

HABITAT SELECTION BY SMALL MAMMALS: SEASONALITY OF
RESPONSES TO CONDITIONS CREATED BY FIRE AND TOPOGRAPHY
IN TALLGRASS PRAIRIE

by

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A MASTER'S THESIS

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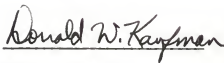
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INTRODUCTION

Fire, an integral abiotic component of the tallgrass prairie ecosystem, has both direct and indirect effects on animal populations and assemblages. Directly, animals, probably a small proportion, are killed by fire and heat. Indirectly, fire affects consumer species through changes in the availability of habitat and food resources. Some of the vegetative characteristics that are altered by fire and that affect food and habitat conditions for animals include species composition, species diversity, primary production, time of flowering, palatability of foliage, and patchiness of plant distribution (Dyer, 1982). Actual changes in these characteristics due to fire are dependent on precipitation, species composition, fire intensity, time of the burn, geographic location and topography (Anderson, 1982). Environmental factors such as the amount and availability of seeds and foliage, structure and density of vegetation, and the availability of nests and safe sites are likely important determinants of density and distribution of small mammals; alteration of these factors by burning tallgrass prairie should, therefore, result in changes in small mammal communities.

As a result of these types of changes, Peromyscus maniculatus on burned prairie increased in numbers following a fire relative to unburned sites in several studies (Tester and Marshall, 1961; Tester, 1965; Schramm and Willcutts, 1983),

whereas Reithrodontomys megalotis, another primarily granivorous species, decreased in numbers after fire relative to unburned areas (Cook, 1959). P. leucopus responded positively to fire when nearby populations could immigrate from nearby woods to the burned prairie site (Springer and Schramm, 1972), but were more common in unburned than burned areas in brush prairie savanna (Beck and Vogl, 1972). Information on effects of fire on Microtus ochrogaster and Blarina hylophaga are limited, but data for other species in both genera suggest that both M. ochrogaster and B. hylophaga would be negatively affected by fire (Cook, 1959; Springer and Schramm, 1972). Other species of small mammals found in tallgrass prairie are undoubtedly affected by prairie fires, but current data are not sufficient to document the role of fire in limiting their distributions and densities.

Research on the effects of fire on small mammals of the tallgrass prairie is being conducted as part of the long-term ecological research project (LTER) at Konza Prairie Research Natural Area (KPRNA). Based on early results of this study, P. maniculatus were most numerous on census lines in recently burned plots and decreased with the time since fire; in contrast, R. megalotis numbers were greatest in plots left unburned for two to four years (Kaufman et al., 1983).

Given the array of experimentally burned and unburned watersheds on KPRNA, and the strong evidence that fire affects small mammal densities and distributions, the patterns of small mammal response to fire can now be examined by studying short-term (immediate and seasonal changes during the first year

after fire) and long-term (multi-year) changes in animal numbers and distributions.

While many studies have documented general effects of fire on certain species of small mammals, few have intensively examined temporal aspects of these responses. In the present study, I examined effects of fire on small mammal populations in tallgrass prairie by studying small mammals on adjacent burned and unburned areas. The objectives were to (1) analyze the temporal changes in habitat utilization by small mammals during the first year after fire relative to populations in unburned areas (2) examine temporal shifts in habitat utilization among upland, breaks, and lowland habitats within both unburned and burned prairie, and (3) gather information on recruitment and residency of individuals in both burned and unburned sites.

STUDY SITE AND METHODS

This study was conducted on Konza Prairie Research Natural Area (KPRNA), a 3,487-ha tallgrass prairie in the Flint Hills approximately 4-10 km south of Manhattan, Kansas. The specific study site, a 5.4-ha trapping grid with 10 by 24 stations set at 15-m spacing, was established in T11S, R7E, Sec. 24, Riley Co., Kansas. The grid was established across two experimental burning treatments, with each treatment burned every fourth year in mid-April. Approximately one-half of the grid (the "burned" grid; 2.56 ha, 114 stations), was located within a 56.95-ha area (Watershed 4B) which was burned in April 1983 (the most recent burn before that was in 1979). The other portion (the "unburned" grid; 2.84 ha, 126 stations) was part of a 17.05-ha treatment (Watershed 4A) which was last burned in 1980 and remained unburned through the first year of this study until subsequently burned in April 1984.

The study area was in a typical Flint Hills site (elevation 408-427 m) including lowland valleys with deep permeable soils, relatively steep-sided hills with hard chert- and flint-bearing limestone layers exposed at the surface, and relatively flat ridge tops with shallow soils. Vegetation was dominated by big bluestem (Andropogon gerardii), little bluestem (A. scoparius), and Indiangrass (Sorghastrum nutans). Dominant shrubs along dry ravines included (Cornus drummondii), buckbrush (Symphoricarpos orbiculatus), and honeylocust (Gleditsia triacanthos); in

addition, small patches of smooth sumac (Rhus glabra), New Jersey tea (Ceanothus herbaceus), and prairie wild rose (Rosa arkansana) were present on rocky slopes.

Three topographic sites, upland, breaks, and lowland, were recognized on the grid with each station assigned to one of the three categories. Combinations of soil and associated vegetation have been used to classify range conditions into range sites that are somewhat similar to our categories (Bidwell, 1966). Our classification was based on visual observation of slope, presence of rocks, and vegetation. Upland stations were on ridge tops where the ground surface was relatively flat with few or no rock fragments present. Breaks sites were typified by rock fragments or consolidated large rocks on the surface. Most breaks stations were on the sides of hills with some in rocky areas on flatter surfaces at the top or base of hills. Lowland stations were characterized by a moderate slope, an absence of rocks, and deep soil. Two dry ravines were present on the site with all stations in or on the edges of the ravine included in lowland.

Small mammals were studied from March 1983 to April 1984. Prior to the controlled fire, small mammals were censused for a total of twelve days from 13 March to 18 April 1983. Following the fire, censuses were conducted for 20 days during 23 April to 27 May 1983. After this intensive trapping, censuses were made for four days every other week until winter weather threatened animal survival (December and January). In 1984 censuses were made for 11 days during February to 18 April. Numbers of

individuals on the two grids were available for June 1984 from other work on the same site.

Two large Sherman live traps (7.6 by 8.9 by 22.9 cm) were placed within one meter of each grid station on every other row of the grid. These traps were checked for two days then traps were moved to the alternate rows for the next two days. All traps were baited with peanut butter in the summer, whereas a mixture of peanut butter and oatmeal wrapped in weighing paper and suspended from the back door was used in spring and autumn. Polyester fiberfill was provided as nesting material in late winter, spring, and autumn.

