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Jon P. Beckmann
Kansas State University

Glennis A. Kaufman
Kansas State University

Donald W. Kaufman
Kansas State University

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INFLUENCE OF HABITAT ON DISTRIBUTION AND ABUNDANCE OF THE EASTERN WOODRAT IN KANSAS

Jon P. Beckmann¹, Glennis A. Kaufman,
and Donald W. Kaufman

*Division of Biology
Kansas State University
Manhattan, KS 66506-4901
beckmann@unr.nevada.edu*

ABSTRACT—Anthropogenic modification of native woodlands and grasslands in the Great Plains has altered the abundance and distribution of many species of mammals. To study habitat effects on the eastern woodrat (*Neotoma floridana*), we surveyed nests of the eastern woodrat in woodlands, grasslands, and croplands along 77 km of secondary roads in three counties in north-central Kansas. All nests were located in woodlands (<2% of habitat), although grasslands and croplands constituted 36% and 62% of habitat surveyed, respectively. In our survey, nests were associated positively with shelterbelts (3.6 nests per 100 m of road edge) but not with shrub patches (1.1 nests per 100 m of road edge) or riparian woodlands (0.3 nests per 100 m of road edge). Consequently, we specifically censused nests in an additional 12 riparian woodlands and 12 shelterbelts. Nests of eastern woodrats were less dense in riparian woodlands (9.4 nests/ha) than in shelterbelts (55.5 nests/ha). Density of woodrat nests decreased as width of a wooded area increased. Further, nests per 100 m of length of woodland did not increase as the width of woodland increased. These patterns suggest that woodland edge, not woodland interior, is the primary factor in abundance of eastern woodrats in this region. Although the eastern woodrat has previously been considered a woodland species, our results suggest that this assessment is incorrect. Our observations demonstrate that anthropogenic modification of the Great Plains, in the form of planted shelterbelts and expanded riparian woodland, likely has increased the distribution and abundance of eastern woodrats, compared to the mid-1800s.

¹ Present address: Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, NV 89512

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Introduction

Anthropogenic modification, destruction, and fragmentation of native woodlands and grasslands have altered the abundance and distribution of many species of mammals in the Great Plains since the mid-1800s (Benedict et al. 1996; Kaufman and Kaufman 1996). Initially, the cutting of woody vegetation for firewood and construction of buildings reduced the extent and types of native woodland (Fleharty 1995). Subsequently, however, woody vegetation increased as a result of trees planted in association with farmsteads and as timber claims. More recently, windbreaks and shelterbelts were planted to reduce wind erosion and provide wildlife habitat (Capel 1988; Samson and Knopf 1994; Fleharty 1995). Fire suppression also led to the colonization of native prairie by a variety of trees and shrubs, especially along the edges of streams and ravines. Because of these activities and changes, woody vegetation in the Great Plains is more abundant today than it was before settlement (Fleharty 1995).

Given this increase in woody vegetation and a strong association of eastern woodrats (*Neotoma floridana*) with woody vegetation (Fitch and Rainey 1956; Rainey 1956; Wiley 1980), eastern woodrats likely are more common in central and western Kansas today than they would have been before settlement. To evaluate this expectation, we assessed habitat use of eastern woodrats by surveying the occurrence of nests and habitat along roadsides in north-central Kansas. We expected woodrats to use a variety of naturally occurring and planted wooded habitats. We also knew from field observations during the last 35 years that woodrats in north-central Kansas often are abundant in shelterbelts, defined here as single to multiple rows of planted trees. Therefore, we used our data to test for differences in association of eastern woodrats with three general types of wooded habitats in our survey: shelterbelts, riparian woodlands, and shrub patches.

