RESPONSE OF SMALL MAMMALS TO CONVERSION OF A SAND SHINNERY OAK WOODLAND INTO A MIXED MID-GRASS PRAIRIE

MICHAEL R. WILLIG, RANDALL L. COLBERT, RUSSELL D. PETTIT, and RICHARD D. STEVENS

Ecology Program, Department of Biological Sciences and The Museum (MRW, RLC, RDS), and Department of Range and Wildlife Management (RDP), Texas Tech University, Lubbock, Texas 79409-3131

ABSTRACT.—Shrubs were removed in two areas of a sand shinnery oak woodland via the aerial application of tebuthiuron, an herbicide that eliminates at least 90 percent of the shrub component (Quercus havardii). A circular grid containing 260 traps was established at each of four sites: two tebuthiuron treated areas and two untreated or control areas. Estimates of density (total rodents and Dipodomys ordii alone) based upon the minimum number known to be alive were obtained for each area during each of four phenological seasons. Habitat variables (percentages of bare ground, ground litter, canopy cover, shrubs, forbs, and grasses, as well as vertical height) were determined for tebuthiuron treated and control sites. Statistical analyses revealed that both total rodent density and D. ordii density changed in response to tebuthiuron-related effects. Species composition (proportional species densities) also differed significantly between treated and untreated areas. Seasonal effects on density and species composition occurred and probably were related to behavioral responses of rodents to temperature and precipitation regimes. Key words: small mammal community; rodents; mixed grass prairie; sand shinnery oak woodland; Dipodomys; tebuthiuron.

Habitat characteristics clearly affect rodent populations. It is well documented that a variety of vegetational characteristics affect species composition of local rodent communities as well as the density of component species (Hansen and Ward, 1966; Tietjen et al., 1967; Johnson and Hansen, 1969; Rosenzweig and Winakur, 1969; Parmenter and MacMahon, 1983; Schroder, 1987; Wywialowski, 1987; Abramsky, 1988; Brown, 1989; Brown and Zeng, 1989). The community and population responses of small mammals to vegetational changes have been studied by inducing modifications through the use of chemical treatment (Johnson, 1964; Johnson and Hansen, 1969; Christian, 1977; McGee, 1982; Sullivan and Sullivan, 1982; Zou et al., 1989), fire clearcutting (Gashwiler, 1970; Sullivan, 1979; Van Horne, 1981), and mechanical removal of select plant species (Parmenter and MacMahon, 1983). Percent cover (Allred and Beck, 1963; Brown et al., 1972; M'Closkey, 1975; M'Closkey and Lajoie, 1975; Rosenzweig et al., 1975; Feldhamer, 1979), vegetation-precipitation relationships (Reynolds, 1958; Brown, 1973; Hafner, 1977), foliage height diversity (Allred and Beck, 1963; Rosenzweig and Winakur, 1969; M'Closkey, 1975; Morris, 1979), foliage density (Rosenzweig and Winakur, 1969; Brown et al., 1972; M'Closkey and Lajoie, 1975; Hafner, 1977), and ground litter (Morris, 1979) are
among the many variables that have been correlated or associated with changes in small mammal densities and community composition.

Munger et al. (1983) suggested that bushes are favorable resource patches that act as proximate cues for rodent activity, whereas results from several other studies pointed toward cover as the main factor affecting rodent populations in arid and semiarid environments (Rosenzweig and Winakur, 1969; Price, 1978; Thompson, 1982; Parmenter and MacMahon, 1983). Nonetheless, Hafner (1977) contended that desert rodent species diversity does not respond to a particular parameter because even animals of the same species are influenced by different environmental factors in different geographical situations. This leads to the question of the importance of shrubs in determining small mammal species composition and abundance in a sand shinnery oak woodland.