Traps were checked daily between 0630 and 1000 h. When daily temperatures exceeded 29 °C, traps were closed at the morning check and reopened between 1800-2000 h. Individual animals were toe clipped and ear tagged (using size 1 monel tags) at first capture. Trap day, grid station, species, sex, age and reproductive condition were recorded for each capture. Individuals were weighed to the nearest 0.5 g using a Pesola balance at the first capture during each four-day census period. P. maniculatus and P. leucopus were aged by pelage characteristics, juveniles are gray, adults are brown, and subadults exhibit a mixture of juvenile and adult pelage. R. megalotis weighing more than 9 g were considered adults. All animals were released at the site of capture.

Relative densities were estimated as the minimum number of animals alive (MNA) for each trap period. The MNA is the sum of the actual number of individuals caught during a given four-day

trap period and the number of individuals that were caught in trap periods before and after but not at that time (Krebs, 1966). The trappability for a species was calculated by first dividing the number of individuals caught in a trap period by the number known to be alive, then averaging this value for all trap periods.

During each trapping period all individuals were classed into one of the following three residency categories modified from those defined by Metzgar (1979): new individuals, young residents, and old residents. The new individuals category included all individuals during the first trapping period in which they were caught, the young residents category included all individuals first caught in the previous trapping period (regardless of age), and the old residents category included all individuals caught in two or more previous trapping periods.

RESULTS

Two hundred twenty-nine small mammals of 14 species were captured 1,632 times from March 1983 to April 1984 (Table 1). The four common species (> 10% of the total number of individuals for all species) were the deer mouse (Peromyscus maniculatus; 29% of individuals, 46% of captures), white-footed mouse (P. leucopus; 26%, 28%), western harvest mouse (Reithrodontomys megalotis; 19%, 14%), and thirteen-lined ground squirrel (Spermophilus tridecemlineatus; 12%, 5%). The relatively uncommon species (< 3% of total individuals) were, in descending order of abundance, the eastern woodrat (Neotoma floridana), Elliot's short-tailed shrew (Blarina hylophaga), prairie vole (Microtus ochrogaster), cotton rat (Sigmodon hispidus), hispid pocket mouse (Perognathus hispidus), least shrew (Cryptotis parva), plains harvest mouse (Reithrodontomys montanus), house mouse (Mus musculus), southern bog lemming (Synaptomys cooperi) and meadow jumping mouse (Zapus hudsonius) (Table 1).

Burned and Unburned Prairie

Number of small mammals captured on the entire grid was low ($N = 12$) prior to the controlled prairie fire (12 days of trapping from 13 March to 18 April 1983). These 12 individuals, representing 3 species, were caught 51 times (Table 2). The number of small mammals increased considerably on both burned and

Table 1. Total numbers of individuals and captures of small mammals in tallgrass prairie during entire study period. Numbers in parentheses are percentages of total individuals and captures.

	Number of Individuals	Total Captures
<u>Peromyscus maniculatus</u>	67 (29)	758 (46)
<u>Peromyscus leucopus</u>	59 (26)	464 (28)
<u>Reithrodontomys megalotis</u>	44 (19)	231 (14)
<u>Spermophilus tridecemlineatus</u>	27 (12)	75 (5)
<u>Neotoma floridana</u>	6 (3)	50 (3)
<u>Blarina hylophaga</u>	8 (3)	19 (1)
<u>Microtus ochrogaster</u>	4 (2)	11 (1)
<u>Sigmodon hispidus</u>	3 (1)	6 (<1)
<u>Perognathus hispidus</u>	2 (1)	5 (<1)
<u>Cryptotis parva</u>	2 (1)	5 (<1)
<u>Reithrodontomys montanus</u>	4 (2)	4 (<1)
<u>Mus musculus</u>	1 (<1)	2 (<1)
<u>Synaptomys cooperi</u>	1 (<1)	1 (<1)
<u>Zapus hudsonius</u>	1 (<1)	1 (<1)
Total	229	1,632

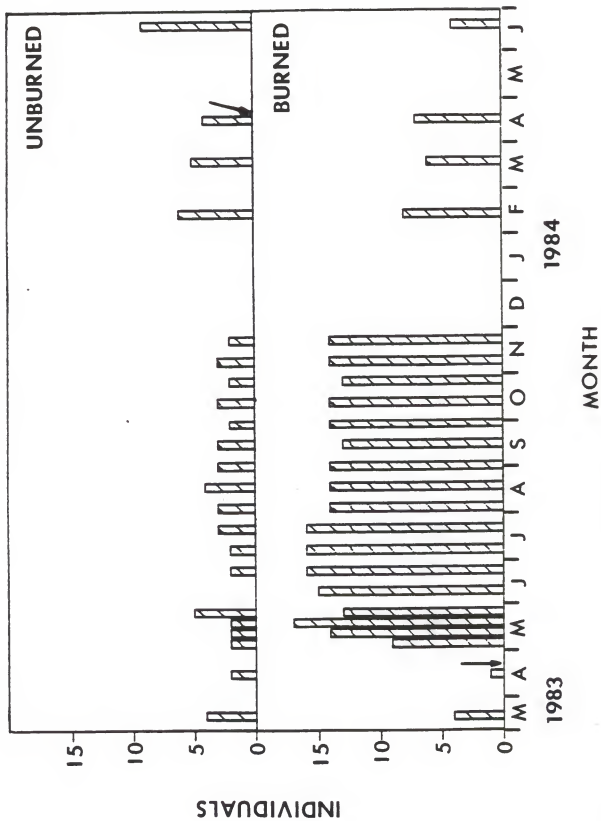
Table 2. Numbers of individuals and captures on the unburned and burned grids both pre-fire (13 March - 18 April) and post-fire (23 April - 16 May). Post-fire individuals captured on unburned and burned grids were counted in the totals of each grid with numbers of individuals caught only on the burned or unburned in parentheses.

