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DISTRIBUTION OF EASTERN WOODRATS IN A GRASSLAND-WOODLAND MOSAIC: INFLUENCE OF VEGETATION AND FIRE

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ABSTRACT—The eastern woodrat is a characteristic, charismatic rodent in the prairie region. We assessed the distribution of eastern woodrats (*Neotoma floridana*) within the mosaic of interspersed grasslands and woodlands on the Konza Prairie Biological Station. In summer 1996 we recorded the placement of eastern woodrat nests in 10 areas that differed in prescribed fire regimes. Although most vegetation in our study sites (>90% of the area) was native tallgrass prairie, all of the nests (n = 122) were associated with woody-shrubby vegetation. Nests of the eastern woodrat were more common along limestone outcrops that had trees and shrubs (16 nests/km) than in the other four types of linear, wooded habitats (<2 nests/km). Seven of 78 nests were damaged or destroyed in areas burned by prescribed fires in April 1997. Large-sized eastern woodrat nests were less common in sites that experienced annual fires than in those sites that had less frequent fires. This pattern suggests that eastern-woodrat nests are vulnerable to prairie fires. The frequency of large eastern woodrat nests may be an indication of time since last burn in a tallgrass prairie ecosystem.

KEY WORDS: Konza Prairie, eastern woodrat, prairie fires, tallgrass prairie

Introduction

The eastern woodrat (*Neotoma floridana*) is a widespread and relatively common rodent in woody-shrubby vegetation found in the western tallgrass prairie, such as that found in the eastern one-half of Kansas (Fitch and Rainey 1956; Rainey 1956; Bee et al. 1980; Finck et al. 1986; Kaufman et al. 1993). In the Flint Hills region of eastern Kansas, eastern woodrats typically occur in habitats that range from forested lowland and riparian sites to sparsely wooded sites, such as shrub patches and limestone outcrops that have scattered shrubs or trees. In these sites, eastern woodrats usually build nests, which consist of branches, twigs, leaves, and bark of trees and shrubs, as well as stems and leaves of herbaceous vegetation. Such nests are built against trees, logs, and various kinds of woody debris, although nests also can be freestanding. Woodrats use various kinds of plant material either to build typical nests in association with limestone outcrops or to construct den sites, which enclose fractures and pockets created by overhanging rock. Typical nests composed of woody materials can have bases that exceed 2 m in the longest dimension, whereas dens in rocky outcrops generally are enclosed by only a small amount of plant material. Regardless of the type of den site, plant material used in nest construction will be vulnerable to prairie fires, even in woody and shrubby vegetation.

Here, we examine the influence of the type and presence of woody-shrubby vegetation, the recent history of prescribed prairie fires, and the presence of limestone outcrops on the distribution of eastern woodrat nests within the Konza Prairie. Additionally, we evaluate the vulnerability of woodrat nests to prairie fires as well as the effect of fire frequency on nest size found in woodland sites.

Methods

Our study was conducted on Konza Prairie, a 3,487 ha research site located 15 km south of Manhattan in the Flint Hills region of eastern Kansas. The site is characterized by dissected hills of Permian-aged limestones and shales. Over 90% of the site is dominated by tallgrass vegetation, which includes big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Schizachryium scoparium*), and switchgrass (*Panicum virgatum*). Embedded in the prairie are woody and shrubby habitats along intermittent streams, eroded ravines, and limestone outcrops. Shrubby vegetation also occurs in scattered sites in uplands, on slopes, and in lowlands where fire has occurred only infrequently during the past 20-30 years. Forested sites are characterized by bur oak (*Quercus macrocarpa*), chinkapin oak (*Q. muehlenbergii*), green ash (*Fraxinus pennsylvanica*), honey locust (*Gleditsia triacanthos*), common hackberry (*Celtis occidentalis*), black walnut (*Juglans nigra*), and American elm

(*Ulmus americana*). These same species of trees are scattered at low densities along limestone outcrops. Common shrubs that also occur along limestone outcrops and in scattered patches throughout the prairie include rough-leaved dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), and aromatic sumac (*R. aromatica*).

In summer 1996 we surveyed the distribution of eastern woodrat nests in 10 areas of Konza Prairie that encompassed 753 ha. These 10 areas differed both in dimensions and in history of fire since establishment of the Konza Prairie in the 1970s. Treatment area designations, size of area, and fire history, defined as the number of times a treatment area was burned, either by prescribed fires or wildfires from spring 1977 to spring 1996, are summarized in Table 1.