The results of the first phase of this project indicated that shelterbelts provided suitable habitat for woodrats, and possibly better habitat than that provided by riparian woodlands. Therefore, we designed a second phase to test for differences in use of shelterbelts versus riparian woodlands by eastern woodrats. We hypothesized that nest density would be much greater in shelterbelts than in the riparian wooded habitats that occurs along prairie streams. Our observations over the last 35 years indicated that woodrats often use very narrow strips of trees and shrubs, and even single trees, for nest sites in central and eastern Kansas. In these cases, woodrats gather food from nearby herbaceous vegetation (Post et al. 1993), including a variety of

native and weedy forbs, grasses, and grain sorghum (personal observation). Use of very narrow or small wooded patches suggested that thin strips of trees and shrubs may have very high densities of woodrat nests. Based on this, we also hypothesized that nest density (number/ha), actually would be higher in narrow rather than in wide woodland belts. We measured woodland widths, so our data could be used to test for an effect of woodland width on nest density. Finally, we considered the effect of habitat width on differences of nest density between shelterbelts and riparian woodland habitats. An understanding of how anthropogenic modification of the Great Plains impacts the distribution and abundance of species is important to the conservation of those species in the region.

Methods

We surveyed nests of woodrats in north-central Kansas during March-October 1996. Nest counts do not provide estimates of number of individuals, but they do provide reasonable indices to woodrat abundance (Vreeland and Tietje 1999), and they are particularly useful for surveying patterns of habitat use. Our use of nest counts enabled us to examine habitat associations in a larger number of sites and for more woodrats than would have been possible by direct sampling of woodrat numbers by use of live traps. A second advantage was that nest counts provided an index of site use during the survey and the two or so preceding years. Therefore, using nest counts avoided the potential bias of estimating the abundance of woodrats only at the immediate time of sampling.

Dominant vegetation types in this region, in terms of the proportion of area occupied, were native mixed-grass prairie (mostly grazed by cattle), planted grasslands, wheat fields, and sorghum fields. Wooded habitats, such as riparian woodlands, shelterbelts, planted shrubs and naturally occurring shrub patches, were much less abundant. Shelterbelts were planted woodlands designed to reduce wind erosion. Some shelterbelts consisted of one or more rows of mature eastern red cedar (*Juniperus virginiana*), some of eastern red cedar and Osage orange (*Maclura pomifera*) or other deciduous trees, and some of only a single row of Osage orange. Riparian woodlands were natural woodlands associated with streams and ravines. These woodlands generally consisted of common hackberry (*Celtis occidentalis*), black walnut (*Juglans nigra*), American elm (*Ulmus americana*), honey locust (*Gleditsia triacanthos*), and oaks (*Quercus spp.*). Naturally occurring shrub patches consisted of wild plum (*Prunus spp.*), smooth sumac (*Rhus glabra*)

and aromatic sumac (*R. aromatica*), whereas planted shrub patches included a variety of non native ornamental plants.

Habitat Association. From 26 March through 6 April 1996 we censused nests of eastern woodrats along roadsides of Smith, Osborne, and Russell Counties in north-central Kansas. We randomly selected four sections of land (1.6 x 1.6 km) in each of the three counties. Only sections that had no urban development and that were completely surrounded by dirt, gravel, or secondary paved roads were used. If a section chosen at random did not meet these criteria, we excluded that section from our survey and randomly chose a new site. Because each of these three counties was square and enclosed 900 sections, we further stratified our sampling by choosing one section from each of the four quadrants (225 sections per quadrant) of each county. We walked all roads around each section and recorded all woodrat nests within 25 m of both road edges. In cropland and grassland, the vegetation typically was short, so it could be surveyed readily by walking and watching for nests. Along wooded edges, the observer walked to the edge of or into private land to make sure that nests within 25 m of the road were seen and verified. Nests on the ground and in trees were counted. No distinction was made between active and inactive nests. Our procedures resulted in a survey of 12.8 km of road edge per section (6.4 km of road x two sides) and a total length of 153 km for all 12 sections. In addition, we used a 1 m measuring wheel to determine the length of each habitat that paralleled each side of all roads surveyed.