Sand shinnery oak (Quercus havardii) predominates on sandy soils in semiarid environments in western Texas, southeastern New Mexico, and western Oklahoma, where it grows on about 2.7 million hectares (Pettit and Jones, 1986). The sand shinnery oak ecosystem is essentially a monoculture, with at least 80 percent of the herbage being oak (Pettit and Jones, 1986). The effect of the shrub component on rodent population parameters has not been studied even though removal of the sand shinnery oak via tebuthiuron treatment drastically alters the habitat by changing cover, food resources, foliage height diversity, and water availability to other plants (McIlvain, 1954; Elwell, 1964; Rechenthin and Smith, 1967; Robison and Fisher, 1968; Jones and Pettit, 1984; Pettit and Jones, 1986). Herein, we assess the response of small mammals to the tebuthiuron-induced conversion of a sand shinnery oak woodland into a mid-grass prairie. We also attempted to identify the potential ecological variables associated with changes in small mammal population density or community composition. The hypotheses for evaluation were that the removal of the sand shinnery oak would affect a change in the overall abundance of small mammals, and that there would be an alteration in species composition, possibly because of herbicide-induced changes in habitat variables. Moreover, Dipodomys ordii density should change in tebuthiuron-treated areas because kangaroo rats, in general, avoid areas of thick cover and are associated more frequently with sparsely vegetated areas (Rosenzweig and Winakur, 1969; Rosenzweig, 1973).

**Materials and Methods**

**Study Site**

The study site is located on the Southern High Plains of Texas (33°22'-33°26' N, 102°37'-102°50' W), about 19 miles N and 4 miles E Plains, Yoakum County. The terrain is relatively flat at an elevation of about 1260 meters. The climate is warm-temperate and semiarid, with fluctuating temperatures during the winter. Annual precipitation averages 41
centimeters, with the majority of the rainfall occurring from May through October (Jones and Pettit, 1984).

The vegetation on the untreated control sites is at least 80 percent (biomass) sand shinnery oak (Pettit and Jones, 1986). Other plants found on the control sites include soapweed (Yucca angustifolia), sand sagebrush (Artemisia filifolia), and prickly pear cactus (Opuntia polyacantha). The vegetation on the treated site is predominantly grasses and forbs; the more common plants include little bluestem (Schizachyrium scoparium), purple threeawn (Aristida purpurea), annual buckwheat (Erigonum annuum), and fleabane (Eriogonum modestum). A complete plant species list for the area is presented in Colbert (1986). Mammals known from the study area include Dipodomys ordii (Ord's kangaroo rat), Onychomys leucogaster (northern grasshopper mouse), Perognathus flavescens (plains pocket mouse), Peromyscus maniculatus (deer mouse), Reithrodonotomys montanus (plains harvest mouse), Sigmodon hispidus (hispid cotton rat), Neosoma micropus (wood rat), Spermophilus spilosoma (spotted ground squirrel), Canis latrans (coyote), Taxidea taxus (badger), Lepus californicus (black-tailed jackrabbit), Sylvilagus audubonii (desert cottontail), Antilocapra americana (pronghorn), and Bos bos (cattle).

Shrub Removal

The study area was chosen because shrubs had been removed via the application of tebuhiuron (Graslan®, N-(4-(1,1-dimethylthyl)-1,3,4-thiadiazol-2-yl)-N,N'-dimethyleurea) pellets (20 percent active ingredients) that were aerially broadcast at an application rate of one-half pound per acre. Grid I was treated in May 1982, whereas grid II was treated in May 1980 and retreated in May 1983. The use of tebuhiuron is the only method that essentially eliminates sand shinnery oak for an extended period and does not directly affect other components of the plant community, except for initial damage to forbs (Jones and Pettit, 1984). Tebuhiuron has been documented to kill more than 90 percent of the sand shinnery oak in the community (Pettit, 1975; Jones et al., 1978; Jones and Pettit, 1984). The two treated areas, although different in treatment times, were chosen because of their current similarity in vegetation, previous and present grazing pattern, and topography. Within each treated area, grid sites were selected randomly. Trapping sites were established on two control areas where sand shinnery oak had never been treated with tebuhiuron. All four sites were within a 1500-hectare area.

