ASSOCIATIONS OF EASTERN REDCEDAR AND SMALL-MAMMAL COMMUNITY STRUCTURE IN THE OKLAHOMA CROSS TIMBERS

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PREFACE AND ACKNOWLEDGMENTS

The purpose of this study was to examine interactions between herbivores, especially small mammals, and eastern redcedar. Studies were designed to examine effects of redcedar invasion on community structure of small mammals and determine the major consumers of redcedar cones and dispersers of redcedar seeds.

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CHAPTER 1

FRUGIVORY OF EASTERN REDCEDAR CONES

INTRODUCTION

Invasive species are a major conservation and management concern in natural ecosystems (Soule 1990) and a serious threat to biodiversity (Heywood 1989, Hobbs and Humphries 1995). An invasive species spreads or is introduced beyond its native range and causes a negative impact on its environment either ecologically or economically (Daehler 2001). Invasive plants can reduce or displace native species and can alter structure and functioning of ecosystems (D'Antonio and Vitousek 1992, Rejmanek 1995, Binggeli 1996, Higgins et al. 2000). Studies in the United States and Australia have shown that invasive species have the capacity for widespread expansion and can threaten ecosystem function (Hobbs and Humphries 1995).

Plant invasions can alter nutrient cycling patterns (Beerling 1995), influence biodiversity (Hobbs and Humphries 1995), and change hydraulics and hydrology (Schmitz et al. 1997). They typically are characterized by a decline in species diversity at all trophic levels within an ecosystem. Hobbs and Huenneke (1992) noted that suppression of fires in ecosystems dominated by fire-adapted species can lead to an invasion of non-native plant species, especially woody species. Recent changes in landscape cover in the Great Plains are resulting from the expansion and invasion of eastern redcedar (*Juniperus virginiana* ; Engle et al. 1987, Smith and Stubbendieck 1990, Gehring and Bragg 1992, Briggs et al. 2002).

Increased abundance of eastern redcedar in the Great Plains has been associated with several changes in ecosystem function. It can lead to a reduction in herbaceous biomass in the canopy zone (Engle et al. 1987, Smith and Stubbendieck 1990), alter species composition and reduce understory light and soil water content (Gehring and Bragg 1992, Briggs et al. 2002), and change biological and physical soil factors (Arend 1950, Broadfoot 1951). Recent inventories indicate an extensive expansion of eastern redcedar populations westward into the rangeland regions of the United States, with significant encroachment in the mixed prairie of Kansas and Oklahoma (Bragg and Hulbert 1976, Snook 1985). It is the most rapidly expanding woody species on rangeland and is increasing in tree size and number of locations occupied (Wilson and Schmidt 1990). Eastern redcedar is invading tallgrass prairie, old fields, and cross timbers where it is altering the landscape and causing shifts in wildlife populations and habitat (Wilson and Schmidtt 1990, Gehring and Bragg 1992, Stone 1998).

The dispersal pattern of eastern redcedar may be influenced by animals. Previous studies have shown that invasion of seeds and seedlings of woody species into old-fields may depend largely on the behavior of their potential consumers (Whelan et al. 1991, Manson and Stiles 1998). Knowing the main consumers of eastern redcedar cones and their rate of consumption may be important for understanding eastern redcedar dispersal. Many studies have concentrated on dispersal of eastern redcedar cones by birds (Phillips 1910, Holthuijzen and Sharik 1984); however, few studies have looked at the potential of mammals as dispersers. Therefore, the objective of this study was to evaluate consumption of eastern redcedar cones by potential guilds of dispersers, including mammalian herbivores.

LITERATURE REVIEW

Eastern Redcedar

Eastern redcedar is a slow-growing but persistent evergreen tree capable of growing to heights of 12-18 m and is native to 37 of the United States (Little 1980). It grows under a wide range of climatic and soil conditions. Annual rainfall within its range varies from about 40 cm in the Great Plains to 150 cm in the Southeast, and length of growing season ranges from 120 to 250 days (Van Haverbeke and Read 1976). Eastern redcedar is most common on dry soils and can occur on soil types ranging from acidic sands to those derived from limestone. It can occur in pure stands or open mixtures with pines or hardwoods (Ferguson et al. 1968). Small inconspicuous male and female flowers appear from February to May on separate trees. The fruit is a berry-like cone, which is fleshy, dark blue, and highly aromatic. These cones usually contain two seeds, but on occasion they may contain three to four (Ferguson et al. 1968). Pollination begins in February in the southern and eastern parts of its range, and fertilization occurs about a month later (Van Haverbeke and Read 1976). Seeds mature in one season, and fruit dispersal of eastern redcedar occurs from September to March in the eastern deciduous forest (Stiles 1980). Natural germination of seeds usually occurs in the early spring during the second year after dispersal, but a few seeds may germinate the first or third year. Delayed germination is caused by embryo dormancy and possibly by an impermeable seedcoat (Fowells 1965).

Eastern redcedar is a pioneer species in vegetational succession (Lassoie et al. 1983). Historically, fire prevented encroachment of eastern redcedar into tallgrass prairies and forest meadows of the central United States (Arend 1950). With the reduction of wildfires, this species has become prominent in much of the Central Plains grasslands, especially in Oklahoma and Kansas (Engle et al. 1987, Engle et al. 1988, Schmidt and Stubbendieck 1993). In Oklahoma, eastern redcedar occupied 0.6 million ha in 1950 but more than 4 million ha by 1989 (Grumbles 1989, Bidwell et al. 1990). The increase in eastern redcedar also has been attributed to an increased seed source resulting from use of the species in shelterbelt plantings and reduced competition due to overgrazing (Bragg and Hulbert 1976, Van Haverbeke and Read 1976).

Eastern redcedar has been associated with several changes in ecosystem function. In Oklahoma, canopy cover in the herbaceous layer was reduced under eastern redcedar compared with adjacent tallgrass prairie (Engle et al. 1987). Smith and Stubbendieck (1990) found an 83% reduction in understory herbaceous biomass in the canopy zone and a pattern of reduced understory light and soil water content. Eastern redcedar also changes other biological and physical soil factors, including producing higher soil pH (Arend 1950), greater surface calcium content, higher surface organic matter, lower bulk density, and greater infiltration rates (Broadfoot 1951). Eastern redcedar not only reduces herbaceous vegetation but alters species composition. Gehring and Bragg (1992) reported a shift from native C_4 species (warm-season grasses) to C_3 species (cool-season grasses) when photosynthetic pathways were intercepted by redcedar canopy. The change in plant diversity can alter wildlife species and numbers.

Seed dispersal by animals

Birds and mammals have long been acknowledged as important agents of plant dissemination. Animals can disperse plants by feeding on fruits of plants and defecating seeds, or by adhesion of fruits or seeds to their fur, feathers, or feet. Several studies have evaluated the concept of seed dispersal from animal ingestion by studying seed germinability after passage through animals. Krefting and Roe (1949) reported that seed germination improved for 8 of 16 species when recovered from bird droppings. Seeds recovered from mammalian scats did not appear to have benefited from digestive action although they were as germinable as controls. Seeds from blueberries and red raspberries passed through deer mice (*Peromyscus maniculatus*) in germinable condition (Krefting and Roe, 1949). Generally, seeds that pass through birds and mammals retain their vitality and are frequently benefited by the process. Drupes and berries benefit by the complete cleaning of the seed from the surrounding pulp and if herbivorous mammals pass the seed, then feces on the ground where the seed lies also benefit the seed (Ridley 1930).

Animals have been considered one of the major causes in the spread of junipers by either spreading seeds or reducing competition from other plants (Johnsen, 1962). Eastern redcedar cones are consumed by many species of animals, possibly leading to widespread seed dispersal if seeds are not damaged in the process (Phillips 1910). At least 71 species forage on eastern redcedar (Van Dersal 1938). Seed dispersal depends heavily upon birds and small mammals (Phillips 1910, Livingston 1972). Birds are responsible for most seed dissemination, with cedar waxwings (*Bombycilla cedrorum*), robins (*Turdus migratorius*), and mockingbirds (*Mimus polyglottus*) being the most common dispersal agents (Phillips 1910). Studies have reported that eastern redcedar seeds pass undamaged through several species of animals (Phillips 1910, Johnsen 1962, Holthuijzen and Sharik 1985). Redcedar seeds passed unharmed through the digestive tract of avian dispersers, yellow-rumped warblers (*Dendroica coronta*) and cedar waxwings (*Bombycilla cedrorum*), and showed a 1.5–3.5-fold greater germination rate than manually depulped seeds (Holthuijzen and Sharik 1985). Juniper fruit and seeds also have been found in feces of mammals, such as raccoons (*Procyon lotor*), foxes (*Vulpes* spp.), bobcats (*Lynx rufus*), chipmunks (*Tamias* spp.), and other small mammals (Phillips 1910). Deer (*Odocoileus* spp.) browse heavily on eastern redcedar in winters when mast production is low (Halls and Crawford 1960, Segelquist and Green 1968), and sheep, goats, and cattle have been considered dispersal agents of junipers (Bray 1904, Parker 1945). According to Phillips (1910), mammal-scattered seed are left in slightly better condition for germination than those scattered by birds. Johnsen (1962) also reported juniper seeds passed unharmed through digestive tracts of several mammals, and germination rate increased compared with control seeds. Specifically, he found that one-seed juniper passed through woodrats (*Neotoma* spp.) and increased germination rate.

Although birds are considered the main consumers and dispersers of eastern redcedar, small mammals also may be playing a role. Numerous studies have associated small mammals with the establishment and removal of woody vegetation in old-fields (Mittelbach and Gross 1984, Ostfeld et al. 1997, Manson et al. 1999, Manson 2000). Overall, however, few general patterns emerged. The majority of studies evaluating seed predation by rodents reported variation in predation rates as a function of habitat type, seed species, and time (Hulme 1993). Manson (2000) reported that survival of neighboring tree propagules was generally positively autocorrelated, suggesting that foraging by mice and voles contributed to a clumped pattern of tree propagule establishment in old-fields. Some studies found that microhabitat influenced seed predation, with seed predation by mice greater in areas with ground cover, particularly dense vegetation (Manson and Stiles 1998, Hulme and Hunt 1999). Manson and Stiles (1998) also reported that abundance of mice was a poor predictor of patterns of seed predation in old-fields. Ostfeld et al. (1997), however, reported that rodent density does appear to have an effect on patterns of seed predation. Low mouse density resulted in higher rates of seed predation in an old-field than at the forest edge, and high mice density increased predation rates for less-preferred tree species (Ostfeld et al. 1997). Edwards and Crawley (1999) found that the highest proportion of seed removal by rodents occurred at the highest seed density. However, Hulme and Hunt (1999) found that rodents were not influenced by relative seed density. Some studies have reported that post-dispersal predation on tree seeds is due predominately to small mammals and not birds or insects within temperate old fields and forests (Whelan et al. 1991, Ostfeld et al. 1994). In the northeastern U.S., white-footed mice (*Peromyscus leucopus*) appear to be the dominant consumers (Gill and Marks 1991, Ostfeld et al. 1997).

STUDY AREA

This study was conducted at the Oklahoma State University Research Range about 11 km southwest of Stillwater in Payne County, OK (36°02'40"–36°04'20"N, 97°09'30"–97°11'39"W). The Research Range was situated on the western fringe of the cross timbers ecoregion, which covers large parts of central Oklahoma and Texas. Climate was continental with an average growing period of 204 days from April to October. Mean annual temperature was 15°C and ranged from an average daily minimum of -4.3°C in January to an average daily maximum of 34°C in August. Average annual precipitation was 831 mm (National Oceanic and Atmospheric Administration

1999). The vegetation was a mosaic of upland forest dominated by blackjack oak (*Quercus marilandica*) and post oak (*Quercus stellata*); tallgrass prairie dominated by little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), rosette panicgrass (*Panicum oligosanthes*), and western ragweed (*Ambrosia psilostachya*); and a small amount of bottomland forest.

METHODS

Experimental Design

Our study was located in the Junkyard pasture of the Research Range. Twelve eastern redcedar trees, ranging in height from 7.6 to 10.7m, were selected in each of 3 vegetation types: tallgrass prairie, cross timbers, and eastern redcedar thicket. To examine frugivory of cedar cones by different animal guilds, I randomly assigned trees to 3 exclosure treatments. The full-exclosure treatment consisted of 2.4-m cattle panels encircling the cedar tree, with 0.9-m-high flashing buried 0.3-m adjacent to the cattle panels. Cedar cones were therefore available to birds and arboreal rodents (e.g., Sciuridae) but not terrestrial rodents or larger mammals. The partial-exclosure treatment consisted solely of 2.4-m cattle panels encircling the cedar tree. This treatment allowed birds and rodents access to cedar cones, but not larger mammals. The no-exclosure treatment allowed cones to all potential consumers. Each treatment type had 4 replications in each vegetation type.

I sampled monthly starting in October 2001 when trees began to produce mature cones and ending in March 2002 at the end of active dissemination of seeds. Four tertiary branches (i.e., 3 branchings from the main stem and about 1.5 m high) were selected on each tree by randomly selecting a bearing to locate the first branch and then rotated 90° to select the other 3 branches (Fig. 1). Sample branches were individually tagged with an aluminum strip, and at monthly intervals the number of cones per sample branch were recorded. Adjacent to each of the sample branches, a branch of similar size and number of cones was covered with screening material. Cones that had fallen from covered branches into the screening material also were counted at monthly intervals. This count was used to estimate proportion of cones that fell off branches naturally. Cones were counted on the same branches in November 2002 to assess habitat and yearly differences in cone production.

Cones were harvested from nonsampled trees. Dishes containing 50 g of these cones were placed under each tree to assess the identity of cone predators (Fig. 1). Two types of containers were used. One was a closed Tupperware (14.4 x 10.3 x 25.2 cm) with a 2.5-cm round hole drilled in the side to allow access to small mammals. The other was an open dish (16.5 x .15 x 23.5 cm) to allow birds or other mammals to feed on the cones. Shelters were built over the open containers to keep cones falling from the tree from going into the container. Two containers of each type were placed under every tree for a total of 144 containers. A measured amount of cones were placed in each container and left for 5 days, after which cones were reweighed to determine the amount of cones consumed. Control containers, which had small holes to allow water evaporation to take place but were closed to prevent animal access to the cones, were used to account for average water loss from the cones during the 5 days. That amount was added to weight of cones removed from containers to determine true consumption.

Data Analysis

An index of redcedar cone production (cones/sampled branch) was developed, and cone production was compared among habitat types and years using repeated measures analysis (PROC MIXED, SAS Institute Inc. 2000). Percent cone loss was calculated by dividing the average number of cones on a branch per tree at time t by the average number of cones at time t-1. The proportion of cone loss was adjusted for cone fall using the covered branches. Data were square-root transformed and checked for normality before statistical analysis. Differences in cone loss between habitats, treatments, and time were compared using repeated measures analysis (PROC MIXED; SAS Institute Inc. 2000). We fitted a multiple variance model and used the Kenward-Roger approximation to calculate effective degrees of freedom (PROC MIXED, SAS Institute Inc. 2000; Kenward and Roger 1997). We used least-squared means separation tests for all significant main effects. The mass (g) of cones consumed from the dishes was calculated by the difference in mass before and after the 5-day period. Cone consumption rate was analyzed using repeated-measures ANOVA to investigate differences among habitat types, exclosures, and types of containers (PROC MIXED; SAS Institute Inc. 2000). We fitted a multiple variance model and used the Kenward-Roger approximation to calculate effective degrees of freedom (PROC MIXED, SAS Institute Inc. 2000; Kenward and Roger 1997).

RESULTS

Cone production varied among the 3 different habitat types over time ($P = 0.006$). In November 2001, cone production was higher in the cedar thicket than in the prairie *(P*

$= 0.047$) and cross timbers ($P = 0.002$). In November 2002, however, there was no difference in cone production by habitat ($P = 0.123$). Cedar habitats had lower ($P < 0.001$) cone production in 2002, but the cross timbers and prairie habitat stayed relatively the same (Fig. 2).

Cone loss on branches did not vary among exclosure types ($P = 0.178$; Fig. 3). A habitat-by-time interaction explained most of the variation in cone removal ($P = 0.024$; Fig. 3). Cone loss in December–January was lower in the cedar habitat, and cone loss in February–March was higher in the cross timbers forest (Figs. 4–5). Overall, a greater percentage of cones were consumed from the cross timbers and prairie habitats (Fig. 5).

Cone consumption from containers varied by several 3-way interactions among habitat, treatment, month, and container (Table 1). Interactions involving container type can be explained by open containers always having a greater loss of cones, but the magnitude of difference varying by habitat, treatment, and month (Figs. 6–8). For example, cone consumption was consistently low for closed containers but was higher for open containers during December and January in cross timbers and prairie habitats (Fig. 6). Similarly, cone consumption was greater for open containers in no- and partial-exclosure treatments then all other container-treatment combinations in December, but only varied by container in other months (Fig. 7). Cone consumption also was consistently higher from open containers in the no-exclosure treatment in all 3 habitats but especially in the cross timbers (Fig. 8).

Cone consumption was analyzed for open containers only, given the lack of consumption for closed containers. Cone consumption in open containers varied by the 3-way interaction of habitat, treatment, and month ($P = 0.003$). Trees with no enclosures had higher cone loss from containers than those with enclosures, especially in the cross timbers in December and January (Fig. 9). Except for the prairie-partial treatment, full and partial enclosures had similarly low cone loss (< 7 g).

DISCUSSION

Redcedar is known to produce larger-than-average crops once every 2–3 years (Fowells 1965). Holthuijzen and Sharik (1985) found a difference in average number of cones between years and among trees. In our study, trees in the cedar thicket may have had a peak year in 2001 and then returned to an average year in 2002; the majority of trees in the cross timbers and prairie may have had average crops in both years. Determination of habitat-specific cone production would require studies over multiple years.

