axes (MamNMS) covaried with axes from vegetation community NMS (VegNMS) during the overall time by station, with MamNMS Axis 1 positively correlated with VegNMS Axis 1 ($r_s = 0.462$, $p < 0.001$), VegNMS Axis 2 ($r_s = 0.134$, $p = 0.008$), and VegNMS Axis 3 ($r_s = 0.325$, $p < 0.001$); MamNMS Axis 2 was positively correlated with VegNMS Axis 2 ($r_s = 0.117$, $p = 0.020$) and negatively correlated with VegNMS Axis 3 ($r_s = -0.348$, $p < 0.001$); MamNMS Axis 3 was negatively correlated with VegNMS Axis 1 ($r_s = -0.114$, $p = 0.023$). For the seasonal ordinations, by station, the July-October period had three axes of the mammal ordinations that covaried with all three axes of the vegetation ordination, the January-March period had two axes of the small mammal

TABLE 5. Eigenvector values of principal component analysis ordination of land uses surrounding sites from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.

	Eigenvectors values		
Land Use	Axis 1	Axis 2	Axis 3
Agricultural row crop	-0.8214	-0.5087	0.0605
Farmstead	-0.0208	0.0290	-0.0162
Brome grass	-0.0664	-0.1407	-0.1402
Brome grass grazed	-0.0118	-0.0249	-0.0248
Brome grass hayed	-0.0032	0.0014	0.0020
Native grass	-0.0651	0.0444	-0.7459
Native grass grazed	-0.0861	0.2314	-0.2440
Native grass hayed	-0.0955	0.2430	-0.0223
Native grass & timber mix	-0.0448	-0.0845	-0.1727
Newly restored grass	-0.0938	0.1504	0.0952
Restored grass	-0.0545	0.1221	0.0278
Restored grass & timber mix	-0.0064	0.0154	-0.0065
8-yr restored grass	-0.1135	0.0445	-0.0213
Marsh	-0.1883	0.4497	-0.0057
Pond	-0.0316	0.0226	-0.4398
Riparian	-0.4613	0.5883	0.1426
River	-0.1222	-0.0386	-0.0211
Road	-0.0652	0.0103	-0.3180
Urban	-0.0671	0.0900	0.0630

ordination that covaried with three axes of the vegetation ordination, and the April-June period had two axes of the small mammal ordination that covaried with two axes of the vegetation ordination (Table 6).

Site-level ordinations had three axes of the small mammal ordination that covaried with three axes of the vegetation ordination during the overall period, with MamNMS Axis1 positively correlated with VegNMS Axis1 ($r_s = 0.677$, $p < 0.001$), MamNMS Axis2 positively correlated with VegNMS Axis3 ($r_s = 0.382$, $p < 0.001$), and MamNMS Axis 3 positively correlated with VegNMS Axis1 ($r_s = 0.272$, $p = 0.005$). The January-March ordination had two axes that covaried for the small mammal and vegetation ordinations, the April-June ordinations had two axes that covaried for the small mammal and vegetation ordinations, and the July-October ordinations had one axis that covaried for the small mammal and vegetation ordinations (Table 7). Ordinations of small mammal community, vegetative community, and landscape characteristics (LanPCA) by site produced a significant correlation between MamNMS axis 1 and VegNMS Axis 1 ($r_s = -0.733$, $p = 0.020$) and between MamNMS Axis 1 and LanPCA Axis 1 ($r_s = -0.833$, $p = 0.002$) during the April-June season.

TABLE 6. Spearman rank correlation results for non-metric multidimensional scaling axes of small mammal communities and vegetation communities at the station level for different time periods from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.

Time	n	Mammal		Vegetation Axis 1	Vegetation Axis 2	Vegetation Axis 3
Overall	395	Axis 1	r_s	0.462	0.134	0.325
			p	**<0.001**	**0.008**	**<0.001**
		Axis 2	r_s	0.075	0.117	-0.348
			p	0.139	**0.020**	**<0.001**
		Axis 3	r_s	-0.114	-0.096	0.033
			p	**0.023**	0.056	0.519
January-March	108	Axis 1	r_s	0.399	0.141	0.504
			p	**<0.001**	0.145	**<0.001**
		Axis 2	r_s	0.218	0.417	0.021
			p	**0.024**	**<0.001**	0.829
		Axis 3	r_s	-0.025	-0.196	-0.069
			p	0.794	**0.043**	0.479
April-June	104	Axis 1	r_s	-0.626	0.175	0.004
			p	**<0.001**	0.076	0.966
		Axis 2	r_s	0.082	-0.093	0.207
			p	0.410	0.350	**0.035**
		Axis 3	r_s	-0.076	0.297	-0.125
			p	0.444	**0.002**	0.205
July-October	183	Axis 1	r_s	-0.466	0.027	0.150
			p	**<0.001**	0.721	**0.043**
		Axis 2	r_s	0.003	0.238	-0.164
			p	0.970	**<0.001**	**0.027**
		Axis 3	r_s	-0.014	-0.053	0.185
			p	0.849	0.478	**0.012**

Note: Significant correlations are shown in boldface

TABLE 7. Spearman rank correlation results for non-metric multidimensional scaling axes of small mammal communities and vegetation communities at site level for different time periods from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.

Time	n	Mammal		Vegetation Axis 1	Vegetation Axis 2	Vegetation Axis 3
Overall	105	Axis 1	r_s	0.677	0.022	0.052
			p	**<0.001**	0.826	0.597
		Axis 2	r_s	0.002	-0.017	0.382
			p	0.983	0.862	**<0.001**
		Axis 3	r_s	0.272	-0.084	-0.088
			p	**0.005**	0.394	0.374
January-March	27	Axis 1	r_s	-0.174	0.146	0.250
			p	0.382	0.464	0.207
		Axis 2	r_s	0.400	-0.067	0.662
			p	**0.038**	0.736	**<0.001**
		Axis 3	r_s	-0.479	-0.116	0.036
			p	**0.012**	0.561	0.856
April-June	27	Axis 1	r_s	-0.606	-0.158	0.340
			p	**<0.001**	0.429	0.082
		Axis 2	r_s	0.016	0.564	0.313
			p	0.936	**0.002**	0.110
		Axis 3	r_s	0.030	-0.320	0.315
			p	0.880	0.103	0.108
July-October	51	Axis 1	r_s	-0.575	0.028	-0.194
			p	**<0.001**	0.842	0.172
		Axis 2	r_s	0.248	0.098	0.020
			p	0.080	0.495	0.887
		Axis 3	r_s	-0.089	-0.060	-0.214
			p	0.534	0.675	0.131

Note: Significant correlations are shown in boldface.

Discussion

The scale at which changes occur in patterns of similarity of small mammal communities can be detected. Associations of these changes with habitat characteristics can provide insight to the processes that are influencing the community and the scale at which those processes operate. If processes occurring at the landscape level (i.e., limitations on dispersal) are the most influential on community structure, then patterns of similarity of small mammal communities should correspond to the landscape characteristics surrounding the sites. If, however, processes at the site level are the most influential determinants of structure, then patterns of community similarities should correlate with similarities in vegetation or other habitat characteristics at the site level. Processes occurring at a finer scale, such as patch within a patch, should produce patterns of similarity of small mammal community structure that are associated with the habitat immediately surrounding the trapping stations.

Temporal variation in the small mammal community structure was observed at both the station and site level (Table 2). Small mammal populations fluctuate seasonally, annually, and multi-annually (Merritt et al. 2001, Brady and Slade 2004). Temporal variation in community structure might be due to the influence of a dominant species (Brady and Slade, 2004). The high relative frequency of *S. hispidus* suggests a disproportionate influence on community structure in native sites (Figure 7) and two 8-yr restored sites (Figure 8). In the newly restored sites (Figure 9), there was no abundant species common among the sites, and no apparent dominance of *S. hispidus* in the summer months, as was seen in the other treatments. Newly restored sites were inhabited mainly by smaller species such as *P. maniculatus*, *M. musculus*, and *R. megalotis*. The

FIGURE 7. Relative frequency of the most abundant small mammal species in the native treatment by site from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. For definition of species abbreviation see Table 1.

