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# Differential Consumption of Eastern Red Cedar (*Juniperus virginiana*) by Avian and Mammalian Guilds: Implications for Tree Invasion

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**ABSTRACT.**—Increased abundance and distribution of eastern redcedar (*Juniperus virginianus*), a native species in the Great Plains, has been associated with changes in ecosystem functioning and landscape cover. Knowledge of the main consumers and dispersal agents of eastern red cedar cones is essential to understanding the invasive spread of the species. We examined animal removal of cedar cones in three habitats (tallgrass prairie, eastern red cedar and woodland-prairie margins) in the Cross Timbers ecoregion using three exclosure treatments during autumn and winter. Exclosure treatments excluded study trees from ungulates, from terrestrial rodents and ungulates or from neither (control). Loss of cones from branches varied by a habitat-time interaction, but was not affected by exclosure type. Loss of cones from containers located under experimental trees varied by a habitat-treatment-time interaction. In December and January, cone consumption from containers in no-exclosure treatments was highest in margins, followed by tallgrass prairie and eastern red cedar habitats. We conclude birds consumed the majority of cones from branches and small- and medium-sized mammals consumed cones on the ground. Both birds and mammals likely contribute to the spread of eastern red cedar but at different scales. Limiting invasion of eastern red cedar in forests may require early detection and selective removal of pioneer seedlings in cross timbers and other habitats that attract a high diversity or density of frugivores.

## INTRODUCTION

Eastern red cedar (*Juniperus virginiana*) has colonized native vegetation at exponential rates in Oklahoma due to fire suppression (Engle *et al.*, 1996) and is rapidly converting remnant native grassland habitats in other areas of the Great Plains of the United States (Gehring and Bragg, 1992; Coppedge *et al.*, 2001; Hoch *et al.*, 2002). Invasion by eastern red cedar impacts ecological and human health by homogenizing diversity, reducing wildlife

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habitat quality, increasing fire risk, altering hydrology and nutrient cycling and producing highly allergenic pollen (Engle *et al.*, 1996; Norris *et al.*, 2001). Fire was a process that historically limited the spread of eastern red cedar, a fire-intolerant species that reproduces solely by seed in contrast to most woody plants of the Great Plains that reproduce vegetatively and can resprout after fire (Briggs *et al.*, 2002). In the absence of fire, eastern red cedar spreads rapidly across the landscape (Bragg and Hulbert, 1976), mostly from animal-driven dispersal of the ripened, fruit-like cones. Eastern red cedar is dioecious, with female cones developing into a blue, berry-like or drupe-like structure (Gleason and Cronquist, 1963).

Junipers (*Juniperus* spp.), in general, are adapted for dispersal by frugivorous vertebrates, especially birds and mammals by virtue of their fleshy, fruit-like cones (Chambers *et al.*, 1999). At least 71 species forage on eastern red cedar (Van Dersal, 1938) and seed dispersal apparently depends heavily upon birds and small mammals (Phillips, 1910; Livingston, 1972). Birds are considered the most efficient and quantitatively important group of vertebrates for dispersing seeds of eastern red cedar, with cedar waxwings (*Bombycilla cedrorum*), robins (*Turdus migratorius*) and mockingbirds (*Mimus polyglottus*) being the most common dispersal agents (Phillips, 1910; Holthuijzen and Sharik, 1985). Eastern red cedar seeds passed unharmed through the digestive tract of yellow-rumped warblers (*Dendroica coronata*) and cedar waxwings and showed a 1.5–3.5-fold greater germination rate than manually depulped seeds (Holthuijzen and Sharik, 1985).

The role of mammals in red cedar dispersal is less well-known, although a variety of mammal species has been identified as dispersal agents for other junipers (Chambers *et al.*, 1999). Red cedar cones and seeds have been found in feces of raccoons (*Procyon lotor*), foxes (*Vulpes* spp.), bobcats (*Lynx rufus*) and small mammals (Phillips, 1910). In addition, mammal-dispersed seeds were left in slightly better condition for germination than those dispersed by birds (Phillips, 1910). Johnson (1962) reported that juniper seeds passed unharmed through digestive tracts of several species, such as woodrats (*Neotoma* spp.), thus enhancing germination rates.