	Unburned		Burned	
	Individuals	Captures	Individuals	Captures
<u>P. maniculatus</u>				
Pre-fire	5 (1)	11	5 (1)	12
Post-fire	2 (0)	18	24 (22)	109
<u>P. leucopus</u>				
Pre-fire	2 (2)	8	3 (3)	19
Post-fire	8 (8)	29	3 (3)	31
<u>R. megalotis</u>				
Pre-fire	0	0	0	0
Post-fire	12 (12)	52	0	0
Other Species				
Pre-fire	1 (1)	1	0	0
Post-fire	8 (8)	21	10 (10)	38
Total small mammals				
Pre-fire	8 (4)	20	8 (4)	31
Post-fire	30 (28)	120	37 (35)	178

unburned portions of the grid in the four weeks immediately following the fire (Table 2). General patterns of differential abundance between the unburned and burned grids established at this time continued into autumn. P. maniculatus were more abundant on the burned than unburned grid, whereas P. leucopus and R. megalotis were more abundant on the unburned than burned grid. These three species were the only species sufficiently abundant to consider in detail for differences in use of burned and unburned prairie and upland, breaks, and lowland sites.

Peromyscus maniculatus.--P. maniculatus were more numerous on the burned than unburned grid during each census period from 1 May to 23 November (Fig. 1). This difference resulted from a large increase in numbers on the burned grid in the first few weeks following the fire on April 20; the number of individuals then remained stable into autumn (Fig. 1). Numbers of individuals on the entire grid changed little during winter (N = 16 in November and 14 in February), but a shift in distribution of individuals between unburned and burned areas did occur. From February to April 1984, the numbers on the unburned and burned grids were no longer significantly different from a random distribution based on the size of area available on each grid. The increase in numbers of P. maniculatus on burned area evident in 1983 also occurred in 1984, with nine in June 1984 on the newly burned grid (the unburned grid in 1983) and four on the grid left unburned for 14 months (the burned grid in 1983).

Figure 1. Number of Peromyscus maniculatus known to be alive for each trap period on unburned and burned grids from March 1983 through June 1984. Arrows indicate when controlled burning occurred.



The average trappability of P. maniculatus individuals for the 20 trapping periods during the year after fire was similar on unburned (0.81) and burned grids (0.84). Trappability on the burned grid was lowest from July through mid-September (0.62) compared to all other times (0.91), with a similar decrease in trappability also observed on the unburned grid.

From May through November, the first capture of new P. maniculatus occurred more frequently on the burned grid (N = 41) than on unburned (N = 13; Table 3). The number of first captures was greater on the burned than unburned grid for both adult (13 captures on burned and 7 on unburned, with 9.5 expected on burned and 10.5 on unburned based on area of the two grids) and young mice (subadult and juveniles; 28 on burned and 6 on unburned, with 16 and 18 expected, respectively). The pattern for adults was not significant ($\chi^2 = 2.46$, d.f. = 1, p > 0.05) although it was for young mice ($\chi^2 = 16.52$, d.f. = 1, p < 0.01).

Forty-eight of the 54 new P. maniculatus individuals were first captured between May and October. Of these, 19 (40%) established residency on the grid (captured during a period greater than one month = old residents). Of animals first captured as young individuals, 36% established residency, whereas 45% of new adults became residents. Sixteen of 39 new individuals (41%) on the burned grid became residents (56% of males and 29% of females) while two of seven (29%) became residents on the unburned grid. One individual was consistently caught on both grids, while four animals moved from one grid to

Table 3. First captures of new Peromyscus maniculatus on burned and unburned grids for 1 May - 23 November 1983.

	Adult		Subadult		Juvenile		All Ages	
	M	F	M	F	M	F	M	F
Burned								
May - Jun	3	3	6	5	3	7	12	15
Jul - 12 Sep	2	1	3	0	1	0	2	4
23 Sep - Nov	2	2	4	1	2	3	3	5
Total	7	6	13	7	8	15	17	24
Unburned								
May - Jun	3	1	4	1	2	3	5	4
Jul - 12 Sep	2	0	2	0	0	0	2	0
23 Sep - Nov	1	0	1	0	1	0	2	0
Total	6	1	7	2	2	4	9	4

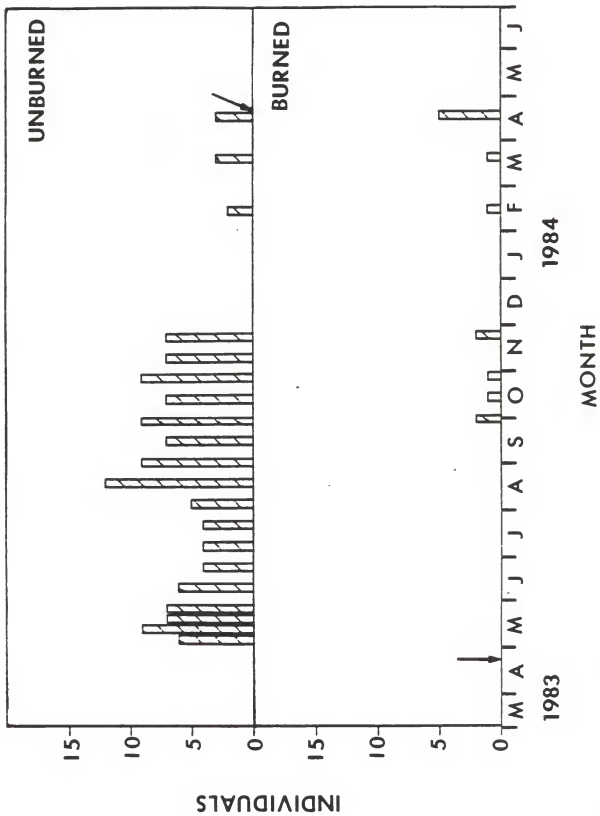
the other; three of these from unburned to burned, and one from burned to unburned.

Reithrodontomys megalotis.--No R. megalotis were captured prior to the fire but twelve adults, all on the unburned grid, were captured in the month following fire (Table 2.) The number of R. megalotis was greatest on the unburned grid during the first month after fire and again in autumn with a decline evident in summer (late June through early August; Fig. 2). No R. megalotis were captured on the burned grid until autumn (Fig. 2). R. megalotis declined from November to February (N = 9 and 3) with similar numbers occurring on the unburned and burned grids from February through April. In June 1984, no R. megalotis were caught on either grid.

The average trappability for R. megalotis on the unburned grid during the year after fire was 0.76 with a decline in trappability occurring in the hot summer months (July to mid-September, average = 0.49 compared to 0.88 for all other time periods). No comparison of trappability could be made between grids due to the low number of individuals caught on the burned.