Birds had access to cones on all trees during the study. Because there was no difference in cone loss in exclosure treatments, the majority of cone loss from branches was probably due to birds. Other studies have reported that birds consume the majority of eastern redcedar seeds (Phillips 1910, Holthuijzen and Sharik 1984). However, there was variation in the rate of cone depletion over time and among habitats. Cedar and prairie habitats had a large loss of cones from October to December, and then the rate of total cone loss leveled out. In cross timbers, total number of cones lost decreased gradually over time. However, percent cone loss increased greatly from February to March (Fig. 4). Cones may have ripened earlier in the prairie and cedar thicket than in cross timbers. Holthuijzen and Sharik (1985) found that cones on some trees ripened quickly during August and September, whereas cones on other trees ripened over a longer period of time. After cones ripened in cross timbers, they may have had more consumption because nearby trees provided perches for birds (Debussche et al. 1982, McDonnell and Stiles 1983).

Cone loss was caused not only by animal predation but also other factors. Ripe cones can be removed from trees by wind and rain. Although we used covered branches to account for natural cone loss, wind might have affected cone loss more on open branches than on covered branches.

Patterns of seed predation vary by habitat type, seed species, and time (Hulme 1993). Differences in exclosure types indicate that birds are not the main consumers of cedar cones on the ground. Trees with no exclosures had the greatest cone loss from containers, indicating that small- and medium-sized mammals are major cone consumers. Photos taken by movement-activated cameras at the end of the study showed opossums (*Didelphis virginiana*) and *Peromyscus* spp. removing cones from open containers. Rodent consumption also was evident from mice feces found in the containers.

Our results indicate consumption of eastern redcedar cones from containers on the ground is based on habitat type and time. Higher seed removal in the cross timbers with no exclosures may have been due to medium-sized mammals, particularly opossums. Ginger et al. (2003) reported that opossums in this area were more prevalent in cross timbers oak habitats, and Kasparian et al. (2002) showed that eastern redcedar cones were consumed by opossums. Because opossums can consume more cones at one time than rodent species, they may have been a significant cone consumer at no-exclosure trees in the cross timbers. Trees with no exclosures and partial exclosures in the prairie habitat had the next highest cone removal from open containers (Fig. 9).

Greater loss of cones in the cross timbers and prairie also may be attributed to microhabitat preferences of small mammals. In other studies, microhabitat influenced seed predation, with predation by mice greater in areas with dense ground cover (Manson and Stiles 1998, Hulme and Hunt 1999). Predation rates may be higher under woody or tall herbaceous vegetation (Bowers and Dooley 1993, Myster and Picket 1993). In our study, redcedar trees in the cross timbers and prairie habitats had greater ground cover than in the cedar thicket habitat (personal observation). Several trees near the cross timbers had nearby thickets of sumac (*Rhus* spp.) and fallen logs and debris, which would provide cover for small mammals. Thick herbaceous vegetation in the prairie also would provide cover for small mammals from predators. Of the no-exclosure treatments, cedar habitat had the lowest cone removal. Small mammals may be avoiding trees near cedar because of less ground cover. Eastern redcedar reduces understory herbaceous vegetation (Gehring 1983, Engle et al. 1987, Smith and Stubbendieck 1990), thereby providing less cover from predators.

Overall, birds appeared to consume the majority of cones from branches, whereas small- and medium-sized mammals consumed cones on the ground. The guilds likely contribute to the spread of eastern redcedar at different scales. Because birds have high mobility and a digestion time (18–20 min) that exceeds their feeding time (3–4 min) on trees, they tend to have a high dispersal efficiency (Holthuijzen and Sharik, 1985). Holthuijzen and Sharik (1985) also found that on average birds dispersed cones more than 12 m from the parent tree. Therefore, eastern redcedar seeds dispersed by birds are spread away from the parent tree. Because the majority of birds feeding on eastern redcedar (cedar waxwings, mockingbirds, robins) are not forest birds, they can spread seeds to more open areas with some structural diversity, such as old-fields. The amount of bird-disseminated seeds dropped into fields is positively associated with the amount of structural complexity in the field (McDonnell and Stiles 1983). Vegetation such as trees and shrubs attract birds by providing perching places (Debussche et al. 1982, McDonnell and Stiles 1983). Therefore, birds would probably defecate more cedar seeds in areas where pioneer trees or shrubs already occurred or along the edges of forests. McDonnell and Stiles (1983) found that bird-disseminated seeds occurred in greater numbers along the forest edge than any other site. Dispersed seeds of eastern redcedar also would be more concentrated along powerlines and fencerows where birds perch.

Eastern redcedar is probably spread on a smaller scale by small mammals. Because rodents lack the mobility of avian species, they probably disperse seeds only a short distance (< 1 ha) from the parent tree. For example, a home range size of 0.1 ha (Lackey et al. 1985) for white-footed mice would provide a radius around the parent tree of 17.8 m. Brewer and Rejmanek (1999) found that several species of rodents disperse seeds < 10 m away from the source in Neotropical forests. The spread of eastern redcedar in certain areas will depend on resident rodent species. *Peromyscus* spp. and eastern woodrats (*Neotoma floridana*) consume eastern redcedar cones (Phillips 1910, Johnsen 1962). Deer mice prefer more open areas and prefer habitats with exposed soil and limited vertical structure (Clark et al. 1998). Therefore, if deer mice are consuming cones, they are probably contributing to the localized spread of cedar in early-successional old-fields away from the invasion front. These would be areas where birds would be less likely to spread eastern redcedar seeds due to lack of vertical structures. White-footed mice (*Peromyscus leucopus*) and eastern woodrats, however, prefer more woodland-type habitats and the occasional grass-forb areas (Caire et al. 1989). These species along with larger species, such as the Virginia opossum, would contribute to cedar invasion into forested areas from the woodland-old field edge.

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Table 1. Results of repeated-measures ANOVA for consumption of eastern redcedar cones in seed predation trials. Effects of factors and interaction terms influencing seed removal rates are reported using Type III sum of squares *F* values.

Factor	df	*F*	Prob.>*F*
Habitat	2, 135	2.41	0.0934
Treatment	2, 135	8.42	0.0004
Month	5, 264	27.64	<.0001
Container	1, 135	51.71	<.0001
Habitat x Treatment	4, 135	1.24	0.2986
Habitat x Month	10, 278	1.21	0.2844
Treatment x Month	10, 278	1.30	0.2314
Habitat x Treatment x Month	20, 284	3.00	<.0001
Habitat x Cont	2, 135	1.31	0.2727
Treatment x Cont	2, 135	2.08	0.1286
Habitat x Treatment x Cont	4, 135	2.34	0.0581
Month x Cont	5, 264	2.62	0.0247
Habitat x Month x Cont	10, 278	1.83	0.0550
Treatment x Month x Cont	10, 278	3.15	0.0008
Habitat x Treatment x Month x Cont	20, 284	1.25	0.2112

Figure 1. Layout for cone and seed-predation sampling in study of frugivory of eastern redcedar in each habitat and exclosure type on Oklahoma State University Research Range, Payne County, Oklahoma.

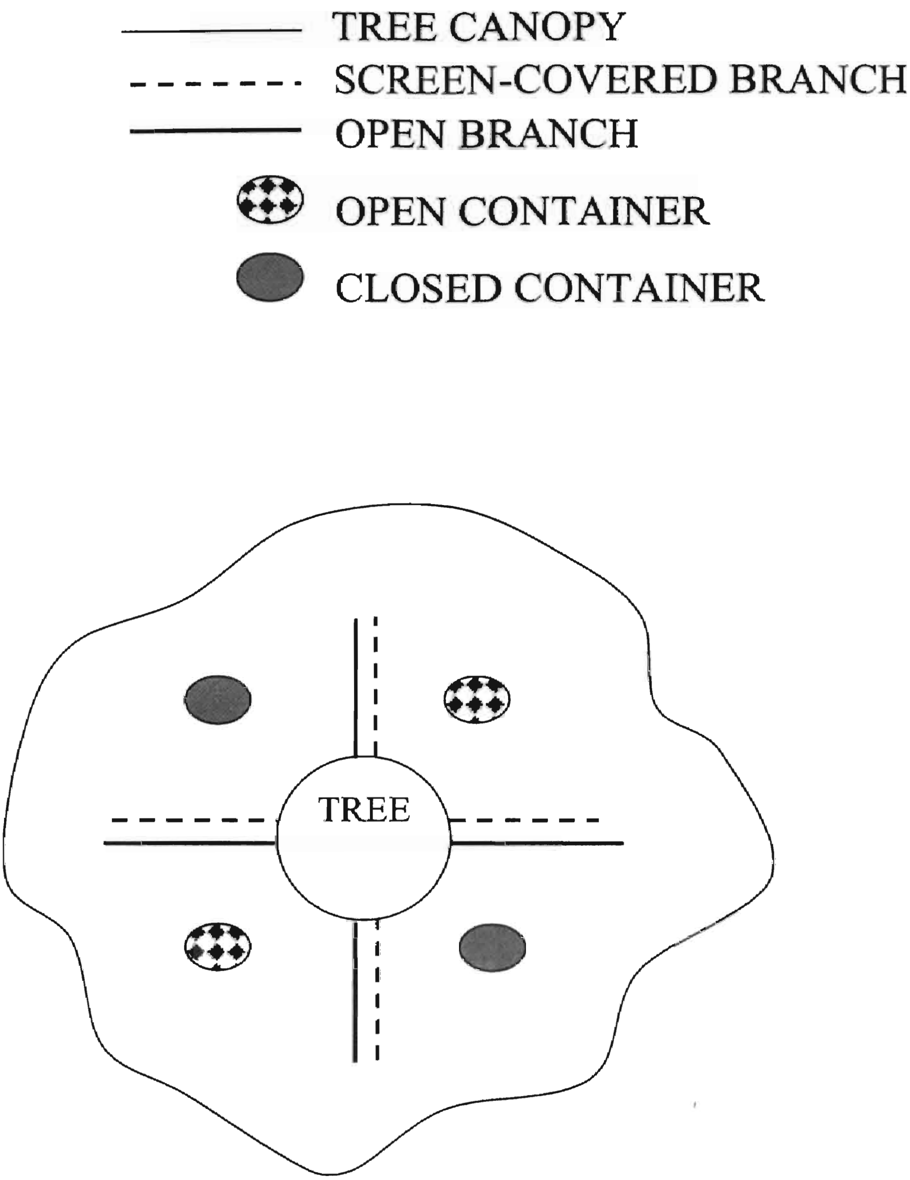

TREE CANOPY
SCREEN-COVERED BRANCH
OPEN BRANCH
OPEN CONTAINER
CLOSED CONTAINER
TREE

Figure 2. Eastern redcedar cones per tertiary branch (+ SE) by habitat type and year (n = 12 replicates/year), Oklahoma State University Research Range, Payne County, Oklahoma.

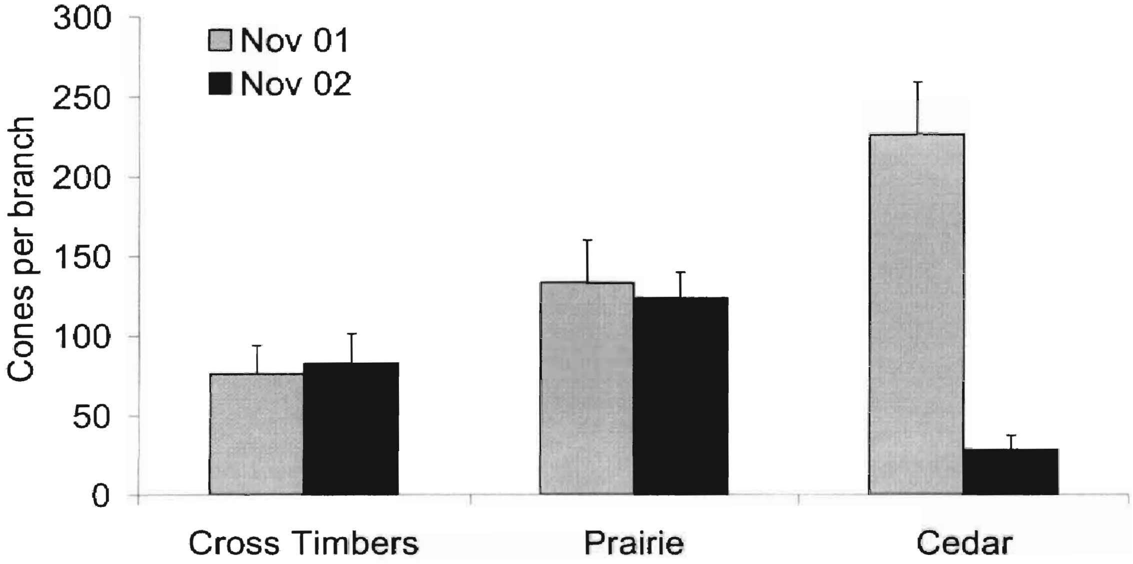
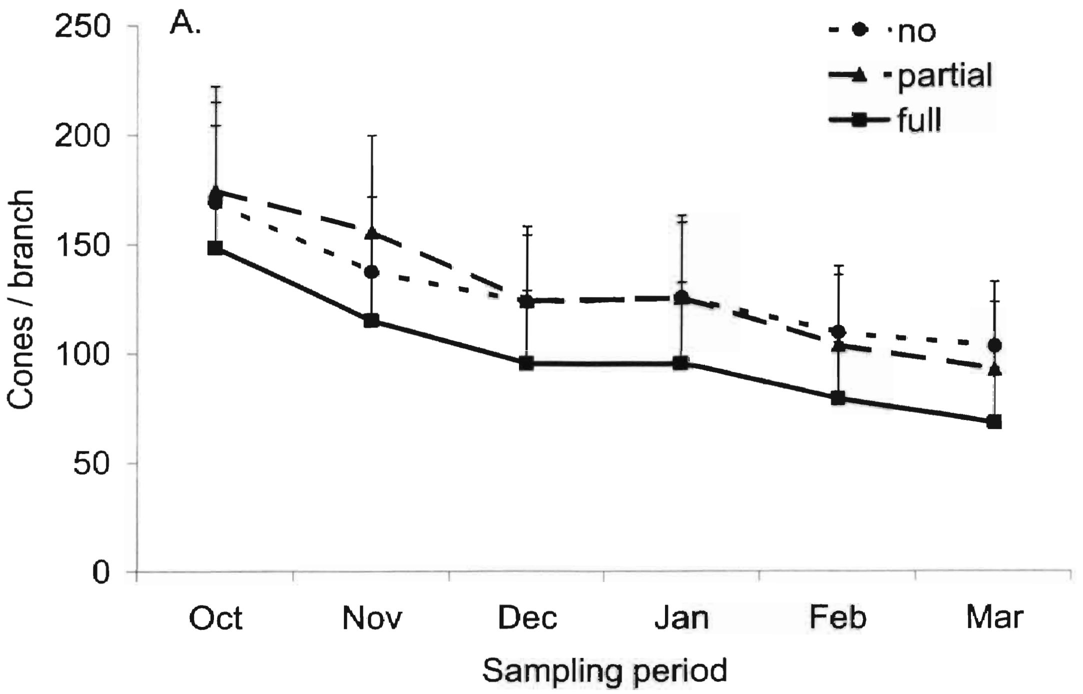

300
250
200
150
100
50
0
Cones per branch
Nov 01
Nov 02
Cross Timbers
Prairie
Cedar

Figure 3. Average number of eastern redcedar cones per branch (+ SE) from October 2001 to March 2002 by (A) exclosure type and (B) habitat type, Oklahoma State University Research Range, Payne County, Oklahoma.


