

Effect of Topography on the Distribution of Small Mammals on the Konza Prairie Research Natural Area, Kansas

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Abstract. Long-term research on small mammals was initiated on the Konza Prairie Research Natural Area in autumn, 1981. Twenty-eight permanent traplines (20 stations per line) were established in fire treatments that were burned at 1- to 20-year intervals in the spring. Small mammals were trapped in summer during 1981-1987 and spring and autumn during 1981-1991. A total of 12 species of rodents and 2 species of shrews was recorded from our prairie sites during the study period. Eight species were sufficiently common with wide distributions across Konza Prairie to warrant analyses of their use of upland, limestone-breaks, and lowland prairie. Five of eight common species were not distributed randomly across topography in burned and unburned sites on Konza Prairie. For example, deer mice (*Peromyscus maniculatus*) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) used more stations in limestone-breaks than in lowland and upland prairie, whereas western harvest mice (*Reithrodontomys megalotis*), white-footed mice (*P. leucopus*), and hispid cotton rats (*Sigmodon hispidus*) used more stations in lowland than in upland and breaks prairie. Fewer species were captured per trap station in upland than lowland and breaks prairie, although plant species richness and diversity are greater on uplands than lowlands on Konza Prairie.

Key words: small mammals, rodents, shrews, topography, fire, tallgrass prairie

Introduction

Although habitat distribution and use have been studied for small mammals, little information is available on the effect of local differences in topography on the distribution of small mammals. This lack of knowledge is conspicuous within the grassland biome, because a topographically rugged landscape is a prominent feature of most unplowed native prairie, including tallgrass prairie. Recent short-term studies of habitat selection of small mammals on the Konza Prairie Research Natural Area near Manhattan, Kansas suggest that topography has an effect on small mammals. For example, deer mice (*Peromyscus maniculatus*) selected limestone breaks (Kaufman *et al.* 1988) or burned uplands (Peterson *et al.* 1985), whereas western harvest mice (*Reithrodontomys megalotis*) selected unburned lowlands (Kaufman *et al.* 1988; Peterson *et al.* 1985). In contrast to these small mammals, hispid cotton rats (*Sigmodon hispidus*) were not affected by fire treatments, but selected lowland over upland prairie (Peterson *et al.* 1985). Topographic effects for other species of small mammals are poorly known.

Studies of vegetation on Konza Prairie suggest differences relative to time since fire and topography. For example, live plant biomass is greater on lowland than on upland prairie (Abrams *et al.* 1986). Plant biomass also was greater on annually burned than unburned lowland prairie, whereas no burning response was found on upland. Additionally, species richness (number of species per plot) was greater on upland than on lowland prairie in both annually burned and unburned sites (Abrams and Hulbert 1987). Differences in plant biomass, composition, and species richness likely influence spatial

distributions of small mammals on Konza Prairie and, more broadly, spatial distributions of small mammals in tallgrass prairie in the Flint Hills.

During 10 years (1981-1991) of sampling small mammals along 580 traplines in prairie on the Konza Prairie, 12 species of rodents and 2 species of shrews were recorded. The common species (> 1% of the community of small mammals) were the deer mouse (4.8 individuals per trapline); western harvest mouse (2.1); Elliot's short-tailed shrew (*Blarina hylophaga*, 1.6); white-footed mouse (*P. leucopus*, 0.89); prairie vole (*Microtus ochrogaster*, 0.55); thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*, 0.33); hispid cotton rat (0.23); and southern bog lemming (*Synaptomys cooperi*, 0.11). Rare species (< 0.5% of the community of small mammals) included the hispid pocket mouse (*Chaetodipus hispidus*, 0.040 individuals per trapline); eastern woodrat (*Neotoma floridana*, 0.028); house mouse (*Mus musculus*, 0.024); plains harvest mouse (*R. montanus*, 0.021); least shrew (*Cryptotis parva*, 0.012); and meadow jumping mouse (*Zapus hudsonius*, 0.0034).

Our primary objective was to examine the effect of topography on the distributions of small mammals on Konza Prairie using a 10-year data set (1981-1991). Specific objectives were to determine (1) if one topographic position (upland, limestone-breaks, or lowland prairie) had more species present on average than others; (2) if the eight common species showed repeated patterns of use across burned and unburned prairie that were related to topography; and (3) if the six rare species showed any observable patterns that were related to topography.

