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DISTRIBUTION OF CARNIVORE BURROWS IN A PRAIRIE LANDSCAPE

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ABSTRACT—Mammals impact prairie ecosystems through burrowing activities. Burrows used by carnivores were studied in four habitat types at the Konza Prairie Biological Station, a native tallgrass prairie near Manhattan, KS. We surveyed nearly 40 km of 10-m-wide transects and counted burrows in upland, slope, and lowland prairie and along ravines. Burrows were placed selectively along slopes (7.3 per km) and to a lesser extent along edges of ravines (4.2), but only infrequently in upland (0.6) and never in lowlands (0.0). We also recorded features (e.g., location, aspect, and slope steepness) along slope transects at a 30 m intervals to estimate availability of these features. Points of hills (18.7 burrows per km) were used more than sides of hills (2.0) or upper ends of ravines (1.5). Burrows on points were placed selectively on steep rather than shallow slopes and on south- and west-facing slopes rather than north- and east-facing slopes.

Key Words: burrows, carnivores, Kansas, tallgrass prairie, topography

Introduction

Small to large mammals, through their foraging, burrowing, and other activities, such as wallowing, urinating, defecating, and trail making, can impact prairie ecosystems through generation of various small-scale disturbances. These disturbances can remove or cover growing vegetation or create local concentrations or "hotspots" of certain nutrients. These disturbances and hotspots can alter nutrient dynamics and provide microsites for plant colonization and establishment at local or fine-scale spatial areas. These impacts can alter plant species composition, which leads to greater

number of species and heterogeneity at a landscape scale (Hartnett and Fay 1998).

Mammalian disturbances have been shown to affect plant communities and ecosystem processes directly. For example, selective feeding on preferred plant species affects those populations of plants directly by reducing their growth and survival (Inouye et al. 1987). Also, grazing by bison (*Bos bison*) and prairie dogs (*Cynomys ludovicianus*) in grasslands increases number of plant species present (Cid et al. 1991), increases uptake of nitrogen from soil (Whicker and Detling 1988), increases concentration of nitrogen in plant shoots (Coppock et al. 1983), and allocates nitrogen to leaves (Jaramillo and Detling 1988). In contrast, number of plant species and diversity were lower in bison wallows, but many of the plant species that colonized wallows were distinct from those occurring in adjacent prairie (McMillan 1999).

Mammalian disturbances also can affect plant communities indirectly by their effect on available resources that limit plants by altering soil structure or chemistry (Chew 1974, 1978). Plant species that colonize animal disturbances such as burrow mounds may differ with type and physical features of the disturbance. For example, annual plants were more likely to colonize badger (*Taxidea taxus*) burrows, whereas perennial species were more likely to colonize pocket gopher (*Geomys bursarius*) mounds (Gibson 1989). Nutrient concentrations also can be affected by deposition of urine or fecal matter, which creates locally high concentrations of certain nutrients (Woodmansee 1978). For example, nutrient dynamics vary among wallows and edges of wallows where concentrations of magnesium and sodium were higher as compared to adjacent prairie where concentrations of total carbon and nitrogen were higher (McMillan 1999).

Mammals also affect the soil profile by their wallowing and burrowing activities. Changing the soil structure may change soil aeration and moisture retention, which then may influence decomposition or mineralization rates by microbes (Inouye et al. 1987). For example, greater soil bulk density, higher soil moisture, and higher soil temperature occurred in bison wallows than in adjacent prairie (McMillan 1999). In contrast to bison wallows, which are concave depressions, disturbances of rodents (e.g., pocket gopher and prairie dogs) typically are made by depositing subsurface soil in a loosely packed mound. Pocket gophers reduced nitrogen near the soil surface and increased heterogeneity of soil nitrogen by moving nitrogen-poor subsurface material to the soil surface (Inouye et al. 1987). This change in soil nitrogen can affect which species colonize these soil patches

and subsequently plant succession on these areas. Further, plant biomass may be enhanced directly adjacent to pocket gopher mounds and burrows and nitrogen availability may be increased over burrows (Reichman et al. 1993).