Our habitat categories were woodland, grassland, cropland, and other. We further subdivided woodlands into shelterbelts, defined as combinations of trees and shrubs planted to either reduce wind erosion or provide wildlife food; riparian woodlands, defined as trees and shrubs along creeks and ravines; and shrub patches, defined as natural or planted acres of shrubs. Grasslands included grazed and ungrazed native prairie, planted and native grasslands used for hay, and unmowed and ungrazed grasslands planted for conservation purposes. Croplands included both fields with growing winter wheat and fields with stubble from wheat, sorghum, and corn. The habitat category "other" made up only 6% of transects and included driveways, farmsteads, farm ponds, and pasture roads. We excluded the habitat category "other" from our analyses.

The proportion of each habitat type available was estimated from total length of each habitat divided by the total length of woodland, grassland, and cropland combined. This caused a small overestimate of the proportion

of woody vegetation because some shelterbelts (oriented parallel to the road) and shrub patches (small) were <25 m in width. It was not possible to obtain permission to measure widths of all of the shelterbelts and shrub patches that were on private land. Thus, total woodland was likely closer to 1.5% than to the estimated 1.7%. This small overestimate would not change the observed association of woodrats with woodland, since even fewer nests would have been expected in woodland than we observed.

Shelterbelts versus Riparian Woodlands. To further evaluate the pattern of occurrence, we counted woodrat nests in an additional 12 shelterbelts and 12 riparian woodlands between late May and mid-October 1996. We stratified our analyses by choosing four paired shelterbelts and riparian woodlands in each of the three counties. We selected these pairs by driving in different regions of each county and first choosing the shelterbelt and then finding a nearby riparian woodland to pair with it. Criteria for shelterbelt selection were as follows: >100 m in length, readily accessible from a road, available for study with permission from the owner/tenant, and near (<4 km) to a riparian woodland of equal length that also was accessible for study. Further, we chose only shelterbelts and riparian woodlands that were ungrazed or lightly grazed to avoid any major influences of livestock on woodrat nesting.

Once a shelterbelt and its paired riparian woodland were chosen, we searched both areas thoroughly and counted all nests. Subsequently, we measured the length and width of the shelterbelts and riparian woodlands. We used the width at the middle and at the two ends of each wooded area to estimate the average width. Active plus inactive nests served as an index of the use of each site by woodrats. Width of wooded sites varied much more among riparian woodlands than among shelterbelts.

Statistical Analyses. We used log-likelihood ratio (G) tests to assess whether woodrat nests were distributed randomly among woodland, grassland and cropland, and among the three woodland types. The expected frequencies were based on proportions of road edge occupied by each habitat type. We used nonparametric Wilcoxon paired-sample (T) tests to determine if the width of wooded areas and density of woodrat nests differed between shelterbelts and riparian woodlands. We used Pearson correlation (r) analyses to test for relationships between nest density and woodland width and between number of nests per 100 m and woodland width. In the case of nest density and woodland width, a plot of the data revealed a curvilinear pat-

tern. Consequently, we log-transformed both variables before conducting the correlation analyses. A probability level of $P < 0.05$ was used to reject our null hypotheses.

Results

Habitat Association. Road edges consisted of 62.1% cropland, 36.2% grassland, and 1.7% woodland. This general pattern was consistent across the three counties (ranges: 59%-64% cropland, 34%-39% grassland, and 1%-2% woodland). We counted 37 nests, and all were in woodland. As would be expected from this pattern, use by woodrats varied significantly among habitats ($G = 300.2$, $d.f. = 2$, $P < 0.001$).

The woodland area along road edges was divided into 54% riparian woodlands, 31% shelterbelts, and 15% shrub patches. Based on nest distribution, eastern woodrats were distributed nonrandomly among shelterbelts, riparian woodland, and shrub patches ($G = 38.0$, $d.f. = 2$, $P < 0.001$). A strong association with shelterbelts (29 nests; 3.6 nests per 100 m road edge) compared to shrub patches (4 nests; 1.1 nests per 100 m road edge) and riparian woodland (4 nests; 0.3 nests per 100 m road edge) caused the observed pattern.