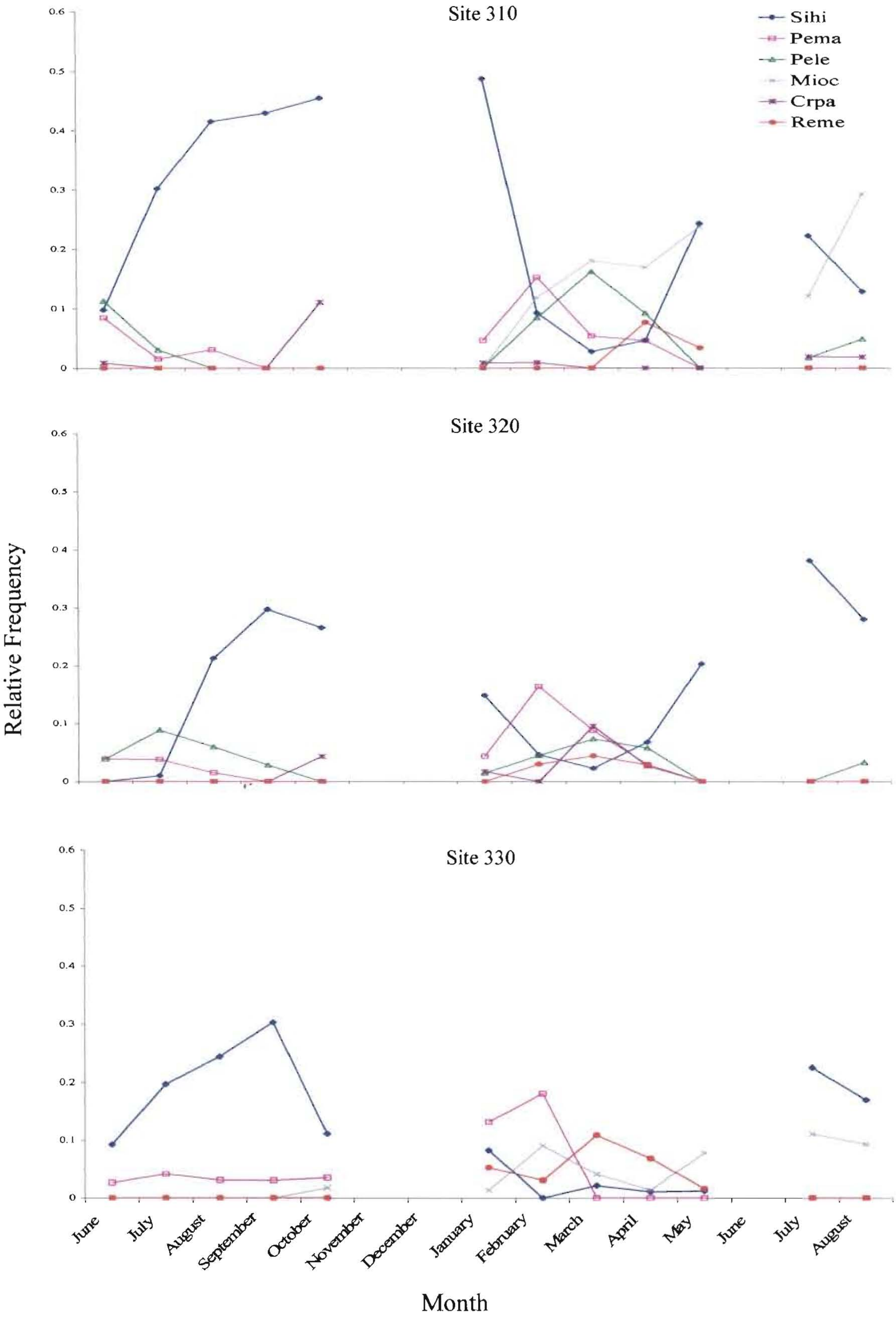

Site 310
Sihi
Pema
Pele
Mioc
Crpa
Reme
Site 320
Site 330
Relative Frequency
0
0.1
0.2
0.3
0.4
0.5
0.6
June
July
August
September
October
November
December
January
February
March
April
May
June
July
August
Month

FIGURE 8. Relative frequency of the most abundant small mammal species in the 8-yr restored treatment by site from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. For definition of species abbreviation see Table 1.