The mammalian fauna is less diverse today than before Euro-American settlement in the northern Flint Hills (Kaufman et al. 1998). For example, nine species of carnivores have been recorded at the Konza Prairie Biological Station (Konza Prairie; Kaufman et al. 1998). Of these, only five are considered common: coyote (*Canis latrans*), raccoon (*Procyon lotor*), American badger, striped skunk (*Mephitis mephitis*), and bobcat (*Lynx rufus*). The remaining carnivores are red fox (*Vulpes vulpes*), long-tailed weasel (*Mustela frenata*), mink (*M. vison*), and least weasel (*M. nivalis*). Extirpated carnivores are gray wolf (*Canis lupus*), both black and grizzly bears (*Ursus americanus* and *U. arctos*, respectively), eastern spotted skunk (*Spilogale putorius*), northern river otter (*Lontra canadensis*), and mountain lion (*Puma concolor*). The extant carnivores show habitat associations across the dissected landscape of Konza Prairie (Finck et al. 1986; McMillan et al. 1997). Raccoons, red foxes, bobcats, striped skunks, mink, and least weasels are found in lowland habitats and in association with woody and brushy habitats along streams, whereas badgers and long-tailed weasels prefer open grasslands. Coyotes are seen commonly in upland, slope, and lowland prairie habitats on Konza Prairie.

Some attention has been given to plant species that colonize the bare soil of badger mounds (e.g., Platt 1975; Gibson 1989). However, no research has been directed at how burrowing and excavating activities of mammalian carnivores might affect soil processes or ecosystem function through changes in nutrient dynamics or rates of mineralization or decomposition associated with mounds. Because of the disturbance made to the soil profile by carnivores digging burrows and the potential impacts of these disturbances on plant communities and landscape processes, we wanted, as a first step in understanding their impact, to survey the distribution of carnivore burrows across the tallgrass prairie landscape (Konza Prairie). Our preliminary observations suggested that carnivore burrows were more common on slopes than in other topographic positions on Konza Prairie. Therefore, we expected to find more burrows associated with the upper edge of the slope prairie than with lowland and upland prairie. If we found this expectation to be true, we then wanted to assess if all positions on a slope were equally likely to be used for burrow placement. Further, we wanted to determine if slope aspect and steepness influenced where burrows were

placed. To test whether carnivore burrows were placed selectively relative to certain classes of topography, slope steepness, and slope aspect, we also estimated availability of the same features in the study area.

Methods

We conducted our research during June and July 1996 on Konza Prairie, a 3,487 ha research site, located near Manhattan in eastern Kansas (Fig. 1). The largest remnants of native tallgrass prairie, such as Konza Prairie, are found on the shallow, rocky soils of the Flint Hills. These grasslands are characterized by xeric uplands and mesic lowlands connected by moderately steeply sloping prairie. This erosional landscape has stream-dissected hills, bench and slope topography in the uplands created by resistant limestone bedrock and less-resistant mudstone layers, and valley bottoms (Oviatt 1998).

Konza Prairie is comprised mostly of tallgrass prairie with limited deciduous forest along streams. Perennial warm-season grasses, such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), dominate the prairie vegetation (Freeman 1998). Grasses common on xeric sites are blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), and buffalograss (*Buchloe dactyloides*). Shrub thickets and small trees occur along the upper reaches of ravines and on slopes associated with limestone outcrops. Rough-leaved dogwood (*Cornus drummondii*), aromatic sumac (*Rhus aromatica*), smooth sumac (*R. glabra*), and buckbrush (*Symphoricarpos orbiculatus*) are the woody plants typically associated with draws and limestone outcrops (Freeman 1998). Riparian areas consist of nearly continuous deciduous forest, which are 10 to 300 m wide and associated with perennial streams. Dominant trees include bur oak (*Quercus macrocarpa*), chinquapin oak (*Q. muehlenbergii*), hackberry (*Celtis occidentalis*), and American elm (*Ulmus americana*; Freeman 1998).