Rodent Trapping

We used a circular grid to trap rodents. Thirteen lines, each comprising 20 medium-sized Sherman live-traps, radiated from a center stake, with the first trap in each line 2.5 meters from the center stake. The remaining traps were placed at five-meter intervals. This spacing was used in order to 1) insure at least eight to 12 traps per home range in the center of the grid, and 2) facilitate the capture of approximately 60 individuals during a trapping session (Anderson et al., 1983). Preliminary results from trapping a circular grid from 25 May to 15 July 1984 suggested that the previously described trap spacing and grid size were appropriate given the small mammal fauna at the sites. Four permanent grids were established, one in each of the treated areas, and one in each control area. Trapping continued until all animals from the center of each grid were captured in accordance with the recommendations of Anderson et al. (1983). This usually required three or four nights of trapping. Trapping sessions were scheduled during the dark phase of the moon to restrict any variation in activity that might be affected by moon light (Price et al., 1984). Because of limitations in the number of available traps, one control site and one treated site were trapped at the same time. The traps were then moved to the replicate sites for additional trapping. The complete trapping regime required eight or nine days each season.

Trapping was aimed at nocturnal and crepuscular rodents only. Larger mammals such as desert cottontails (Sylvilagus audubonii) and black-tailed jackrabbits (Lepus californicus)
were excluded because of trap size. Diurnal rodents such as the spotted ground squirrel
(Peromyscus spilosoma) were not marked when captured, and thus do not appear in the
overall evaluation of rodent density and species composition. A granola mixture was used
as bait, cotton Nestlets were placed in each trap to prevent rodent hypothermia. Upon
initial capture, rodents were uniquely toe-clipped, weighed, and identified to sex and
species. Trap location was recorded for initial as well as subsequent captures of previously
captured individuals.

Trapping was conducted in four sessions defined by seasonal foliage changes that occur in
the area. The first session was in the winter after all leaves had fallen from the oaks (19 to
27 January 1985). Trapping was restricted to only three nights on each grid. The second
period occurred during oak refoliation in the spring (13 to 20 May 1985). The third
trapping session occurred in the summer during maximum plant development (10 to 17
August 1985). The last period was during the autumn dormancy, after the first frost but
before leaf fall (9 to 19 November 1985).

Vegetation Sampling

A summary of vegetation sampling methods is offered by Daubenmire (1968), the original
source for most of the following procedures. A permanent line transect was established
across each grid to measure the same points every trapping season. A frame of 0.25 square
meter was placed at 30 points spaced equidistantly along the transect. At each point, the
highest vegetation within the frame was measured for vertical height. Then, using either a
Canon AE-1 35-mm or a Minolta XG-7 35-mm camera, and focusing from directly above
the center of the frame, a photograph was taken of the quadrat. The resultant slides were
projected onto a screen of 0.5 by 0.5 meters that was divided into 100 sections. This enabled
an accurate estimation of the percentages of bare ground, ground litter, and canopy cover.
Also, a step-point analysis was performed to determine vegetation composition. A transect
was walked for 100 steps across each grid. Bare ground, litter, or plant species identity was
recorded at the end of each step. If bare ground or litter was recorded, the identity of the
closest plant species was also noted. Percentage of shrubs, forbs, and grasses was
determined from these data.

Population Estimation

We designed the study to take advantage of features of plotless or distance sampling
(Anderson et al., 1983), but because of methodological limitations associated with low
capture success, limited our analyses to a more simple index of density. The minimum
number of individuals known to be alive (Nmin) on each grid per trapping session was used
as the index of density. This enumeration method has been used several times in studies
concerning dispersal (Krebs et al., 1976; Stafford and Stout, 1983; Williams and Cameron,
1984) and demography (Krebs, 1966; Yahnner, 1983). Moreover, recent studies indicate
density estimates based upon Nmin and more complex procedures (JOLLY method for open
populations, CAPTURE method for closed populations) are highly correlated; in fact, the
magnitude of these estimates differed by no more than 30 percent (S. Blair, personal
communication). Regardless, the bias of underestimating density should be consistent in all
treatments, thereby not affecting statistical comparisons.