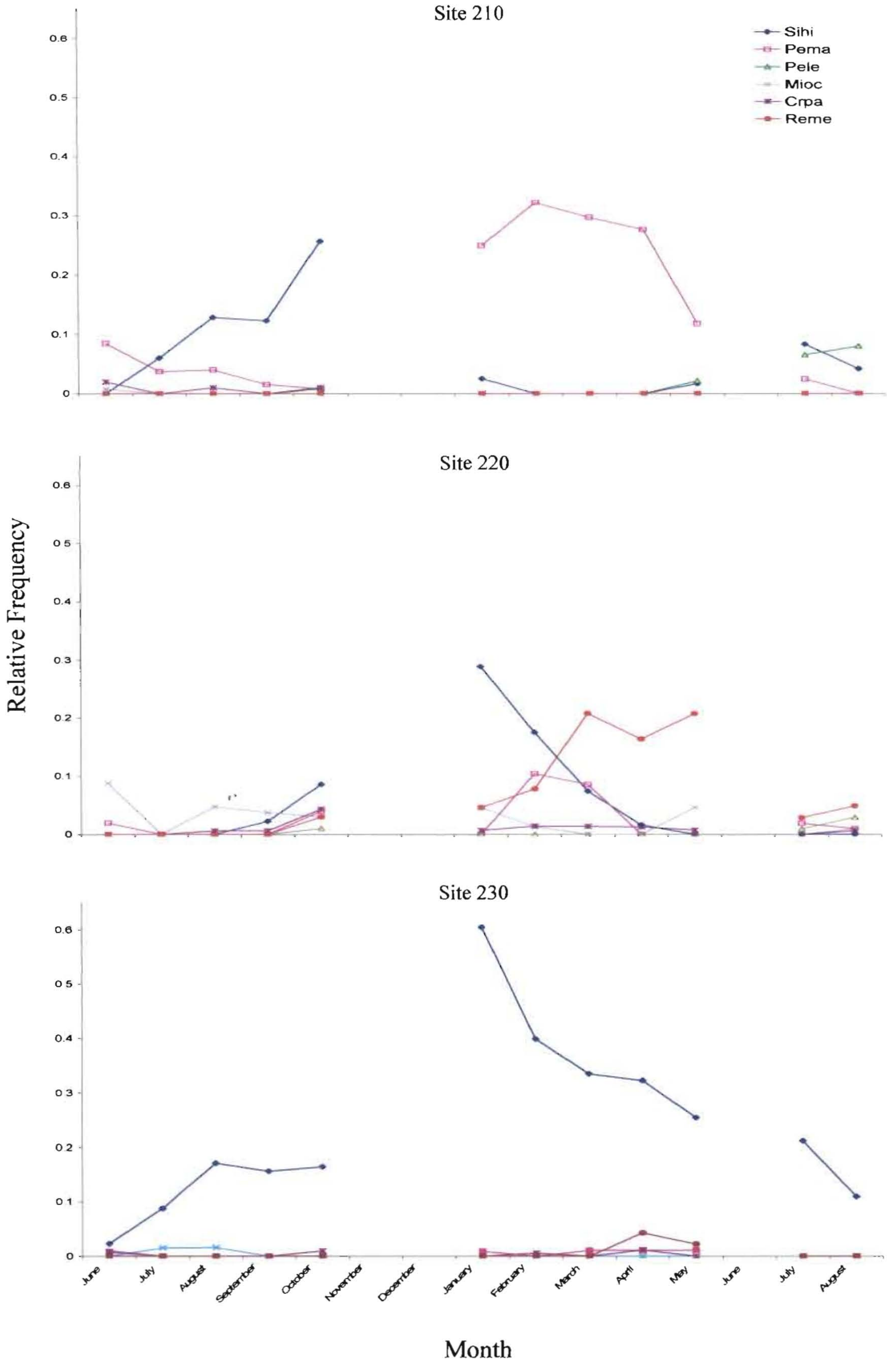
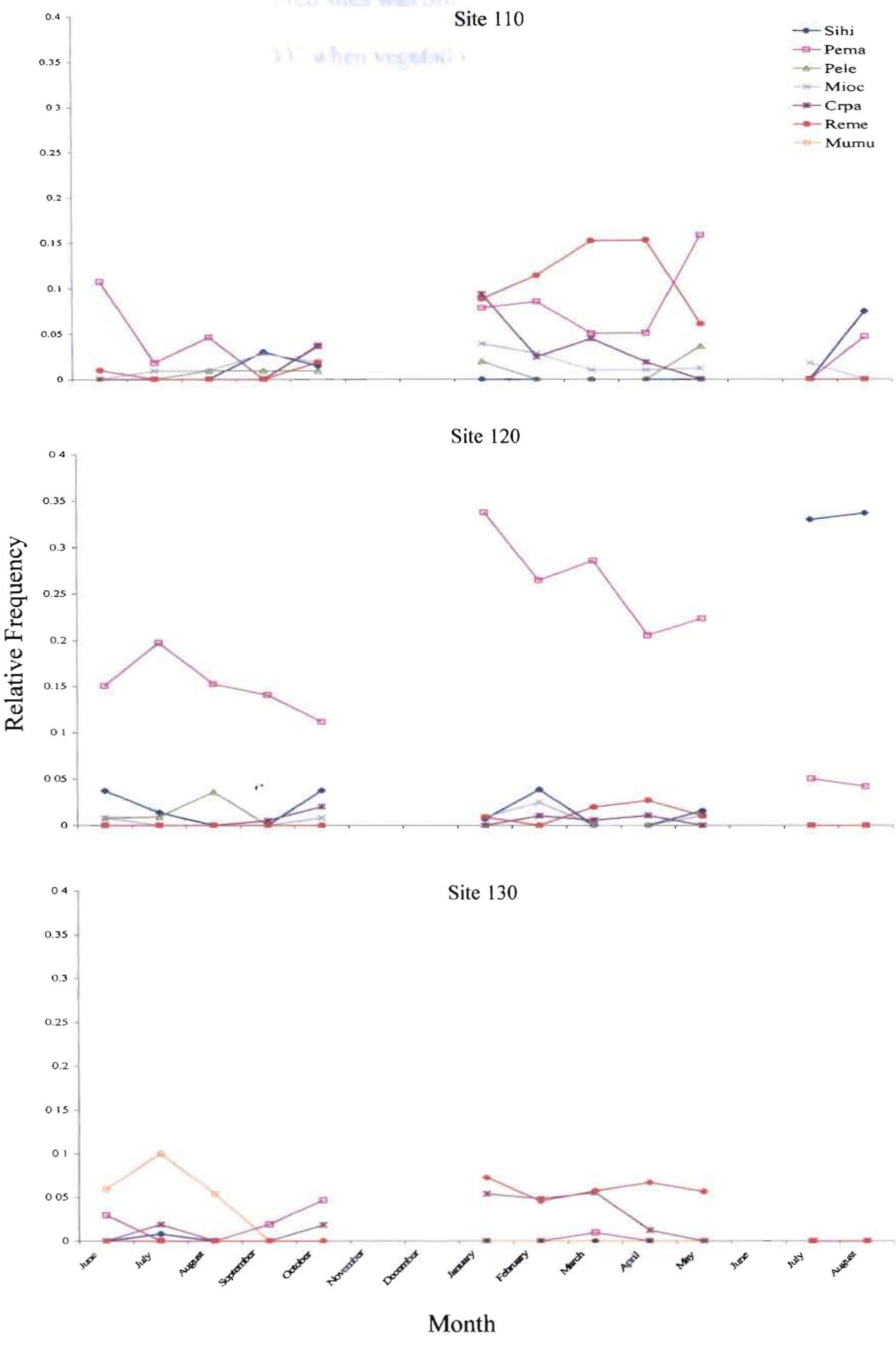

Site 210
Sihi
Pema
Pele
Mioc
Crpa
Reme
0.6
0.5
0.4
0.3
0.2
0.1
0
Site 220
Site 230
Relative Frequency
June
July
August
September
October
November
December
January
February
March
April
May
June
July
August
Month

FIGURE 9. Relative frequency of the most abundant small mammal species in the newly restored treatment by site from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas. For definition of species abbreviation see Table 1.


Site 110
Sihi
Pema
Pele
Mioc
Crpa
Reme
Mumu
Site 120
Relative Frequency
Site 130
June
July
August
September
October
November
December
January
February
March
April
May
June
July
August
Month

exception in the newly restored sites was Site 120, which was dominated by *S. hispidus* in July 2005 and August 2005 when vegetation structure became similar to the other treatments.

Temporal variation in vegetation occurred seasonally, with shifts from cool season grasses and forbs in the spring, to warm season grasses and forbs in the summer and fall, to dormant or dead vegetation in the winter. There was a successional shift in vegetation in the newly restored sites, from annual grasses and forbs early in the study to perennial grasses and forbs at the conclusion of the study. Monthly mowing of newly restored sites during the first summer, accidental burning of Site 210 in November 2004, and a flood during June 2005 also contributed to temporal variations in vegetation structure.

Temporal changes in small mammal communities corresponded with changes in vegetation during the overall time of the investigation. The association of small mammal community structure with habitat corresponds with results of previous studies of grassland small mammal communities (Dueser and Porter 1986, Synder and Best 1988, Diffendorfer et al. 1996, Falout and Nelson 1997). Although there was a significant relationship between small mammal community structure and vegetation structure at the site level for the overall time period, and the April-June and July-October seasons, the highest predictability of small mammal community structure was by station level vegetation during the overall time of the investigation. Thus, the associations found at the station level can explain the association of small mammal community structure with habitat at the site level. Small mammal community structure covaried with landscape characteristics only during the April-June season, during which time small mammal community structure also had an association with vegetation structure at the station, site, and landscape level.

The present investigation demonstrated variation among stations within sites in terms of vegetation communities and corresponding variation in small mammal community structure. The processes that cause small mammal communities to be associated with vegetation structure appear to operate at a finer scale than the extent of sites examined. The general lack of association between landscape characteristics and small mammal community structure suggests differential access is not a confounding factor in this system, except, perhaps, during the April-June season. During that time, processes occurring at a larger scale appear to influence small mammal communities more than during other times of the year. Dispersal of small mammals during this season might occur more frequently than other times of the year due to individuals born in the fall establishing home territories and the increase in reproductive activity. Thus, differential access to preferred habitats at the landscape level might be more influential on small mammal community structure during this season than at other times.

The ability to detect patterns of similarity of small mammal communities and their association with the structure of the plant communities was essential to this investigation and only could be accomplished by examination of multiple scales, by collecting species-level vegetation data. The relationship between small mammal community structure and vegetation structure at the site level would have resulted in the conclusion that the ecological neighborhoods approximated the size of the habitat patches had this investigation been conducted using one spatial scale, but finer resolution demonstrated that associations at the station level could explain the site-level similarities, and that the approximate neighborhood for the processes governing small mammal community structure was smaller than the extent of the patch. Likewise, the association of small mammals with landscape characteristics during the April-June season might have been missed if multiple temporal scales had not been examined.