From May through November, more R. megalotis individuals were first caught on the unburned grid (N = 34) than on the burned (N = 5). First captures for both adults and young were significantly greater on the unburned than burned grid (adults: N = 20 on burned, 3 on unburned, $\chi^2 = 10.93$, d.f. = 1, $p < 0.01$; young: N = 14 and 2, $\chi^2 = 7.86$, d.f. = 1, $p < 0.01$). Only 27% (N = 10) or new R. megalotis captured between 23 April and

Figure 2. Number of Reithrodontomys megalotis known to be alive for each trap period on unburned and burned grids from March 1983 through June 1984. Arrows indicate when controlled burning occurred.

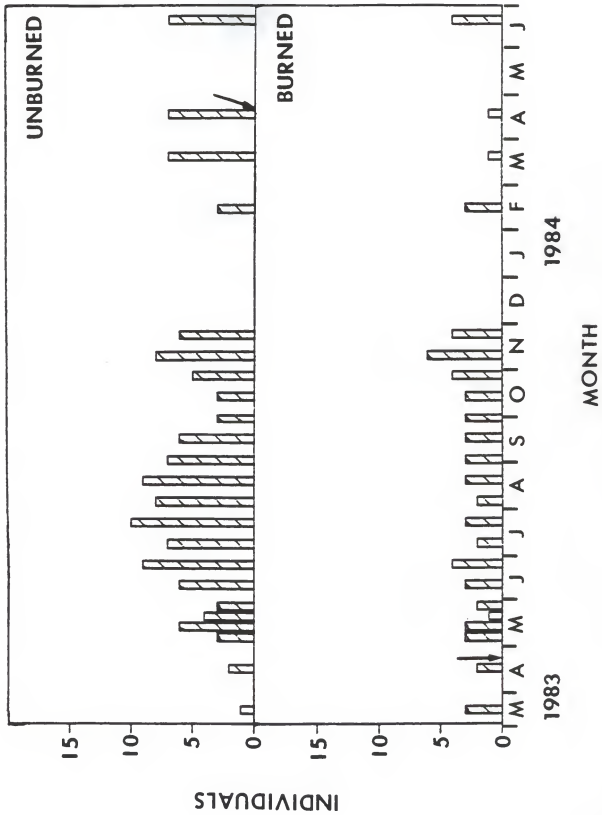


28 October became residents with 7 of 20 adults (35%) [and 3 of 14 (21%) new young animals] staying on the unburned grid. No individuals first captured on the burned grid (N = 3) became residents, and one individual first caught on the unburned grid was also caught on the burned and did not become a resident of either.

Peromyscus leucopus.--During the month after fire, the number of individuals increased on the unburned area from two to eight, but did not change on the burned portion of the grid (Table 2). The number of P. leucopus increased from March through June when peak density was reached (Fig. 3). Numbers remained high for all trapping periods through November, with the exception of late September and early October when an apparent decline occurred. More individuals were captured on the unburned than burned grid from May through November (although these numbers were not significantly different for the four trapping periods with sufficient individuals to test for differences). The number of P. leucopus declined over winter (N = 10 in November to 6 in February) with no detectable shift in distribution on burned and unburned grids (Fig. 3). Although the 1983 unburned grid was burned in April 1984, trapping during June 1984 detected no change in P. leucopus distributions between the two grids, i.e., more individuals remained on the newly burned grid than on the portion burned in 1983.

Trappability was high for P. leucopus and differed very little between unburned (0.95) and burned grids (0.93). In

Figure 3. Number of Peromyscus leucopus known to be alive for each trap period on unburned and burned grids from March 1983 through June 1984. Arrows indicate when controlled burning occurred.



contrast to P. maniculatus and R. megalotis, no major decline in trappability occurred during the summer months (average for July to mid-September = 0.93 on the unburned and 0.95 on the burned grid).

From 23 April to 23 November, more new P. leucopus individuals were first captured on the unburned than burned grid (N = 35 on unburned, 11 on burned). First captures for both adult (N = 18 on unburned, 6 on burned) and young (N = 17 on unburned, 5 on burned) animals were significantly greater on the unburned than burned grid (adults: $\chi^2 = 4.87$, d.f. = 1, p < 0.05; young: $\chi^2 = 5.41$, d.f. = 1, p < 0.05). The percentage of new animals that established residency was 39.0% (16 of 41) with 39.4% (13 of 33) of individuals first captured on the unburned grid becoming residents and 37.5% (3 of 8) of the individuals on the burned becoming residents. Approximately the same percent of adult and young animals became residents on the unburned grid (39% and 40% respectively), whereas 50% of adults and no young (0 of 2) established residency on the burned. One individual was first caught on the burned grid and moved to the unburned where it remained.

Other species.--The number of S. tridecemlineatus known to be alive on the study site was greater during the four weeks of May with 4, 7, 10, and 9 individuals than during other time periods. Some movement from one grid to another occurred, but the numbers on the two grids were similar with no obvious preference for burned or unburned observed. Of the 27 new individuals marked

between May and October, 14 were first captured on the the unburned and 13 on the burned grid. After May when traps were closed during the day, very few ground squirrels were captured limiting any further comparisons.

No other small mammal species were sufficiently abundant for a comparison of numbers on burned and unburned grids.