Methods

Long-term research on small mammals was initiated on the Konza Prairie Research Natural Area south of Manhattan, Kansas in autumn, 1981. Konza Prairie is located within the Flint Hills and is characterized by steep-sided hills with wide valleys and flat ridges (for more detailed description, see Kaufman *et al.* 1988). Konza Prairie is divided into areas with prescribed burning treatments that vary from 1 to 20 years between spring fires (for more details on the Konza Prairie and location of treatment sites, see Zimmerman 1993). Our study utilized a total of 14 treatment sites with three experiencing annual fire for various lengths of time (1A since 1972, 1D since 1978, and N1B since 1988). Eleven treatment sites had periodic fires that were preceded and followed by various lengths of time with no fire

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(2C and 2D burned every other year since 1977 and 1978, respectively; 4B, 4D, 4F, 4G, and N4D burned once every 4 years since 1979, 1974, 1981, 1980, and 1988, respectively; and 10A and 10D burned once every 10 years since 1981 and 1986, respectively). Two treatments (20B and N20B) were not burned between 1981 and 1991, but differed in length of time with no fire in that N20B was burned in an accidental fire in 1980, whereas 20B was unburned since 1973. All study sites were ungrazed by large mammalian herbivores during our study.

Each experimental fire treatment had two permanent traplines (20 traps per station per line). Each station had two large Sherman live traps (7.6 by 8.9 by 22.9 cm) placed within 1 m of the permanent station marker. For more details on traplines, stations, and trapping procedures, see Kaufman *et al.* (1988). Because of the extensive topographical relief, we attempted to place the two traplines within an experimental treatment such that 40% of the stations would occur in upland, 20% in limestone-breaks, and 40% in lowland prairie. These percentages were attempted in our initial placement of traplines to try to standardize the number of stations in different topographic categories for the many fire treatment sites. All stations within a treatment site were categorized as occurring in either upland, breaks, or lowland prairie (for more description of topographic positions, see Kaufman *et al.* 1988).

Spring and autumn data for small mammal traplines were accumulated for 10 years from autumn 1981 to spring 1991, whereas summer data were accumulated from 1981 to 1987. These data were divided into four data sets, annual burns, periodic burns (first year after fire with more than 1 year since fire), short-term unburns (2-4 years without fire), and long-term unburns (5-20 years without fire). Some experimental fire treatments appeared in only one data set (e.g., 1D), whereas others appeared in a maximum of three data sets (e.g., N1B, Table 1). The parameter that was evaluated for each data set was the presence/absence of a species at each station during each sampling period. A value of 1 was recorded if a species was present at a station, whereas a value of 0 was recorded if a species was absent.

Table 1. Number of times a treatment site appeared in data sets for annual burns, periodic burns (2-20 year interval), short-term unburns (2-4 years), and long-term unburns (5-20 years) in summer (SU), autumn (AU), and spring (SP) on Konza Prairie Research Natural Area, Kansas.

Site	Annual			Periodic			Short			Long		
	SU	AU	SP	SU	AU	SP	SU	AU	SP	SU	AU	SP
1A	2	4	3	--	--	--	--	--	--	--	--	--
1D	6	10	10	--	--	--	--	--	--	--	--	--
N1B	--	2	2	--	1	1	--	--	--	6	7	7
2C	--	--	--	2	2	2	1	3	2	--	--	--
2	--	--	--	1	3	2	2	2	2	--	--	--
4B	--	--	--	2	2	2	4	8	8	--	--	--
4D	--	--	--	2	2	2	4	6	5	--	--	--
4F	--	--	--	1	3	3	5	7	7	--	--	--
4G	--	--	--	1	2	1	5	6	6	--	--	--
N4D	--	--	--	--	1	1	--	2	2	6	7	7
10A	--	--	--	--	1	1	3	3	3	3	5	4
10D	--	--	--	1	1	1	1	2	1	--	1	1
20B	--	--	--	--	--	--	--	--	--	6	10	10
N20B	--	--	--	--	--	--	2	2	3	4	7	7

A log-likelihood ratio test (G -test) was used to test whether proportions of stations with and without a particular species present were equal across topographic positions within each of the four data sets. G -statistics that were greater than the critical test statistic ($P = 0.05$) were partitioned to determine which topographic positions differed in use by each species. Results from the four data sets then were compared to look for commonality of topographic patterns among burned and unburned treatments. G -tests also were used to assess the effect of topography on the number of species present at a station. The maximum number of species that possibly could occur at a station was eight (two traps set for four consecutive nights) within each trapping period.