Nests were located by visually searching the 10 areas during 312 hours of walking in June-July 1996. When a nest was found, we recorded location, type of vegetation in which the nest was placed, and characteristics of the site on which the nest was built. We made no distinction between nests that were active or inactive, as all nests showed evidence of having been used within the last two years. We assigned nests to one of nine habitat categories based on vegetation and physical features near each nest. Eight of these categories were subsets of woody-shrubby vegetation present on Konza Prairie, and the ninth category was abandoned anthropogenic structures. The eight categories of woody-shrubby vegetation were based on dominant vegetation (trees versus shrubs), width of patch, and presence or absence of proximity to a stream or ravine, rather than on the presence of specific tree or shrub species.

Our nine habitat categories were forest, narrow forest, linear woodland, headwater woodland, stream woodland, shrub thickets, isolated trees, limestone outcrop, and anthropogenic structures. The first three categories (forest, narrow forest, and linear woodland) were dominated by trees of various species, which were not associated with a stream but differed from each other in the width of forested habitat that was associated with each category. Forest had a width of >15 m of trees, narrow forest was 5-15 m wide, and linear woodland was <5 m wide. Both the fourth and fifth categories, headwater woodland and stream woodland, were associated with reaches of small streams, but they varied in types of dominant vegetation. Headwater woodland was dominated by trees or shrubs, whereas stream woodland was dominated only by trees. In addition, these two differed in placement and width of streams. Headwater woodland was associated with headwater reaches that had a width <3 m, whereas stream woodland was

TABLE 1

FEATURES AND FIRE HISTORY FOR TEN AREAS (TREATMENTS) AT KONZA PRAIRIE BIOLOGICAL STATION (KANSAS) STUDIED FOR EASTERN WOODRAT NEST DISTRIBUTION

Treatment Area	Size (ha)	No. of burns[a]	Limestone outcrop lengths (m)	No. of nests	Nest density (per 10 ha)
N1A	94	13	1700	41	4.4
2D	48	12	300	0	0.0
N2A	101	10	900	17	1.7
N1B	121	9	400	11	0.9
N4A	99	6	50	4	0.4
FA	11	5	0	0	0.0
N20A	83	4	1100	28	3.4
N4D	136	3	600	8	0.6
20C	36	3	0	13	3.6
20B	24	1	0	0	0.0
Total	753	-	5050	122	1.6

[a] Indicates the number of years between spring 1977 and spring 1996 that the treatment was burned.

associated with reaches of prairie streams that had a width of >3 m. Headwater woodland was sometimes associated with wooded ravines. The four remaining categories (shrub thickets, isolated trees, limestone outcrops, and anthropogenic structures) were unique. The shrub thickets were dominated by shrubs, usually rough-leaved dogwood or smooth sumac, and they were highly variable in size. This habitat occurred in both upland and lowland areas and in the absence of streams and ravines. Isolated trees were individual trees that were >20 m from the nearest wooded site. Limestone outcrops often had fractures and overhanging rock, and were associated with a narrow band of trees and shrubs. Anthropogenic structure consisted of building foundations and other debris, remnants of abandoned farm sites.

We measured lengths and widths of forest, narrow forest, linear woodland, headwater woodland, stream woodland, and limestone outcrops in each study site using a 1 m measuring wheel. These six habitats were relatively linear. The only exceptions were some forest sites that were >50 m wide. Measured lengths were used as an estimate of availability of each habitat type. Nests also were found in patches of the other habitat types, but these numerous patches were small and irregularly shaped, so no linear measurements of these habitats were estimated.

Later, in February-March 1997, we surveyed for eastern woodrat nests in six areas that were scheduled to be burned in April 1997. We marked each eastern woodrat nest, measured the diameter of the base of each nest, and assigned the nest to a habitat type. Subsequently, nests were categorized using diameter as follows: small-sized (0.1-1.2 m in diameter), intermediate-sized (1.3-2.0 m), or large-sized (>2.1 m). The treatment areas in which nests were located (labeled as NTA, N1A, N1B, K4A, SB, and SC on Konza maps), encompassed >700 ha. Individual treatment areas varied in size, topograpy, and recent history of prairie fire. The six sites were burned by prescribed prairie fire during 3-9 April 1997. For each fire, we recorded wind speed and direction, intensity of fire, and direction of headfire at each of the sites. After 10 April, we revisited all nest sites and recorded the status of each nest (burned, partially burned, or unburned).

Statistical Analyses

We used log-likelihood ratio tests (G) to determine whether the nests of eastern woodrats were distributed randomly among study sites and among vegetation. The expected frequency among sites was based on the area of the various study sites. The expected frequency among vegetation types was based on the lengths of the different linear habitats. We also used G tests to determine if sizes of nests differed among treatments that had different fire histories, and to evaluate whether treatment site, habitat conditions, or nest size had an effect on the likelihood that a nest would burn. We used Pearson correlation analyses to test for relationships between number or density of nests and size, and between density and vegetative characteristics of study sites.