A.
Cones / branch
250
200
150
100
50
0
Oct
Nov
Dec
Jan
Feb
Mar
Sampling period
no
partial
full

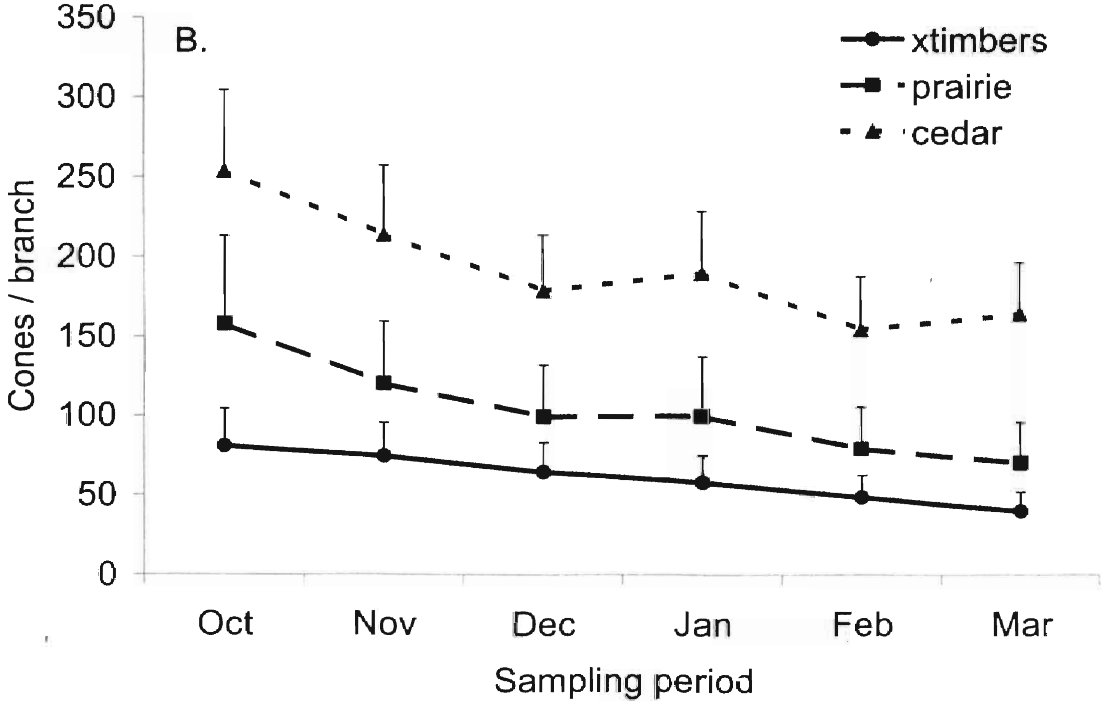
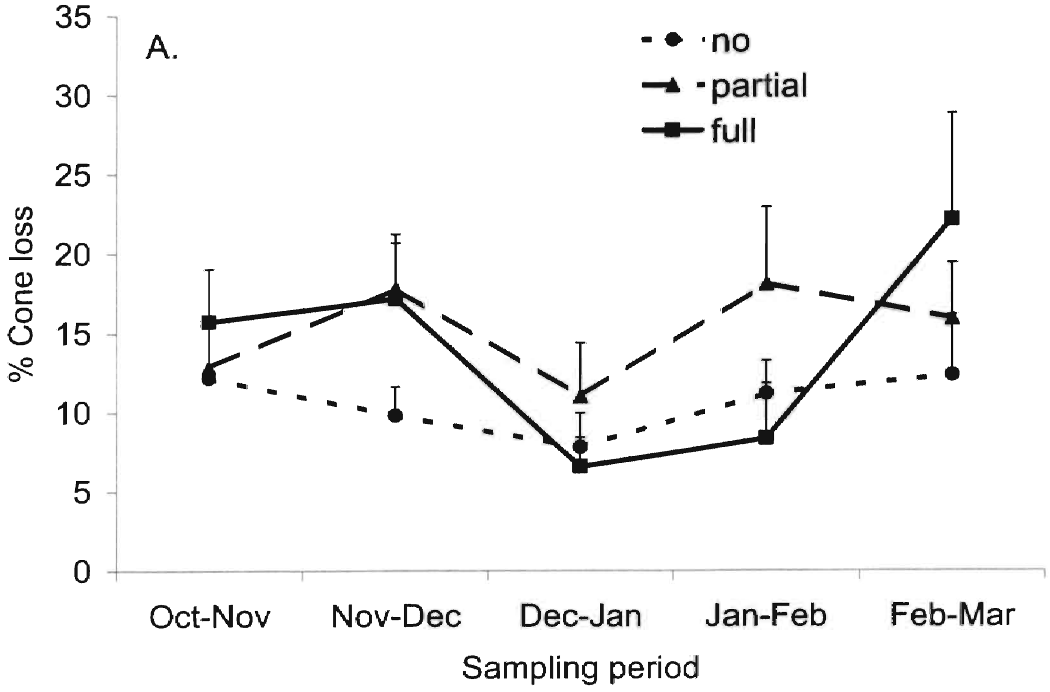
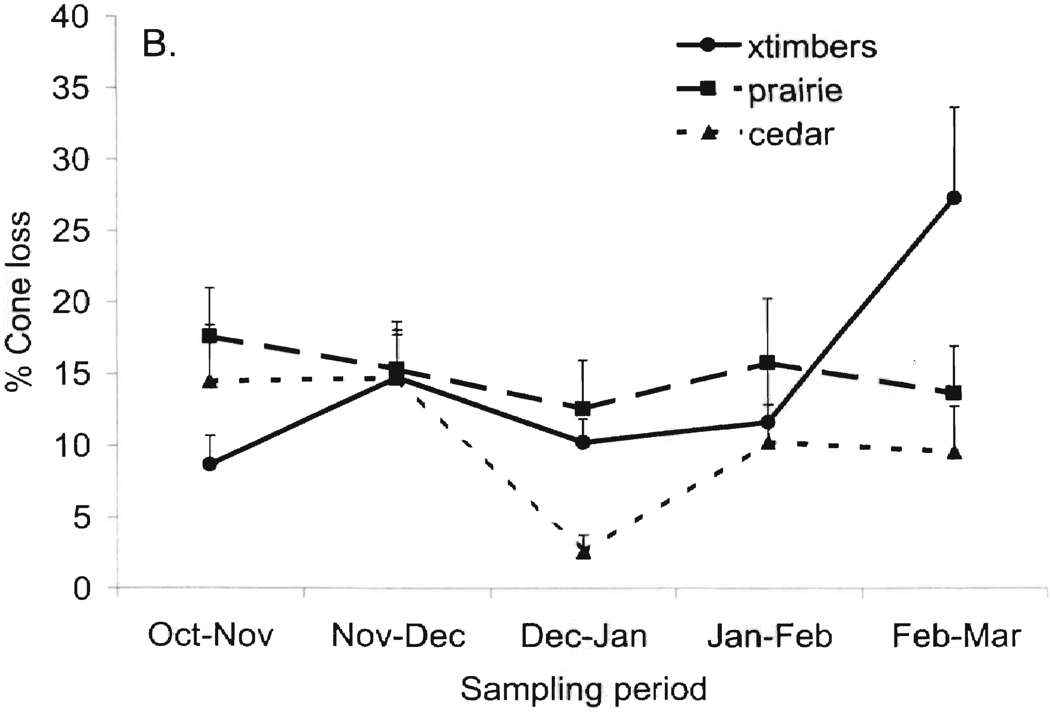

B.
Cones / branch
350
300
250
200
150
100
50
0
Oct
Nov
Dec
Jan
Feb
Mar
Sampling period
xtimbers
prairie
cedar

Figure 4. Average percent cone loss from branches of eastern redcedar (+ SE) by month in 2001–2002 for (A) exclosure type and (B) habitat type, Oklahoma State University Research Range, Payne County, Oklahoma.

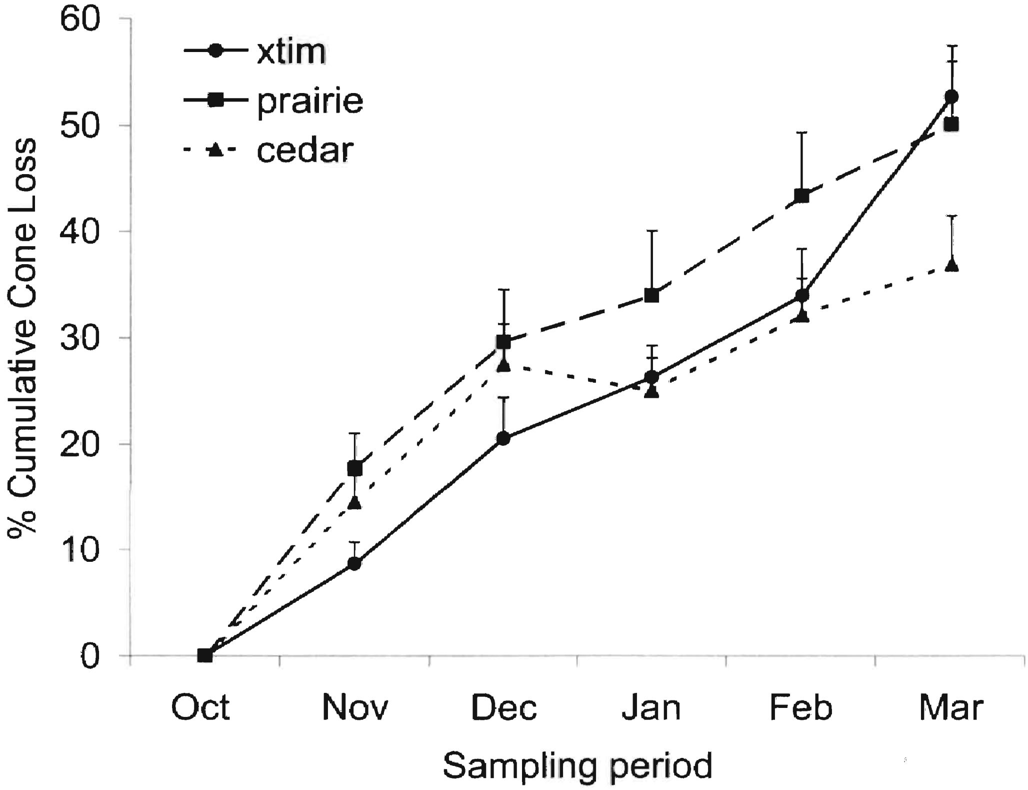


A.
no
partial
full
% Cone loss
0
5
10
15
20
25
30
35
Oct-Nov
Nov-Dec
Dec-Jan
Jan-Feb
Feb-Mar
Sampling period



B.
xtimbers
prairie
cedar
% Cone loss
0
5
10
15
20
25
30
35
40
Oct-Nov
Nov-Dec
Dec-Jan
Jan-Feb
Feb-Mar
Sampling period

Figure 5. Cumulative percent cone loss on branches of eastern redcedar (+ SE) from 2001 to 2002 for habitat types in Oklahoma State University Research Range, Payne County, Oklahoma.



60
50
40
30
20
10
0
xtim
prairie
cedar
% Cumulative Cone Loss
Oct
Nov
Dec
Jan
Feb
Mar
Sampling period

Figure. 6. Average loss of eastern redcedar cones (+ SE) from 50-g containers for each habitat-container combination from October 2001 to March 2002, Oklahoma State University Research Range, Payne County, Oklahoma.

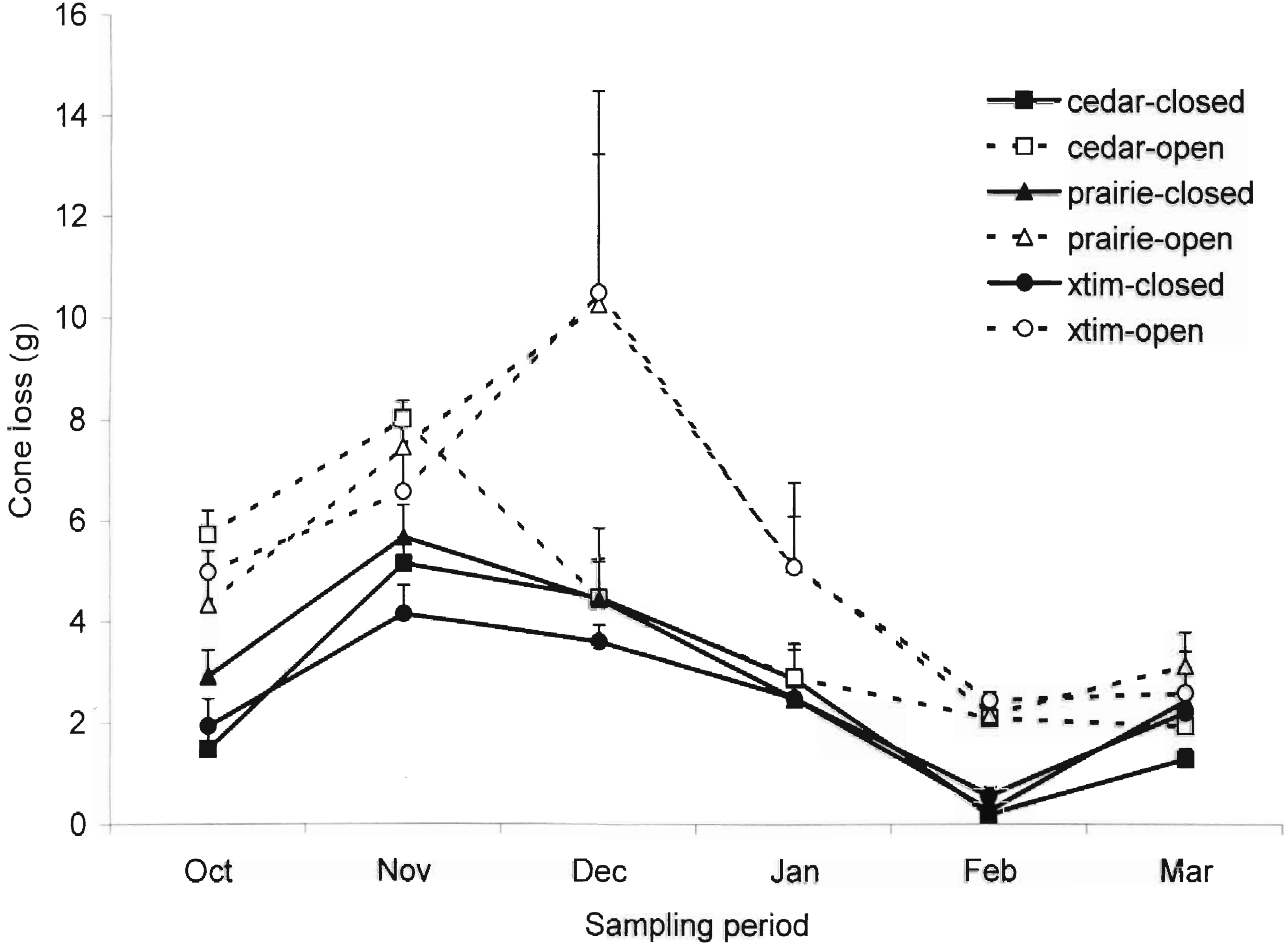

16
14
12
10
8
6
4
2
0
Cone loss (g)
Oct
Nov
Dec
Jan
Feb
Mar
Sampling period
cedar-closed
cedar-open
prairie-closed
prairie-open
xtim-closed
xtim-open

Figure 7. Average loss of eastern redcedar cones (+ SE) from 50-g containers for each exclosure-container combination from October 2001 to March 2002, Oklahoma State University Research Range, Payne County, Oklahoma.

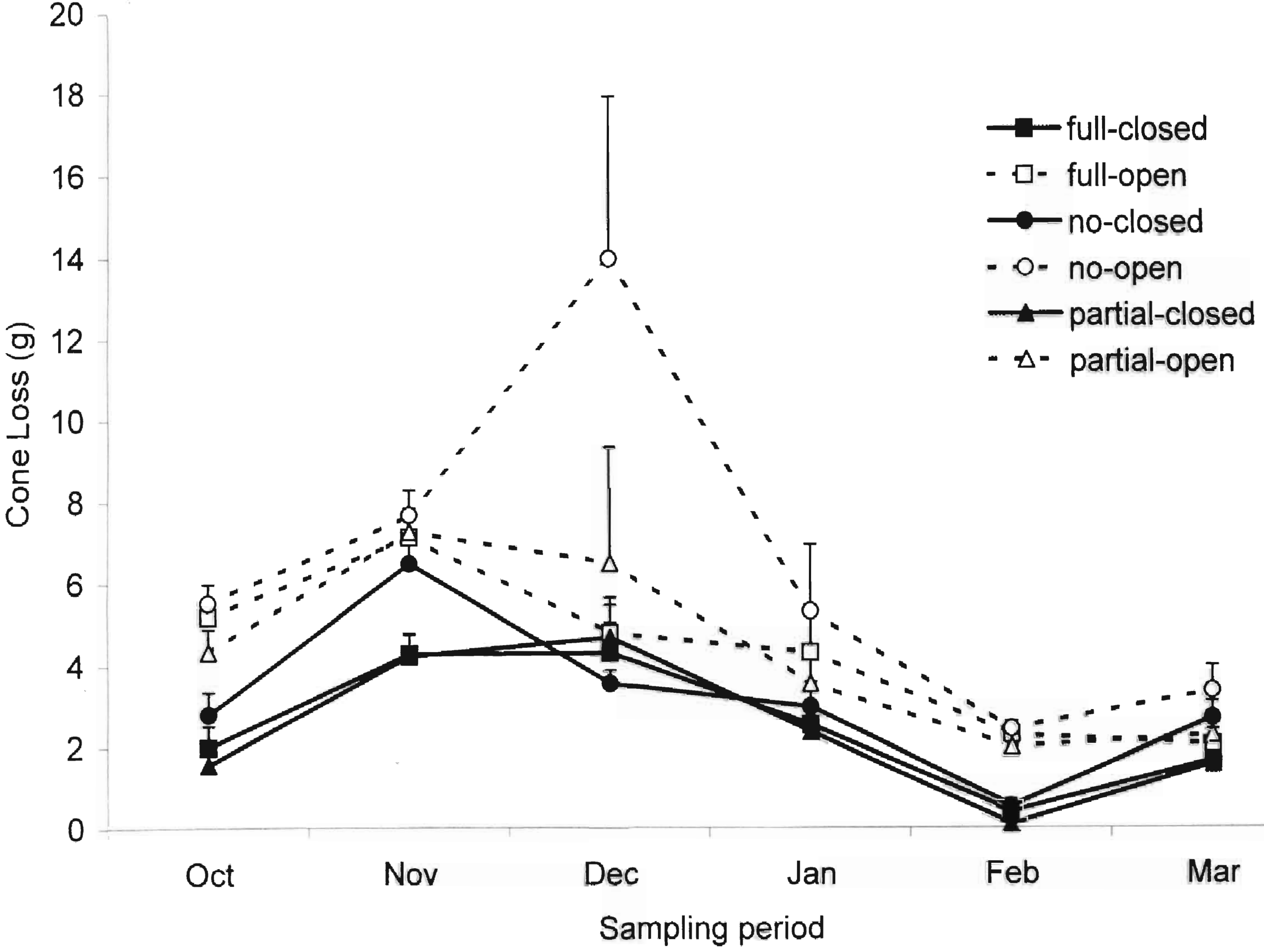

20
18
16
14
12
10
8
6
4
2
0
Cone Loss (g)
Oct
Nov
Dec
Jan
Feb
Mar
Sampling period
full-closed
full-open
no-closed
no-open
partial-closed
partial-open

Figure 8. Average loss of eastern redcedar cones (+ SE) from 50-g containers for each exclosure-container combination by habitat type, October 2001-March 2002, Oklahoma State University Research Range, Payne County, Oklahoma.