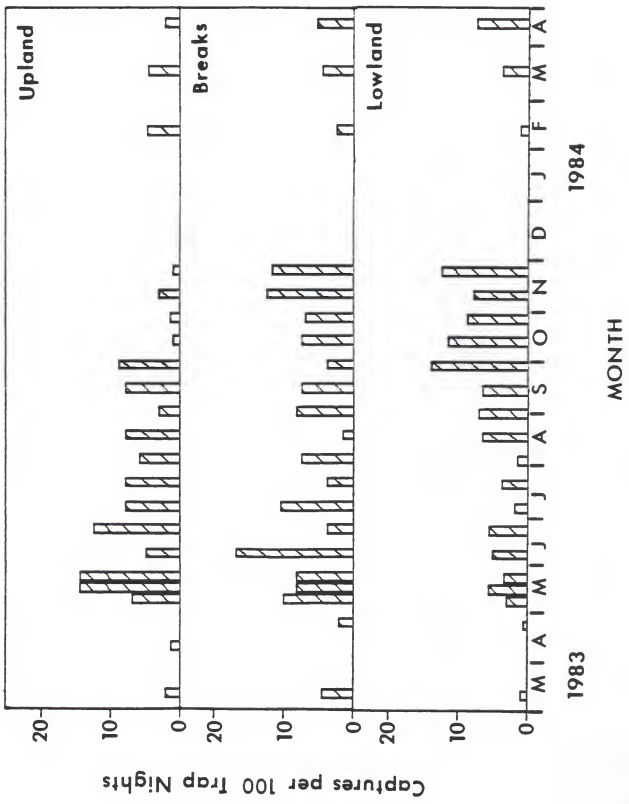
Upland, Breaks, and Lowland Sites

Peromyscus maniculatus.--Deer mice used the three topographic sites within both the unburned and burned grids in a nonrandom fashion. During the year after fire, use of breaks (7.22 captures per 100 trap nights (TN)) was greater than use of upland (5.90) and lowland (5.64) on the burned grid, whereas use of breaks (1.33) and uplands (1.59) was greater than use of lowland (0.09) on the unburned grid (Table 4). Although these patterns were significant, a more detailed examination of use of topographic sites demonstrated seasonal shifts in use of topographic sites on the burned grid that did not occur on the unburned grid (Table 4, Fig. 4). On the unburned grid, capture data were combined for spring-summer 1983, late summer-autumn 1983, and late winter-spring 1984 categories since captures were limited. Use of the three topographic sites during these three time periods remained relatively constant with more captures in upland and breaks than in lowland (Table 4). In contrast, use of topographic sites on the burned grid was focused in the breaks and upland following the fire as it tended to be prior to the

Table 4. Trap nights (TN) and captures per 100 trap nights for *P. maniculatus* by topographic site on unburned and burned grids. Chi-square significance levels: * = $p < 0.05$, ** = $p < 0.01$, blank = too few captures for testing.

	Upland		Braks		Lowland		Chi Square
	TN	Captures/ 100 TN	TN	Captures/ 100 TN	TN	Captures/ 100 TN	
Unburned							
Pre-fire	350	2.86	400	0.25	510	0.00	
Post-fire	3,144	1.59	3,612	1.33	4,584	0.09	57.7 **
23 Apr - 18 Aug	1,572	1.02	1,806	0.83	2,292	0.04	19.0 **
29 Aug - 23 Nov	1,050	1.52	1,200	1.17	1,530	0.06	18.7 **
4 Feb - 18 Apr	522	3.45	606	3.13	762	0.26	20.2 **
Burned							
Pre-fire	260	1.54	340	1.76	540	0.37	
Post-fire	2,340	5.90	3,048	7.22	4,872	5.64	7.9 *
23 Apr - 27 May	546	8.79	708	8.19	1,140	3.16	28.4 **
6 Jun - 7 Jul	312	8.33	408	10.29	648	4.17	14.7 **
18 Jul - 18 Aug	312	7.05	408	4.17	648	3.86	4.9
29 Aug - 26 Sep	312	6.41	408	6.37	648	9.10	3.3
7 Oct - 23 Nov	468	1.50	612	9.31	972	9.98	31.4 **
4 Feb - 18 Apr	390	3.85	504	3.97	816	3.80	0.2

Figure 4. Peromyscus maniculatus captures per 100 trap nights at upland, breaks, and lowlands on burned habitat for all trap periods from March 1983 through April 1984.



fire. By late fall, the pattern shifted to increased use of lowland habitat and decreased use of upland with the use of breaks habitat changing little with the exception of a slight increase in October and November (Fig. 4, Table 4). Use of topographic sites on the burned grid was not different from a random pattern during summer (mid-July through September) and late winter-spring (February to April) 1984.

During spring 1983 (May through June), distribution on uplands, breaks, and lowlands on the burned grid were similar for all three residency classes (3 by 3 contingency table: $\chi^2 = 5.95$, $d.f. = 4$, $p > 0.05$). New individuals were captured too infrequently in other seasons to test for differential use of topographic sites on the burned grid. All resident classes showed the same seasonal pattern of habitat use as previously described for P. maniculatus. In addition, capture success on upland, breaks, and lowland on the burned grid were not significantly different between males and females in either spring, summer, or autumn (3 by 2 contingency tables, $\chi^2 = 0.37$, 0.66, and 1.38, $d.f. = 2$, $p > 0.05$). Similar comparisons could not be made on the unburned grid due to insufficient captures.

Most individual deer mice were not restricted to a single topographic site and readily moved from one site to another. For example, only 20% of 25 P. maniculatus captured 5 or more times on the burned grid were recorded in a single topographic site. These 25 mice were caught three or more times in a total of 111 trap periods with an average of 4.4 trap periods per individual. Deer mice were caught in two different topographic sites in 60%

of the 111 cases, whereas captures in only one topographic site occurred in 32% of these cases. Individual mice were captured in all three topographic sites in 9% of the 111 cases.

Reithrodontomys megalotis.--For total captures of western harvest mice on the unburned grid from 23 April 1983 to 18 April 1984 (post-fire) use of lowland (2.29 captures per 100 trap nights) was greater than breaks (1.96) and upland (0.41). Captures at upland, breaks, and lowland were significantly different from the expected random distribution during all but one month (mid-July to mid-August) when captures were sufficient to perform a chi-square test (Table 5). Seasonal shifts in use of topographic sites occurred, with captures more common at breaks in spring, a non-significant difference in late summer, and a preference for lowlands from autumn until the following spring (Fig. 5). The few captures of R. megalotis on the burned grid were concentrated in the lowland during the year after fire.

Comparisons across topographic sites for R. megalotis could not be made for resident classes or for males and females due to insufficient captures.

Peromyscus leucopus.--In contrast to the other species examined, P. leucopus occurred predominantly in lowland on both unburned and burned areas and exhibited no seasonal pattern of habitat use (Table 6, Fig. 6). The significant non-random distribution across topographic sites was evident for all trap periods analyzed with captures per 100 trap nights greatest on

Table 5. Trap nights (TN) and captures per 100 trap nights for *R. megalotis* by topographic site on unburned and burned grids. Chi-square significance levels: * = $p < 0.05$, ** = $p < 0.01$, blank = too few captures for testing.

	Upland		Breaks		Lowland		Chi Square
	TN	Captures/ 100 TN	TN	Captures/ 100 TN	TN	Captures/ 100 TN	
Unburned							
Pre-fire	350	0.00	400	0.00	510	0.00	
Post-fire	3,144	0.41	3,612	1.96	4,584	2.29	42.3 **
23 Apr - 27 May	732	0.82	846	2.60	1,068	1.59	7.4 *
6 Jun - 7 Jul	420	0.00	480	2.50	612	1.31	10.6 **
18 Jul - 18 Aug	420	0.71	480	1.67	612	1.31	1.6
29 Aug - 26 Sep	420	0.24	480	2.29	612	2.94	9.5 **
7 Oct - 23 Nov	630	0.48	720	1.25	918	3.38	18.9 **
4 Feb - 18 Apr	522	0.00	606	1.48	762	3.02	16.9 **
Burned							
Pre-fire	260	0.00	340	0.00	540	0.00	
Post-fire	2,340	0.08	3,048	0.03	4,872	0.39	13.5 **

Figure 5. Reithrodontomys megalotis captures per 100 trap nights at upland, breaks, and lowlands on unburned habitat for all trap periods from March 1983 through April 1984.