Results of the present investigation suggest that the investigators perception of a "patch" was not be the appropriate scale for investigations of patterns and processes. When a site was assigned a treatment type in this study, it was assumed a "patch" type, but the results suggest that the small mammals perceived the heterogeneity of the "patch" at a finer scale. It is expected that most systems have within patch variation, so investigations into processes that determine community structure within those systems should be scaled relevant to the organism.

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APPENDICES

Appendix A. Presence/absence of vegetation species and variables by site from June 2004 to August 2005 at the Flint Hills National Wildlife Refuge, Kansas. Category LBWS signifies litter, bare ground, water, and stem. (X indicates presence, - indicates absence)

Variable/Species	Common name	Site								
		110	120	130	210	220	230	310	320	330
Woody										
Rosa arkansasa	Arkansas rose	-	-	-	-	-	-	X	X	X
Rhus glabra	Smooth sumac	-	-	-	-	-	-	-	X	X
Cornus drummondii	Dogwood	-	-	-	-	-	-	X	X	X
Symphoricarpos orbiculatus	Coralberry	-	-	-	-	-	-	X	X	X
Rubus ostryifolius	Blackberry	-	-	-	-	-	-	X	X	-
Woody debris		-	-	-	-	-	-	X	-	-
Grass										
Andropogon gerardii	Big bluestem	X	X	-	X	X	X	X	X	X
Schizachyrium scoparium	Little bluestem	X	X	-	X	X	X	X	X	X
Panicum virgatum	Switchgrass	X	X	X	X	X	X	X	X	X
Sorghastrum nutans	Indian grass	X	X	X	-	X	X	X	X	X
Bouteloua curtipendula	Side-oats grama	X	X	-	-	-	-	-	X	X
Setaria viridis	Green foxtail	X	X	X	X	X	-	-	X	X
Elymus virginicus	Virginia wild rye	-	-	-	X	X	-	-	-	-
Panicum capillare	Witchgrass	X	X	X	-	-	-	X	-	-
Echinochloa crus-galli	Barnyard grass	X	X	X	-	-	-	-	-	-
Digitaria sanguinalis	Crab grass	X	-	-	-	-	-	-	-	-
Eriochloa contracta	Prairie cupgrass	X	-	-	-	-	X	-	-	-
Aristida oligantha	'Three awn	-	-	-	-	X	X	-	-	-
Bromus inermis	Smooth brome	-	X	X	-	-	-	-	X	-
Sorghum halepense	Johnson grass	X	-	X	X	-	-	-	-	-
Tridens flavus	Purpletop	-	X	-	-	-	-	X	-	-
Agrostis hyemalis	Agrotis	X	X	-	-	X	X	X	-	X
Panicum acuminatum	Panicum	X	X	-	-	-	-	X	-	X
Sporobolus vaginiflorus	Tall dropseed	-	X	-	-	X	X	X	-	-
Bromus tectorum	Downy chess	X	X	X	-	-	-	X	-	-
Elymus smithii	W. wheat grass	X	X	-	-	-	-	-	-	-
Hordeum pusillum	Little barley	-	X	X	-	-	-	-	-	-
Unknown grass		X	X	X	X	X	X	X	X	X
Forbs										
Rumex crispus	Curlydock	-	X	X	X	-	X	X	-	-
Oxalis stricta	Wood sorrel	-	X	X	-	-	-	X	-	-
Solanum ptycanthum	Black nightshade	X	X	X	-	-	X	X	X	X
Solanum rostratum	Buffalo bur	-	X	-	-	-	-	-	-	-
Erigeron strigosus	Daisy fleabane	X	X	X	-	X	X	-	X	-
Convolvulus arvensis	Field bindweed	X	X	X	-	-	X	-	-	-
Polygonum punctatum	Smartweed	X	X	X	X	X	X	-	-	-

Appendix A cont.

Variable/Species	Common name	Site								
		110	120	130	210	220	230	310	320	330
Forbs										
Ambrosia artemisifolia	Common ragweed	X	X	-	X	X	X	X	X	X
Ambrosia trifida	Giant ragweed	-	-	-	X	X	-	-	-	X
Amaranthus rudis	Pigweed	X	X	X	-	X	X	X	-	-
Cassia fasiculata	Showy partridge pea	X	X	-	X	X	X	-	-	-
Desmanthus illinoensis	Illinois bundleflower	X	X	-	X	X	X	-	X	-
Helianthus annuus	Common sunflower	X	X	X	X	X	-	X	X	X
Amorpha canescens	Leadplant	-	-	-	-	-	-	X	X	X
Amorpha fructicosa	False blue indigo	-	-	-	-	-	-	X	X	X
Solidago missouriensis	Goldenrod	-	-	-	X	-	-	X	X	X
Euphorbia corollata	Flowering spurge	-	-	-	-	-	-	-	-	X
Alvia picheri	Blue pitcher sage	-	X	-	-	-	-	-	-	X
Psoralea tenuflora	Surf pea	-	-	-	-	-	-	X	X	X
Fragaria virginiana	Strawberry	-	-	-	-	-	-	X	X	-
Lespedeza cuneata	Sericea lespedeza	-	X	-	X	X	X	X	X	-
Lespedeza spp.	Lespedeza	-	-	-	-	-	X	-	X	X
Gaura coccinea	Scarlet gaura	X	-	X	X	-	X	X	X	X
Teucrium canadense	American germainder	-	-	-	X	X	X	X	X	X
Xanthium strumarium	Cocklebur	X	-	-	-	-	-	-	-	-
Apocynum cannabinum	Hemp dogbane	-	X	-	X	X	X	-	X	X
Asclepias syriaca	Milkweed	-	X	-	X	X	X	-	X	X
Asclepias verticillata	Whorled milkweed	-	-	-	X	-	X	X	X	-
Helanthus tuberosus	Jerusalem artichoke	-	-	-	-	-	-	-	X	-
Conyza canadensis	Horseweed	X	X	X	-	X	X	X	-	-
Vernonia baldwini	Ironweed	-	-	-	X	-	-	X	-	X
Carex spp.	Sedge	-	-	-	X	X	X	-	-	-
Artemisia campestris	Silver sage	-	-	-	-	X	X	X	X	X
Tradescantia bracteata	Spiderwort	-	-	-	-	-	-	X	-	X
Trifolium pratense	Prairie clover	-	-	-	X	-	X	-	X	X
Verbena stricta	Verbena	-	-	-	-	-	-	-	X	-
Glycine max	Soybean	-	X	X	-	-	-	-	-	-
Abutilon theophrasti	Velvet leaf	X	X	X	-	-	-	-	-	-
Capsella bursa-pastoris	Shepard's purse	X	X	X	-	-	-	-	-	-
Cirsium undulatum	Thistle	-	-	-	X	-	-	-	-	-
Lactuca serriola	Prickly lettuce	X	X	X	-	X	-	-	-	-
Lactuca serriola	Prickly lettuce	X	X	X	-	X	-	-	-	-
Rudbeckia hirta	Black-eye susan	X	X	-	-	-	-	-	-	-
Penstemon grandiflorus	Beard's tongue	-	-	-	-	-	-	-	-	X
Cichorium intybus	Chicory	-	-	X	-	-	-	-	-	-

Appendix A cont.