Statistical Methods

Model 1 two-way (tebuthiuron treatment versus season) Analysis of Variance (ANOVA)
was used to compare the relative abundance after arcsine (angular) transformation (Sokal
and Rohlf, 1981) of shrubs, forbs, and grasses, as estimated from the step-point analysis,
using SAS program Proc GLM (SAS Institute, 1985). Four ecological variables (vertical
height, percent bare ground, percent ground litter, and percent canopy cover) were analyzed
via mixed-model nested two-way ANOVA, with two grouping factors and one trial factor
(BMDP2V-Dixon and Brown, 1979). The two grouping factors were tebuthiuron
<table>
<thead>
<tr>
<th>Source of variation</th>
<th>DF</th>
<th>Sum of squares</th>
<th>Mean squares</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forbs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>Treatment (T)</td>
<td>1</td>
<td>0.151</td>
<td>0.151</td>
<td>6.02</td>
<td>0.049</td>
</tr>
<tr>
<td>Season (S)</td>
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<td>0.280</td>
<td>0.140</td>
<td>5.59</td>
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</tr>
<tr>
<td>T x S</td>
<td>2</td>
<td>0.217</td>
<td>0.109</td>
<td>4.33</td>
<td>0.068</td>
</tr>
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<td>Error</td>
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<td>0.150</td>
<td>0.025</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Grasses</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>0.405</td>
<td>0.405</td>
<td>27.30</td>
<td>0.002</td>
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<td>Season (S)</td>
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<td>0.419</td>
<td>0.210</td>
<td>14.14</td>
<td>0.005</td>
</tr>
<tr>
<td>T x S</td>
<td>2</td>
<td>0.265</td>
<td>0.133</td>
<td>8.95</td>
<td>0.016</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>0.089</td>
<td>0.015</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Shrubs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
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<td>0.083</td>
<td>111.11</td>
<td>0.001</td>
</tr>
<tr>
<td>Season (S)</td>
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<td>0.010</td>
<td>0.005</td>
<td>0.67</td>
<td>0.548</td>
</tr>
<tr>
<td>T x S</td>
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<td>0.046</td>
<td>0.023</td>
<td>3.09</td>
<td>0.120</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>0.045</td>
<td>0.007</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Treatment and season; the trial factor comprised two grids within each treatment. The vertical height analysis had 30 replications within each grid, whereas each of the other three variables had 19 replications within each grid. Percent bare ground, percent canopy cover, and percent ground litter were subjected to arc sine transformation, in order to meet the assumption of normality and homoscedasticity for ANOVA (Sokal and Rohlf, 1981); tebuthiuron treatment and season were the main effects tested. Population size, as estimated by minimum number known to be alive, was analyzed by model I two-way ANOVAs (tebuthiuron treatment versus season), followed by the Welsch Step-Up Procedure, a multiple comparison test (Sokal and Rohlf, 1981). Regardless of the significance of the ANOVA, a series of more powerful *a priori* comparisons of tebuthiuron treated versus control grid densities were conducted within each season (Sokal and Rohlf, 1981).

A Chi-Square Contingency Test (Zar, 1984) was conducted on the number of initial captures of each species for each season to determine if tebuthiuron treatment affected small mammal species composition. If a significant Chi-square value resulted, the proportional contribution of each species to the overall Chi-square value was calculated as a means of identifying taxa affecting significance.

**Results and Discussion**

**Floral Analysis**

*Composition.*—The two-way ANOVA for shrub abundance (Table 1, Fig. 1) indicated a highly significant difference (*P* = 0.001) between tebuthiuron treated and untreated areas. Season did not have an effect (*P* = 0.548), and season affected all tebuthiuron treated and untreated areas equally, as no evidence suggested an interaction (*P* = 0.120). Grass abundance also showed effects of tebuthiuron treatment (Table 1); however, the treatment effects were dependent on season (the interaction was significant, *P* = 0.016). In particular, the greater abundance of
Figure 1. Seasonal comparison (winter, spring, and autumn) of floral composition (percent grasses, forbs, and shrubs) in the tebuthiuron treated and untreated grids within the sand shinnery oak woodland.

Grasses in tebuthiuron treated grids is magnified in the winter compared to spring or autumn (Fig. 1). The percentage of forbs was significantly different between tebuthiuron treated and untreated areas ($P = 0.049$); a consistent difference existed among seasons ($P = 0.043$) as well (Table 1, Fig. 1). In general, tebuthiuron treatment caused a significant change in shrub, grass, and forb abundance, whereas seasonal variation existed in forb and grass abundance, but not in shrub abundance.