Knowing the main consumers of eastern red cedar cones and their rate of consumption is essential for understanding invasion mechanisms of eastern red cedar. Many studies have described dispersal of eastern red cedar cones by birds (Holthuijzen and Sharik, 1984; Holthuijzen *et al.*, 1986), but few studies have looked at the potential of mammals as dispersers. We hypothesized that eastern red cedar dispersal and establishment are facilitated by both mammals and birds and that cone removal will be dictated by habitat preferences of these different frugivore guilds. Therefore, our primary objective was to compare consumption of eastern red cedar cones between potential guilds of dispersers among different habitat types. A secondary objective was to compare cone production among habitat types.

#### MATERIALS AND METHODS

*Study area.*—Our study was conducted at the Oklahoma State University Research Range about 11 km southwest of Stillwater in Payne County, Oklahoma (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 extends into Kansas and Texas (Hoagland *et al.*, 1999). 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). Cross timbers vegetation was a mosaic of oak forest, tallgrass prairie

and thickets of eastern red cedar. The forest is an upland hardwood type dominated by blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*) with coralberry (*Symphoricarpos orbiculatus*), eastern red cedar, poison ivy (*Toxicodendron radicans*), roughleaf dogwood (*Cornus drummondii*), redbud (*Cercis canadensis*) and American elm (*Ulmus americana*) as understory woody dominants (Ewing *et al.*, 1984). Tallgrass prairie habitats were dominated by little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), rosette panic grass (*Panicum oligosanthes*) and western ragweed (*Ambrosia psilostachya*). Eastern red cedar has invaded both oak forest and tallgrass prairie and, in some locations, dominated the vegetation with dense canopy cover that reduced understory vegetation.

*Experimental design.*—We selected 12 eastern red cedar trees, ranging in height from 7.6 to 10.7 m, in each of three habitat types: tallgrass prairie, eastern red cedar and woodland-prairie margins. Trees selected for the margin habitat were located on the boundary between patches of cross timbers forest and tallgrass prairie. Canopies of trees in margins were isolated from neighboring trees either naturally or by felling of limbs of adjacent trees. This isolation was conducted to limit arboreal mammal (*e.g.*, Scuriidae) movement that would mimic bird use of fully-exclosed trees (*see below*). We did not sample trees in forest interiors because of limited availability of large, cone-bearing eastern red cedars in this habitat. In addition, the design and intent of our exclosure treatments would have necessitated removal of neighboring trees to isolate experimental trees in the oak forest.

We randomly assigned trees to three exclosure treatments to examine frugivory of cedar cones by different animal guilds. The full-exclosure treatment consisted of 2.4-m wire mesh (15 × 20 cm) cattle panels encircling the eastern red cedar tree, with 0.9-m-high solid metal flashing buried 0.3-m adjacent to the panels. Eastern red cedar cones were, therefore, available to birds but not terrestrial rodents or larger mammals. The partial-exclosure treatment consisted solely of 2.4-m wire mesh panels encircling the experimental tree, which allowed birds and rodents access to red cedar cones, but not larger mammals (*e.g.*, ungulates). The no-exclosure treatment allowed all potential consumers access to cones. Each treatment type had four replications in each vegetation type ( $n = 36$  experimental trees).

*Branch experiment.*—We monitored loss of cones on branches to estimate consumption of cones ripening on trees. We sampled monthly starting in October 2001, when female cones began to mature into fruit, and ending in March 2002, at the end of active dissemination of seeds. We selected four tertiary branches (*i.e.*, the third branching from the main stem) and about 1.5 m above the ground 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 tagged individually 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 fell from covered branches into the screening material were counted at monthly intervals 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.

We recognize that cone loss from branches can be caused by factors other than animal frugivory. Ripe cones can be removed from trees by wind and rain. Although we used covered branches to account for natural cone loss, weather events might have affected cone loss more on open branches than on covered branches. Holthuijzen *et al.* (1986) estimated that 17.9% of the unripe cone crop dropped due to wind or other natural causes. Conversely, it is likely that red cedar has cones evolved to prevent premature drop during stochastic climatic events. Such drop would greatly reduce the chances for consumption and