Variable/Species	**Common name**	**Site**								
		110	**120**	**130**	**210**	**220**	**230**	**310**	**320**	**330**
Forbs										
Cacalia tuberosa	Indian plantain	-	-	-	-	-	-	-	X	-
Aster pilosus	Hairy aster	-	X	-	-	-	-	X	X	X
Coreopsis grandiflora	Coreopsis	-	-	-	-	-	X	-	-	-
Stellaria media	Chickweed	X	X	-	-	-	-	-	-	-
Lamium amplexicaule	Henbit	X	X	X	-	-	-	-	-	-
Taraxacum officinale	Dandelion	-	X	-	-	-	-	-	-	-
Specularia perfoliata	Venus looking-glass	X	-	X	-	-	-	-	-	-
Tragopogon dubius	Goats beard	X	-	-	-	-	-	-	-	-
Medicago lupulina	Black medic	-	-	-	X	-	-	-	-	-
Polygonum scandens	False buckwheat	-	-	-	X	-	-	-	-	-
Verbascum blattaria	Moth mullein	-	-	-	-	-	-	X	-	-
Asclepias viridis	Green antelopehorn	-	-	-	-	-	-	X	-	X
Trifolium repens	Trifolium	-	X	-	-	-	-	-	-	-
Gutierrezia dracunculoides	Broomweed	-	-	-	-	-	-	X	X	-
Unknown forb		X	X	X	X	X	X	X	X	X
LBWS										
Litter		X	X	X	X	X	X	X	X	X
Bare Ground		X	X	X	X	-	X	X	X	X
Water		-	-	X	-	-	-	-	-	-
Stem		-	-	X	-	-	-	-	-	-

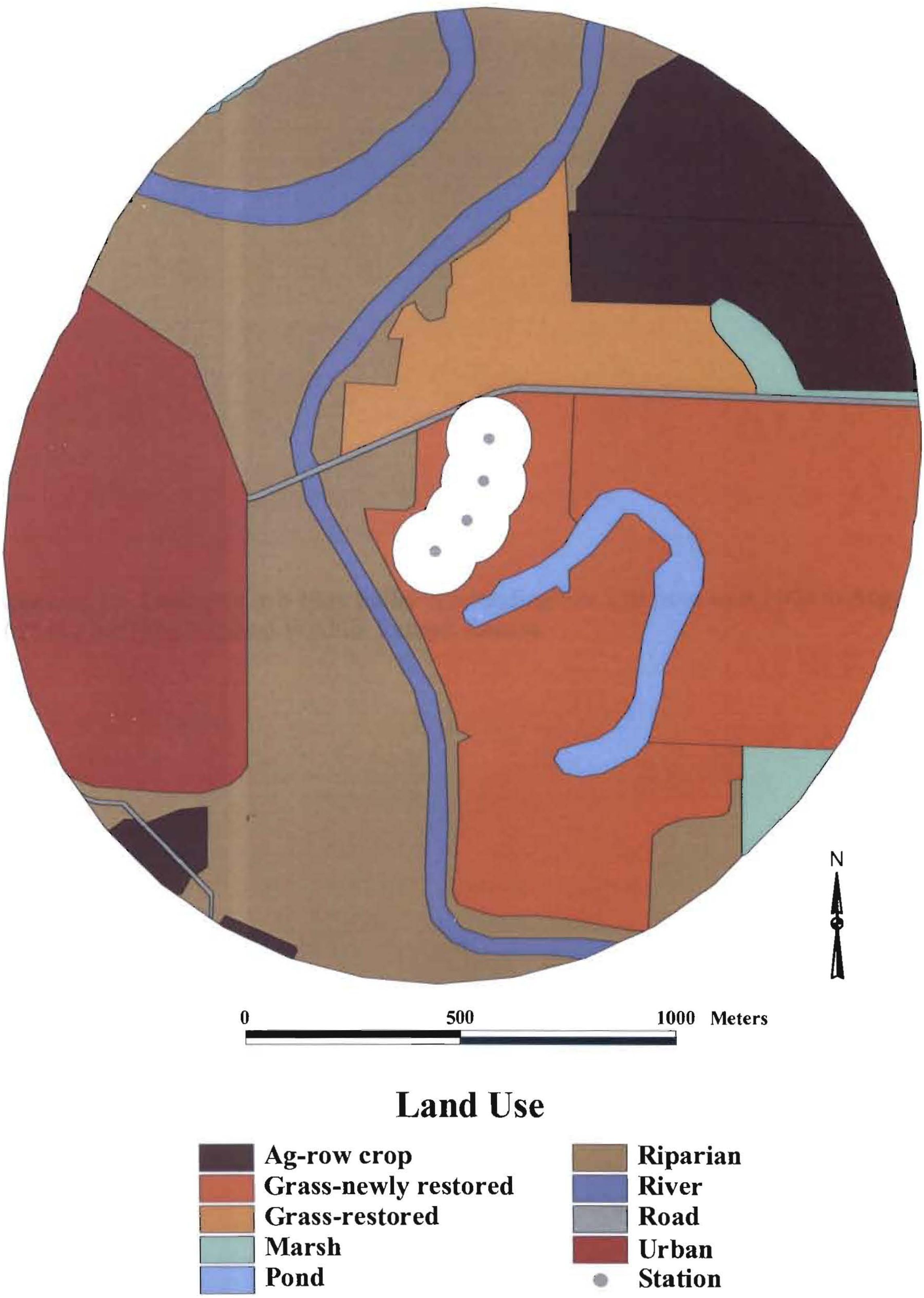
Appendix B. Land uses in a 1 km buffer surrounding Site 110 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
500
1000 Meters
Land Use
Ag-row crop
Farmstead
Grass-native
Grass-native-grazed
Grass-native-hayed
Grass-newly restored
Grass-restored
Marsh
Riparian
Road
Station

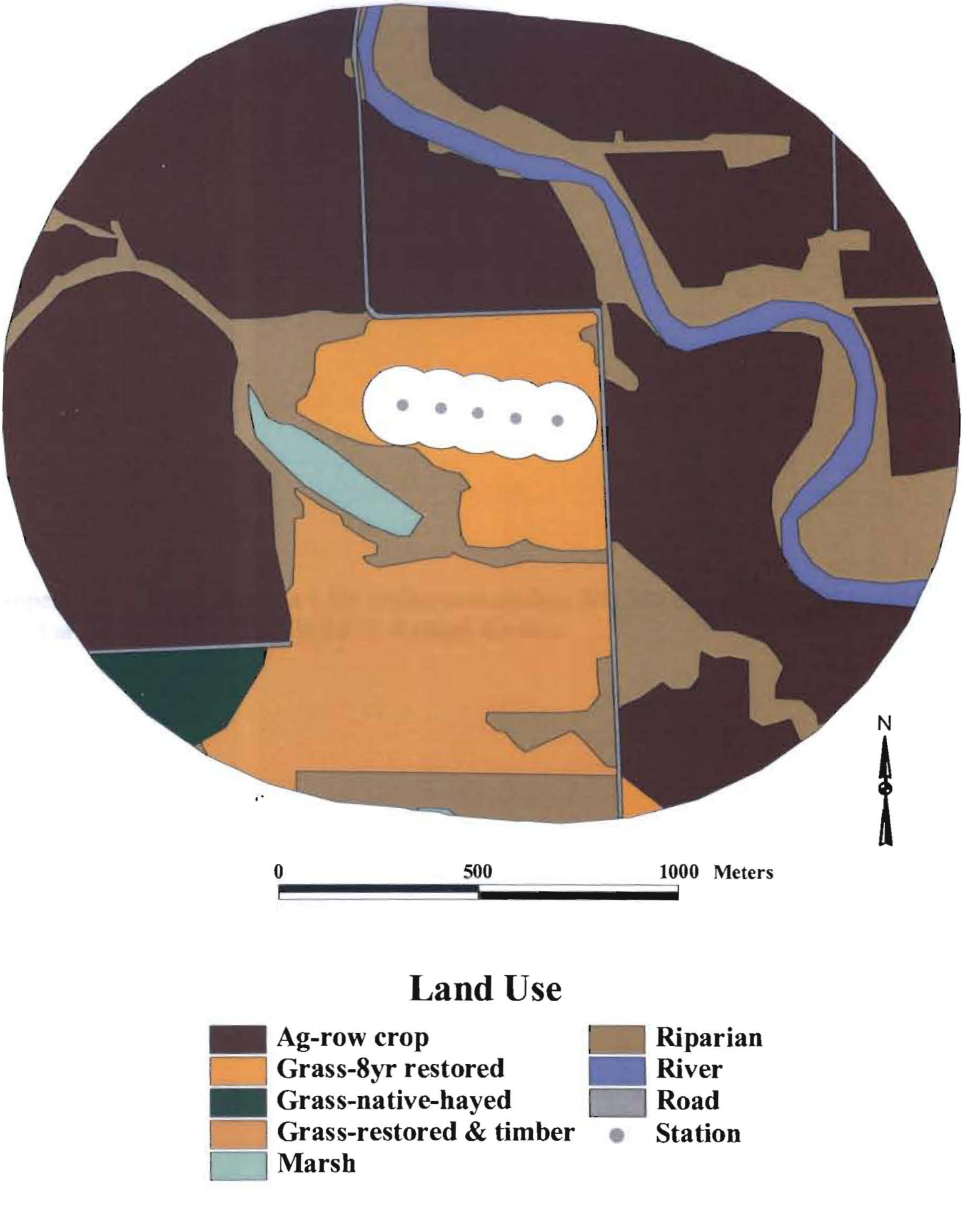
Appendix C. Land uses in a 1 km buffer surrounding Site 120 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
500
1000 Meters
Land Use
Ag-row crop
Farmstead
Grass-brome-hayed
Grass-native-grazed
Grass-native-hayed
Grass-newly restored
Station
Grass-restored
Pond
Riparian
River
Road
Urban