Results

All eastern woodrat nests found (n = 122) were in woody and shrubby vegetation even though prairie vegetation dominated our study sites (> 90% of the area). Of these nests, 82 (67%) were associated with limestone outcrops, 10 (8%) with narrow forest, 8 (6%) with forest, 7 (6%) with headwater woodland, 7 (6%) with isolated trees, 4 (3%) with shrub thickets, 2 (2%) with stream woodlands, and 2 (2%) with anthropogenic structures. Unexpectedly, no eastern woodrat nests were associated with linear woodland. Most nests were associated with an individual tree (70%), 10 species of trees were used, and most nests were built on the ground (93%).

The number of nests varied widely among study sites (Table 1), but it was not correlated with size of the sites ($r = 0.38$, $d.f. = 8$, $P > 0.10$). Number and density of nests per site (nests/10 ha) also did not correlate with number of burns from 1977 to 1996 (number of nests: $r = 0.43$, $d.f. = 8$, $P > 0.10$; density of nests: $r = 0.19$, $d.f. = 8$, $P > 0.10$). However, eastern woodrat nests showed a strong association with limestone outcrops, but not with the other four linear habitats ($G = 180$, $d.f. = 4$, $P < 0.001$). Of the five linear habitats with nests, nest density was higher in limestone outcrops (16.4 nests/km) than in the four other linear habitats, all of which were fairly equal (narrow forest: 1.8 nests/km; headwater woodland: 1.1 nests/km; forest: 1.0 nests/km; and stream woodland: 0.5 nests/km). Further, the number of nests in a study site was correlated positively with the length of limestone outcrop within a site ($r = 0.91$, $d.f. = 8$, $P < 0.001$).

In spring 1997, proportions of small, intermediate, and large nests differed significantly between annually burned sites (n = 44 nests in N1A and N1B) and infrequently burned sites (n = 34 in NTA, K4A, SB, and SC) ($G = 9.1$, $d.f. = 2$, $P < 0.05$). Annually burned sites contained a smaller proportion of large nests (16% large, 36% intermediate, and 48% small nests) than did infrequently burned sites (47% large, 21% intermediate, and 32% small nests). Seven of the 78 nests were burned in prescribed prairie fires in spring 1997. Two of these nests were only partially burned. More small and intermediate nests (13% of 55) burned than large nests (0% of 23; $G = 5.2$, $d.f. = 1$, $P < 0.05$). Nests associated with limestone outcrops appeared more vulnerable to fire than nests in other wooded habitats, because six of 46 nests burned in outcrops, whereas one of 32 nests burned in other habitats, but these proportions were not statistically different ($G = 2.6$, $d.f. = 1$, $P > 0.10$).

Discussion

Eastern woodrats nests were associated strongly with wooded habitats in the dissected landscape of Konza Prairie, as expected from previous work (Finck et al. 1986; Kaufman et al. 1993; McMillan and Kaufman 1994). Other earlier works also noted the use of wooded limestone outcrops on Konza Prairie (Kaufman et al. 1983; Finck et al. 1986; Kaufman et al. 1993) and elsewhere in eastern Kansas (Fitch and Rainey 1956; Rainey 1956). Not only did eastern woodrats use wooded outcrops, but they preferentially selected this narrow, linear habitat over other linear or two-dimensional wooded areas. The preferential use of narrow, linear wooded habitats by eastern woodrats also was found for shelterbelts and riparian zones in north-central Kansas (Beckmann et al. 2001).

Frequent use of wooded limestone outcrops by eastern woodrats likely reflects the availability of fractures in the limestone for nesting as well as the availability of exposed ledges and overhangs for den sites. We found no eastern woodrat nests in other sites on Konza Prairie, which lacked suitable woody vegetation for use by eastern woodrats (e.g., 2D, 20B, and FA). The branches, twigs, bark, and foliage from trees and shrubs facilitated enclosing fractures and overhanging rock areas for den sites or contributed to building nests along the base of the exposed limestone outcrop. Eastern woodrat nests were rare along outcrops adjacent to grass habitat that lacked such woody resources. Additionally, trees and shrubs on limestone outcrops provided food resources such as fruits, nuts, and seeds. Post et al. (1993) recorded that seeds, fruits, and foliage from forbs and grasses above and below outcrops were eaten. Further, trees and shrubs associated with outcrops likely provide open travel lanes for eastern woodrats because of reduced understory vegetation adjacent to the outcrop and reduced risk of predation in a grass-only habitat.