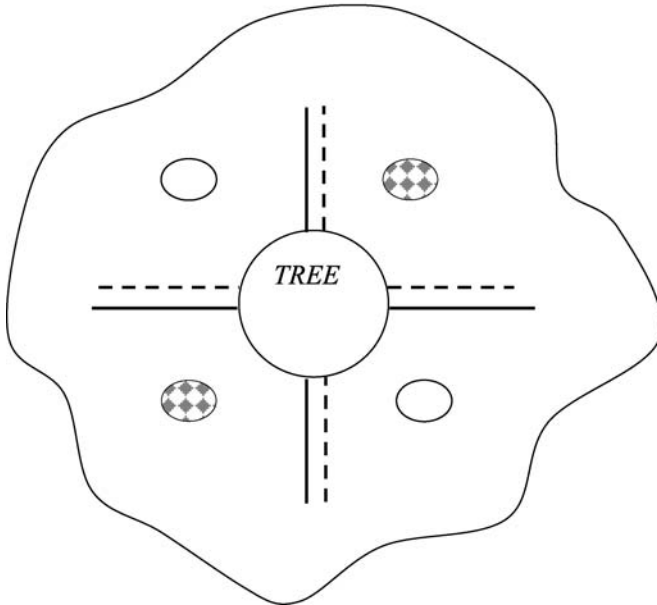
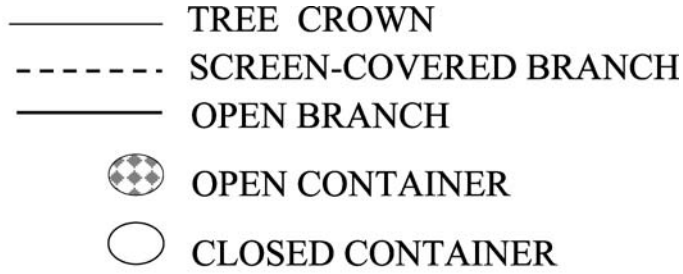


FIG. 1.—Sampling design by experimental unit (individual tree) to evaluate cone consumption of eastern red cedar on Oklahoma State University Research Range, Payne County, Oklahoma

dispersal. Therefore, loss on open branches may be an accurate representation of actual consumption.

*Container experiment.*—We harvested cones from non-sampled trees and placed them in containers under each experimental tree to identify predators of fallen (senesced), but viable, cones (Fig. 1). Two types of plastic containers were used. One type was closed ( $14.4 \times 10.3 \times 25.2$  cm) with a 2.5-cm round hole cut in the side to allow entry by small mammals. The other type was an open tray ( $16.5 \times 0.15 \times 23.5$  cm) to allow birds and mammals to remove cones. Shelters were built over the open containers to keep cones falling from the tree into the container. Two containers of each type were placed under every tree ( $n = 144$

containers). A measured amount of cones (50 g) was placed in each container and left for 5 d, after which we reweighed cones to determine the mass of cones removed. 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 correct for average water loss from the cones during the 5 d.

*Data analysis.*—Cone production, as number of cones per branch, was compared among habitat types and years using repeated-measures analysis of variance (ANOVA; PROC MIXED; SAS Institute Inc., 2000). Cone loss from branches (*i.e.*, estimated consumption) was calculated as a percentage 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 natural cone fall using the number of fruit recovered from 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 ANOVA. 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 removed from containers was calculated by the difference in mass before and after the 5-d period corrected for water loss. Cone removal rate was averaged within container type for each tree and was analyzed using repeated-measures ANOVA to investigate differences among habitat types, exclosures, and types of containers (PROC MIXED; SAS Institute Inc., 2000). Given the lack of removal from closed containers, we also analyzed cone removal for open containers only. 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

*Branch experiment.*—Cone production by red cedars varied among the 3 different habitat types over time (habitat by time interaction,  $P = 0.006$ ). In November 2001 cone production was greater in the cedar habitat than in the prairie ( $P = 0.047$ ) and woodland-prairie margin habitats ( $P = 0.002$ ). In November 2002, however, there was no difference in cone production by habitat ( $P = 0.123$ ). Trees in cedar habitats had lower ( $P < 0.001$ ) cone production in 2002 than in 2001, but cone production in the margin and prairie habitats were similar across years (Fig. 2).

Cone loss on branches did not vary among exclosure types ( $F_{2,60} = 3.50$ ,  $P = 0.178$ , Fig. 3A), and a habitat-by-time interaction explained most of the variation in cone loss ( $F_{8,105} = 2.34$ ,  $P = 0.024$ ). Cone loss in December–January was least in the cedar habitat, and cone loss in February–March was greatest in the woodland-prairie margins (Fig. 3B). Other interactions were not significant ( $P > 0.332$ ).