Shelterbelts versus Riparian Woodlands. Mean lengths of shelterbelts and paired riparian woodlands were 274 m; the range was 103-509 m. Shelterbelts ($X \pm 1$ SE) were much narrower (7.3 ± 1.3 m) than riparian woodlands (54.6 ± 15.4 m) ($T = 0$, $n = 12$, $P < 0.001$). This difference in width led to a woodland area that was much smaller for shelterbelts (0.21 ± 0.07 ha) than for riparian woodlands (1.59 ± 0.60 ha; $T = 0$, $n = 12$, $P < 0.001$).

Nest density, however, was much greater in shelterbelts (55.5 ± 23.1 nests/ha) than in riparian woodlands (9.4 ± 4.3 nests/ha) ($T = 7$, $n = 12$, $P < 0.01$). Further, the density of nests decreased significantly as woodland width increased ($r = -0.72$, $d.f. = 22$, $P < 0.001$; Fig. 1). The negative relationship was highly significant for riparian woodlands ($r = -0.75$, $d.f. = 10$, $P < 0.01$), but not for shelterbelts ($r = -0.46$, $d.f. = 10$, $0.15 > P > 0.10$). The lack of a pattern for shelterbelts likely was caused by the absence of woodrat nests from one shelterbelt of medium width. The overall pattern of decreasing nest density with increasing width was not caused by inclusion of data from both types of woodlands (Fig. 1).

Since area increased per length of woodland as the width increased, we expected the number of nests to increase with width. However, the number

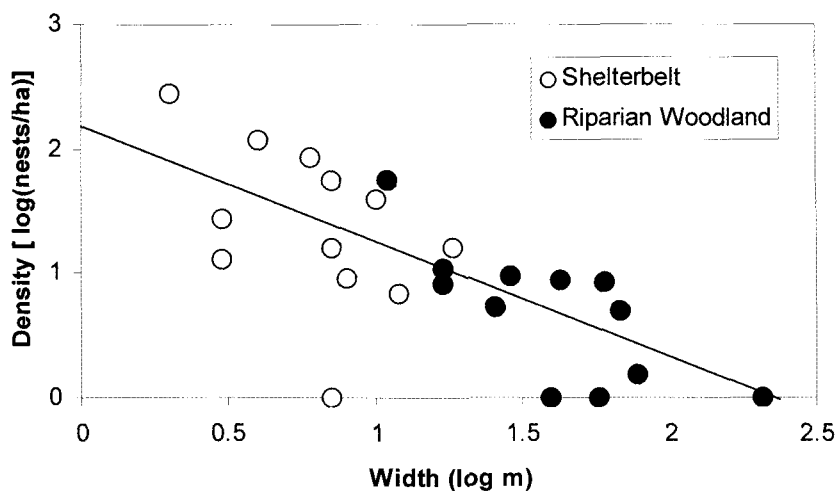


Figure 1. Density of nests [$\log(\text{nests/ha})$] of eastern woodrats (*Neotoma floridana*) relative to width of wooded habitats ($\log \text{ m}$) for 12 shelterbelts (open circles) and 12 riparian woodlands (closed circles) in north-central Kansas during 1996. The solid line represents the regression equation [$\log \text{ density} = 2.17 - 0.95(\log \text{ width})$] fitted to the data from all 24 sites.

of nests per 100 m of woodland did not change as woodland width increased ($r = -0.19$, $d.f. = 22$, $P > 0.10$; Fig. 2). This overall lack of correlation was not caused by combining observations from the two habitats because neither habitat showed a significant correlation (shelterbelts: $r = -0.11$, $d.f. = 10$, $P > 0.10$; riparian woodlands: $r = -0.27$, $d.f. = 10$, $P > 0.10$). On average, shelterbelts had $2.5 (\pm 0.6)$ nests per 100 m, riparian woodlands had $2.3 (\pm 0.6)$ nests per 100 m, and all 24 wooded sites combined had $2.4 (\pm 0.6)$ nests per 100 m.