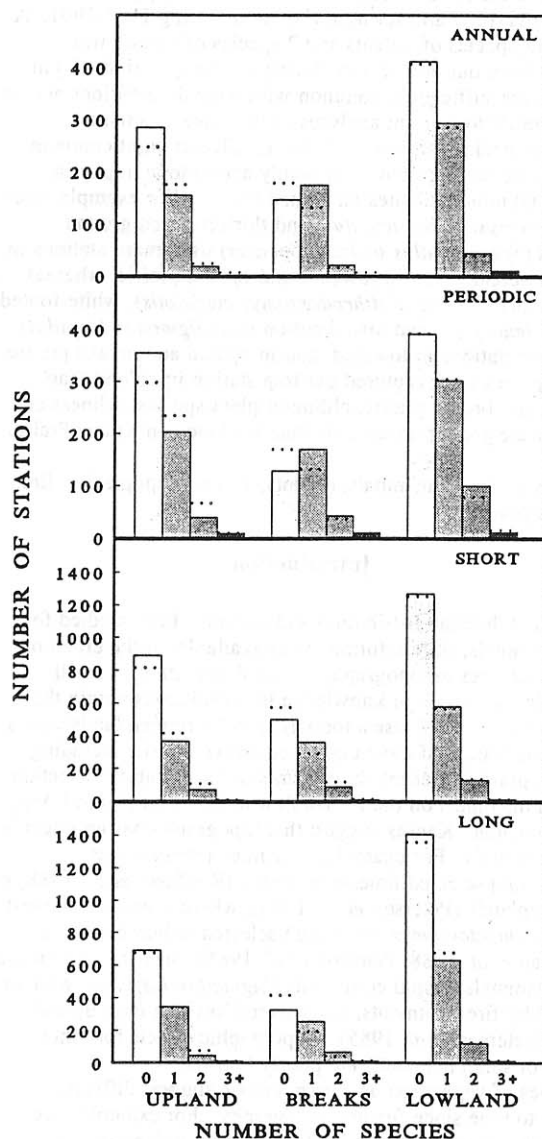


FIG. 1. Observed number of stations with zero, one, two, and three or more species present in upland, limestone-breaks, and lowland prairie in annual burns, periodic burns, short-term unburns (2-4 years), and long-term unburns (5-20 years) on the Konza Prairie Research Natural Area. Dotted lines on bars indicate the expected frequency for each category given a random distribution.

Table 2. Number of stations and number of stations used by small mammals in upland (U), limestone breaks (B), and lowland (L) in annual burns, periodic burns (first year after fire with 2-20 years unburned), short-term unburns (2-4 years), and long-term unburns (5-20 years) on the Konza Prairie Research Natural Area, Kansas.

Category	Annual			Periodic			Short			Long		
	U	B	L	U	B	L	U	B	L	U	B	L
Stations	458	342	760	606	350	804	1336	952	1992	1088	658	2174
Deer mouse	131	180	286	201	186	277	264	315	256	210	229	199
Western harvest mouse	15	4	37	40	22	57	78	78	289	72	47	268
Elliot's short-tailed shrew	14	14	23	24	15	46	73	61	144	81	54	217
White-footed mouse	2	2	20	18	25	83	22	33	116	25	22	120
Prairie vole	13	4	21	9	3	13	52	32	30	34	27	56
Thirteen-lined ground squirrel	7	12	6	8	17	23	24	27	9	25	30	26
Hispid cotton rat	7	0	13	5	10	30	2	2	14	3	0	4
Southern bog lemming	1	0	2	0	1	0	7	5	16	7	3	20

Results

A total of 14 species of small mammals was captured at 11,520 stations from 1981 to 1991 on the Konza Prairie. In descending order of the number of stations used, these species were the deer mouse (2,734 stations), western harvest mouse (1,007), Elliot's short-tailed shrew (766), white-footed mouse (488), prairie vole (294), thirteen-lined ground squirrel (214), hispid cotton rat (90), southern bog lemming (62), hispid pocket mouse (24), eastern woodrat (20), house mouse (15), plains harvest mouse (12), least shrew (7), and meadow jumping mouse (2). Statistical analyses were made for the eight common species, whereas these tests were not possible for the six rare species because of a lack of available data.