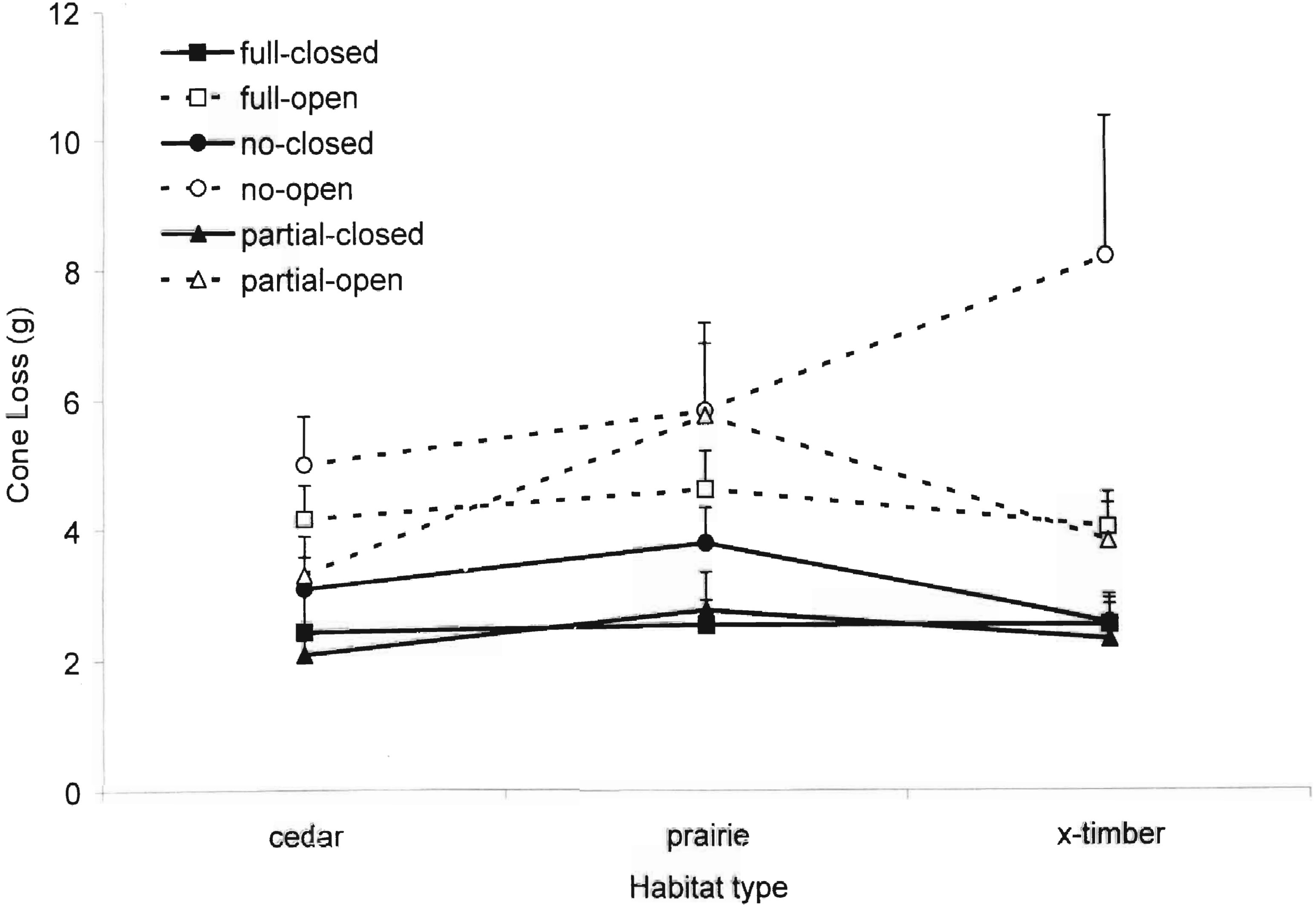
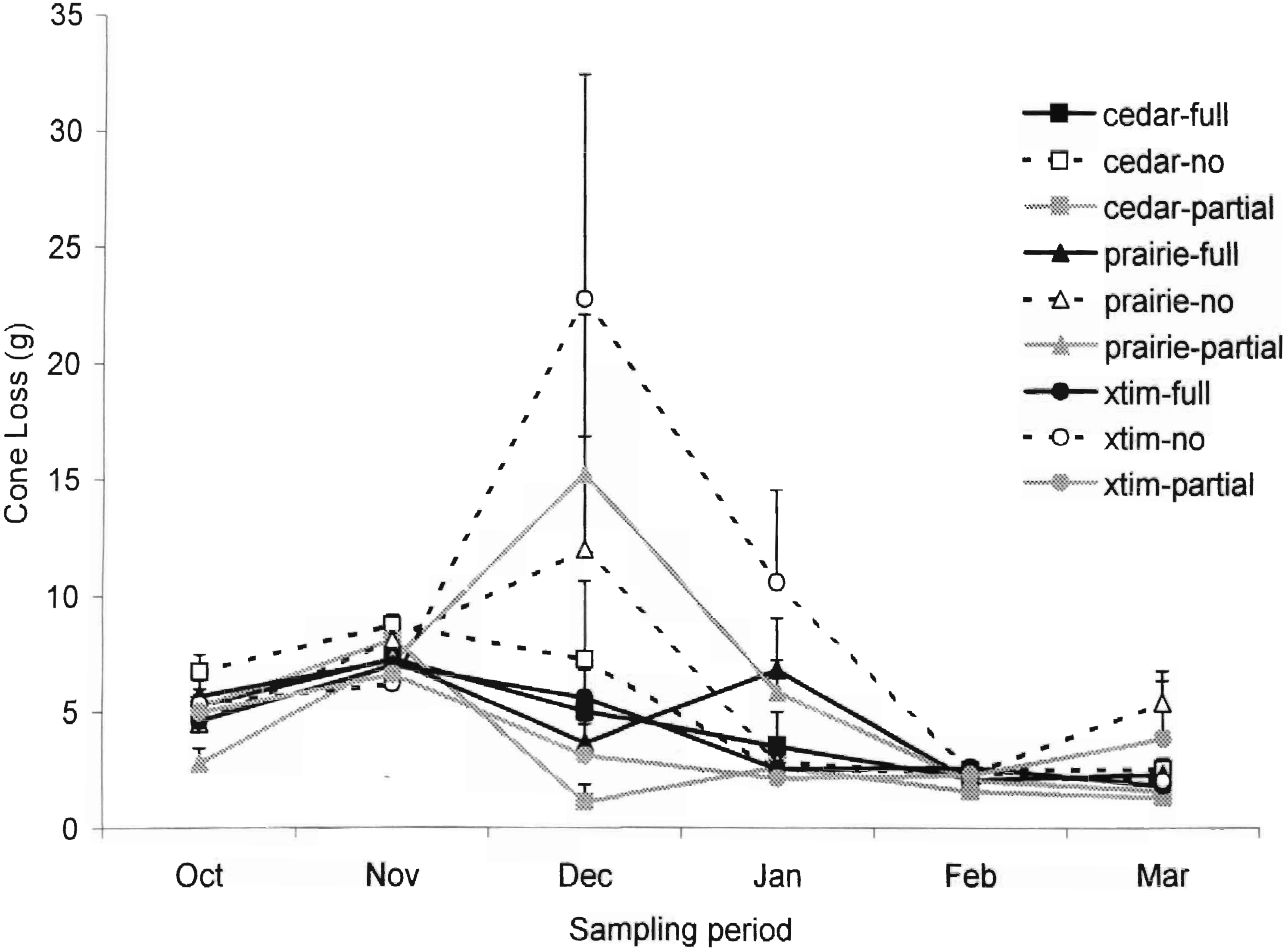

12
10
8
6
4
2
0
Cone Loss (g)
full-closed
full-open
no-closed
no-open
partial-closed
partial-open
cedar
prairie
x-timber
Habitat type

Figure 9. Average loss of eastern redcedar cones (+ SE) from open 50-g containers for each habitat-exclosure combination from October 2001 to March 2002, Oklahoma State University Research Range, Payne County, Oklahoma.


35
30
25
20
15
10
5
0
Cone Loss (g)
Oct
Nov
Dec
Jan
Feb
Mar
Sampling period
cedar-full
cedar-no
cedar-partial
prairie-full
prairie-no
prairie-partial
xtim-full
xtim-no
xtim-partial

CHAPTER 2

EFFECTS OF EASTERN REDCEDAR ON COMMUNITY STRUCTURE OF SMALL MAMMALS

INTRODUCTION

Recent changes in landscape cover in the Great Plains are resulting from the expansion and invasion of eastern redcedar (*Juniperus virginiana*; Engle et al. 1987, Smith and Stubbendieck 1990, Gehring and Bragg 1992, Briggs et al. 2002). Increased abundance of eastern redcedar in the Great Plains has been associated with several changes in ecosystem function. It can lead to a reduction in herbaceous biomass in the canopy zone (Engle et al. 1987, Smith and Stubbendieck 1990), alter species composition, reduce understory light and soil water content (Gehring and Bragg 1992, Briggs et al. 2002), and change biological and physical soil factors (Arend 1950, Broadfoot 1951). Recent inventories indicate an extensive expansion of eastern redcedar populations westward into the rangeland regions of the United States, with significant encroachment in the mixed prairie of Kansas and Oklahoma (Bragg and Hulbert 1976, Snook 1985). It is the most rapidly expanding woody species on rangeland and is increasing in terms of tree size, area occupied, and number of locations (Wilson and Schmidt 1990). Eastern redcedar is not only invading the tallgrass prairie but also old fields and cross timbers, where it is altering the landscape and causing shifts in wildlife populations and habitat (Wilson and Schmidtt 1990, Gehring and Bragg 1992, Stone 1998).

Changes in vegetation by plant succession or invasion can alter spatial variation in small-mammal communities due to individual and population responses to landscape features and shifts in local vegetation (Schweiger et al. 2000). Individual species of small mammals have different vegetational or structural preferences and respond differently to composition and structural changes in vegetation. By altering the landscape, abiotic environment, and local vegetation, eastern redcedar likely is changing the suitability of habitat for small-mammal species at several different scales. Therefore, small-mammal communities could be altered by invasion of eastern redcedar.

Landscape characteristics, such as the spatial arrangement and size of habitat patches, can affect localized ecological patterns and processes (Forman and Gordon 1986). Animal species respond to several scales of landscape characteristics and resource aggregation (Ward and Saltz 1994, Pedlar et al. 1997). Species thrive or disappear and populations grow or decline based on response to changes in their habitats (Estes 1996). Understanding temporal and spatial scales at which organisms perceive and respond to their environment is a central issue in ecology (Wiens 1989), and investigations of habitat relationships for wildlife species at varying scales are becoming common.

Compositional and structural changes of vegetation can alter the suitability of habitat for small-mammal species (Kaufman and Fleharty 1974, M'Closkey and Lajoie 1975). Vegetation or structural preferences have been demonstrated for several small-mammal species; however, studies of micro- and macrohabitat use of rodents are inconsistent (Jorgensen and Demarais 1999). Some authors have suggested that small-mammal distributions and habitat-selection strategies are sensitive to variance in local vegetative structure (Dueser and Shugart 1978, Swihart and Slade 1990). Swihart and Slade (1990) concluded that capture frequencies of several species of small mammals fluctuated extensively with changes in the vegetation around traps. They found that a reduction in captures of harvest mice (*Reithrodontomys* spp.) and deer mice coincided with a reduction in forbs, and captures of white-footed mice increased with an increase in wooded habitat around traps.

Other studies have shown that large-scale features of habitat can affect spatial distributions of small mammals (Foster and Gaines 1991, Barrett et al. 1995, Collins and Barrett 1997, Manson et al. 1999). Manson et al. (1999) found that capture probabilities of mice and voles were better predicted by macrohabitat features than by variation in the microhabitat around individual trap stations. Distance from the forest edge predicted *Microtus* and *Peromyscus* captures better than variation in vegetation cover at the microhabitat level. The landscape context of habitat fragments can have strong species-specific effects on spatial distributions of small mammals along with local vegetative composition (Schweiger et al. 2000). For example, distribution of white-footed mice was influenced by complex interactions among landscape features, patch size, adjacency to the forest, and local vegetative structure (Schweiger et al. 2000). Understanding how the interaction between macrohabitat and microhabitat affects species responses to changes in landscape structure warrants further exploration.

The overall goal of this study was to examine effects of eastern redcedar invasion on community structure of small mammals. My specific objectives were to compare small-mammal communities in tallgrass prairie, old field invaded by cedar, and cross timbers and evaluate mammalian spatial data relative to vegetation and eastern redcedar occurrence at different scales.

Given known effects of eastern redcedar on vegetative communities (i.e., decreased herbaceous understory and change in species composition; Smith and

Stubbendieck 1990; Gehring and Bragg 1992), several demographic consequences were possible within the small-mammal community. I hypothesized that small-mammal communities would be altered in areas with increasing amounts of eastern redcedar. I also predicted that overall diversity of small mammals would be lower where eastern redcedar was prevalent as a result of reduced aboveground plant biomass and cover. In the old-field site, prairie species, such as deer mice (*Peromyscus maniculatus*), fulvous harvest mice (*Reithrodontomys fulvescens*), plains harvest mice (*Reithrodontomys monatnus*), and cotton rats (*Sigmodon hispidus*), should be prevalent in the open areas and their densities should decrease with increasing cedar (Geortz 1964, Hanchey and Wilkins 1998, Schweiger et al. 2000). Woodland species, white-footed mice (*Peromyscus leucopus*) and eastern woodrats (*Neotoma floridana*), should be prevalent in the cedar stands and their densities should decrease with decreasing cedar (Kaufman et al. 1983, McMurry et al. 1993). In the tallgrass-prairie site, deer mice, fulvous harvest mice, prairie voles (*Microtus ochrogaster)*, and cotton rats would be common, except in the small patches of eastern red cedar where white-footed mice should occur (Caire et al. 1989, Schweiger et al. 2000). The cross timbers site would contain woodland voles (*Microtus pinetorum*), white-footed mice, and eastern woodrats due to the increased amount of woodland vegetation (Schweiger et al. 2000). White-footed mice and woodrats should be more prevalent in the cross timbers site than in areas with an increased amount of cedar because the forest has more understory cover.

STUDY AREA

This study was conducted on three sites at the Oklahoma State University Research Range (CTER) located about 11 km southwest of Stillwater in Payne County, OK (36°07' N, 97°04' W). One site in each of 3 vegetational types was used to evaluate interactions between small mammals and eastern red cedar: 1) tallgrass prairie adjacent to cross timbers, 2) cross timbers, and 3) old-field that had been invaded by eastern redcedar trees in half of the plot. This region was located within a subtropical humid climate zone. Mean annual temperature was 15°C and ranged from an average daily minimum of –4.3°C in January to an average daily maximum of 34°C in August. The average annual precipitation was 831 mm (National Oceanic and Atmospheric Administration 1999).

The tallgrass-prairie site previously was used for livestock grazing during summer, and fires burned the site in 1991 and 1996. Dominant herbaceous species were little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and western ragweed (*Ambrosia psilostachya*). The prairie site also contained isolated motts of sumac (*Rhus* spp.), oaks (*Quercus* spp.) and eastern redcedar. Soils belong to the Grainola-Lucien complex (fine, mixed, thermic Vertic Haplustalfs) and the Zaneis-Huska complex (fine-loamy, mixed, thermic Udic Argiustolls) classified as Shallow Prairie and Loamy Prairie range sites (Henley et al. 1987).

The cross timbers site was dominated by post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) in the overstory. The understory was dominated by buckbrush (*Symphoricarpos orbiculatus*), greenbriar (*Smilax bona-nox*), poison ivy, winged sumac (*Rhus copallinum*), smooth sumac (*R. glabra*), and eastern redcedar. Soils belong to the Harrah Pullasiki complex (fine-loamy, siliceous, thermic Ultic Paleustalfs) classified as Loamy Bottomland range site and the Stephenville-Darnell complex (fine-loamy, siliceous, thermic Ultic Haplustalfs) classified as the Shallow Savannah range site (Henley et al 1987).

The old-field site previously was used for livestock grazing during summer and was burned in 1996. Dominant herbaceous species were little bluestem, Indiangrass, threeawn species (*Aristida* spp.), and western ragweed. Eastern redcedar invaded the western and southern section of the site. In 1996 the cedars were mechanically removed with a rotary saw in the northeastern portion of the site. Soils consist of Renfrow loam (fine, mixed, thermic Udertic Paleustolls) and the Zaneis Huska complex along with Coyle loam classified as Claypan Prairie and Loamy Prairie range sites (Henley et al. 1987).

METHODS

Trapping

Trapping grids (180 m x 180 m) were sampled in each of 3 vegetation types: tallgrass prairie, cross timbers forest, and old-field invaded by eastern redcedar. Each grid was divided into 225 12 x 12-m cells. Two traps were placed in each cell, and each trap was 6 m from each other throughout the grid (Fig. 1).

Animals were trapped using Sherman live traps (7.6 x 8.9 x 22.9 cm) baited with oatmeal and provided with cotton for warmth during cold weather (<1.7°C). Trapping was conducted seasonally from May 2001 to August 2002 in May, August, November, and February (i.e., 6 trapping periods). Within a season, one grid was trapped for 5 consecutive days, followed immediately by a 5-day trapping run on another grid until all 3 grids were sampled. Traps were set right before sunset and checked every morning.

All captured rodents were sexed, aged (adult, juvenile), and weighed with a spring scale. Larger rodents (e.g., cotton rats and wood rats) were marked using ear tags, and all other species were toe-clipped for future identification (Animal Care and Use Committee 1998).