Discussion

Eastern woodrat nests were associated positively with woodland habitats rather than grassland or cropland habitat. This pattern is consistent with previous work in the central Great Plains (Fitch and Rainey 1956; Rainey 1956; Wiley 1980). Although this pattern is not unexpected, it further quantifies the avoidance by woodrats of nonwoodland habitats within the

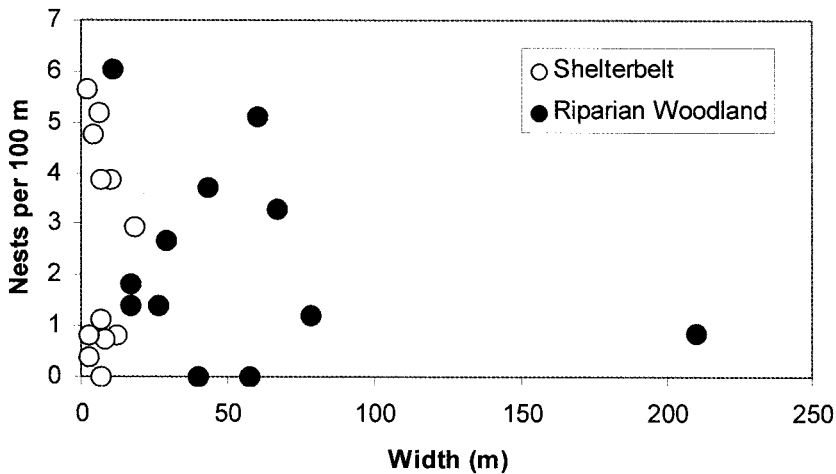


Figure 2. Numbers of nests of eastern woodrats (*Neotoma floridana*) per 100 m relative to width of wooded habitats for 12 shelterbelts (open circles) and 12 riparian woodlands (closed circles) in north-central Kansas during 1996.

complex landscape created by farming, ranching, and other anthropogenic manipulations in north-central Kansas. Our primary objective for initiating these surveys was to test the hypothesis that anthropogenic woodlands, such as shelterbelts, provide suitable habitat for eastern woodrats. Our data support this hypothesis since woodrat nests were associated strongly with shelterbelts, but not with riparian woodland or shrub patches. We designed the road survey to census nests in numerous sites over a geographically large area, and thereby avoiding any bias in pattern detection created by intensive study of a small, local site. However, total woodland habitat was quite small (2-3 km of the total road edge), and our observations of nests ($n = 37$) did not allow determination of habitat associations in the detail we sought.

To enhance our analysis of woodrat use of anthropogenic woodlands, we subsequently focused our efforts on two of the most common woodland habitats in central Kansas, planted shelterbelts and natural riparian woodlands. The results of this comparison supported our hypothesis that planted shelterbelts provide suitable habitat for eastern woodrats. In fact, based on nest density, the shelterbelts provided better habitat for woodrats than did

the riparian woodlands. Given this association and the presence of tree plantings in many local areas that would not have had trees or shrubs before settlement (Fleharty 1995), we conclude that eastern woodrats occur in more areas locally and likely reach a much higher abundance regionally in central and western Kansas today than before settlement. The positive association between woodrats and shelterbelts as revealed by our surveys of habitats and nests along road edges also supports this pattern. Further, it must be noted that many of our wooded riparian areas in both phases of our study either would not have existed or would have been much narrower before settlement.

The eastern woodrat has previously been considered a woodland species, but is this assessment correct? Are these rodents dependent on the woodland edge or on the woodland interior, or both? We addressed this question by evaluating changes in density in relation to increasing woodland width. If woodrats require primarily the conditions available in the interior of wooded sites, then nest density should increase as width increases, that is, from very narrow linear woodlands (one shrub or tree in width) to more two-dimensional woodlands. Further, density should asymptote when width reaches a point where the edge to interior ratio was very small. In contrast, if woodland edges provide the most suitable conditions, we would expect that nest density would be highest in very narrow woodlands and decrease as woodland width increases. The basis for this prediction is that linear woodlands have a high proportion of edge to interior, whereas wide patches of woodland have a high proportion of interior to edge. Ecologically, the herbaceous plant matrix in which the narrow woodland is embedded should provide better food resources for a woodland edge species than does the plant matrix in the woodland interior. This pattern would not be true for a woodland interior species.