The number of species present at a station ranged from zero to five. The maximum number of species present at a station was three in upland, and five in both limestone-breaks and lowland prairie. In both burned and unburned treatments, the proportion of stations with zero, one, two and \geq three species of small mammals was not equal across the three topographic positions (annual burn: $\chi^2 = 41.7$, $d.f. = 6$, $P < 0.01$; periodic burn: $\chi^2 = 52.9$, $d.f. = 6$, $P < 0.01$; short-term unburn: $\chi^2 = 55.0$, $d.f. = 6$, $P < 0.01$; long-term unburn: $\chi^2 = 62.3$, $d.f. = 6$, $P < 0.01$). In both burned treatments (annual and periodic), upland was overrepresented in stations with no species present, breaks in stations with one species present, and lowland prairie in stations with two and three or more species (Fig. 1). Short-term unburned sites mirrored results for burned sites, whereas in long-term unburned sites, lowland was overrepresented in stations with no species present and limestone-breaks prairie in stations with one or two species present (Fig. 1).

Deer mice did not use topographic positions randomly in either burned or unburned prairie (Table 2; annual: $\chi^2 = 47.9$, periodic: $\chi^2 = 44.3$, short-term unburn: $\chi^2 = 159.7$, long-term unburn: $\chi^2 = 233.9$; all $d.f. = 2$ and all $P < 0.01$). In both burned and unburned prairie, deer mice selected breaks over upland and lowland, although relative use of breaks was lower in unburned than in burned prairie (Fig. 2). Use of lowland was greater than that of upland in annually burned prairie, whereas upland was used more than lowland in unburned prairie. Upland and lowland were not used differentially in periodic burns.

Western harvest mice selectively used topographic sites in annually burned and unburned prairie (Table 2; annual: $\chi^2 = 11.2$, short-term unburn: $\chi^2 = 72.8$, long-term unburn: $\chi^2 = 34.3$; all $d.f. = 2$ and all $P < 0.01$), but not in periodic burns ($\chi^2 = 0.3$, $d.f. = 2$, $P > 0.05$). In short- and long-term unburns, western harvest mice selected lowland over upland and limestone-breaks prairie (Fig. 2). For annual burns, they also used lowland more than limestone-breaks, but not significantly more than upland.

White-footed mice also did not use topographic positions randomly in either burned or unburned prairie (Table 2; annual: $\chi^2 = 12.7$, periodic: $\chi^2 = 31.0$, short-term unburn: $\chi^2 = 40.5$, long-term unburn: $\chi^2 = 21.5$; all $d.f. = 2$ and all $P < 0.01$). White-footed mice used lowland more than upland and breaks in both burned and unburned prairies, except that lowland was not used more than breaks in periodic burns (Fig. 2). Additionally, white-footed mice used breaks over upland in periodic burns and short-term unburns.

Thirteen-lined ground squirrels differentially used topographic sites in all four types of burned and unburned prairie (Table 2; annual: $\chi^2 = 9.8$, periodic: $\chi^2 = 10.5$, short-term unburn: $\chi^2 = 30.0$, long-term unburn: $\chi^2 = 25.0$; all $d.f. = 2$ and all $P < 0.01$). Ground squirrels selected limestone breaks over lowland except in periodic burns (Fig. 2). Additionally, breaks were selected over upland prairie in periodic burns and long-term unburns.

Cotton rats selectively used topographic positions in burned and short-term unburned prairie (Table 2; annual: $\chi^2 = 10.0$, periodic: $\chi^2 = 13.9$, short-term unburn: $\chi^2 = 7.5$, long-term unburn: too few stations used to test statistically; $d.f. = 2$ and $P < 0.01$ for burn treatments and $P < 0.05$ for short-term unburns). Lowland was selected over upland by cotton rats in periodic burns and short-term unburns, but not in annual burns (Fig. 2). In contrast, lowland was selected over breaks in annual burns, but not in periodic burns or short-term unburns.