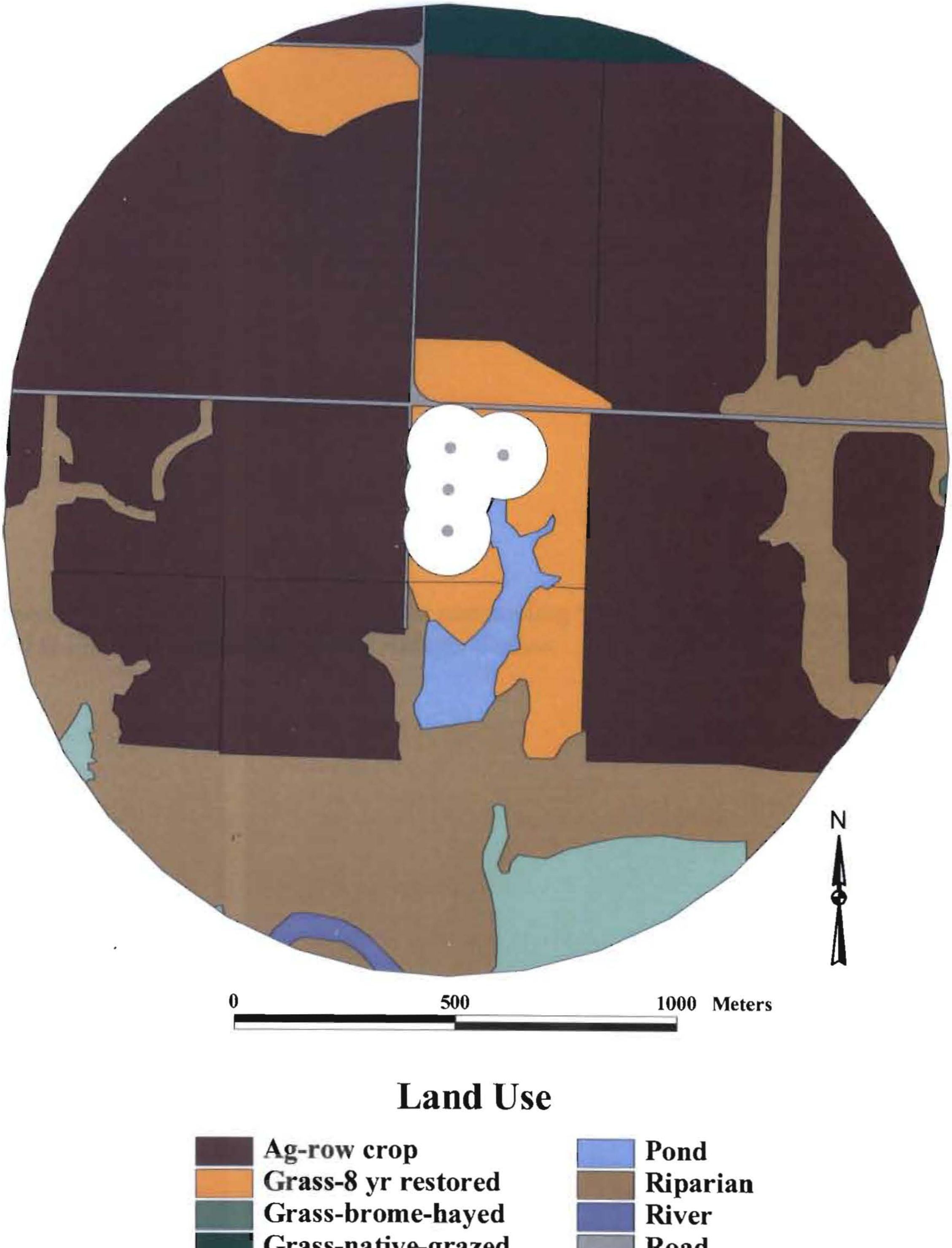
Appendix D. Land uses in a 1 km buffer surrounding Site 130 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
500
1000 Meters
Land Use
Ag-row crop
Grass-newly restored
Grass-restored
Marsh
Pond
Riparian
River
Road
Urban
Station