Vegetation Sampling

Vegetational data consisted of percent cover of eastern redcedar, understory vegetation and overstory vegetation. Percent cover of eastern redcedar was visually estimated in all 225 cells in each habitat type. Understory vegetation (< 1 m) was sampled using a 1-m^2 frame. Four samples taken in each cell were averaged to give one estimate for each cell. Variables included percent cover of forb, legume, grass, woody vegetation, bareground, rock, litter, moss, *Opuntia*, and dead material. Overstory vegetation was sampled using a densiometer (Lemmon 1957). Four sample points from each cell were averaged to give one estimate for each cell. At each sample point a measurement was taken in each of the 4 cardinal directions.

Data Analysis

I used data only from species with enough captures to effectively run a particular analysis. Some species (*Chaetodipus hispidus, Blarina brevicada*) had too few captures (< 10) to be used in any analysis. Characteristics of small-mammal communities were compared among grid types using plots of rank abundance and ordination techniques. Overall species composition was first evaluated in the 3 plots using detrended correspondence analysis (DCA) with CANOCO (ter Braak and Smilauer 1988) software with default options. Eight small-mammal species were used to ordinate all cells in each habitat type ($n = 675$). DCA is an indirect gradient analysis technique used to identify factors influencing characteristics of communities that vary along compositional gradients (Peet et al. 1988, Palmer 1993). DCA uses the weighted averages of species abundance to generate species-site joint plots in which sample scores in the ordination diagram lie at the centroids of the positions of species that occur in them. Sites close to a particular species are likely to have a high abundance of that species and those farther away a lower abundance. The effect of habitat type on species abundance was assessed by comparing sample scores and species scores in the first two DCA dimensions. Eigenvalues produced from the DCA represent the correlation between species' scores and sample scores (maximum value = 1.0). I used correlation of DCA axis scores with vegetation variables to identify gradients represented by the DCA ordination axes.

Rank-abundance analysis (Begon et al. 1996) was used to determine differences in the structure of small-mammal communities in the 3 habitat types. The log of the number of individuals was used as an index of abundance, and species were assigned a rank from 1 (most abundant) to 7 (least abundant). The relationship between species rank and abundance in small-mammal communities was compared among the 3 habitats using multiple linear regression (PROC REG, SAS Institute Inc. 2000).

Stepwise logistic regression (PROC LOGISTIC; SAS Institute Inc. 2000) was used to assess the association between occurrence of individual small-mammal species and eastern redcedar cover, total overstory cover, and understory vegetation. In each habitat type, probability of capture of each species at each cell was regressed against vegetational variables. Models were fitted using a maximum-likelihood method, and variables were brought into the model using a significance value of 0.15 (Hosmer and

Lemeshow 2000). The Hosmer and Lemeshow test (Hosmer and Lemeshow 2000) was used to test goodness-of-fit of the model.

For each habitat type, I reduced the number of vegetational variables using correlation analyses. For pairs of variables that were highly correlated with each other ($|r| > 0.5$), I eliminated the member of the pair that was most highly correlated with other variables in the data set. In the tallgrass prairie, litter and herbaceous cover were negatively correlated ($r = -0.61$, $P < 0.0001$), and cedar and overstory cover were positively correlated ($r = 0.66$, $P < 0.0001$). In the cedar old-field, cedar and forb cover were negatively correlated ($r = -0.67$, $P < 0.0001$), litter and cedar cover were positively correlated ($r = 0.58$, $P < 0.0001$), bareground and litter were negatively correlated ($r = -0.55$, $P < 0.0001$), and overstory cover was positively correlated with cedar ($r = 0.84$, $P < 0.0001$) and litter cover ($r = 0.58$, $P < 0.0001$) and negatively correlated with forb cover ($r = -0.58$, $P < 0.0001$). In the cross timbers, herbaceous and forb were positively correlated ($r = 0.53$, $P < 0.0001$), bareground and litter cover were negatively correlated ($r = -0.76$, $P < 0.0001$), and herbaceous ($\mathrm{r} = -0.69$, $\mathrm{P} < 0.0001$) and forb cover ($\mathrm{r} = 0.53403$, $\mathrm{P} < 0.0001$) were negatively correlated with percent overstory cover. Variables eliminated from logistic regression analyses were herbaceous and overstory cover in the tallgrass prairie; forb, litter, and overstory cover in the cedar old-field; and herbaceous, litter, and overstory cover in the cross timbers.

I was specifically interested in the association of eastern redcedar and the probability of capture of small mammals. Therefore, I regressed probability of capture for all small-mammal species with adequate data in each habitat type against eastern redcedar as the only independent variable. I also conducted logistic regression analyses at different grid sizes to determine the spatial scale at which individual species of small mammals were affected by eastern redcedar. Adjacent cells in each grid were placed in groups of 9 and 25 to provide 3 spatial scales: cell (12 x 12 m), 9 cells (36 x 36 m) and 25 cells (60 x 60 m). Eastern redcedar data for each scale were determined by averaging measurements from the cells.

RESULTS

Small-mammal Communities by Habitat

I recorded 1,184 small mammal captures representing 10 species and 523 unique individuals in 40,500 trap nights between May 2001 and August 2002 (Appendix A). Percent cover for each vegetation class varied among the 3 habitats with cedar old-field having the greatest amount of cedar, followed by cross timbers and tallgrass prairie (Table 1).

Detrended correspondence analysis revealed similarity in species composition among cells occurring in the tallgrass prairie and cedar old-field site compared with the cross timbers (Fig. 2). The first two axes of the DCA ordination accounted for 33.3% of the variance associated with species data. The small-mammal communities were separated along DCA axes 1 and 2 (Fig. 2). Axis 1 separated the community in the cross timbers (e.g., woodland vole, eastern woodrat, white-footed mouse) from communities in the other 2 habitats. That separation was associated with a vegetational gradient from grasses and forbs to greater amounts of woody understory, cedar, litter, and overstory cover (Table 2, Fig. 2). Communities in the cedar old-field and tallgrass prairie were partially separated on axis 2, which was associated with a vegetational gradient from forb and woody understory cover to increasing cedar cover and bareground (Table 2). The prairie site and open areas of the cedar old-field site were dominated by cotton rats, fulvous harvest mice, plains harvest mice, and prairie voles. Cedar-invaded areas of the old-field site were characterized by white-footed mice and deer mice.

Rank-abundance analysis showed that species richness and evenness differed between the cross timbers plot and the other 2 habitats (Fig. 3). The slope of the linear regression equation in the rank-abundance curves was an index of species diversity, or rather equitability (Southwood 1966). Comparison of the slopes in the rank-abundance curves indicated that small-mammal communities inhabiting the cross timbers had a less even distribution of species than those from the cedar old-field ($P = 0.005$) and the tallgrass prairie ($P = 0.023$). There was no difference between the tallgrass prairie plot and the cedar old-field plot ($P = 0.075$). Species richness and evenness generally were higher in the cedar old-field and tallgrass prairie than in the cross timbers forest.

Species-specific Relationships to Habitat and Vegetational Variables

Percent cover of eastern redcedar consistently affected the probability of capture of small mammals across all species-habitat models (Tables 3–5). Results of the Hosmer-Lemeshow goodness-of-fit test indicated that all logistic models presented adequately fit the data. Although many other variables had effects, there was considerable variation among species and habitat types (Tables 3–5).

For example, in the tallgrass prairie site, all 4 rodent species were associated with eastern redcedar cover. All 3 prairie species were negatively correlated with cover of cedar, whereas the one woodland species (white-footed mouse) was positively correlated with cedar. Three of the 4 rodent species were associated with percent woody understory cover. Prairie voles were negatively correlated with woody cover, whereas white-footed mice and cotton rats were positively correlated with it. Only 2 rodent species, white-footed mice and cotton rats, were positively associated with litter. All other vegetational variables were associated with ≤ 1 rodent species in the tallgrass prairie site (Table 3).

In the cedar old-field site, 3 of the 4 species were associated with eastern redcedar. Plains harvest mice and cotton rats, considered prairie species, were negatively correlated with cedar, and white-footed mice were positively associated with cedar. Percent herbaceous cover was positively correlated with white-footed mice, whereas deer mice were negatively correlated. All other vegetation variables were associated with ≤ 1 rodent species in the cedar old-field site (Table 4).

In the cross timbers site, eastern woodrats and white-footed mice were positively associated with woody understory cover. Percent cover of cedar was positively correlated with white-footed mice and woodland voles. Woodland voles also were positively correlated with forb cover, whereas eastern woodrats were negatively correlated. All other vegetational variables were associated with ≤ 1 rodent species in the cross timbers site (Table 5).

Logistic regression models conducted with cedar as the sole vegetational variable provided a more detailed illustration of the affect that cedar had on the probability of capture of small mammals. White-footed mice were positively correlated with cedar in all 3 habitat types (Table 6). The estimated probability of capture for white-footed mice was more sensitive to increases in cedar cover in the cedar old-field and tallgrass prairie habitats, doubling with an increase in cedar cover from 0 to 20%, than in the cross timbers (Figure 4). Plains harvest mice in the cedar old-field, and cotton rats and fulvous harvest mice in the tallgrass prairie were negatively correlated with eastern redcedar (Table 6). The estimated probability of capture decreased by 50% for plains harvest mice as cedar cover increased from 0 to 20% in the cedar old-field and decreased by 50% for cotton rats and fulvous harvest mice as cedar cover increased from 0 to 35% in the tallgrass prairie (Figure 4).

Individual species of small mammals responded to eastern redcedar at different scales in different habitat types. In the tallgrass prairie site, fulvous harvest mice were negatively associated with cedar at only the smallest scale (12 x 12 m ; coefficient = -0.026, $P = 0.0288$), and prairie voles were negatively associated with cedar at only the largest scale (60 x 60 m ; coefficient = -0.194, $P = 0.0572$). Cotton rats were negatively correlated with cedar at all 3 scales: small (coefficient = -0.039, $P = 0.0003$), medium (36 x 36 m ; coefficient = -0.061, $P < 0.0001$), and large (coefficient = -0.071, $P = 0.0002$), whereas white-footed mice were positively correlated with cedar at all 3 scales: small (coefficient = 0.037, $P < 0.0001$), medium (coefficient = 0.106, $P < 0.0001$), and large (coefficient = 0.144, $P < 0.0001$).

In the cedar old-field, plains harvest mice were negatively correlated with cedar at the smallest scale (coefficient = -0.046, $P < 0.0001$) and the medium scale (coefficient = -0.043, $P = 0.0004$). Deer mice were not affected by cedar at any of the scales, whereas white-footed mice were positively correlated with cedar at all 3 scales: small (coefficient = 0.034, $P < 0.0001$), medium (coefficient = 0.05, $P < 0.0001$), and large (coefficient = 0.053, $P < 0.0001$).

In the cross timbers, white-footed mice were positively associated with cedar at only the smallest scale (coefficient = 0.012, $P = 0.0434$). Woodland voles were positively correlated with cedar at the medium scale (coefficient = 0.124, $P = 0.0003$), but not the small or large scale. Eastern woodrats were not affected by cedar at any scale.

DISCUSSION

Small-mammal Communities by Habitat

The results provided mixed support relative to my *a priori* predictions. First, these data did not support my hypothesis that small-mammal diversity would be lower in the cedar-old field plot. Species richness and evenness were higher in the tallgrass prairie and cedar old-field than the cross timbers, indicating that diversity would be higher in these 2 plots. Sullivan et al. (1999) similarly found that species diversity and richness were higher in 8–10-year-old clearcuts than in forest areas in west-central British Columbia. In our study, the tallgrass prairie and cedar old-field site contained both open and woody areas, whereas the cross timbers consisted mostly of overstory cover and little herbaceous understory. Johnson et al. (1979) reported that species richness of small mammals was highest in edge habitat, where all or most of the forest species plus some open-habitat specialists could be found. My results were similar with prairie and woodland species found in the tallgrass prairie and the cedar old-field habitats but only woodland species in the cross timbers.

Previous studies at CTER found that white-footed mice, cotton rats, and eastern woodrats responded to successional changes in habitat (McMurry et al. 1993, 1994, 1996). White-footed mice and eastern woodrats were captured most frequently in late-successional areas with high amounts of woody dicots, whereas cotton rats had the highest numbers in early-successional habitats with greater amounts of grasses. Densities of all rodents were higher in early and late succession and lowest on forest habitats with little herbaceous cover (McMurry et al. 1993, 1994, 1996). These results support my findings that diversity and abundance was lowest in the cross timbers. However, although cedar old-field and tallgrass prairie had a similar diversity of small mammals, the tallgrass prairie site had an overall greater abundance of small mammals. The majority of species in the cedar old-field plot also occurred in open, non-invaded areas (Figure 5).

Composition of small mammals communities also varied among habitats (Figure 3). Composition in tallgrass prairie was similar to that in cedar old-field plots, but highly dissimilar to the cross timbers forest. Other studies also reported that the change in species communities was greatest between grassland and woodland communities than among other habitat types (Hanchey and Wilkins 1998, Kaufman et al. 2000). In my study, grassland and generalist species were mostly associated with the tallgrass prairie and cedar old-field sites, whereas woodland species were mostly associated with the cross timbers. Swihart and Slade (1990) also found that species composition changed with an increase in wooded habitats. Increased woody vegetation led to a decrease in harvest mice and deer mice and an increase in white-footed mice.

The most salient finding of the study was that small-mammal community structure shifted along gradients of increasing eastern redcedar. Overall, eastern redcedar was the most important vegetation factor in modeling probability of capture of most species in cedar old-field and tallgrass prairie habitats. In these sites, prairie species generally decreased and a single woodland species (i.e., white-footed mice) increased with increasing redcedar (Figure 6). Eastern redcedar, however, did not appear to have as much of an effect on species composition in the cross timbers. My results were similar to Chapman (2000) who showed a decline in grassland birds and a concurrent increase of shrub- and woodland-associated birds with increasing cedar. Coppedge et al. (2001) also found that open-habitat generalist and woodland bird species in western Oklahoma generally increased with increasing woody plant cover, whereas many grassland species decreased.

Species-specific Relationships to Habitat and Vegetational Variables

It is worth noting that population growth rates (λ) of most species of small mammals in all 3 sites exceeded 1.0 during the study period (Appendix B). These trends were likely due to population recovery following a major regional ice storm that occurred in December 2000–January 2001 just before my study (Clark et al. in press). Winter storms can cause catastrophic declines in small-mammal populations, followed by an increase in population following the event (Mihok et al 1985). Therefore, my results may be relevant to expanding populations of small mammals but not necessarily more stable communities of small mammals.

The probability of occurrence of the white-footed mouse was positively correlated with cedar in all 3 habitats and with woody cover in 2 habitats, which supported my predictions. Schweiger et al. (2000) similarly reported that captures of white-footed mice were positively associated with a dense woody canopy. White-footed mice also were positively associated with cedar at all 3 scales in the tallgrass prairie and cedar old-field site, but at only the smallest scale in the cross timbers site. Cedar cover appeared to facilitate the occurrence of white-footed mice in areas they might not normally be found. Similarly, in Kansas, the species was captured more frequently closer to patch edges and within large wooded patches close to contiguous forest (Schweiger et al. 2000). The white-footed mouse occurs in deciduous forests, riparian woodlands, and shrub-dominated sites, and rarely uses areas without woody structure (Kaufman et al. 1983). In the cross timbers forest, however, there is already sufficient canopy cover. Because white-footed mice were selecting cedar at the small scale, it appears that they are selecting small stands of cedar within woodland habitat.

Cotton rats in Oklahoma are limited to habitats with dense grass, forbs, or low-growing woody vegetation (Caire et al. 1989). The results of my study were consistent with these observations and supported my predictions. I found that the probability of occurrence of cotton rats was negatively correlated with cedar and litter and positively correlated with woody vegetation < 1m in height. Geortz (1964) also found that cotton rats usually avoided areas where tree canopy shaded ground cover. At CTER, relative densities of cotton rats increased in response to increased production of monocots (McMurry et al. 1994). When cedar moves into an area, it reduces the herbaceous ground cover under the canopy zone (Engel et al. 1987, Smith and Stubbendieck 1990). In fact, cotton rats were negatively associated with cedar at all 3 scales, indicating that cotton rat populations would decrease with not only a large-scale invasion of cedar, but also the appearance of a few scattered trees.

Prairie voles were negatively correlated with cedar and woody, as expected. The prairie vole is commonly found in grassy areas with legumes (Marquis and Batzli 1989). Prairie voles were influenced more by cedar at the largest scale, suggesting that prairie voles avoided landscapes where eastern redcedar was prominent.

Occurrence of woodland voles, in contrast, was positively correlated with forb and cedar cover. Woodland voles occur in woodland habitats, such as savannah edge, upland and bottomland woods (Caire et al. 1989). Woodland voles were probably positively correlated with forbs, because forbs and grasses are a main part of their diet (Cengel et al. 1978). Voles also could be attracted to cedar because their seedlings would be a source of food. Meadow voles (*Microtus pennsylvanicus*) are known to gnaw tree seedlings and can be an important agent of tree mortality (Ostfeld and Canham 1993).

Occurrence of the eastern woodrat was positively correlated with woody cover and negatively correlated with forbs. My results were similar to McMurry et al. (1993), who found that woodrats selected areas with increased woody vegetation for their greater structural complexity. Woodrats were not affected by cedar at any scale, indicating that an increase or decrease in cedar may not influence the population. Eastern woodrats, however, were not captured in the cedar old-field plot where there was a high density of cedar. Therefore, although woodrats were not affected by cedar patches throughout the cross timbers, they may decrease in numbers in areas where eastern redcedar has invaded prominently.