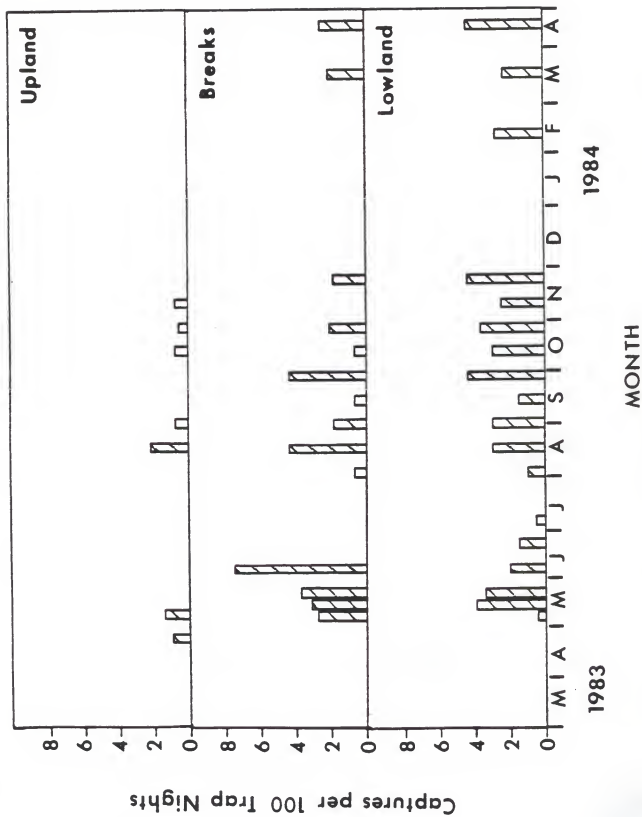


Table 6. Trap nights (TN) and captures per 100 trap nights for *P. leucopus* by topographic site on unburned and burned grids. Chi-square significance levels: * = $p < 0.05$, ** = $p < 0.01$, blank = too few captures for testing.

	Upland		Breaks		Lowland		Chi Square
	TN	Captures/ 100 TN	TN	Captures/ 100 TN	TN	Captures/ 100 TN	
Unburned							
Pre-fire	350	0.00	400	0.00	510	1.57	
Post-fire	3,144	0.13	3,612	0.64	4,584	5.21	271.7 **
23 Apr - 18 Aug	1,572	0.19	1,806	0.89	2,292	4.75	108.2 **
29 Aug - 23 Nov	1,050	0.09	1,200	0.42	1,530	5.29	100.3 **
4 Feb - 18 Apr	522	0.00	606	0.33	762	6.43	66.0 **
Burned							
Pre-fire	260	0.00	340	0.29	540	3.33	
Post-fire	2,340	0.00	3,048	0.26	4,872	3.35	157.5 **
23 Apr - 18 Aug	1,170	0.00	1,524	0.20	2,436	3.04	73.2 **
29 Aug - 23 Nov	780	0.00	1,020	0.29	1,620	4.51	72.4 **
4 Feb - 18 Apr	390	0.00	504	0.40	816	1.96	

Figure 6. Peromyscus leucopus captures per 100 trap nights at upland, breaks, and lowlands on unburned habitat for all trap periods from March 1983 through April 1984.

lowland. All but 27 of 274 captures on the unburned grid and 9 of 190 on the burned occurred at lowland stations. The uplands were totally avoided on the burned grid and accounted for only 4 of 274 captures on the unburned.

Comparisons across topographic sites for P. leucopus could not be made for residency classes or for males and females due to too few captures in upland and breaks.

Other species.--Captures of S. tridecemlineatus indicated use of breaks and lowlands, but an avoidance of uplands. The number of captures at upland, breaks, and lowland respectively were 5, 24, and 16 for burned and 4, 9, and 17 for unburned. Although individuals and captures were limited it appears that differential use of the sites on burned and unburned grids occurred with more captures at break sites on the burned grid but in lowland on the unburned.

The few N. floridana captured (N = 6) remained exclusively in the lowlands except one individual that constructed a house surrounding and under rocks on the breaks and a second individual only captured once at a breaks station.

Use of topographic sites could not be examined for any or the less abundant species.

DISCUSSION

The richness of the small mammal assemblage on the study site (14 species) and the species present were expected from known distributional ranges and from results of previous studies in tallgrass prairie, including those conducted on Konza Prairie. Given the basic natural history known for the species present, however, the relative abundances of some species were unexpected. For example, captures of M. ochrogaster and B. hylophaga, species common in lush grassland conditions, were rare on the study site. On the other hand, P. leucopus, a woodland species, and S. tridecemlineatus, a species usually associated with short-grass conditions, were more abundant than expected.

Peromyscus maniculatus.--Selection by deer mice of burned prairie habitats over nearby unburned sites has been well documented, e.g., oak savanna in Minnesota (Tester and Marshall, 1961; Tester 1965), restored prairie in Illinois (Schramm and Willcutts, 1983), pine grassland savanna in South Dakota (Bock and Bock, 1983), and tallgrass prairie on KPRNA (Kaufman et al., 1983; Kaufman et al., in review). Therefore, the significantly higher number of P. maniculatus on burned compared to unburned portions of the grid during the first growing season after a 1983 spring fire, and again in 1984 when the other portion of the grid was burned, was expected. In addition, the greater number of adults recruited and the number of individuals establishing

residency on the burned grid support the greater suitability of this site for deer mice.

Although the actual causes of the differential use of burned and unburned sites are unknown, it seems likely that the opening of the soil surface due to the removal of litter by fire (suggested by Tester, 1965; Kaufman et al., in review) and an increase in food availability also due to litter removal (suggested by Kaufman et al., 1983; Kaufman et al., in review) play a role in the habitat use response exhibited by deer mice.

This preference for burned habitat continued until late winter and early spring 10 to 12 months after the fire. A shift from significantly more individual mice on burned to a non-significant difference over winter was not seen in an earlier study in which numbers remained higher on burned sites than on unburned 11 months after fire (Kaufman et al., in review). This over-winter change in distribution may have resulted from reduced seed availability due to a declining seed supply as well as from increasing litter accumulation on the burned grid.