We assessed the distribution of carnivore burrows on upland prairie, slope prairie, lowland prairie, and ravines associated with the upper slope and bench of the grassland (Fig. 2a). Upland prairie was characterized by relatively flat hilltop areas, which had shallow soils and relatively xeric conditions. Slope prairie occurred on sides of hills; top edges of slopes often were found where limestone strata outcropped. Some outcropping limestone formed ledges up to 1 m in height, whereas others produced rocky grassland due to limestone fragments on the soil surface. Lowland prairie

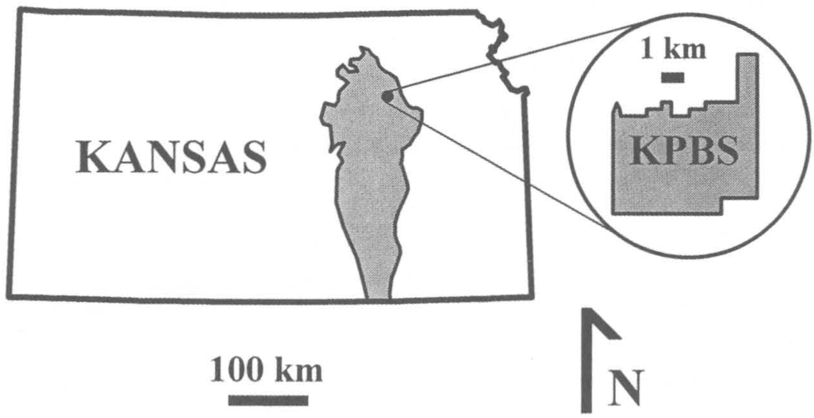

Figure 1. Location of the Konza Prairie Biological Station (KPBS) in the Flint Hills (shaded area) in Kansas. Drawing by Dawn M. Kaufman.

was typified by mesic and deep loamy soil, which was relatively flat or only gently sloped. Ravines included open washout areas, which lacked woody vegetation and were dominated by prairie vegetation; deeply eroded areas, which were bordered by prairie vegetation or by moderate shrubby vegetation [e.g., sumac (*Rhus* spp.)]; and dry creek beds with woody vegetation [e.g., oaks (*Quercus* spp.) and cottonwood (*Populus deltoides*)].

Transects, which were 10 m wide, were placed in upland, slope, and lowland prairie, and along ravines (Fig. 2a). Because we wanted to assess areas where carnivores, primarily coyotes and badgers, lived, we placed transects in locations only where ≥1 km of contiguous habitat could be surveyed in each habitat type. This resulted in transects that differed in total length sampled for carnivore burrows (upland = 9.0 km, slopes = 12.1 km, lowland = 7.5 km, and ravines = 11.0 km). Further, we divided the 12.1 km slope prairie transects into points of hills, sides of hills, and interior slopes of hills (Fig. 2b). Points were those regions having convex curvature at the ends of narrow extensions of hills, whereas interior slopes were those regions that had concave curvature and served as heads of drainages, which led eventually into ravines. Side slopes occurred between points and interior slopes. Because of the nature of the slope, transect lengths varied for these slope positions (points = 3.9 km, sides = 5.5 km, and interior slopes = 2.7 km).

We counted each active or inactive burrow along each transect, but did not include diggings that resulted from attempts to excavate prey. We did not