*Container experiment.*—Cone removal from containers varied by several 3-way interactions among habitat, treatment, month and container (Table 1). Interactions involving container type were explained by open containers always having a greater loss of cones, but the magnitude of difference varied by habitat, treatment and month. Cone removal from open containers varied by the 3-way interaction of habitat, treatment and month ( $P = 0.003$ ). The interaction was manifest in December and January, when removal peaked at 10–25 g from the 50-g containers (Fig. 4). During that period, containers under trees in no-exclosure treatments, ordered by margin, prairie and cedar habitats, had the greatest cone removal (Fig. 4). Except for high cone loss in the prairie partial-exclosure treatment, full and partial exclosures lost similar amounts of cones ( $< 7$  g).

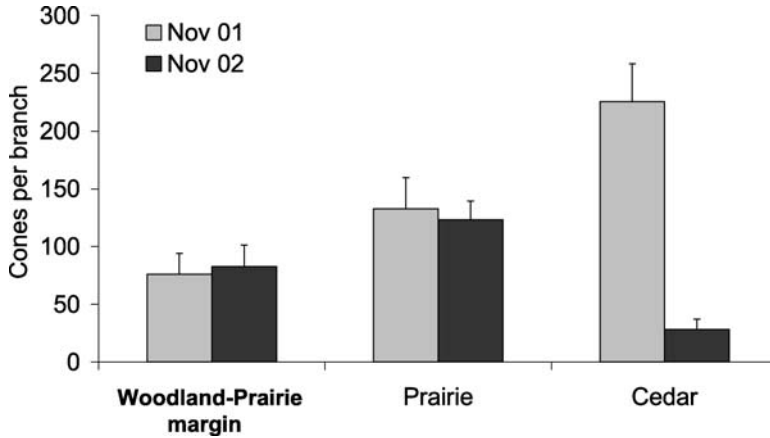


FIG. 2.—Eastern red cedar cones per tertiary branch (+ se) by habitat type and year (n = 12 replicates/year), Oklahoma State University Research Range, Payne County, Oklahoma

DISCUSSION

*Branch experiment.*—Cones mature in eastern red cedar within one growing season (Chambers *et al.*, 1999), and the species is known to produce larger-than-average crops of cones once every 2–3 y (Fowells, 1965). Holthuijzen and Sharik (1985) found a difference in average number of cones between years and among trees. In our study, cone production of trees in the cedar habitat appeared to peak in 2001 and then returned to an average year in 2002; the majority of trees in the woodland-prairie margin 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, although sciurids also may have consumed cones from branches. Other studies have reported that birds consume the majority of eastern red cedar cones (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 woodland-prairie margins, total number of cones lost decreased gradually over time. However, percent cone loss increased greatly from February to March (Fig. 3). Cones may have ripened earlier in the prairie and cedar thicket than in margins, then were consumed by avian frugivores. 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 woodland-prairie margins, they may have had more consumption because nearby trees provided perches for birds (Debussche *et al.*, 1982; McDonnell and

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FIG. 3.—Average cone loss (%) from branches of eastern red cedar (+ se) by month in 2001–2002 for (A) exclosure type and (B) habitat type, Oklahoma State University Research Range, Payne County, Oklahoma