Deer mice were negatively correlated with grass and positively correlated with legumes. Other studies reported that deer mice prefer open habitats, are associated negatively with woody canopies (Schweiger et al. 2000), and avoid lowland prairie with forbs and shrubs (Clark et al. 1998). Deer mice were not affected by cedar at any scale, indicating that an increase or decrease in cedar would not affect the population. Deer mice probably avoided thick grassy vegetation and were not affected by cedar because they prefer habitats with exposed soil and limited vertical structure (Clark et al. 1998).

Occurrence of plains and fulvous harvest mice was negatively correlated with cedar. Hanchey and Wilkins (1998) also found that abundance of fulvous harvest mice was positively correlated with grasses and negatively associated with woody material. Both species prefer more grassy habitats, with fulvous harvest mice occurring more in areas with heavy grass cover and plains harvest mice using areas of more sparse cover (Spencer and Cameron 1982). Both species were negatively associated with cedar at only the smallest scale. This result suggests that these species would avoid areas immediately surrounding eastern redcedar trees but still occur in landscapes with limited cedar invasion to their small home-range size. Geortz (1963) reported a mean home range of 0.17 ha for male and 0.21 ha for female plains harvest mice in Payne Co., Oklahoma.

Eastern redcedar has become invasive in Oklahoma and other Great Plains rangelands due to the suppression of wildfire and other factors (Norris et al. 2001, Briggs et al. 2002). My data suggest that invasion of redcedar is a serious concern to the diversity and abundance of small mammals associated with prairie habitat. The majority of prairie species were negatively correlated with cedar. Small-mammal species composition can change with an increase in eastern redcedar cover. In fact, an increase in overstory cover from 0 to 30% cedar would change a species-rich prairie community to a depauperate community dominated by 1 species, the white-footed mouse (Figures 5, 6). Therefore, although the habitat is changing from prairie to woodland, the small mammal community is not. Swihart and Slade (1990) found similar results when they assessed small-mammal community structure at different successional stages of habitat in northeastern Kansas. Early in the study, they found that forbs dominated the habitat and this led to an irruption of harvest mice and deer mice, but low numbers of white-footed mice. During the middle of their study, the area shifted to grass and wooded habitats, where there was a reduction in the number of harvest mice and deer mice and an increase in white-footed mice. Increased availability of wooded habitat enabled increased numbers of white-footed mice to occupy the area. At the end of their study, they used brush removal, mowing and plowing to remove the woody vegetation. These management activities resulted in increased levels of grass and forb habitat, and subsequent increase in deer mice and decrease in white-footed mice. Overall, Swihart and Slade (1990) also found a decrease in prairie species and an increase in white-footed mice with an increase in wooded habitats

It is necessary to remove eastern redcedar to manage for prairie species of small mammals in native grassland areas. Encroachment of eastern redcedar can be controlled with proper grazing management and carefully planned prescribed burning. Eastern redcedar is especially sensitive to fire because of its thin bark. Therefore, implementing a 3–5 year rotation of prescribed fire is the easiest and most cost-effective control method (Engle and Kulbeth 1992). Small trees (< 2 m) are killed by fire if surrounded by enough fuel; however, in areas with larger trees (> 2 m), prescribed fires do not provide for 100% kill (Engle and Kulbeth 1992). Larger trees must be mechanically removed and then burned or these trees will persist for decades.

Although eastern redcedar management is relatively simple, recognizing the problem, understanding the consequences to native biodiversity, and preventing its encroachment are difficult challenges. Implementing proper educational programs for wildlife managers and landowners and monitoring redcedar establishment may prevent the loss of native biodiversity in vulnerable grassland systems.

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Table 1. Percent cover by category in each of the 3 habitat types (COF = cedar old-field, CTF = cross timbers forest, TGP = tallgrass prairie) at Oklahoma State University Research Range, Stillwater, Oklahoma, May 2001 – August 2002. Percent grass, forb, woody vegetation, legume, bareground, litter, dead standing material, and rock were all measured at < 1-m in height.

Habitat	Cedar	Grass	Forb	Woody	Legume	Bareground	Litter	Dead	Rock	Overstory
COF	19.3	31.0	13.1	0.3	2.3	8.3	50.3	0.9	0.0	15.2
CTF	11.9	5.6	1.1	14.0	0.1	6.5	86.6	2.4	0.0	81.5
TGP	3.5	39.9	21.0	7.1	2.1	0.4	66.1	1.1	0.5	6.2

Table 2. Results of detrended correspondence analysis for small mammal composition data from tallgrass prairie, cedar old-field, and cross timbers habitats on the Oklahoma State University Research Range from May 2001 to August 2002. Only correlations with P < 0.05 are reported.

	Detrended correspondence analysis	
	Axis 1	Axis 2
Eigenvalue	0.81	0.57
% Variance of all axes	19.5	33.3
Length of gradient	5.35	3.86
Correlations		
overstory cover	0.687	0.196
cedar	0.464	0.431
grass	-0.497	-0.197
forb	-0.584	-0.207
woody	0.329	-0.222
bareground	0.165	0.229
litter	0.491	——
legume	-0.158	——

Table 3. Logistic regression relating probability of occurrence of small mammal species in tallgrass prairie to vegetation cover, Payne County, Oklahoma, 2001-2002; b = regression slope; P = p-value; p(GOF) = Hosmer and Lemeshow goodness-of-fit test.

		Vegetation cover (%)					
Species	Statistic	Cedar	Forb	Rock	Litter	Woody	P(GOF)
Prairie vole	b	-0.238	-0.042			-0.071	0.607
	P	0.117	0.055			0.032	
White-footed mouse	b	0.043		0.309	0.054	0.046	0.833
	P	0.036		0.039	0.016	0.019	
Fulvous harvest mouse	b	-0.019					0.414
	P	0.159					
Cotton rat	b	-0.034			-0.045	0.044	0.199
	P	0.039			0.017	0.028	

Table 4. Logistic regression relating probability of occurrence of small mammal species in cedar old-field to vegetation cover, Payne County, Oklahoma, 2001-2002; b = regression slope; P = p-value; p(GOF) = Hosmer and Lemeshow goodness-of-fit test.

		Vegetation cover (%)				
Species	Statistic	Cedar	Grass	Legume	Bareground	p(GOF)
White-footed mouse	b	0.062	0.030			0.269
	P	<.0001	0.068			
Deer mouse	b		-0.047	0.232		0.817
	P		0.009	0.002		
Plains harvest mouse	b	-0.047				0.151
	P	0.001				
Cotton rat	b	-0.202			-0.097	0.266
	P	0.008			0.029	

Table 5. Logistic regression relating probability of occurrence of small mammal species in cross timbers forest to vegetation cover, Payne County, Oklahoma, 2001-2002; b = regression slope; P = p-value; p(GOF) = Hosmer and Lemeshow goodness-of-fit test.

		Vegetation cover (%)				
Species	Statistic	Cedar	Forb	Woody	Bareground	p(GOF)
Woodland vole	b	0.026	0.465			0.572
	P	0.143	<.0001			
Eastern woodrat	b		-0.683	0.049		0.738
	P		0.059	0.013		
White-footed mouse	b	0.028		0.035	-0.038	0.814
	P	0.009		0.022	0.071	

Table 6. Logistic regression results modeling the probability of capture of each species in 3 habitat types with percent of cedar cover as the independent variable.

Habitat	Species	n	Coefficient	S.E.	P	p(GOF)[a]
Cedar-old field	White-footed mouse	62	0.0590	0.00903	<.0001	0.0076
Cedar-old field	Deer mouse	31	0.0140	0.00818	0.0877	0.1203
Cedar-old field	Plains harvest mouse	36	-0.0468	0.0142	0.0010	0.1506
Tall-grass prairie	White-footed mouse	61	0.0569	0.0176	0.0012	0.0056
Tall-grass prairie	Cotton rat	135	-0.0397	0.0161	0.0138	0.5943
Tall-grass prairie	Fulvous harvest mouse	105	-0.0194	0.0137	0.1588	0.4139
Tall-grass prairie	Prairie vole	33	-0.2187	0.1524	0.1512	0.4557
Cross timbers	White-footed mouse	81	0.0226	0.0101	0.0255	0.1868
Cross timbers	Eastern woodrat	29	-0.00459	0.0150	0.7599	0.8848
Cross timbers	Woodland vole	17	0.0161	0.0161	0.3173	0.6749

[a] Hosmer and Lemeshow test was used to test goodness of fit of the model.

Figure 1. Grid layout and design to investigate small mammal community structure in 3 habitat types: tallgrass prairie, cedar old-field and cross timbers forest. Sherman traps were equally distributed throughout the grid at Oklahoma State University Research Range, Payne County, Oklahoma, May 2001 to August 2002.

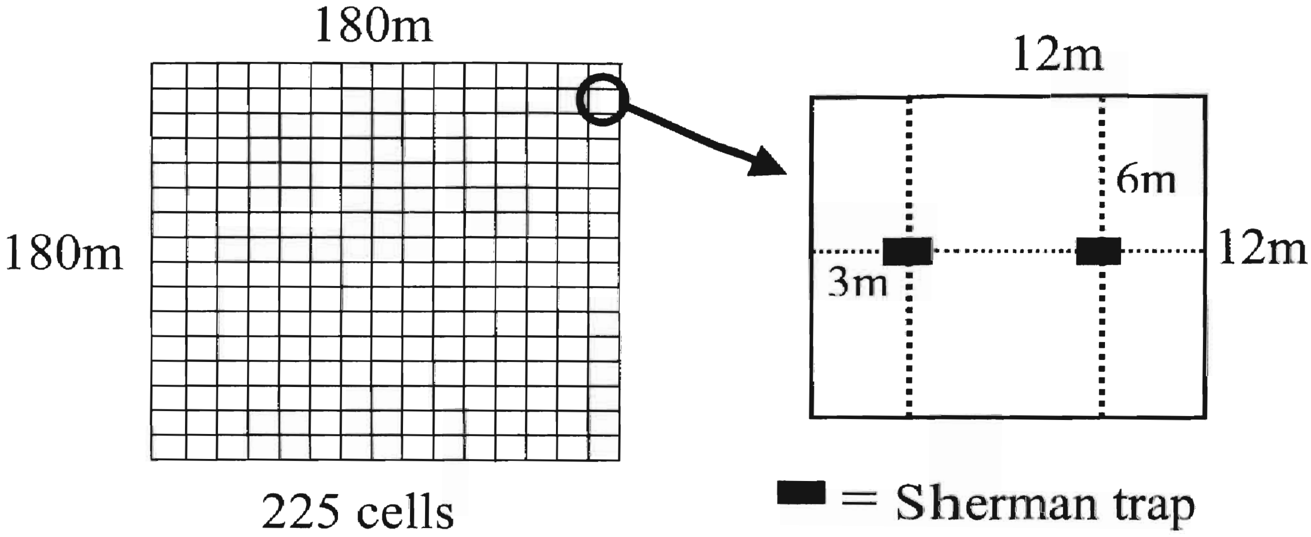

180m
180m
225 cells
12m
12m
6m
3m
■ = Sherman trap

Figure 2. Detrended Correspondence Analysis (DCA) ordination bi-plot depicting species scores (solid symbols) for small mammals in 3 habitat types: tallgrass prairie (TGP), cedar-invaded old-field (COF), and cross timbers forest (CTF). Each open symbol represents one cell in a habitat type. Envelopes with —— represent cells in the cedar old-field, envelopes with ---- represent cells in the cross timbers forest, and envelopes with ..... represent cells in the tallgrass prairie. Axis 1 depicts a gradient of increasing woody cover and Axis 2 depicts a gradient from forb and woody understory cover to cedar and bareground cover. Species abbreviations: Moch = Microtus ochrogaster, prairie vole; Mpin = Microtus pinetorum, woodland vole; Nflo = Neotoma floridana, eastern woodrat; Pleu = Peromyscus leucopus, white-footed mouse; Pman = Peromyscus maniculatus, deer mouse, Rful = Reithrodontomys fulvescens, fulvous harvest mouse, Rmon = Reithrodontomys montanus, plains harvest mouse, and Shis = Sigmodon hispidus, cotton rat.

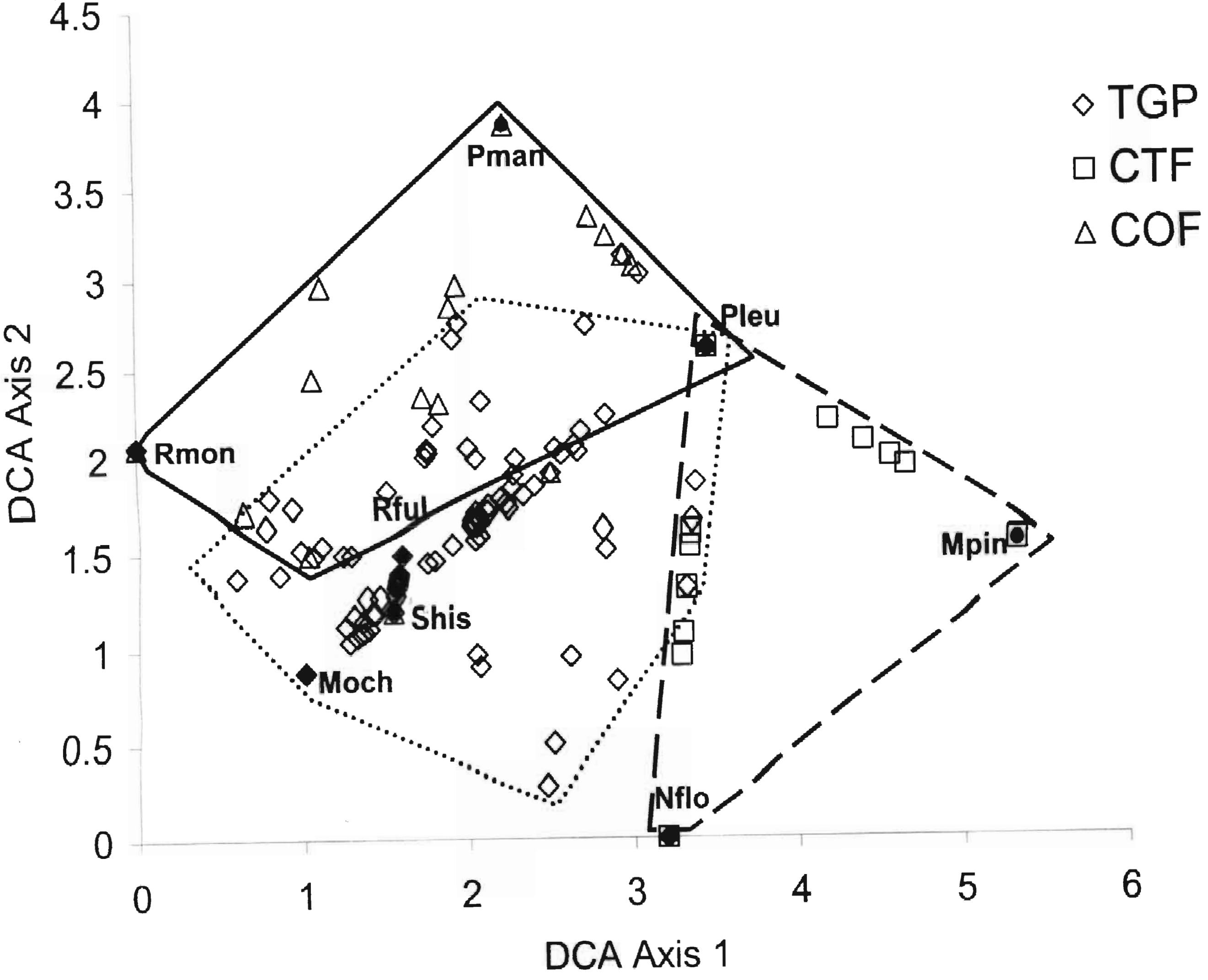

4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
DCA Axis 2
0
1
2
3
4
5
6
DCA Axis 1
◇ TGP
□ CTF
△ COF
Pman
Pleu
Rmon
Rful
Shis
Moch
Nflo
Mpin

Figure 3. Rank abundance patterns of rodent communities inhabiting 3 sites: tallgrass prairie (TGP), cedar old-field (COF), and cross timbers forest (CTF) at Oklahoma State University Research Range, Payne County, Oklahoma, May 2001- August 2002. The log number of individuals of each species is ranked from most abundant (1) to least abundant (5-7).