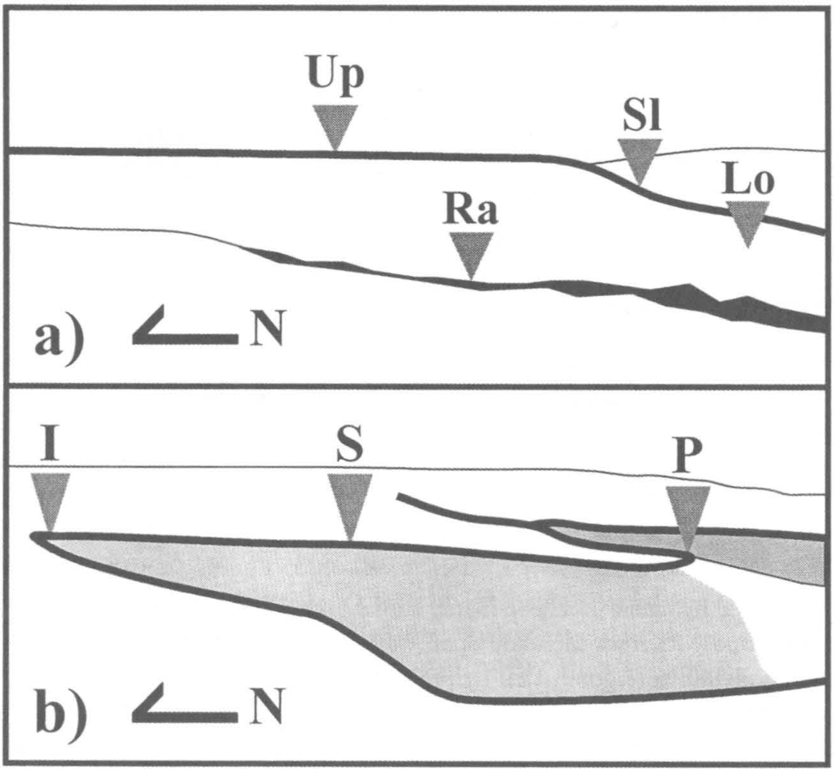

Figure 2. Location of habitats sampled for carnivore burrows at the Konza Prairie Biological Station, Kansas. **(a)** An oblique side view typical of topographic positions sampled, which included upland prairie (Up), slope prairie (Sl), lowland prairie (Lo), and upper edges of ravines (Ra; designated by the black area). **(b)** An oblique side view typical of slope prairie positions sampled, which included points of hills (P), side slopes (S), and interior slopes (I). Shaded areas represent shadows seen in photograph of topographic relief on Konza Prairie. Drawing by Dawn M. Kaufman.

record the latter because, although these disturbances might have a similar effect on the landscape, we did not want to mix the causes of the disturbances. That is, diggings where prey (e.g., prairie rodents) is excavated represent foraging areas for a carnivore at a site selected by the prey, whereas burrows represent sites where carnivores chose to den or seek shelter. Further, if our expectations of carnivore burrow distribution were supported, we wanted to be able to interpret the results relative to life history strategies of carnivores such as coyotes and badgers. Therefore, we arbitrarily

excluded any burrow with an opening that had a diameter $\leq$10 cm or any burrows where the displaced soil volume was $\leq$10,000 cm^3 (volume of 10 cm x 20 cm x 50 cm) because the likelihood that these represented burrows of badgers or coyotes was small. Areal openings of burrows in slope prairie that could be measured averaged 224 $\pm$ 12 cm^2 (1 *SE*, $n = 72$; range: 76 cm^2 to 608 cm^2), whereas volume of displaced soil averaged 0.071 $\pm$ 0.008 m^3 ($n = 63$; range: 0.01 m^3 to 0.311 m^3). Further, <25% of the burrows had openings <150 cm^2. Some burrows were excavated in the preceding season, as evidenced by freshly displaced soil and absence of vegetation on the disturbance area; however, most burrows were more than 1 year old, as revealed by visible degradation of both opening and erosion of displaced soil, and in some cases the presence of vegetation.

At each burrow on a slope, we measured both the aspect of the slope by using a hand-held compass and the steepness of the slope by using a clinometer. To estimate availability of these features in the slope environment, we also measured aspect and steepness systematically at 30 m intervals (hereafter referred to as stations) along the total length of the slope transect (12.1 km). Frequency of availability of slope positions varied [points: $n = 137$ (33.3%), sides: $n = 188$ (45.6%), interior slopes: $n = 87$ (21.1%)]. We placed each burrow into one of eight aspect classes, each representing 45°, relative to the direction of its opening (north = N and NNE; northeast = NE and ENE; east = E and ESE; southeast = SE and SSE; south = S and SSW; southwest = SW and WSW; west = W and WNW; and northwest = NW and NNW). Each station also was placed into one of these eight aspect classes to estimate the frequency of occurrence of aspect classes in the slope environment. Further, we assigned each burrow to one of three slope categories: shallow (slopes between 5° and 16°), intermediate (slopes between 17° and 20°), and steep (slopes between 21° and 28°). Again, we applied the same procedure for the stations to obtain frequencies of slope steepness.