Historically, prairie fires caused by lightning or set by Native Americans likely killed young trees and shrubs and thereby prevented invasion of prairie by trees and shrubs (Briggs and Gibson 1992; Hartnett and Fay 1998). Before European settlement, trees and associated shrubby understory were reported as common only along rivers and large creeks in the tallgrass prairie. Smaller patches of shrubs and trees also occurred along wooded streams as well as ravines, outcrops, and springs that were infrequently burned due to slopes and aspects of the hills, and less often grazed by bison (*Bos bison*). The sparseness of woody vegetation in native tallgrass prairie even along limestone outcrops still is evident in the Flint Hills region today where native prairies have been and continue to be burned frequently.

Because of fire suppression since European settlement, woody vegetation appears to be much more common and widely distributed in the Flint Hills today (Briggs and Gibson 1992; Hartnett and Fay 1998). For example, most outcrops with woody-shrubby vegetation on Konza Prairie, including those we studied, would have been dominated by grass in the late 1800s (references above). As a result, eastern woodrats are likely more common and widespread today in the tallgrass prairie region, such as on Konza Prairie and in many areas of the Flint Hills, than they were in the mid-1800s. The positive effect that woody vegetation has on the distribution of eastern woodrats is evident from their association with woody-shrubby habitats. All nests found were in wooded habitats, which occupied <10% of the study areas. No nests were observed within prairie, which occupied >90% of the study areas, available on Konza Prairie. Further, the number of eastern woodrat nests increased as the trees and shrubs increased near an outcrop.

Although frequent fire is known to prevent the invasion of prairie by shrubs and trees, we did not find a clear inverse relationship between the number of fires during the past 20 years and the number of nests at a study site. This lack of pattern was unexpected. Frequent fires should prevent expansion of woody-shrubby vegetation as well as decrease the amount of woody vegetation present. However, over a 20-year period, fire will not kill all trees and shrubs, especially where fire cannot travel readily, such as through barriers (e.g., streams, ravines, and outcrops) or through areas that lack sufficient fuel (e.g., interiors of shrub patches). As a result, we suggest that the number of eastern woodrat nests at each study site likely was related more to topography and the amount of woody vegetation present in the late 1970s than to current fire management practices. The pattern observed likely reflects the history of prescribed fire and livestock grazing before the last 20 years. Prescribed fire treatments on annual and biennial cycles were begun only in 1984 (N1A), 1985 (N2A), or 1988 (N1B). All sites had considerable amounts of woody vegetation before frequent burns were initiated. Thus, the number of eastern woodrat nests in sites should decrease with ongoing fire management over the next 20 years.

Nests built by woodrats in small patches of trees and shrubs within a matrix of prairie should be vulnerable to damage or complete destruction by prairie fires. Consistent with this expectation, we found a smaller proportion of large nests in annually burned sites (16%) than in less frequently burned areas (47%). Furthermore, a portion of the marked nests was damaged or destroyed by the prescribed 1997 prairie fire, although we expected the proportion burned to be higher than the 9% that we recorded. The low percentage of burned nests observed may reflect the manner in which prescribed fires are conducted on Konza Prairie. Prescribed fires are initiated only when winds are low and relative humidity moderate to high. Further, prescribed fires are contained by fire guards, backfires, and other control measures to confine them to a relatively small size (typically <200 ha). Prairie wildfires, often driven by a strong wind, usually burn a higher proportion of plant litter, burn farther into or through woody-shrubby patches, kill a larger proportion of shrubs and trees, and burn more woody debris than a typical prescribed prairie fire. These effects were evident during and following a wildfire that burned >2,000 ha of Konza Prairie in about 12 hours in spring 1991 (Briggs and Gibson 1992; Hartnett and Fay 1998). Because of such differences between natural and prescribed fires, eastern woodrat nests should be more vulnerable to destruction by wildfire than by prescribed fires.

Today, eastern woodrats are common and widespread throughout woody and shrubby habitats in the northern and central Flint Hills (Finck et al. 1986; Kaufman et al. 1993; McMillan and Kaufman 1994; this study). Because of the active suppression of fires and subsequent increase in woody-shrubby vegetation following European settlement, eastern woodrats likely are more abundant on Konza Prairie, in the Flint Hills, and in other grassland ecosystems than they were before settlement (Beckmann et al. 2001). Continued suppression of fire in tallgrass prairie in much of the Flint Hills suggests that eastern woodrats are likely to increase in overall abundance as trees and shrubs increase in abundance and distribution.

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