Habitat variables.—Four habitat variables (percent bare ground, percent canopy coverage, percent ground litter, and vertical height) were chosen to evaluate differences between untreated sand shinnery oak and
tubuthiuron treated areas of shrub removal. The data for each variable were compared in a mixed model two-way nested ANOVA, evaluating differences related to tubuthiuron treatment, season, and grids within treatment (Table 2). Percent ground litter was not significant for main treatment effects or for interaction terms. Percent bare ground also was not significantly different between tubuthiuron treatments ($P = 0.092$); however, a significant difference among seasons was detected ($P = 0.003$). No interaction between tubuthiuron treatment and season occurred ($P = 0.253$). Vertical height was significantly different only between tubuthiuron treated and control areas ($P = 0.012$). Percent canopy cover was significantly different between tubuthiuron treated and control areas ($P = 0.005$), as well as among seasons ($P = 0.006$). These differences were consistent in that the interaction between tubuthiuron treatment and season was not significant ($P = 0.588$). Canopy cover and vertical height were the only variables significantly affected by tubuthiuron application, whereas canopy cover and bare ground were the only variables that differed seasonally. No evidence of interaction between tubuthiuron treatment and season existed for any of the four habitat variables.

**Faunal Analysis**

*Species composition.—* Rodent species captured in the treated area included *D. ordii, O. leucogaster, Perognathus flavescens, R. montanus, N. micropus, S. hispidus, and Peromyscus maniculatus.* *D. ordii* was the most often captured every season, except in the autumn, when *O. leucogaster* was trapped most often. Both *D. ordii* and *O. leucogaster* were captured in every season. *S. hispidus* was caught only in summer. *Perognathus flavescens* was trapped in every season except winter. *N. micropus* and *Peromyscus maniculatus* were caught only in the spring (one individual of each species). *R. montanus* was captured in the spring and autumn.

The rodent species trapped in the untreated areas were *D. ordii, O. leucogaster, P. maniculatus, N. micropus, P. flavescens,* and *Mus musculus.* *D. ordii* and *O. leucogaster* were caught in every season, with *D. ordii* being captured most often every season except autumn, when trap success for every species was low. *N. micropus* was caught in winter, whereas *M. musculus* was caught only in the autumn. Overall, seven species were captured in treated areas and six species were trapped in control areas. In both areas, *D. ordii* was captured most often except in autumn. It is possible that *O. leucogaster* was more abundant in both the treated and control areas in the autumn because of an unusually high population of grasshoppers, one of their chief sources of food (Davis, 1978) in summer and early autumn. All species caught in the untreated areas were caught in the treated areas, with the exception of *M.*
Table 2. Mixed model two-way (tebuthiuron treatment versus season) nested (replicate grids within cells) ANOVA for ground litter, bare ground, vertical height, and canopy cover. Abbreviations are: DF, degrees of freedom; MS, mean square; P, significance level.

<table>
<thead>
<tr>
<th>Source</th>
<th>Ground litter</th>
<th>Bare ground</th>
<th>Vertical height</th>
<th>Canopy cover</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF</td>
<td>MS</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Tebuthiuron: T</td>
<td>1</td>
<td>1.767</td>
<td>3.43</td>
<td>0.113</td>
</tr>
<tr>
<td>Season: S</td>
<td>2</td>
<td>2.330</td>
<td>4.52</td>
<td>0.063</td>
</tr>
<tr>
<td>T x S</td>
<td>2</td>
<td>0.322</td>
<td>0.62</td>
<td>0.367</td>
</tr>
<tr>
<td>Error 1</td>
<td>6</td>
<td>0.515</td>
<td>0.114</td>
<td>6</td>
</tr>
<tr>
<td>Tebuthiuron: G</td>
<td>18</td>
<td>0.092</td>
<td>1.02</td>
<td>0.440</td>
</tr>
<tr>
<td>Season: G</td>
<td>18</td>
<td>0.072</td>
<td>0.80</td>
<td>0.695</td>
</tr>
<tr>
<td>T x G</td>
<td>36</td>
<td>0.071</td>
<td>0.79</td>
<td>0.783</td>
</tr>
<tr>
<td>S x G</td>
<td>36</td>
<td>0.065</td>
<td>0.72</td>
<td>0.872</td>
</tr>
<tr>
<td>T x S x G</td>
<td>108</td>
<td>0.090</td>
<td>0.679</td>
<td>174</td>
</tr>
</tbody>
</table>