We used log-likelihood ratio tests (G) to determine if burrows were distributed randomly among the available topographic features of interest. Expected frequencies for burrows in upland, slope, lowland, and ravine sites were calculated from the proportion of length of transects that occurred in each habitat type. For distribution of burrows along slopes, we calculated expected frequencies for burrows based on proportions as related to the length of transects assigned to point, side, and interior slopes. We also calculated burrows per km of transect as an index to burrow abundance in upland, slope, lowland, and ravine sites and in points, sides, and interior slopes of hills.

Because too few burrows occurred on sides and interior slopes of hills, we only analyzed effects of slope steepness and aspect on burrow placement on points of hills (73 burrows and 137 stations in the slope environment). We again used G tests to test for preferences of carnivores. For aspect, we calculated expected frequencies for burrows for each class from proportion of stations in that class in the environment. Similarly, we calculated expected frequencies of burrows for steep, intermediate, and shallow slopes from proportions of stations in those classes. Further, we estimated burrows per 10 stations as an index to abundance of burrows in each aspect class and for each slope steepness category.

Results

A total of 139 carnivore burrows were counted along 39.6 km of transects (Table 1). Burrows occurred significantly more often on slopes and along ravines than in upland and lowland sites (G = 125.9, *d.f.* = 3, P <0.001). Further, burrows were associated more strongly with slopes than with ravines (G = 9.7, *d.f.* = 1, P <0.01). Within slope prairie, carnivores selectively chose points of hills over sides and interior slopes of hills for burrow locations (G = 96.9, *d.f.* = 2, P <0.001; Table 2). This positive association was quite strong as the number of burrows per km was 9 to 12 times higher on points than on sides and interior slopes of hills. The relative abundances of burrows across these habitat categories ranked as point slopes (18.7 per km) and ravines (4.2), followed by side slopes and interior slopes (1.5-2.0; Tables 1 and 2). Upland and lowland prairie were used infrequently if at all (0-0.6 burrows per km).

Carnivores did not differentiate between intermediate slopes (burrows = 35, stations = 59) and steep slopes (burrows = 31, stations = 39; G = 1.4, *d.f.* = 1, P > 0.10) on points of hills, so these two classes were pooled before additional analysis. Carnivores preferred steep and intermediate slopes (burrows = 66, stations = 98) to shallow slopes (burrows = 7, stations = 39) on limestone breaks (G = 15.7, *d.f.* = 1, P < 0.001). Almost four times as many burrows occurred on intermediate to steep slopes (6.7 burrows per 10 stations) than occurred on shallow slopes (1.8 burrows per 10 stations).

Slope aspect also influenced placement of burrows, as carnivores preferentially dug more burrows on point slopes that faced south and west than on those that faced north and east (G = 57.3, *d.f.* = 7, P < 0.001; Table 3). The most preferred directions for the opening of the burrows were south (11.5 burrows per 10 stations) and southwest (11.2 burrows per 10 stations). Interestingly, 90% of the burrow openings faced from southeast to west,

TABLE 1
NUMBER AND RELATIVE ABUNDANCE OF CARNIVORE BURROWS IN FOUR HABITAT TYPES, KONZA PRAIRIE BIOLOGICAL STATION

	Burrows		
Topographic position	Number per km	Number	Transects (km)
Upland	0.6	5	9.0
Slope	7.3	88	12.1
Lowland	0.0	0	7.5
Ravine	4.2	46	11.0
Total		139	39.6

although only 53% of the stations were located or available on points of hills that faced in these directions.