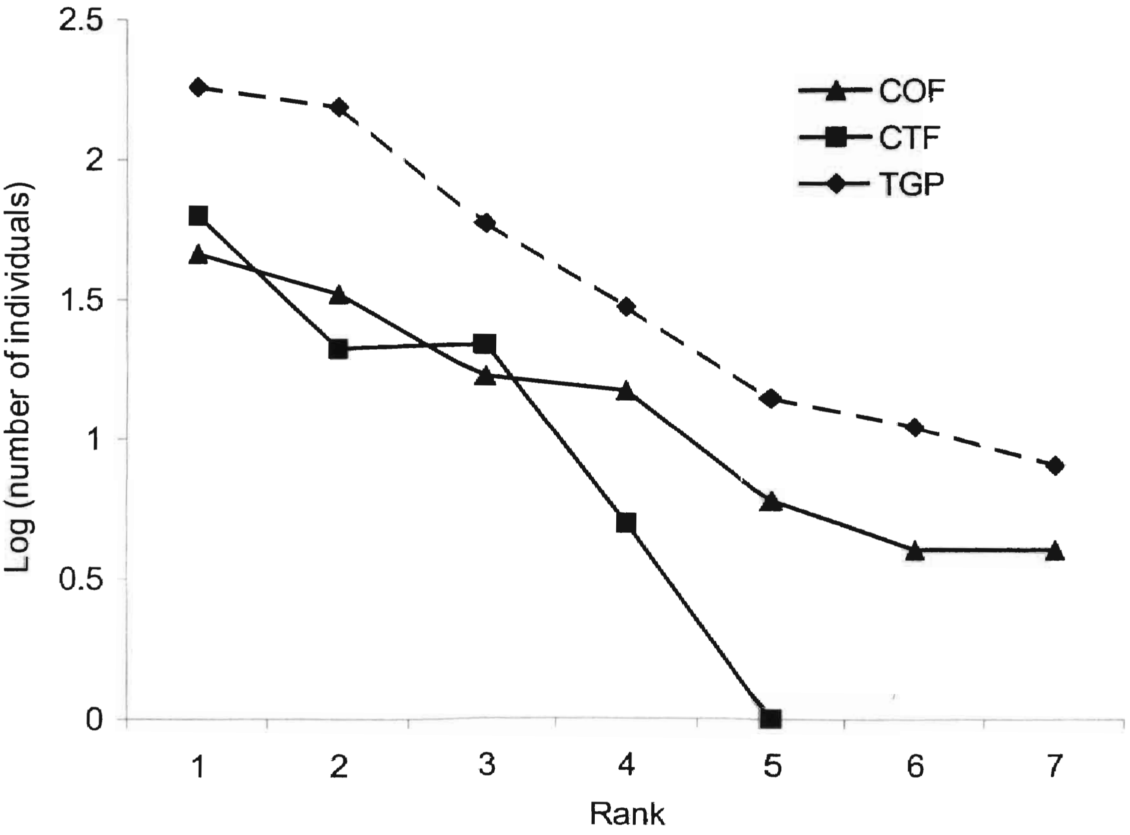

2.5
2
1.5
1
0.5
0
Log (number of individuals)
1
2
3
4
5
6
7
Rank
COF
CTF
TGP

Figure 4. Estimated probability of capture of 4 species of rodents in different habitat types: white-footed mouse in tallgrass prairie (A), cedar old-field (B), and cross timbers forest (C), cotton rat in tallgrass prairie (D), fulvous harvest mouse in tallgrass prairie (E), and plains harvest mouse in cedar old-field (F). Observed proportions of captures are the plotting points. Predictions are based on logistic regression models using percent of eastern redcedar in a 12- x 12-m cell as the independent variable.

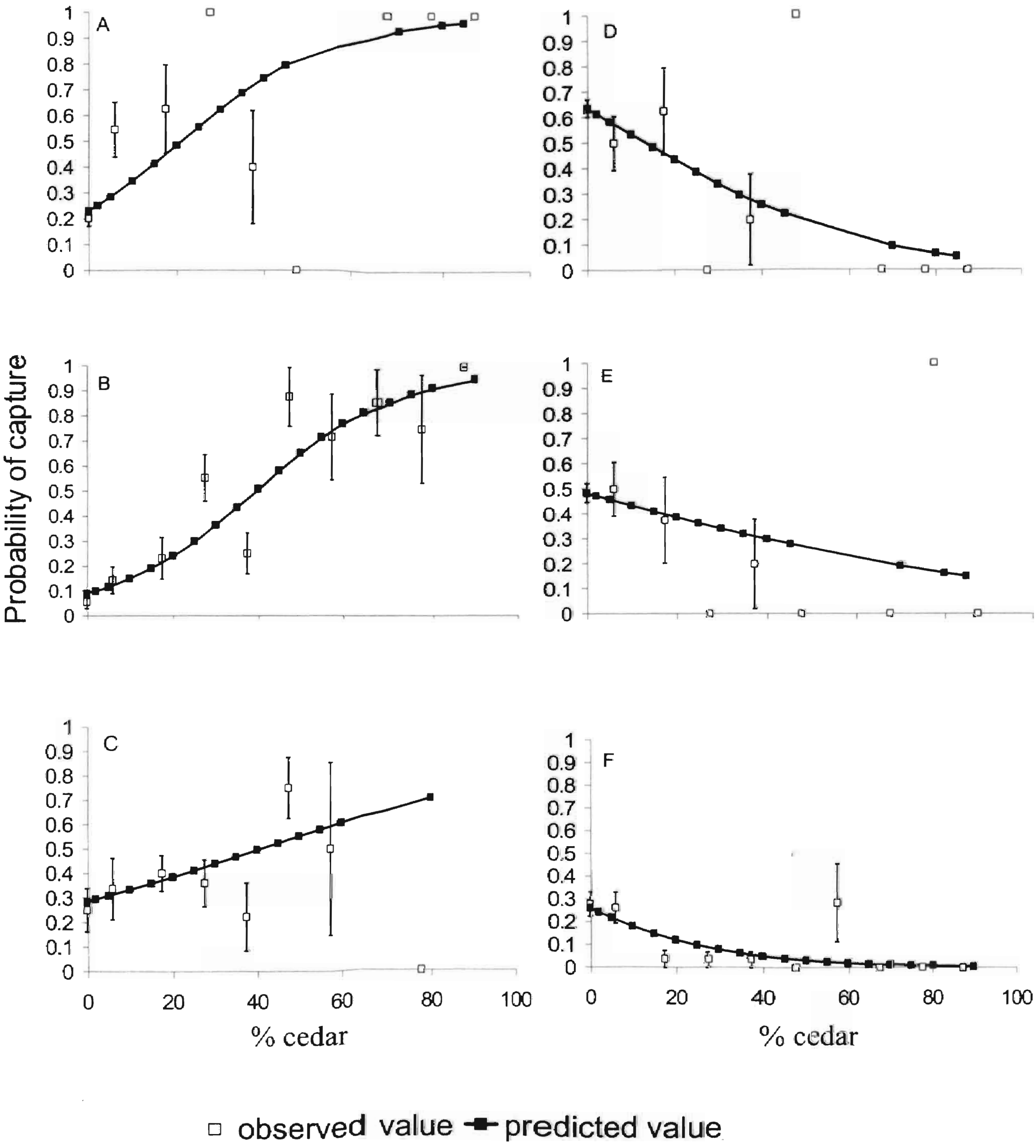

A
B
C
D
E
F
Probability of capture
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
20
40
60
80
100
% cedar
% cedar
□ observed value
■ predicted value

Figure 5. Number of captures of 4 small-mammal species (deer mouse, cotton rat, white-footed mouse, and plains harvest mouse) in each cell in the cedar old-field site in relation to percent cedar, Oklahoma State University Research Range, Payne County, Oklahoma, May 2001-August 2002.

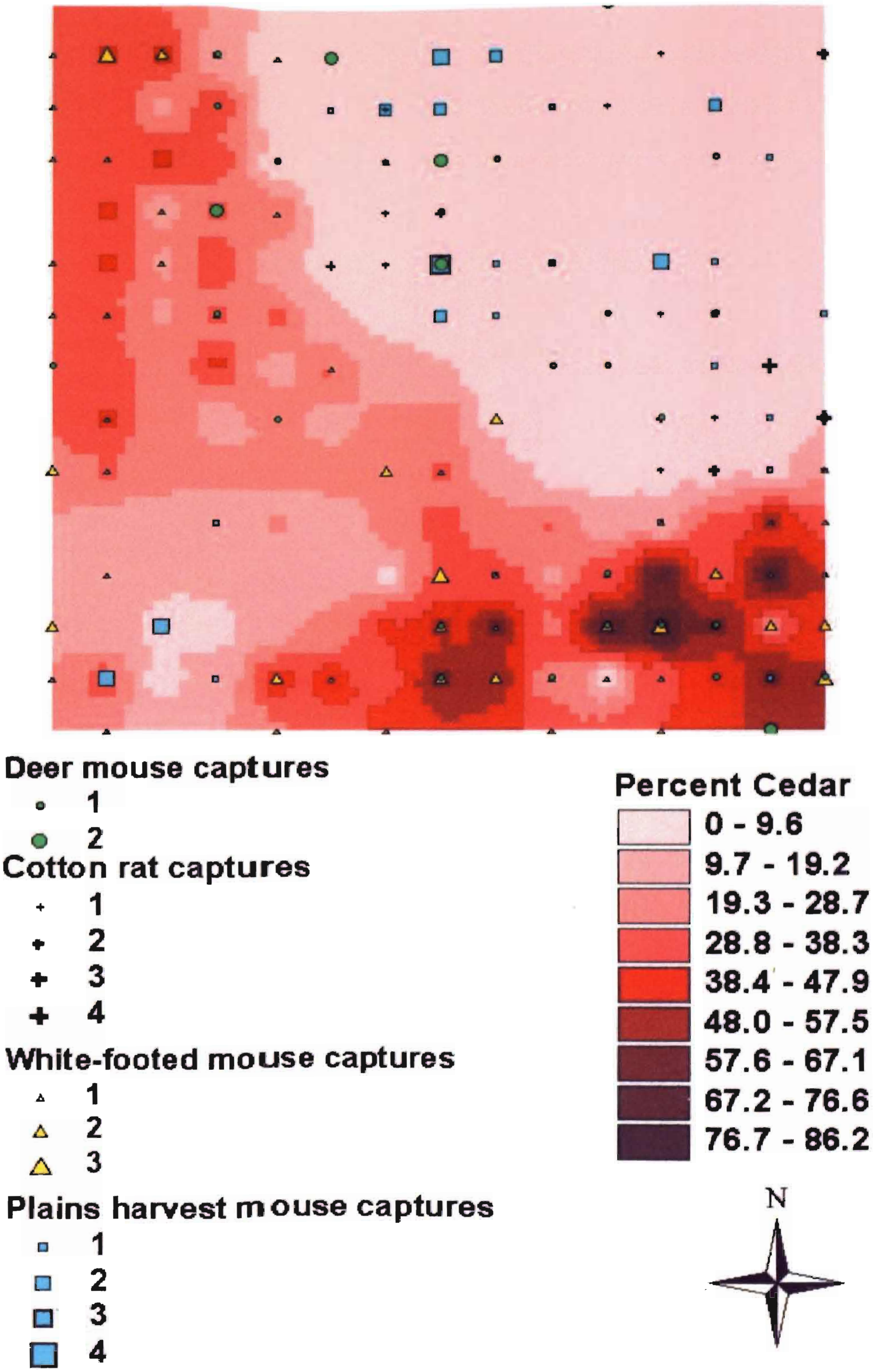
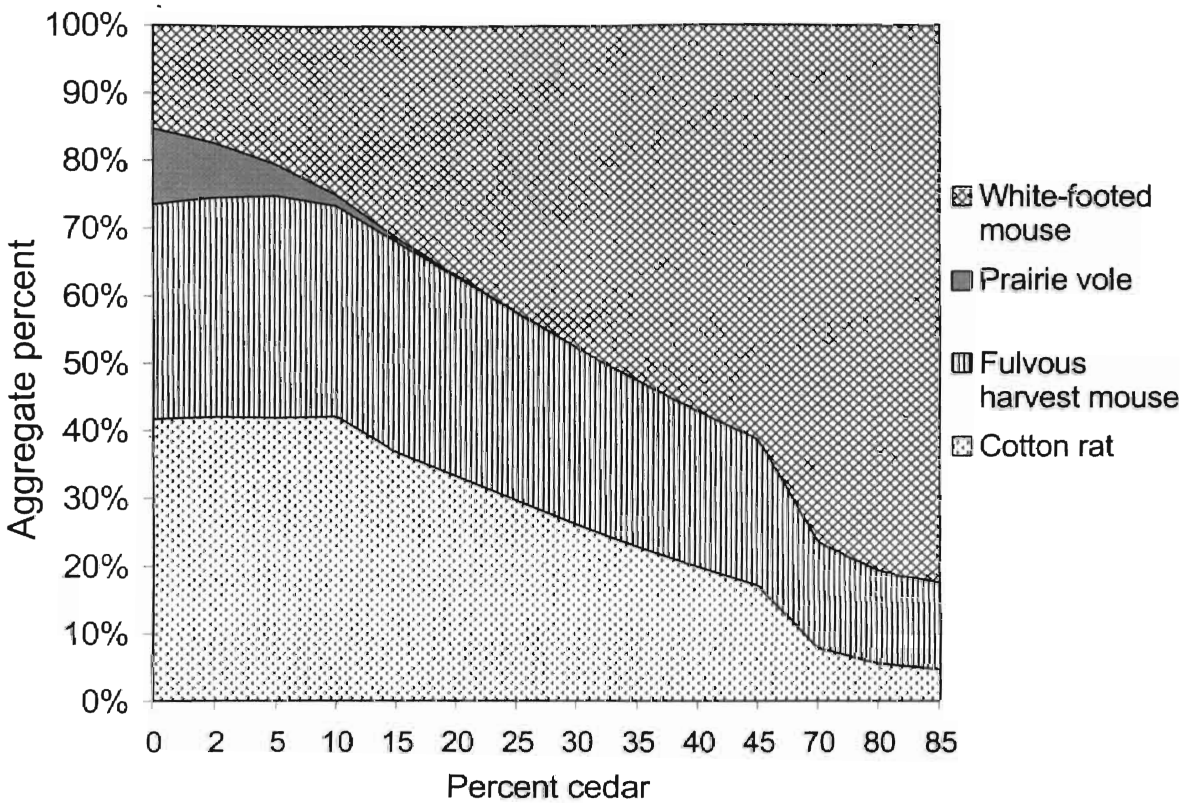

Deer mouse captures
1
2
Cotton rat captures
1
2
3
4
White-footed mouse captures
1
2
3
Plains harvest mouse captures
1
2
3
4
Percent Cedar
0 - 9.6
9.7 - 19.2
19.3 - 28.7
28.8 - 38.3
38.4 - 47.9
48.0 - 57.5
57.6 - 67.1
67.2 - 76.6
76.7 - 86.2
N

Figure 6. Predicted changes in relative composition of the small mammal assemblage in the tallgrass prairie with changes in % cover of eastern redcedar at Oklahoma State University Research Range, Payne County, Oklahoma, May 2001 to August 2002. Relative proportion calculated from changes in estimated probability of capture for each species modeled as a function of eastern redcedar cover in a 12- x 12-m cell.


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Aggregate percent
0
2
5
10
15
20
25
30
35
40
45
70
80
85
Percent cedar
White-footed mouse
Prairie vole
Fulvous harvest mouse
Cotton rat

APPENDIX A

Species capture data for the 3 habitats from May 2001 to August 2002 at Oklahoma State University Research Range, Payne County, Oklahoma.

Species	Habitat	# individuals	Total Captures
Cotton rat	Cedar old-field	13	31
	Cross timbers	1	3
	Tallgrass prairie	127	346
Deer mouse	Cedar old-field	17	39
	Tallgrass prairie	10	24
Eastern woodrat	Cross timbers	12	48
	Tallgrass prairie	14	28
Elliot's short tailed shrew	Cross timbers	4	4
Fulvous harvest mouse	Cedar old-field	4	4
	Tallgrass prairie	104	183
Hispid pocket mouse	Cedar old-field	5	7
Plains harvest mouse	Cedar old-field	30	52
	Tallgrass prairie	6	15
Prairie vole	Cedar old-field	3	6
	Tallgrass prairie	29	42
White-footed mouse	Cedar old-field	38	79
	Cross timbers	47	116
	Tallgrass prairie	42	128
Woodland vole	Cross timbers	17	29

APPENDIX B

Minimum number known alive (MNKA) and population growth rates (λ) for rodent species in different habitats at Oklahoma State University Research Range, Payne County, Oklahoma.

We used the minimum number known alive (MNKA) as an index to abundance for each species in each plot. MNKA was used because several species had low capture rates (Krebs 1966). For individual species, population growth rates (λ) were estimated using minimum number known alive (MNKA) using the following equation:

$$\lambda = N_{t+1} / N_t$$

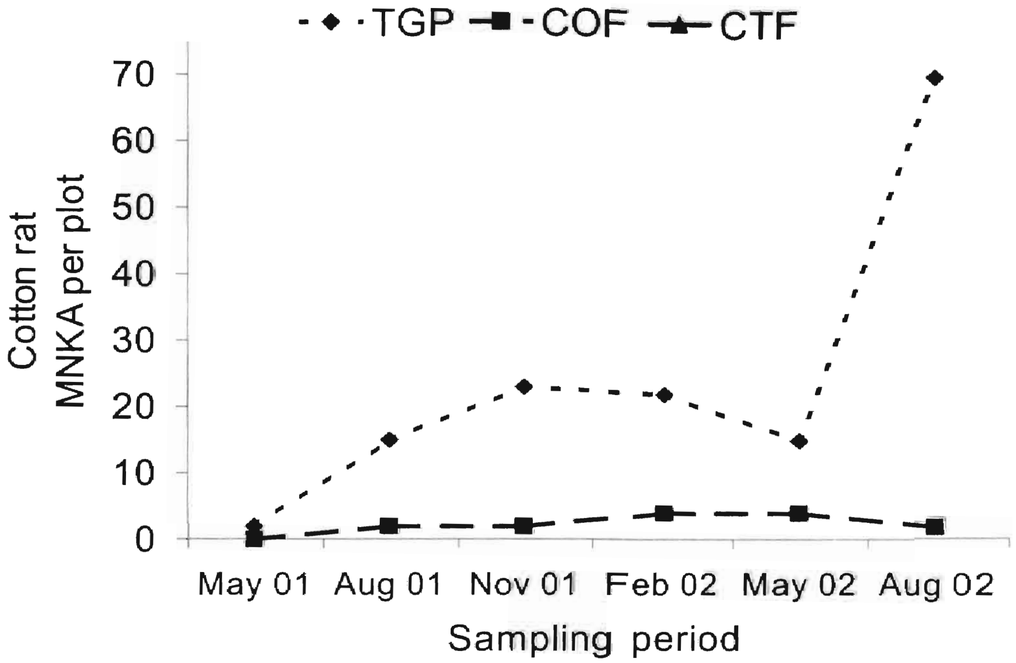
where N_t = MNKA at time t, and N_{t+1} = MNKA at time t + 1. Population growth rates were calculated for each species in each habitat type, resulting in 5 λ values for each species over 6 sampling periods. Data are reported as average values of λ for each species in each habitat type.