A negative relationship between nest density and woodland width could occur only if eastern woodrats were associated more strongly with woodland edge rather than woodland interior. The negative pattern that we recorded was striking. In terms of actual estimates of nest density observed, the narrowest woodland (2 m width) had the equivalent of 280 nests/ha, that is, a spacing of 18-19 m between nests along the length of the 2 m wide woodland. Alternatively, the widest woodland (210 m width) had only 0.4 nests/ha. Intermediate to these values, three woodlands of 17-18 m width averaged 12 nests/ha, and two woodlands of 57-60 m width averaged 4 nests/ha. The association with woodland edge was sufficiently strong to override any effect of width, so nests per unit length of linear woodland did

not increase as width increased. In fact, the widest woodland had one of the lowest numbers of nests per 100 m of length that we recorded. Because the number of nests per 100 m did not increase with width and because the decrease in nest density with increased width fit the same pattern for both riparian woodlands and shelterbelts, the observed association of eastern woodrats with woodland edge seems quite robust. We conclude that the eastern woodrat should be considered an edge species, rather than a woodland species, in this region.

Our initial analysis of nest density using a paired-sample test indicated that woodrats were more abundant in shelterbelts than in riparian woodlands. Given the negative effect of width on nests/ha and the lack of an effect of width on nests per 100 m, the lower density in riparian woodlands than in shelterbelts likely was caused by riparian sites being wider than shelterbelts rather than by riparian sites having a lower quality of environmental features. In fact, the wide range of nest densities in both shelterbelts and riparian woodlands points to a wide range of environmental quality in both types of wooded habitats studied. Although environmental quality apparently varied widely in both woodland types, patterns of density suggested that narrow woodlands associated with adjacent herbaceous habitats provided, on average, more food or higher quality of food, compared to the interiors of most wide patches of wooded habitats. Consistent with the importance of nearby herbaceous vegetation, our field observations in north-central Kansas indicate that woodrats frequently build nests in or at the base of a lone tree (the extreme case of wooded edge) where all or nearly all foraging must be done in nearby herbaceous habitats.

Our observations further demonstrate that woody vegetation can be planted to enhance woodrat abundance and that such plantings would be best arrayed as narrow strips and not as large, wide patches. In north-central Kansas, eastern woodrats frequently use narrow woodlands planted as wildlife habitat or as hedgerows (Kaufman et al. 2000). Consistent with our observations in north-central Kansas, woodrats in eastern Kansas are common in narrow wooded vegetation, such as that found along limestone outcrops (Fitch and Rainey 1956; Rainey 1956). We also have observed similar use of narrow woodlands on the Konza Prairie Biological Station, and elsewhere in the Flint Hills region, of eastern Kansas (Finck et al. 1986).

Additionally, our observations on eastern woodrats raise the question of whether declining populations of the Allegheny woodrat (*N. magister*) in the eastern United States are related in part to changes in availability and distribution of forest or woodland edges and not just to changes in tree composition (Balcom and Yahner 1996). Changes in species composition of

forest trees during the last 30-40 years have occurred, but sizes of stands of mature forest within the geographic range of the Allegheny woodrat also may have increased due to the cessation of logging in parts of the region (Balcom and Yahner 1996).

Distribution and abundance of woodrat nests observed during this study, coupled with known increases in woody vegetation since settlement, support the view that eastern woodrats are much more common in central and western Kansas today than in the mid-1800s. This increase likely is related not only to the numerous shelterbelts and other planted woodland habitats, but also to the general increase of woody vegetation caused by more than 100 years of fire suppression (Flehart 1995). Fire suppression and land management practices that led to changes in riparian woodlands also are likely to have increased the average width and occurrence of such woodlands since settlement. These patterns of increased woody vegetation apply not only to central and western Kansas, but also to many other areas in the Great Plains. Our observations point to the dynamic nature of patterns of abundance and distribution of native animals that can adapt to anthropogenic changes to prairie landscapes. This dynamic aspect also means that conservation plans and efforts must be based on an understanding of historical patterns and causes of change in individual species and not just today's patterns of abundance and distribution.

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