Discussion

Carnivores selectively placed burrows on prairie slopes on Konza Prairie. Previous studies of habitat selection by carnivores in grasslands have associated badgers and coyotes with these types of habitats. For example, badgers and coyotes have been found associated with upland or rolling prairies (Stains and Baker 1958; Halloran and Glass 1959; Andersen and Fleharty 1967; Choate and Fleharty 1975; Finck et al. 1986), slope prairie (Snead and Hendrickson 1942; Finck et al. 1986), or rough breaks terrain (Stains and Baker 1958; Walker 1978) in the Great Plains. Further, previous studies have found burrows and diggings of badgers associated with breaks or slope habitats (Snead and Hendrickson 1942; Finck et al. 1986), whereas dens of coyotes were found on top of hills where short grasses and sumac thickets occurred (Andersen and Fleharty 1967).

On prairie slopes, carnivores selectively placed burrows on points (18.7 per km) over the sides (2.0 per km) and interior (1.5 per km) regions. Some advantages of placing burrows on points of slopes include a large field of view and little blockage of that view by prairie vegetation. Our visual observations on Konza Prairie also indicated that the field of view continually decreases in width and depth as one moves from points of hills to side slopes to interior slopes of hills.

TABLE 2
NUMBER AND RELATIVE ABUNDANCE OF CARNIVORE BURROWS IN SLOPE PRAIRIE HABITAT, KONZA PRAIRIE BIOLOGICAL STATION

	Burrows		
Slope position	Number per km	Number	Transects (km)
Point	18.7	73	3.9
Side	2.0	11	5.5
Interior	1.5	4	2.7
Total		88	12.1

On points of hills, carnivores selectively placed burrows on south- to west-facing slopes over north- to east-facing slopes. Several studies in the Great Plains have suggested that burrows or dens of coyotes have a directional orientation (Gier 1968; Althoff 1980; Hallett et al. 1985). However, the results of these studies are not in agreement, as two studies suggest that coyote burrows are placed on south-facing slopes and banks (Gier 1968; Hallett et al. 1985) and a third study suggests that burrows of coyotes faced east to north (Althoff 1980). Our pattern of distribution of carnivore burrows on points of hills agreed with the results of Gier (1968) and Hallett et al. (1985) for slope aspect. However, more importantly, we also determined relative abundance of eight different classes of slope aspect by systematically sampling aspect at 30 m intervals along the 12.1 km transect of slope prairie. Therefore, we were able to demonstrate that use of points of hills that faced south to west was not caused by a superabundance of point slopes that faced these directions on our study site. Further, we also demonstrated that carnivores do not place burrows randomly, as aspects of burrows differed in proportion to that available in the environment.

Placing burrows on south- to west-facing slopes on Konza Prairie could have several advantages for carnivores. First, burrows facing south to west would receive greater solar radiation per area and be warmer than those facing north to east. This difference in microclimate would be enhanced from late fall to early spring when the sun is low in the southern sky. Further, young carnivores, when active outside the burrow, likely would benefit from both higher levels of heat available from solar radiation and from warm soil on slopes that face south to west as compared to those that face north to east. Finally, burrows on points that faced south to southwest would have a more

TABLE 3
NUMBER AND RELATIVE ABUNDANCE OF CARNIVORE BURROWS AND ASPECT FREQUENCY ALONG SLOPE TRANSECTS, KONZA PRAIRIE BIOLOGICAL STATION

	Burrows		
Slope aspect[a]	Number per 10 stations	Number	Aspect frequency
North	0.0	0	14
Northeast	0.8	1	13
East	2.1	4	19
Southeast	5.0	8	16
South	11.5	15	13
Southwest	11.2	19	17
West	8.9	24	27
Northwest	1.1	2	18
Total		73	137

[a]Slope aspects are categorized as follows: north = N and NNE; northeast = NE and ENE; east = E and ESE; southeast = SE and SSE; south = S and SSW; southwest = SW and WSW; west = W and WNW; and northwest = NW and NNW.

favorable microclimate than those on north-facing slopes during winter and spring when prevailing winds on Konza Prairie come from the north.