The response to fire by P. maniculatus occurred within a few weeks. Numbers reached a peak by the third week of May and then remained stable until late autumn. This immediate response was not examined in earlier studies. The increase in numbers observed during the first month after fire is likely a combination of birth on the grid as well as immigration of individuals to the site. The large proportion of juveniles captured during the first month after fire on the burned portion of the grid supports the idea that more individuals were born on

the burned area. However, if new animals seen after the fire were still in the nest when the area was burned, a similar number would have been expected on the two grids based on the equal number of animals on the two areas before fire. Movement of individuals from unburned to burned areas was observed and probably accounted for the majority of new adults first captured on the burned grid throughout the study.

In addition to the general differences in habitat use between burned and unburned prairie, captures suggest a non-random use of the three topographic sites within burned and unburned prairie and differing between them. Factors important in influencing the use patterns of upland, breaks, and lowland habitat observed in this study may include (1) abundance and availability of food, (2) structure, density, and composition of living vegetation, (3) density of standing dead vegetation, (4) density, depth, and distribution of mulch (=litter), and (5) distribution and availability of nest, burrow, and safe sites.

In unburned prairie, the pattern of use among topographic sites remained relatively stable throughout the study period (May 1983 to April 1984) with uplands used slightly more than breaks and a relative avoidance of lowland areas. Findings on nearby unburned treatment plots on KPRNA showed that more litter was present on lowland sites than on breaks and uplands (Kaufman et al., in review). It is likely that a similar pattern occurred on the unburned grid in this study; and may partially explain the avoidance of this habitat by P. maniculatus. Greater use of areas with sparse ground cover has been shown for P. maniculatus

in strip-mined sites in Illinois, an old field in Kansas, and cultivated fields (e.g., Hansen and Warnock, 1978; Houtcooper, 1978; and Kaufman and Kaufman, unpublished data). In addition, P. maniculatus may be attracted to upland habitat because of reduced litter accumulation and the type of seeds available, whereas break sites probably provide the easiest access to burrows and protective safe sites due to the relative dense rock cover.

Seasonal shifts in habitat use by deer mice occurred on the burned grid but not on the unburned. The lack of any seasonal pattern on the unburned grid was not surprising since the area had remained unburned for three to four years; thus, additional litter or standing dead accumulation should not occur as rapidly on unburned areas as on newly burned sites. On the burned grid, uplands and breaks were preferred over lowland in spring, no differential use was observed from mid-July through September, and an avoidance of uplands and increased use of lowland was observed through autumn. These patterns may represent a response to seasonal changes in vegetation including increased seed set of grasses on lowlands in autumn and seasonal changes in occurrence of flowering forbs and seeds produced across different topographic sites. The greater abundance of forbs and amount of grass on lowlands than on the other sites in autumn (Kaufman et al., in review) may partially explain the shift to greater use of that habitat. In addition, individuals may be moving to lowlands in autumn seeking greater cover and protection before the onset of harsh weather. Since individuals were shown to move across

topographic sites, it is possible that a large number live on break sites where burrow entrances were common and forage into the surrounding upland and break habitats in accordance with food availability.

The only time period when captures were not significantly different among topographic sites occurred in spring 1984. The relatively few captures at lowlands in spring, as compared to autumn, may be a result of reduced food density as well as the buildup of standing dead in lowlands associated with high production in the first growing season after fire. Vegetative production on lowland plots at KPRNA has been found to be greater on burned than unburned treatment sites (Hulbert, unpublished data).

Reithrodontomys megalotis.--Differences in numbers of R. megalotis (including the number of new individuals) between the burned and unburned portions of the grid from May through November suggest that unburned tallgrass prairie is selected over burned. The preference for unburned habitat was previously shown in California grassland (Cook, 1959) and at KPRNA (Kaufman et al., 1983). Reasons for the low density of R. megalotis on burned prairie may include direct mortality due to nest destruction (Erwin and Stasiak, 1979), and the removal of the protective litter layer where nests are constructed (Shump, 1974). In contrast, Vacanti and Geluso (1985) reported greater densities of western harvest mice on burned tallgrass prairie in late summer and continuing for one year after a May fire.

The continued greater use of unburned habitat through autumn contrasts with that found by Kaufman et al. (in review) who reported no significant difference in numbers between burned and unburned prairie in autumn. In addition, Cook (1959) reported an increase in numbers of R. megalotis on burned annual grassland in California during the time of maximum seed production of the annual grasses (summer). Assuming a similar pattern for tallgrass prairie, an influx of R. megalotis should occur in fall when seed production of the dominant grasses occurs. An increase in numbers of harvest mice in autumn was suggested by Kaufman et al. (in review), but was not found in the current study. The large numbers of P. maniculatus on the burned area during autumn may have limited the use of that site by R. megalotis. Vegetative production (peak aboveground biomass) in lowland sites on KPRNA was less in 1983 than 1981, 1982, or 1984 and at uplands was the same as 1982, but lower than in 1981 and 1984 (Hulbert, unpublished data). This reduction in biomass in 1983 would result in less protective cover and litter accumulation than in other years, and possibly caused the delay in movement of harvest mice to the burned site until the following spring.

R. megalotis began to move onto the burned grid in spring 1984, 10 to 12 months after the fire. All new individuals captured from February to April 1984 (N = 6) were captured on the burned area, and by April more R. megalotis were present on the burned grid. These data suggest that some characteristics of sites burned 10 to 12 months prior attract individuals during the spring months. The most likely of these is the buildup of litter

and standing dead material from the first growing season, making it possible for the harvest mice to construct nests and exploit the high seed source that may exist on the burned area. Kaufman et al. (in review) found similar results with the number of R. megalotis in spring being greatest on annually burned sites, but in summer on sites left unburned for two to four years.

Capture data for R. megalotis indicate a non-random use of the three topographic sites. Harvest mice avoided uplands on the unburned grid throughout the study, with more captures at breaks and lowlands. The greater number of captures at break stations on the unburned grid in spring was surprising since the amount of litter was less at these sites in an autumn study (Kaufman et al., in review), and a similar relationship of litter across topographic sites would be expected for spring. The shift from a random distribution in summer to a preference for lowlands in fall may be due to greater litter accumulation or seed production on that site than at uplands or breaks. The preference for tall lush vegetation has been shown for R. megalotis (e.g., Kaufman and Fleharty, 1974; Abramsky, 1978) and aboveground nests have been found to be most common in lowland reestablished prairie in Nebraska (Erwin and Stasiak, 1979).