THI TEXAS JOURNAL OF SCIENCE VOL. 45, NO. 1, 1993
SMALL MAMMAL DENSITIES

Table 3: Pure model I two-way ANOVA of variance (tebuthiuron treatment versus season) comparing density indexes for all species and only *D. ordii* based upon minimum number known to be alive (*N*<sub>mn</sub>).

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sums of squares</th>
<th>Mean squares</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total Species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>506.25</td>
<td>506.25</td>
<td>27.37</td>
<td>0.001</td>
</tr>
<tr>
<td>Season (S)</td>
<td>3</td>
<td>2696.75</td>
<td>898.92</td>
<td>48.59</td>
<td>0.000</td>
</tr>
<tr>
<td>T x S</td>
<td>3</td>
<td>244.75</td>
<td>81.58</td>
<td>4.41</td>
<td>0.041</td>
</tr>
<tr>
<td>Error</td>
<td>8</td>
<td>148.00</td>
<td>18.50</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Dipodomys ordii</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>1</td>
<td>441.00</td>
<td>441.00</td>
<td>22.05</td>
<td>0.002</td>
</tr>
<tr>
<td>Season (S)</td>
<td>3</td>
<td>2225.25</td>
<td>741.75</td>
<td>37.09</td>
<td>0.000</td>
</tr>
<tr>
<td>T x S</td>
<td>3</td>
<td>367.50</td>
<td>122.50</td>
<td>6.12</td>
<td>0.018</td>
</tr>
<tr>
<td>Error</td>
<td>8</td>
<td>160.00</td>
<td>20.00</td>
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</tr>
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</table>

*musculus*, whereas *S. hispidus* and *R. montanus* were the only species from the treated area that were not caught in the untreated area.

In Chi-Square Contingency Tests for spring, autumn, and winter, species composition (the number of individuals captured in summer was too low to perform a meaningful test), data from untreated grids were combined and data from control grids were combined. These combined data sets were tested as untreated and treated areas for each season. Species composition for the autumn season was independent of tebuthiuron treatment (*X^2^ = 5.52, df = 2, P > 0.05*). No significant difference in species composition existed between treated and untreated areas. In contrast, a highly significant difference in species composition (*X^2^ = 165.23, df = 2; P < 0.001) occurred in winter because of tebuthiuron treatment. More than half the Chi-square value (approximately 56 percent) was attributable to the higher than expected number of *O. leucogaster* captured in the untreated areas, and about 30 percent was due to *Peromyscus maniculatus* and *N. micropus*, which were combined to meet Chi-square grouping rules (Sokal and Rohlf, 1981). The remainder was due to the larger than expected numbers of *D. ordii* in the treated areas. Species composition in spring was significantly different in treated and untreated areas (*X^2^ = 7.04, df = 2, 0.05 > P > 0.025), also mainly because of the high numbers of *O. leucogaster* (approximately 71 percent). The remaining 29 percent of the deviation was due to the slightly higher numbers of *D. ordii*, *P. maniculatus*, *R. montanus*, *P. flavescens*, and *N. micropus* in the treated areas.