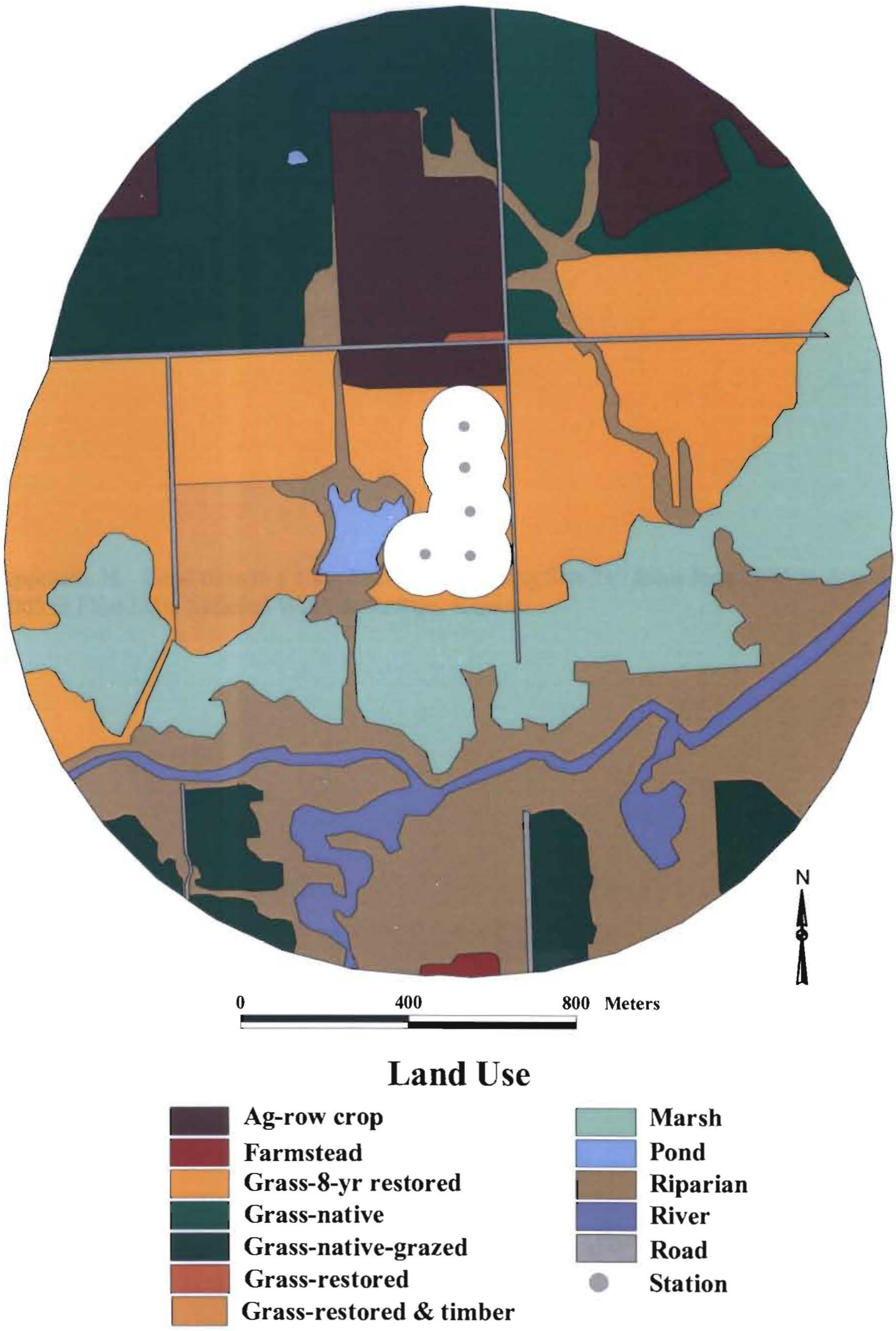
Appendix E. Land uses in a 1 km buffer surrounding Site 210 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
500
1000 Meters
Land Use
Ag-row crop
Grass-8yr restored
Grass-native-hayed
Grass-restored & timber
Marsh
Riparian
River
Road
Station

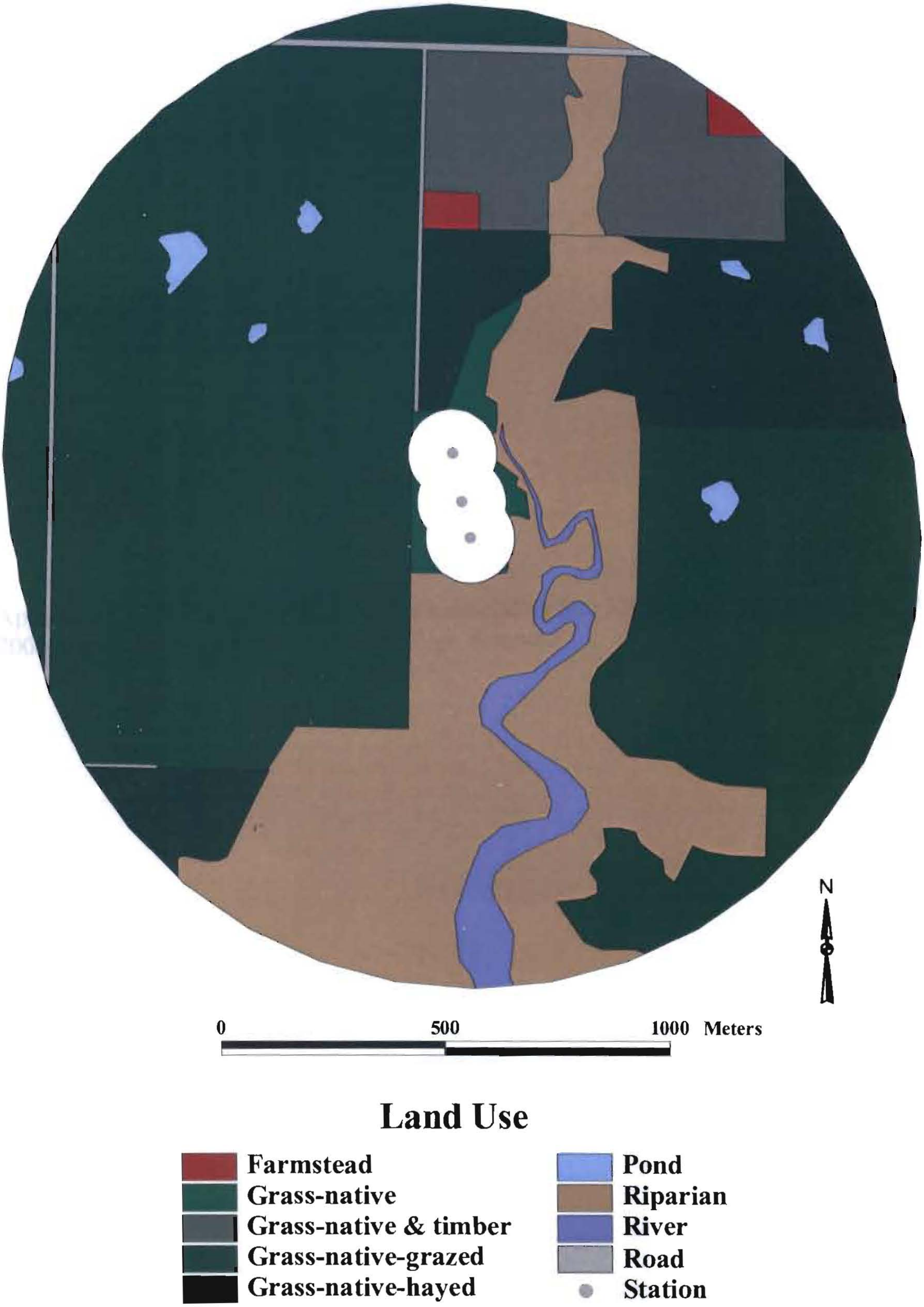
Appendix F. Land uses in a 1 km buffer surrounding Site 220 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
500
1000 Meters
Land Use
Ag-row crop
Grass-8 yr restored
Grass-brome-hayed
Grass-native-grazed
Marsh
Pond
Riparian
River
Road
Station