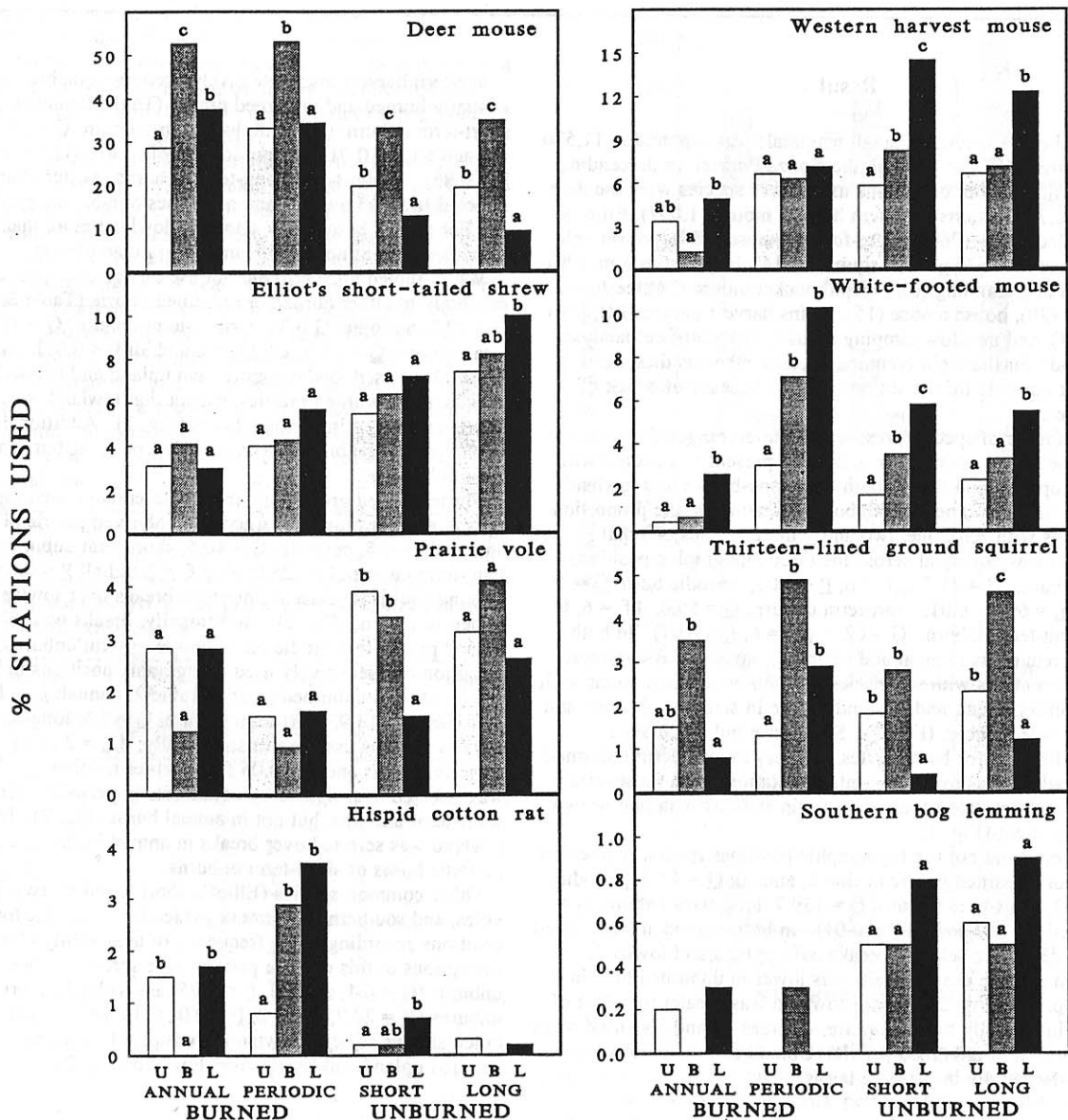
Other common species (Elliot's short-tailed shrews, prairie voles, and southern bog lemmings) tended to use the topographic positions according to the frequency of availability (Table 2). Exceptions to this random pattern were shrews in long-term unburns ($\chi^2 = 6.4$, $d.f. = 2$, $P < 0.05$) and voles in short-term unburns ($\chi^2 = 20.7$, $d.f. = 2$, $P < 0.01$). In these situations, short-tailed shrews selected lowland over upland, whereas prairie voles selected upland and breaks over lowland (Fig. 2).