On points of hills, carnivores selectively placed burrows on intermediate to steep slopes over shallow slopes. The preferential use of steeper slopes over shallower slopes on points of hills suggests that carnivores choose sites that typically are well drained. Previous studies of coyotes have shown that their burrows usually are located in well-drained sites (Gier 1968; Hallett et al. 1985). Another potential advantage of using steeper slopes for burrows is the benefit of a shallower digging angle. Therefore, the energy cost required would be less to transport excavated soil to the surface as compared to level surfaces. Further, less vegetation occurs on steep slopes on Konza Prairie and, therefore, the carnivore would have less interference from vegetation when digging a burrow.

Although carnivores preferred slope prairie for burrows (7.3 burrows per km) to the other three habitats, they did use ravines (4.2 burrows per km) more often than upland prairie (0.6 burrows per km) and totally avoided lowland prairie (0.0 burrows per km). The use of the upper edges of ravines is consistent with carnivores choosing sites that are well drained. In contrast

to slope prairie and ravines, burrows in lowland prairie can flood because of surface and belowground flow of water. In wet seasons that have occurred during the last 23 years on Konza Prairie, we have observed numerous lowland sites that became so saturated with water that overland flow occurred. A disadvantage of placing burrows in uplands on Konza Prairie would include shallow soils, which often are <50 cm and seldom >1 m in thickness (Oviatt 1998). This shallow soil would limit the depth to which burrows could be dug due to underlying Permian-age limestone.

Given that carnivores prefer to place their burrows on slope prairie and to a lesser extent on the upper edges of ravines, this distribution of burrows may have profound effects on ecosystem processes in tallgrass prairies and other rolling grasslands underlain with limestone rocks, which tend to be erosional environments (Oviatt 1998). Further, the preferential placement of burrows on points of slopes that have steep angles is important as well. Previously studied mammalian disturbances on Konza Prairie, such as bison wallows and pocket gopher mounds, tend to occur primarily on level surfaces. That is, bison wallows are established in uplands, terraces, and lowlands, areas with little or no slope (McMillan 1999). Physical disturbances to the soil profile such as wallows of bison and mounds of pocket gophers and prairie dogs have shown differences between the nutrient dynamics and processes in tallgrass prairie and other grasslands. We therefore hypothesize that displacement of soil by carnivores digging and excavating burrows will affect nutrient dynamics and processes and help to maintain higher number of plant species and patchiness in the tallgrass prairie.

Conclusions

Through their digging activities, carnivores disrupted the soil profile and exposed areas of bare soil more frequently on slope prairie and especially on steep points of hills than in other prairie sites. Previous studies of other disturbances on Konza Prairie suggest that carnivore disturbances and the spatial distribution of such impacts may have consequences on the spatial distribution of nutrients and plant species within the tallgrass prairie landscape. For example, grazing by bison reduces the litter layer and increases exposure of soil, which increases heterogeneity in the landscape (Briggs et al. 1998). This patchiness, induced by grazing, trampling, and wallowing by bison, leads to differences in fuel loads and thus burning patterns at the landscape level, which creates a positive feedback system, which further increases and reinforces patchiness in the environment. Because carnivore burrows also reduce or eliminate the litter layer and increase

exposed soil on the surface layer, these burrows also create fire shadows and reinforce the patchiness and heterogeneity in the tallgrass prairie and other types of rolling prairie ecosystems. Although it has been shown by simulated rainfall experiments on upland sites with a low-gradient slope (6%) that overland flow does not erode soil in tallgrass prairie (Koelliker and Duell 1990), experiments have not been done on steeper slopes where vegetation is lacking. Our general observations suggest that carnivore-burrowing activities do alter the microtopography on the slopes and especially on the points of the hills. Thus, we suggest that more attention should be given to the natural history and habits of prairie carnivores and how they might impact prairie ecosystem processes and nutrient dynamics as well as plant communities at local and landscape levels through the physical disturbances of burrowing activities.

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