Peromyscus leucopus.--The density and number of first captures of new individuals for P. leucopus were greatest on the unburned grid. This finding is opposite of findings in a restored prairie in Illinois where P. leucopus immigrated to a burned site from a nearby woodland (Springer and Schramm, 1972).

Habitat conditions on the tallgrass prairie used in this study are strikingly different than riparian woodlands and deciduous forests where white-footed mice are most common (e.g., Getz, 1961; Fleharty and Stadel, 1968; Kaufman and Fleharty, 1974; Kaufman et al., 1983). On the trapping grids P. leucopus occurred mostly in the shrubby ravines and associated area in the lowlands, and only occasionally in shrub-dominated areas extending from the ravines and on hillsides.

The only nearby woody vegetation which could have served as a source of immigrating individuals was a small stand of trees in the burned area, approximately 200 meters from the grid and connected by a ravine. Population responses observed for P. leucopus on burned and unburned grids may have been a response to fire or simply correlated to the amount of available preferred habitat and/or food on the two grids.

P. leucopus preferred lowland habitats on both unburned and burned grids throughout the study, probably as a response to the presence of shrubs and ravines. The effect of fire on shrubs can be devastating, but shrubs can survive in moist ravines and lowland sites where the burn is seldom as complete. The relatively high numbers of P. leucopus was unexpected, although with the exception of the infrequent wood rat (N. floridana) no other mice are commonly found in this habitat.

Other species.--The relatively high numbers of S. tridecemlineatus observed in spring were unexpected based on its noted preference for sparse open grasslands (Struebel and

Fitzgerald, 1978). Such areas provide good burrow sites but have sparse enough cover to allow for unobstructed movement and vision. Most captures of this species occurred on breaks and lowland habitats with no consistent preference for unburned or burned prairie.

Larger numbers of M. ochrogaster were expected on the study site, especially on the unburned grid where a significant litter layer was present. Kaufman et al. (1983) reported only 21 captures of prairie voles for three seasons of censusing on fire treatment plots on KPRNA from autumn 1981 to summer 1982, and only ten captures in plots which had fire history similar to that of the unburned plot in the current study. This time period may represent the low period of a population cycle, but the data gathered to date (Kaufman et al., unpublished data) are not yet sufficient to determine whether vole populations cycle on KPRNA.

The importance of a well-developed litter layer for Microtus species has been documented in a number of studies of grassland sites with different amounts of litter due to grazing, mowing, or burning (e.g., Birney et al., 1976; Lemen and Clausen, 1984; Tester and Marshall, 1961; Getz, 1961; Zimmerman, 1965). The litter layer and standing dead in tallgrass prairie increase with time since fire, and tiller density and yield of grasses decrease (Hulbert, 1969). The amount of green succulent forage, therefore, is negatively related to time since fire and litter accumulation is positively related. Litter accumulation may exceed the optimum threshold for Microtus (Birney et al., 1976); in tallgrass prairie the optimum may be exceeded in plots which

have not been burned for three to four years. Since both litter and forage are important to M. ochrogaster, plots unburned for two to three years may provide optimum food and cover.

Little information is available on habitat preference for B. hylophaga, but based on studies of similar species (B. carolinensis and B. brevicauda) greater numbers were expected on the unburned grid where a deeper litter layer had accumulated. In restored prairie of Illinois, the density of B. brevicauda was reduced by burning, but after two years numbers were comparable to areas left unburned for four years (Springer and Schramm, 1972). It is possible that more B. hylophaga and C. parva were present in the study area but were under-represented because of low trap success.

SUMMARY

Fire and topography altered distribution and density of small mammal populations in tallgrass prairie. The response to fire by P. maniculatus and R. megalotis occurred within one month, with patterns observed during this time consistent throughout the remainder of the study. Continued study is needed to determine the relative importance of immigration and reproduction to individual recruitment and population densities in burned and unburned prairie.

Life history characteristics may be responsible for the opposite preference for burned versus unburned prairie exhibited by deer mice and western harvest mice. Since both species are seed eaters, an increase in seed availability following fire should have a positive effect on both species. However, R. megalotis require dead plant material in order to construct aboveground nests, and the removal of litter was probably a key factor in the absence of this species in the burned area.

Seasonal habitat responses for both P. maniculatus and R. megalotis are likely responses to seasonal changes in vegetative conditions as well as associated changes in food abundance and/or availability. A greater understanding of how food availability and diets are influenced by burning of tallgrass prairie will help explain the effects of fire and topography on the distributions of small mammals in tallgrass prairie.

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HABITAT SELECTION BY SMALL MAMMALS: SEASONALITY OF
RESPONSES TO CONDITIONS CREATED BY FIRE AND TOPOGRAPHY
IN TALLGRASS PRAIRIE

by

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ABSTRACT

Numbers and habitat distribution of small mammals were examined on unburned and burned tallgrass prairie in the Flint Hills of eastern Kansas. Live trapping was conducted from March 1983 through April 1984 on a 5.4 ha trapping grid on Konza Prairie Research Natural Area. Approximately one-half of the grid (2.56 ha) was burned by a controlled fire on 20 April 1983; the other portion of the grid (2.84 ha) was burned on 18 April 1984. Two hundred twenty-nine small mammals of 14 species were captured 1,632 times during the study. Distribution of captures on burned and unburned prairie and at trapping stations in different topographic sites was examined for the three common species: Peromyscus maniculatus, Reithrodontomys megalotis, and Peromyscus leucopus. The number of individuals was greater on the burned area than unburned for P. maniculatus but more R. megalotis and P. leucopus were captured on the unburned. Most new individuals were caught on the preferred habitat type for P. maniculatus and R. megalotis, and preference for burned or unburned areas was evident within one month after fire.

Seasonal patterns of use occurred at the three topographic sites for P. maniculatus on the burned grid and R. megalotis on the unburned, but not for P. leucopus on either grid. Nonrandom distributions for P. maniculatus on the burned grid occurred in spring, with more captures at upland and breaks sites, and in autumn, with more captures at lowland sites. Captures of R.

megalotis were more abundant at breaks sites in spring and at lowland sites in autumn through the following spring; differences were not significant in summer. Seasonal shifts across habitat types were likely related to seasonal changes in vegetation between unburned and burned grids and differences in vegetation structure, amount of litter, and food availability among the topographic sites examined.