*Species densities.*—The way in which tebuthiuron affected rodent density (*N*<sub>mn</sub>) depended upon season (a significant interaction, *P* = 0.041; Table 3); for the most part, the interaction related to the magnitude of the effect of the conversion, rather than to its direction. Mean densities
of all rodents were never higher in the untreated areas compared to the treated areas (Fig. 2). The two-way ANOVA for abundances (N_{min}) of D. ordii (Table 3) produced similar results, with a significant season by tebuthiuron treatment interaction (P = 0.018). Again, the interaction was affected mostly by variation in the degree to which tebuthiuron areas exhibited elevated densities compared to untreated areas. The average density of D. ordii on the untreated areas never exceeded that of the treated areas (Fig. 3). Orthogonal a priori comparisons (Sokal and Rohlf, 1981) of total rodent numbers within each season indicated significant differences between treated and untreated areas in all seasons except summer; whereas, only winter showed a significant difference in D. ordii densities between treated and control areas. The Welsch Step-Up Procedure (Sokal and Rohlf, 1981), although less powerful than either ANOVA or a priori comparisons, revealed seasonal differences in rodent density within treated and within control areas in tebuthiuron treated areas. Winter and summer total density indices were each significantly different (P < 0.05) from all other seasons; whereas autumn and spring total density indices were statistically indistinguishable (P > 0.05). In the control areas, winter total density was significantly different than both spring and summer total density indices, whereas spring, summer, and autumn densities were statistically indistinguishable. In tebuthiuron
treated areas, the winter density index for *D. ordii* was statistically
different than that for all other seasons; spring, summer, and fall density
indices for *D. ordii* were statistically indistinguishable. In untreated areas,
density indices of *D. ordii* were statistically indistinguishable.

**Overview**

Canopy cover and vertical height are important determinants of rodent
species composition and abundance in arid or semi-arid environments
(Rosenzweig and Winakur, 1969; Price, 1978). In our study also, rodent
densities were higher in treated areas, which exhibited greater canopy
cover and vertical height, than in control areas in each season. *D. ordii*
abundance paralleled seasonal changes in percent bare ground;
abundance was highest in the winter, followed by autumn, spring, and
summer. This parallels observations that Merriam’s kangaroo rat (*D.
merriami*), a congener of *D. ordii*, had an affinity for feeding in areas of
bare ground (Rosenzweig and Winakur, 1969; Rosenzweig, 1975).

Like other studies involving habitat manipulation (Rosenzweig and
Winakur, 1969; Brown et al., 1972; Rosenzweig et al., 1975; Feldhamer,
1979), rodent species composition and density were affected by
tebuthiuron-induced changes in sand shinnery oak habitats. Rodent
numbers increased in tebuthiuron treated areas. Moreover, seasonal
fluctuations in $N_{\text{max}}$, whether indicative of behavioral responses or actual changes in density, were different in treated and untreated areas, as indicated by significant interaction terms in the ANOVA and detailed in $A$ priori and $A$ posteriori analyses. In part, these results contrast with those of Parmenter and MacMahon (1983), who found that shrub removal had no effect on *Peromyscus maniculatus*, *Perognathus parvus*, *Onychomys leucogaster*, and *Spermophilus armatus* in a sagebrush dominated shrub-steppe ecosystem in southwestern Wyoming. In that study, shrubs were removed manually without subsequent replacement by other plants. In our study, the absolute increase in rodent density may be a response to shrub removal, the subsequent dominance of the grass component, or both. As in the work of Parmenter and MacMahon (1983), species composition did not change in our study. Rosenzweig and Winakur (1969) considered the biotic variability of arid environments to provide many opportunities for specialization. The sand shinnery oak ecosystem, as well as the mid-grass prairie that resulted from tebuthiuron application, was dominated by generalist rodents. *D. ordii* has been described as a good generalized competitor (Garner, 1974, Parmenter and MacMahon, 1983); the other species caught in this study are plastic with regard to food and habitat requirements (Davis, 1978).

We hypothesize that the rodent community that presently characterizes sand shinnery oak habitats is a relictual subset of the original mid-grass prairie rodent fauna that was sufficiently generalized to survive the transition. More specialized rodents may not have persisted in the shrub-dominated flora and insufficient time has elapsed to obtain a shrub-adapted suite of species. It is not surprising then, to observe no change in species composition as a result of tebuthiuron-induced reconversion to mid-grass prairie. The effect of the drastic alteration in plant species composition and structure was to differentially modify constituent species abundances, rather than alter species composition.

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**Literature Cited**

SMALL MAMMAL DENSITIES