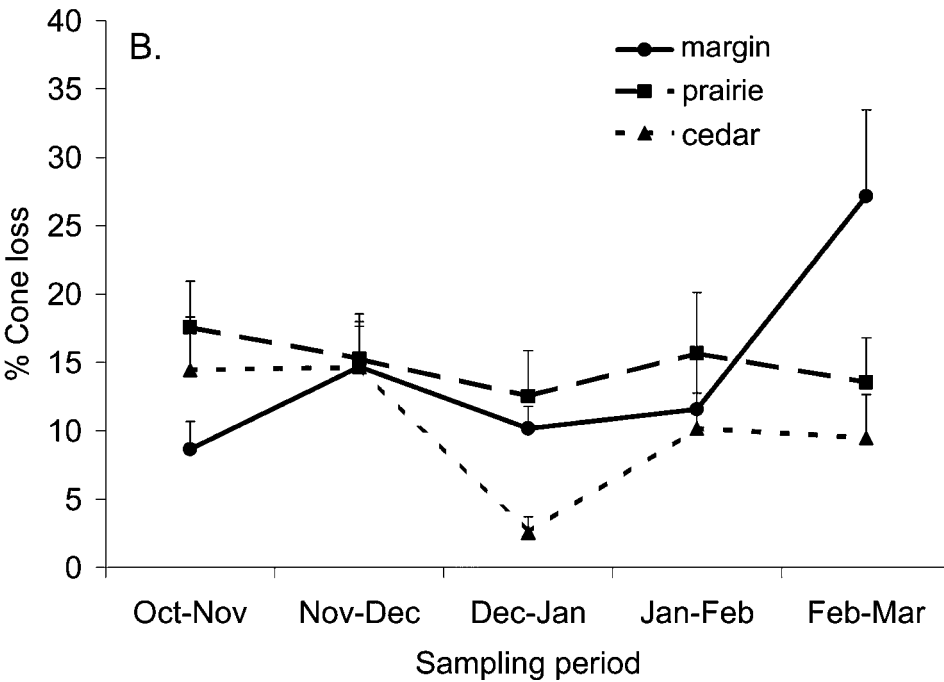
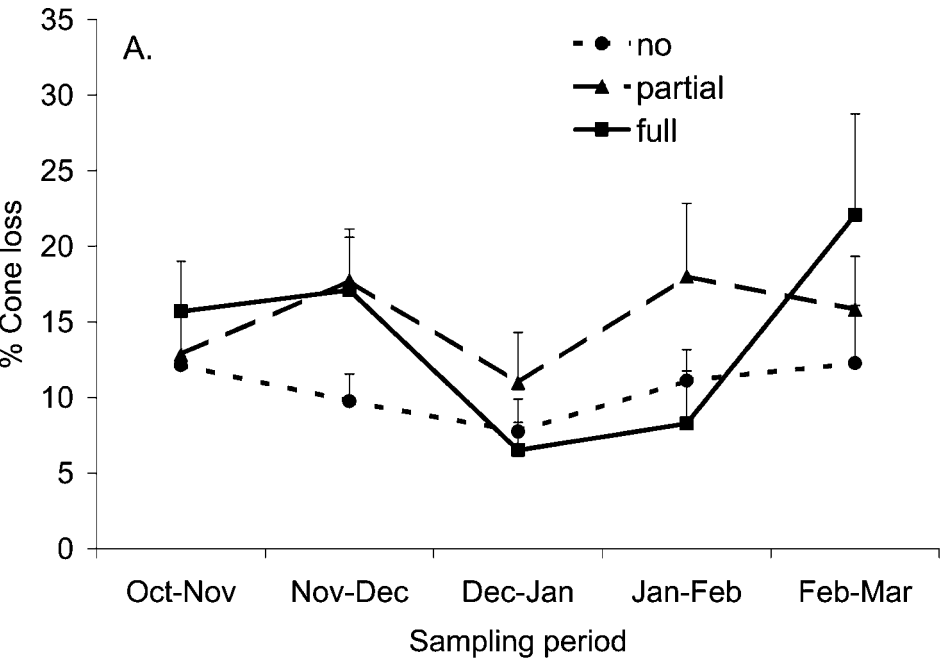




TABLE 1.—Results of repeated-measures ANOVA for removal of eastern red cedar cones from containers in seed predation trials (container experiment). Effects of factors and interaction terms influencing seed removal rates are reported using Type III sum of squares *F* values

Factor	df	F	P > F
Habitat	2, 135	2.41	0.093
Treatment (exclosure type)	2, 135	8.42	<0.001
Month	5, 264	27.64	<0.001
Container	1, 135	51.71	<0.001
Habitat × Treatment	4, 135	1.24	0.299
Habitat × Month	10, 278	1.21	0.284
Treatment × Month	10, 278	1.30	0.231
Habitat × Treatment × Month	20, 284	3.00	<0.001
Habitat × Cont	2, 135	1.31	0.273
Treatment × Cont	2, 135	2.08	0.129
Habitat × Treatment × Cont	4, 135	2.34	0.058
Month × Cont	5, 264	2.62	0.025
Habitat × Month × Cont	10, 278	1.83	0.055
Treatment × Month × Cont	10, 278	3.15	<0.001
Habitat × Treatment × Month × Cont	20, 284	1.25	0.211

Stiles, 1983). Temporal variation in bird abundance among habitats also may explain this effect, but we do not have the data to address that possibility.

*Container experiment.*—Differences among exclosure types indicated that birds were not the main removal agents of cedar cones in dishes on the ground. Trees with no exclosures had the greatest cone loss from containers, indicating that small- and medium-sized mammals were major cone removers. 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 removal also was evident, as we found mice feces in the containers.