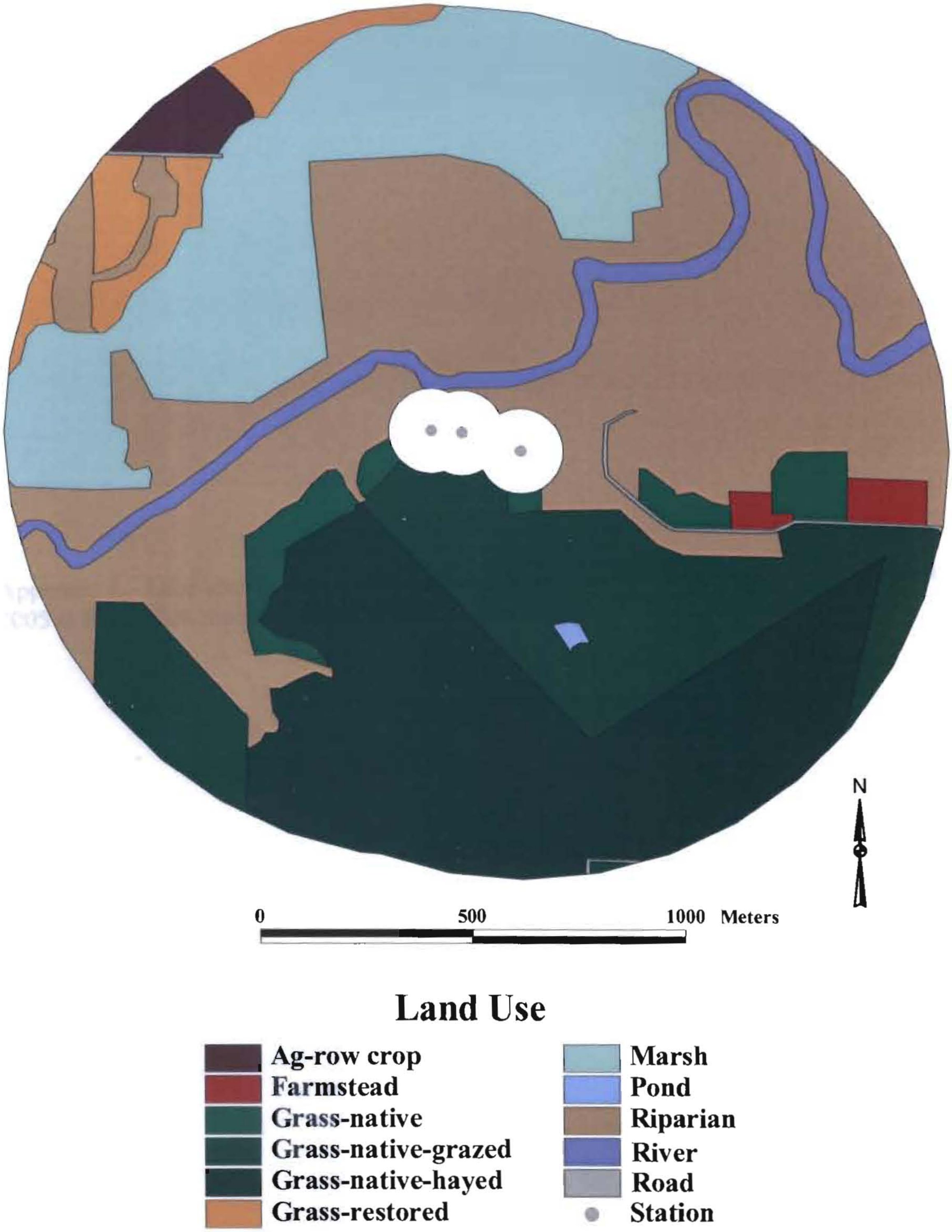
Appendix G. Land uses in a 1 km buffer surrounding Site 230 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
400
800 Meters
Land Use
Ag-row crop
Farmstead
Grass-8-yr restored
Grass-native
Grass-native-grazed
Grass-restored
Grass-restored & timber
Marsh
Pond
Riparian
River
Road
Station

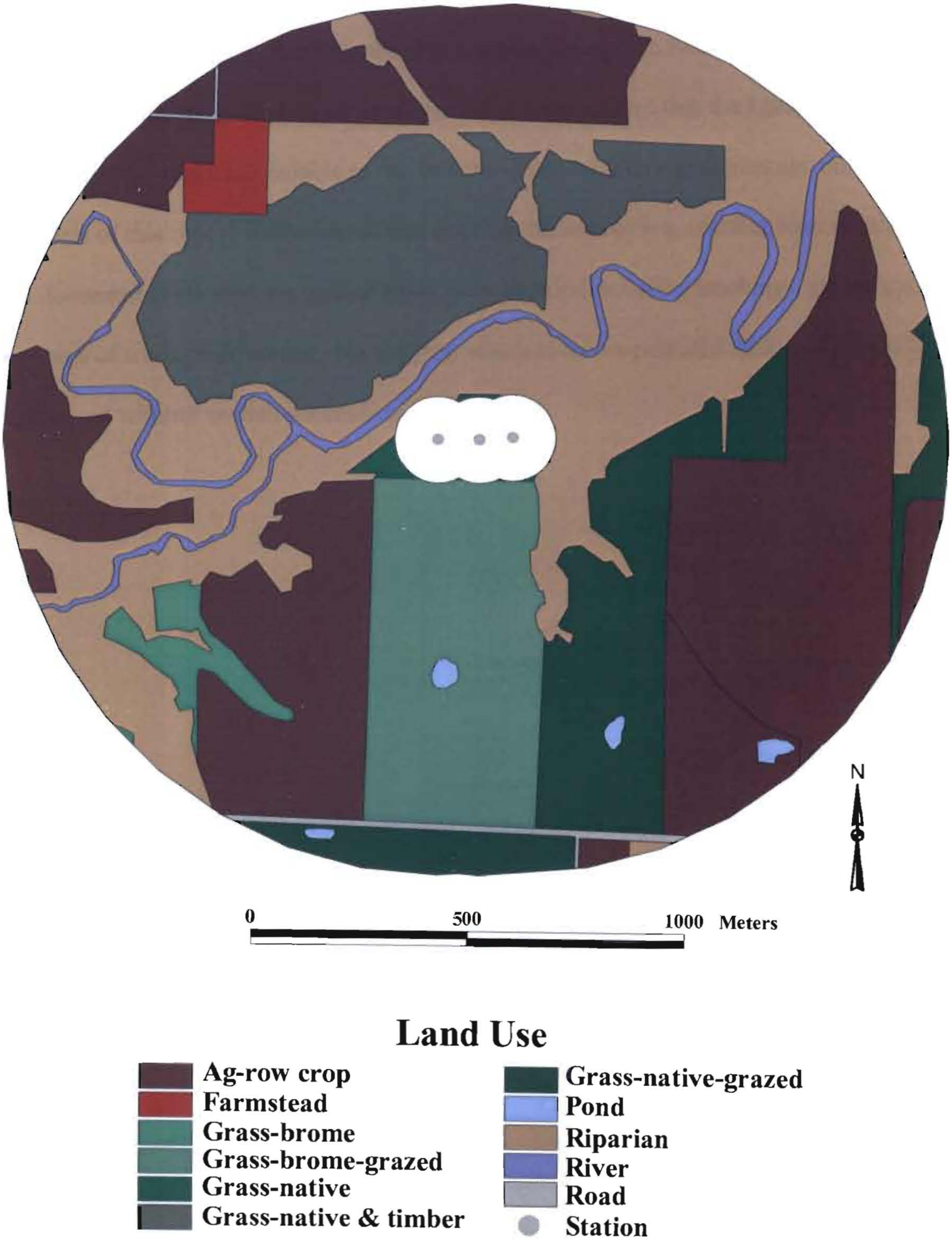
Appendix H. Land uses in a 1 km buffer surrounding Site 310 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
500
1000 Meters
Land Use
Farmstead
Grass-native
Grass-native & timber
Grass-native-grazed
Grass-native-hayed
Pond
Riparian
River
Road
Station

Appendix I. Land uses in a 1 km buffer surrounding Site 320 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
500
1000 Meters
Land Use
Ag-row crop
Farmstead
Grass-native
Grass-native-grazed
Grass-native-hayed
Grass-restored
Marsh
Pond
Riparian
River
Road
Station

Appendix J. Land uses in a 1 km buffer surrounding Site 330 from June 2004 to August 2005 at Flint Hills National Wildlife Refuge, Kansas.


N
0
500
1000 Meters
Land Use
Ag-row crop
Farmstead
Grass-brome
Grass-brome-grazed
Grass-native
Grass-native & timber
Grass-native-grazed
Pond
Riparian
River
Road
Station

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Signature of Author

21 April 2006

Date

Ecological Neighborhoods of Small Mammal Communities at Flint Hill National Wildlife Refuge, Kansas: a Multi-scale Comparison of Community and Habitat Structure

Title of Thesis

Signature of Graduate Office Staff

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