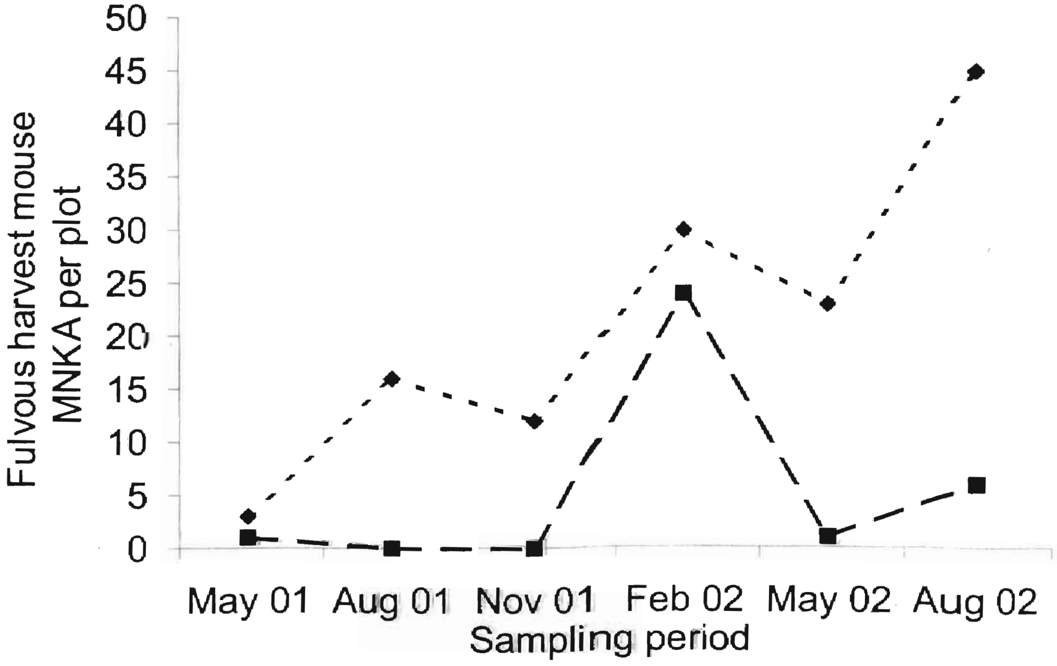
Table B1. Average values for λ for the 7 most abundant small-mammal species in the three habitat types (SE = standard error, LCL = lower 95% confidence limit, UCL = upper 95% confidence limit,) from May 2001 to August 2002 at the Oklahoma State University Research Range, Stillwater, Oklahoma.

Species	Habitat	λ	SE	LCL	UCL
White-footed mouse	Tallgrass prairie	0.97	0.34	0.03	1.92
White-footed mouse	Cedar-old field	0.89	0.21	0.32	1.47
White-footed mouse	Cross timbers	1.70	1.00	-1.08	4.48
Cotton rat	Tallgrass prairie	3.07	1.32	-0.59	6.73
Cotton rat	Cedar-old field	1.13	0.31	0.12	2.13
Fulvous harvest mouse	Tallgrass prairie	2.26	0.84	-0.07	4.59
Prairie vole	Tallgrass prairie	1.53	0.60	-0.15	3.21
Eastern woodrat	Cross timbers	1.17	0.29	0.35	1.98
Woodland vole	Cross timbers	2.31	0.83	-0.01	4.62
Deer mouse	Cedar-old field	1.47	0.83	-0.83	3.78

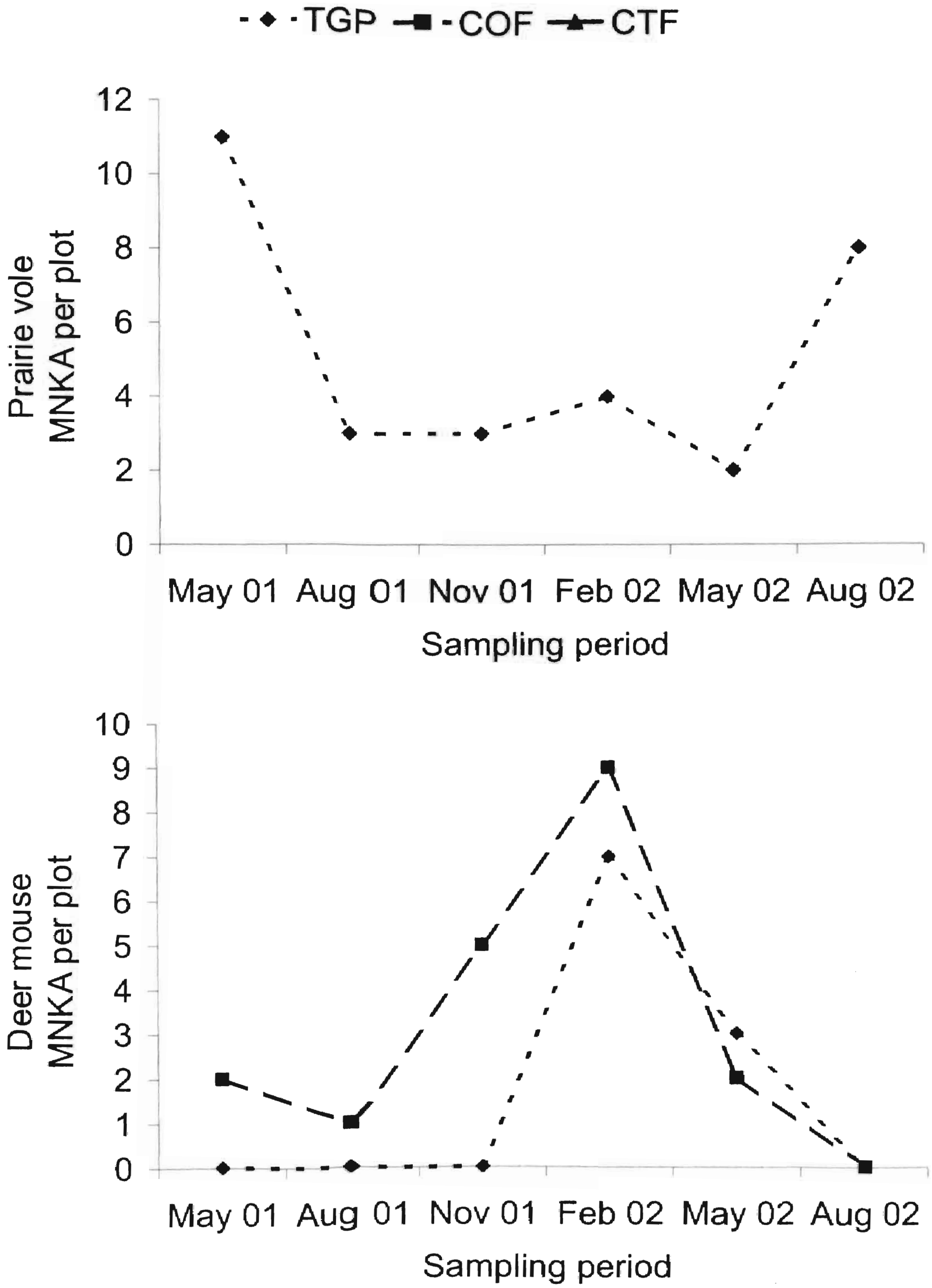
APPENDIX B

Minimum number known alive (MNKA) for 8 rodent species: cotton rat, fulvous harvest mouse, prairie vole, deer mouse, plains harvest mouse, white-footed mouse, eastern woodrat, and woodland vole. For each rodent, MNKA was calculated for each sampling period and any habitat types where the rodent was captured from May 2001 to August 2002.

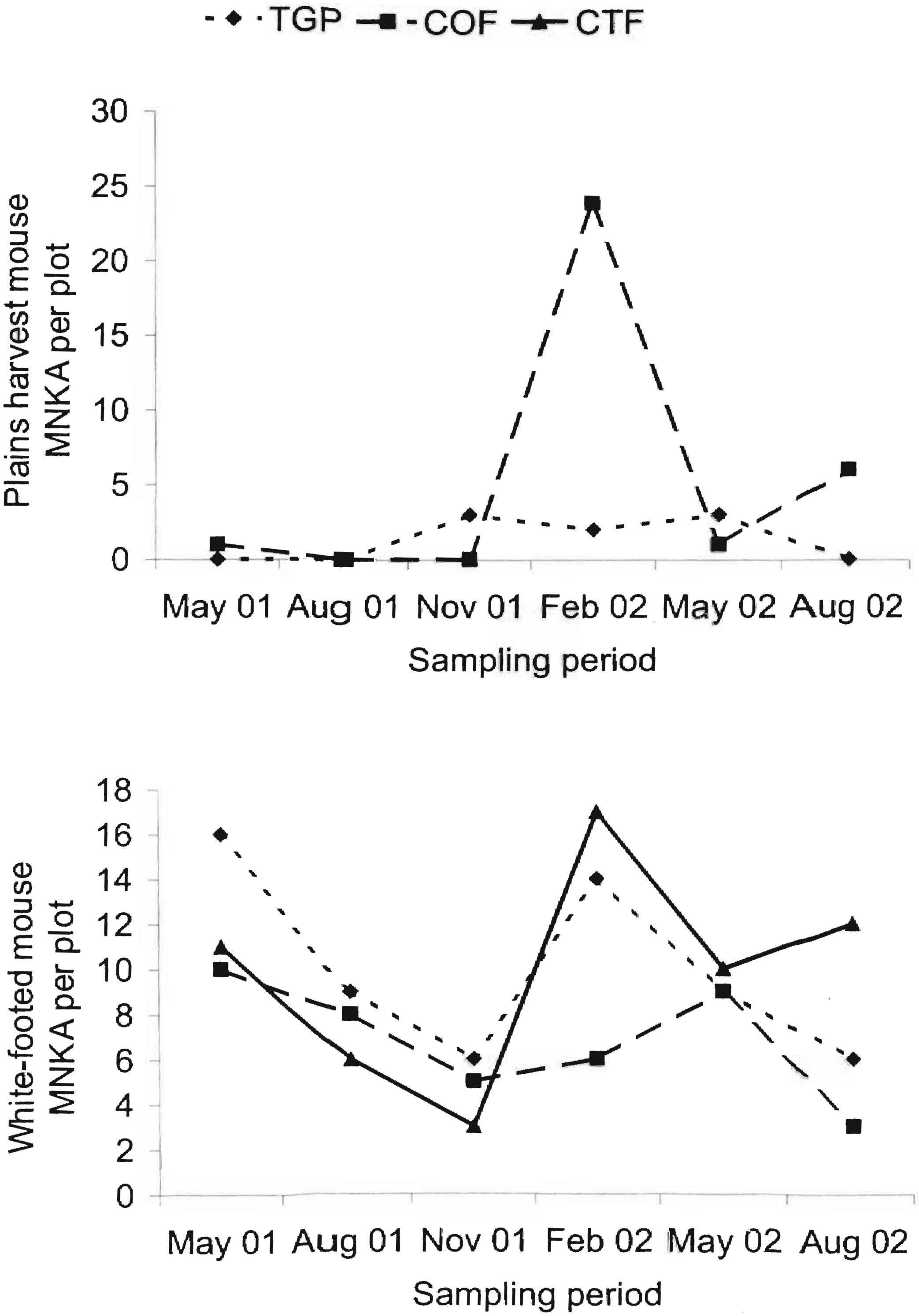




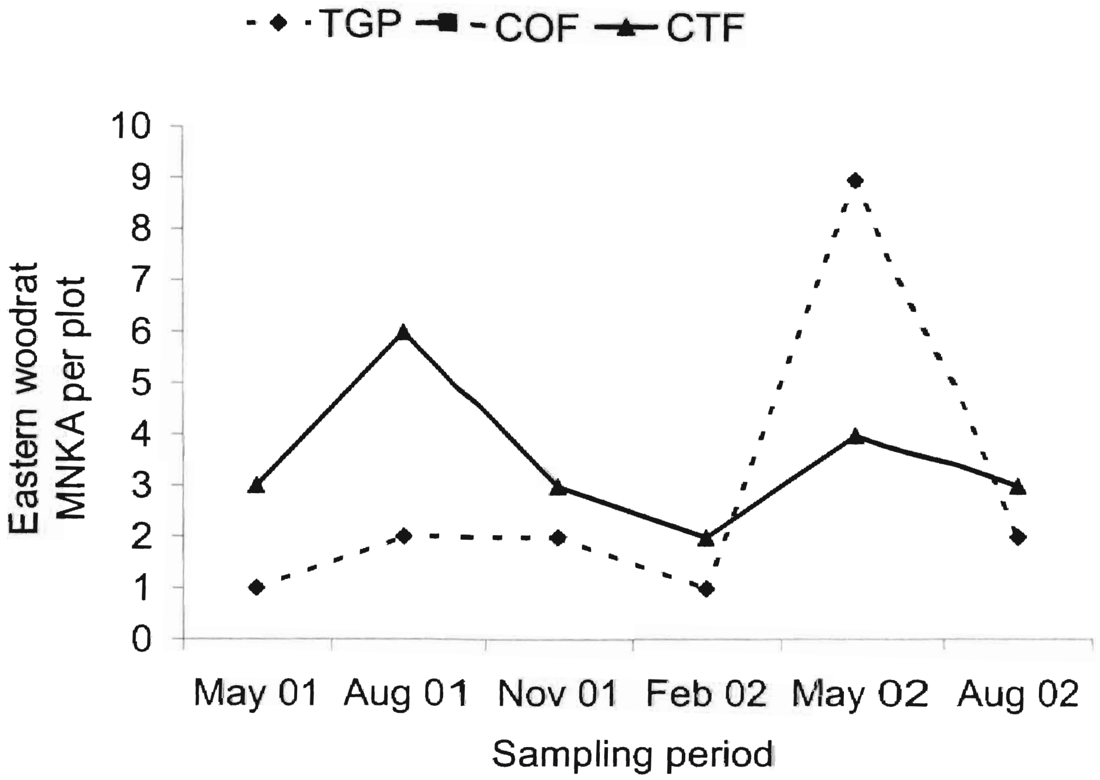
APPENDIX B

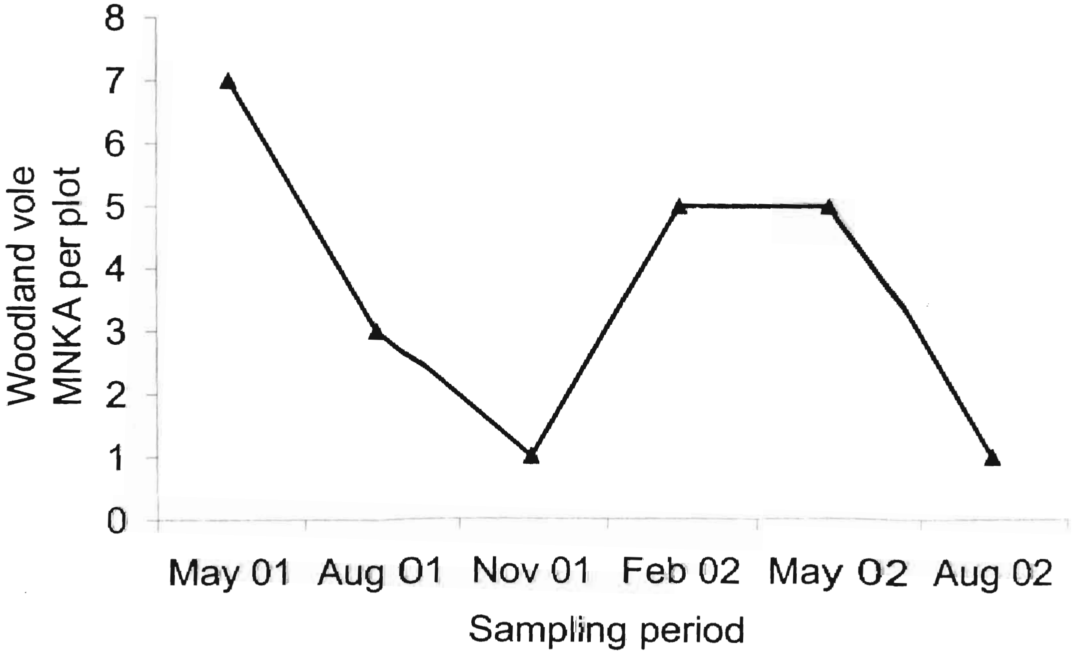

TGP
COF
CTF
Prairie vole MNKA per plot
12
10
8
6
4
2
0
May 01
Aug 01
Nov 01
Feb 02
May 02
Aug 02
Sampling period
Deer mouse MNKA per plot
10
9
8
7
6
5
4
3
2
1
0
May 01
Aug 01
Nov 01
Feb 02
May 02
Aug 02
Sampling period

APPENDIX B


TGP
COF
CTF
Plains harvest mouse MNKA per plot
30
25
20
15
10
5
0
May 01
Aug 01
Nov 01
Feb 02
May 02
Aug 02
Sampling period
White-footed mouse MNKA per plot
18
16
14
12
10
8
6
4
2
0
May 01
Aug 01
Nov 01
Feb 02
May 02
Aug 02
Sampling period

APPENDIX B


TGP
COF
CTF
Eastern woodrat
MNKA per plot
10
9
8
7
6
5
4
3
2
1
0
May 01
Aug 01
Nov 01
Feb 02
May 02
Aug 02
Sampling period


Woodland vole
MNKA per plot
8
7
6
5
4
3
2
1
0
May 01
Aug 01
Nov 01
Feb 02
May 02
Aug 02
Sampling period

VITA

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Master of Science

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