Patterns of seed predation by mammals vary by habitat type, seed species and time (Hulme, 1993). Our study was consistent with these patterns, as removal of eastern red cedar cones from containers on the ground was related to habitat type and time. Cone removal was maximal in the woodland-prairie margins in December and January in the no-exclosure treatment, and may have been due to medium-sized mammals, particularly opossums. Ginger *et al.* (2003) reported that opossums were most likely captured in oak forest in the cross timbers, and Kasparian *et al.* (2002) documented consumption of eastern red cedar cones by opossums. Several medium-sized species of mammals have been implicated in consumption and dispersal of *Juniperus*. For example, raccoons, ringtail (*Bassariscus astutus*), gray fox (*Urocyon cinereoargenteus*), coyotes (*Canis latrans*) and several species of lagomorphs consume cones of other juniper species (*J. ashei* and *J. occidentalis*; Chavez-Ramirez and Slack, 1993; Schupp *et al.*, 1997a). A study of seed dispersal along an ecotone from an Utah juniper (*J. osteosperma*) woodland to an annual grassland documented that lagomorphs dispersed juniper seeds, but also showed that the number and proportion of fecal pellets containing juniper seeds peaked in the woodland and declined rapidly away from the woodland margin (Schupp *et al.*, 1997b).

Greater loss of cones in the woodland-prairie margins and prairie also may be attributed to microhabitat preferences of rodents. Microhabitat influences seed predation by rodents, with predation by mice greater in areas with dense ground cover (Manson and Stiles, 1998; Hulme and Hunt, 1999). Predation rates by small mammals may be higher under woody or

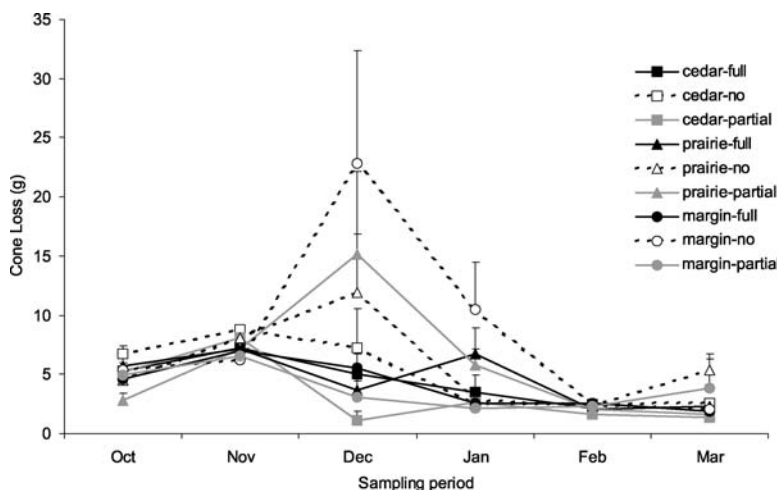


FIG. 4.—Average 5-d removal (g) of eastern red cedar cones ( $\pm$  SE) from open containers holding 50 g of cones for each habitat-exclosure combination on a monthly basis from October 2001 to March 2002, Oklahoma State University Research Range, Payne County, Oklahoma

tall herbaceous vegetation (Bowers and Dooley, 1993; Myster and Pickett, 1993). Several trees in our margin habitat had nearby thickets of sumac (*Rhus* spp.), fallen logs and debris that would provide cover for small mammals. Thick herbaceous vegetation in the prairie also provided cover for small mammals from predators. Of the no-exclosure treatments, cedar habitat had the lowest total cone removal. Eastern red cedar reduces understory herbaceous vegetation (Engle *et al.*, 1987; Smith and Stubbendieck, 1990), thereby providing less cover from predators. Small mammals may be avoiding trees near cedar because of less ground cover.

Numerous studies have associated small mammals with establishment and removal of woody vegetation in old-fields (Mittelbach and Gross, 1984; Ostfeld *et al.*, 1997; Manson *et al.*, 1999; Manson, 2000). 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). Microhabitat can influence seed predation and establishment, with seed predation by mice greater in areas with ground cover, particularly dense vegetation (Manson and Stiles, 1998; Hulme and Hunt, 1999). Habitat type also influences which small mammal species has the strongest effects on consumption, dispersal and succession of woody species (Ostfeld *et al.*, 1997).