Table 3. Mean percentage of stations used in upland, limestone-breaks, and lowland prairie by rare species on Konza Prairie Research Natural Area, Kansas.

Species	Upland	Breaks	Lowland
Hispid pocket mouse	0.09 (0.08)	0.61 (0.06)	0.13 (0.05)
Eastern woodrat	0.09 (0.11)	0.36 (0.31)	0.10 (0.07)
House mouse	0.06 (0.05)	0.10 (0.08)	0.22 (0.08)
Plains harvest mouse	0.14 (0.10)	0.15 (0.18)	0.08 (0.03)
Least shrew	0.12 (0.06)	0.03 (0.03)	0.03 (0.04)
Meadow jumping mouse	0.02 (0.02)	--	0.03 (0.04)

Standard errors are given in parentheses.

Of the rare species, hispid pocket mice were observed in limestone-breaks prairie proportionally more than in upland or lowland prairie, although variability (*SE*) of use of stations was similar between topographical positions (Table 3). Similarly, eastern woodrats used breaks stations more frequently than those in upland and lowland, but use of breaks also had the greatest variability. The house mouse, a nonnative species, was the only rare species that was observed in lowland more frequently than upland or breaks. Variability in use by house mice was similar across upland, breaks, and lowland prairie. Least shrews were observed more in upland than in breaks and lowland with similar levels of variability. The plains harvest mouse was the only rare species that showed similar use of two topographic positions (upland and breaks) with a slightly lower use of lowland prairie. Meadow jumping mice were observed once each in upland and lowland, but never in limestone breaks.

**FIG. 2.** Percentage of stations used in upland (U), limestone-breaks (B), and lowland (L) prairie in annual and periodic burns and short-term (2-4 years) and long-term (5-20 years) unburns by eight common small mammal species on the Konza Prairie Research Natural Area. Letters above bars within each fire treatment that are not the same indicate significant differences.

Discussion

When we initiated our long-term study of small mammals in tallgrass prairie, we expected unique species-specific patterns in use of local topographic conditions because of major differences in the natural history of rodents and shrews found in eastern Kansas (Bee *et al.* 1981). Our results support this general expectation for common species such as deer mice and thirteen-lined ground squirrels, which selectively used the limestone breaks, and western harvest mice, white-footed mice, and hispid cotton rats, which selectively used lowland. However, differential use was statistically nonsignificant for Elliot's short-tailed shrews, prairie voles, and southern bog lemmings. Differential association with topographic position was suggested by patterns of station use for rare species, but abundance and station use were too low to test statistically.

Lowland prairie was selected more than other habitats by western harvest mice, white-footed mice, and hispid cotton rats. Harvest mice used lowland prairie at a landscape scale (our study) and at a microscale (Peterson *et al.* 1985), although Brillhart *et al.* (this volume) failed to demonstrate differential use of lowland and upland on small experimental plots. Selective use of lowlands by cotton rats was evident at a microscale in small experimental patches (Brillhart *et al.* this volume, Peterson *et al.* 1985) and at a landscape scale on Konza Prairie (our study). However, cotton rats may select upland over lowland prairie in summer (Brillhart *et al.* this volume). Our pattern for cotton rats primarily represents autumn use, because 81% of the stations used by cotton rats occurred during autumn sampling periods. Selective use of lowland by white-footed mice likely was due to wooded ravine habitats, which they prefer (Clark *et al.* 1987), being spatially closer to lowland than upland and breaks. Use of trap stations in our study also suggested greater use of lowland over upland and breaks by house mice. This species, which is most common around human habitation (Kaufman and Kaufman 1990), may use ravines and nearby lowland as dispersal corridors more frequently than other topographic features.