*Implications to tree invasion.*—Chambers *et al.* (1999) pointed out that although it is commonly held that birds are the most important dispersal agents for *Juniperus* and that mammals are of incidental importance, the relative importance of birds and mammals in dispersal likely varies by species of *Juniperus*, species of potential dispersers and site conditions. A total of 65% of the cones of eastern red cedar trees in Virginia was dispersed by birds, whereas 29% of cones dropped from the trees by natural causes (Holthuijzen *et al.*, 1986). In our study, birds (and perhaps arboreal mammals) appeared to remove most cones from branches, whereas small- and medium-sized mammals removed cones on the ground. Therefore, we suspect that guilds of frugivorous birds and mammals both contribute materially to the dispersal of eastern red cedar. However, the relative importance of these

guilds in seedling germination, tree establishment and invasion is unknown. Carefully designed experiments are necessary to untangle the multiple factors involved in dispersal success (Chambers *et al.*, 1999). For example, the relative proportion of cone consumption by mammalian frugivores, which typically digest the fleshy pulp of the cone but defecate the seeds unharmed (Chavez-Ramirez and Slack, 1993; Schupp *et al.*, 1997a), and by rodent granivores, which consume and destroy seeds, needs to be studied to understand the overall dispersal efficiency of mammals. In addition, relative germination success after consumption by birds and mammals also needs to be determined.

Guilds of bird and mammal frugivores likely contribute to the spread of eastern red cedar 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 red cedar seeds dispersed by birds are spread away from the parent tree. Because the majority of birds feeding on eastern red cedar (cedar waxwings, mockingbirds, robins) are not forest obligates, they will 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 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 red cedar also are more concentrated along powerlines and fencerows where birds perch (Holthuijzen *et al.*, 1986). Medium-sized mammals, such as carnivores and lagomorphs, may spread red cedar seeds at scales approaching that of birds because of longer gut retention times and movements exceeding 1 km (Chavez-Ramirez and Slack, 1993; Chambers *et al.*, 1999). For example, a coyote consuming red cedar cones and moving within the next 12–24 h could disperse seeds several km from the source tree.

Eastern red cedar is probably spread on a smaller scale by rodents. In addition, rodents may act primarily as seed predators, in which case dispersal would not occur. However, neither the use of pulp versus seed nor the fate of harvested seeds (*e.g.*, caching vs. consumption) by rodents has been studied in any species of *Juniperus* (Chambers *et al.*, 1999). In any case, because rodents lack the mobility of avian species, they probably disperse seeds only a short distance (<100 m) from the parent tree. For example, a home range of 0.1 ha (Lackey *et al.*, 1985) for white-footed mice (*Peromyscus leucopus*) 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. Spread of eastern red cedar in certain areas will depend on resident rodent species. *Peromyscus* spp. and eastern woodrats (*Neotoma floridana*) consume eastern red cedar cones (Phillips, 1910; Johnson, 1962). Deer mice (*P. maniculatus*) prefer open areas, 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 and population increases in existing stands 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 red cedar seeds due to lack of vertical structures.

Invasion of oak forest in the cross timbers by eastern red cedar, although slow due to reduced growth of the species under shade (evidenced by the lack of cone-bearing trees in the forested areas of our study area), could accelerate due to mammal foraging of red cedar

cones along the woodland-prairie margin followed by deposition of seeds nearby under the forest canopy. For example, white-footed mice (*Peromyscus leucopus*) and eastern woodrats prefer woodland habitats with occasional grass-forb areas (Caire *et al.*, 1989). In our study area, white-footed mice were positively associated with eastern red cedar occurrence (Horncastle, 2003). These rodent species, along with larger species such as lagomorphs, Virginia opossums and other frugivorous carnivores, could contribute to cedar invasion into forested areas from woodland-old field or woodland-prairie margins.

The elimination of fire is considered the key reason that eastern red cedar has increased throughout Great Plains grasslands (Hoch *et al.*, 2002), as well as the forest-prairie mosaic of the cross timbers ecoregion. Socioeconomic factors and changes in land-use practices limit the present use of fire to control eastern red cedar expansion (Hoch *et al.*, 2002). Management strategies other than fire may be effective at small scales to slow animal-driven dispersal of the species. For example, removal of potential bird perches, such as fencelines and individual trees in prairie patches, may slow dispersal and subsequent colonization of grasslands by eastern red cedar. Similarly, management strategies to reduce the risk of eastern red cedar invasion in forests may include early detection and selective removal of pioneer seedlings in cross timbers habitats and possibly other habitats that attract a high diversity or density of frugivores.

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