Limestone-breaks prairie was used selectively more than other habitats by deer mice and thirteen-lined ground squirrels. Kaufman *et al.* (1988) reported that deer mice selected limestone breaks in unburned prairie, but exhibited no differential use of topography during the first year after fire. In contrast to results reported in the 1-year study by Kaufman *et al.* (1988), deer mice selected breaks over upland and lowland prairie in both annually and periodically burned prairie in our 10-year study. When only upland and lowland prairie were available in small experimental patches, deer mice used upland over lowland stations (Brillhart *et al.* this volume, Peterson *et al.* 1985). The overall pattern of habitat use for deer mice is selection of limestone-breaks habitat over uplands or lowlands, regardless of the burn history of the site. However, the change from secondary use of lowlands in the first year after fire to secondary use of uplands in years following the first year postburn likely reflects the deterioration of the lowlands from a habitat of high productivity and no litter in the first year after fire (Abrams *et al.* 1986, Kaufman *et al.* 1988) to a habitat with standing dead vegetation and an increasing amount of litter present on the soil surface (Kaufman *et al.* 1988). Our results for thirteen-lined ground squirrels were similar to results from a 13-ha grid on Konza Prairie (Clark *et al.* 1990) where ground squirrels selected limestone breaks and avoided lowland prairie.

Use of trap stations also suggested greater use of limestone breaks over other habitats by hispid pocket mice and eastern woodrats. Pocket mice likely used breaks because of the lack of litter and the large amount of exposed soil surface (Kaufman *et al.* 1988). Higher use of limestone breaks by woodrats probably reflects availability of the rocky outcrop and shrubs that provide the resources for dens.

Prairie voles differentially used upland over lowland in short-term unburned prairie; however, no preferences were shown on burned sites or long-term unburns in our study. Selection of upland by voles also was shown on a 13-ha grid on Konza Prairie following 2-4 years after a fire (Bixler and Kaufman 1995). Use of trap stations also suggested greater use of upland over other habitats by least shrews. Least shrews were associated with upland communities in tallgrass (Clark *et al.* this volume) and mixed grass prairie (Choate and Fleharty 1975).

Elliot's short-tailed shrews and southern bog lemmings showed little differential use of upland, limestone-breaks, and lowland prairie. Elliot's short-tailed shrews were shown to select lowland and avoid upland prairie on a site 2-4 years after fire (Clark *et al.* this volume), whereas our study showed this pattern only in long-term unburns and not in short-term unburns. For southern bog lemmings, only 62 of 11,520 stations (0.5%) were used during our study, so selective use of lowland prairie may become evident as data continue to accumulate from ongoing, yearly, spring and autumn sampling.

The repeatability of patterns of small mammal use of topographic positions on Konza Prairie shows the strength of the topographic effect on habitat selection by small mammals given the complex management plan and the variability in climate, soil, spatial scale, and parameters evaluated in this and other studies. Our study used the presence/absence of a species at a station to assess use of topography, whereas other studies used individual captures of each species (Bixler and Kaufman 1995, Brillhart *et al.* this volume, Clark *et al.* 1990 and this volume, Peterson *et al.* 1985). Spatial scales of studies included small experimental patches (0.04 ha) in upland and lowland prairie on a 2-ha site (Brillhart *et al.* this volume, Peterson *et al.* 1985); in three microhabitats from upland to lowland prairie on a 13-ha grid (Bixler and Kaufman 1995, Clark *et al.* 1990 and this volume); and in three microhabitats in spatially explicit traplines scattered across the landscape of Konza Prairie (Kaufman *et al.* 1988 and our study). However, studies of topographic associations at additional sites are required to ascertain whether the patterns we observed are universal across tallgrass prairie and other topographically diverse grasslands.

Finally, number of species of small mammals recorded per station ranked, in ascending order, as upland, breaks, and lowland. In contrast, shallow, rocky upland had more species of plants than deep-soil lowland prairie on Konza Prairie (Abrams and Hulbert 1987, Gibson and Hulbert 1987). A pattern of high richness and diversity of plant species on upland and low richness and diversity on lowland prairie and the opposite pattern for use by small mammals appears counterintuitive. Rather, one might expect higher diversity in plants to promote greater diversity of small mammals in these topographic sites. However, plant biomass is higher in lowland than in upland prairie (Abrams *et al.* 1986), suggesting that patterns shown in small mammal use may be influenced more by productivity than by the diversity of vegetation. Currently, small mammal use and vegetation cannot be compared on limestone breaks of Konza Prairie, because no measure of plant biomass or species richness and diversity is available.

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