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Effects of shrub defoliation on grass cover and rodent species in a Chihuahuan desert ecosystem

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Treatment of a nine-hectare desert shrub community with an herbicide (dicamba) resulted in reduction of the live canopy of creosotebush, *Larrea tridentata*, and an increase in coverage of bush muhly, *Muhlenbergia porteri*. After treatment, *Dipodomys merriami* was replaced by *Dipodomys ordii* as the dominant species. On untreated control areas, *D. merriami* maintained dominance. These changes are interpreted to result from a release of growth inhibition of *M. porteri* by creosotebush and habitat structure selection in *Dipodomys*.

Introduction

Recently Schroder & Rosenzweig (1975) presented experimental data on manipulation of rodent populations which support an hypothesis that habitat selection resulted in the elimination of interspecific competition between the congeners, *Dipodomys merriami* and *Dipodomys ordii*. They found that artificial manipulation of populations did not produce long-term shifts in the population balances of the congeners and suggested this was due to habitat selection. Schroder & Rosenzweig questioned whether population manipulations would have produced similar results under less favorable conditions (such as below average rainfall).

Experimental manipulation of ecosystems is a powerful tool for obtaining insight into the structure and dynamics of the system (Chew, 1974). As part of the U.S./I.B.P. Desert Biome Program, we conducted studies on the effects of defoliation of shrubs by herbicide on the components of a Chihuahuan Desert ecosystem. These studies provided data which can be used to test the hypothesis that habitat selection may result in reduction of interspecific competition between closely related species of heteromyid rodents. They also provided data useful in interpreting the relationships of shrubs and certain grasses in the Chihuahuan Desert.

Methods

The study site was a 9 ha area approximately 5 km E of the Desert Biome Jornada Site, which is 40 km NNE Las Cruces, Dona Ana, New Mexico. The site is part of the drainage of the watershed on which the Jornada Site is located (Whitford, 1976). The study site was located at the lower end of the alluvial fan of the Dona Ana Mountains. Soils were coarse sand to gravel alluvia, and supported a Chihuahuan desert shrub community (Table 1). The soil composition was as follows: stones greater than 2 mm diameter made up 16 per cent of the

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weight; the remaining soil fraction was 63 per cent sand, 16 per cent silt and 21 per cent clay by volume. Soils were the same on the treated and untreated areas.

The 75-year average annual rainfall for this area is 211 mm (Houghton, 1972). Ambient temperature and rainfall were recorded at a weather station on the Jornada Site for the duration of this study.

Pretreatment measurements of vegetation and densities of small mammals were made in July 1971. Herbicide was applied by aerial spraying in September 1971 and again in September 1972. Dicamba herbicide (Banvel®, Vesicol Chemical Company, Chicago) was applied at $2{\cdot}5\ \mathrm{kg\,.\,ha^{-1}}$.

Vegetation was sampled before and after treatment on nine 5×100 m belts. One belt was positioned randomly within each of the nine hectares. Within each belt the number of each species present and the height and width of the canopy of each shrub were recorded. From these measurements, density, canopy cover and canopy volume were calculated. Measurements were taken only of living plants or of those portions of plants remaining alive after treatment by herbicide.

In April 1974, after our trapping data suggested that the mammalian fauna on the sprayed area had undergone a change, we selected a control area 1 km away from the treated area. On this area we established a trapping grid identical to that used on the treated site. A comparison was made in 1975 using belt transects on the control area to assess changes in canopy cover not attributable to the herbicide treatment. We established one 5×100 m belt along the boundary of each side of the treated area and measured the height and width of each species. Pretreatment, treated, boundary and control trapping areas were compared statistically by means of analysis of variance (Sokal & Rohlf, 1969).

Rodents were sampled over four consecutive nights at each sampling period. Treated and control areas were trapped simultaneously in mid-summer during each year of the study. Sherman livetraps baited with cracked milo were set on a 150×150 m grid of 100 stations with double traps at alternate stations. The grid was located in the center of the herbicide-treated area. Traps were checked at dawn, and trapped animals were marked by removal of one toe on the left front foot and released. Population densities were estimated by the Lincoln Index. When insufficient numbers of marked animals were captured to provide an accurate estimate, the total number of different individuals captured over the four-night period was used as a minimal estimate of the population density. On the control areas the minimal estimate approached the Lincoln Index estimate, whereas on the treated sites the large differences were the result of fewer recaptures.

Results

Drought conditions persisted from November 1970 until the end of June 1972 (218 mm rainfall) with the monthly maximum (40·4 mm) occurring in October 1971. This resulted in little growth of perennial forbs or annual grasses and forbs. Above average rainfall occurred nearly every month from June 1972 to August 1973 (611 mm). Extremely dry conditions persisted from September 1973 to July 1974 (25 mm) followed by wet conditions for the remainder of 1974 (> 300 mm).

Treatment with dicamba herbicide resulted in a marked decrease in shrub cover and a marked increase in cover of one species of grass, *Muhlenbergia porteri* (Tables 1 and 2). Shrubs recovered from the greatest reduction in canopy found in 1973 and by 1975 there was some increase in canopy in *Larrea tridentata*, *Flourensia cernua* and *Prosopis glandulosa* when compared with 1973 (Table 1). There was also a general increase in grass cover after treatment with herbicide; however, in only one species, *M. porteri*, was the increase in cover significantly different from the untreated border and control areas (t tests for unequal sample sizes, $P = 0{\cdot}05$) (Table 2).

Herbicide treatments had no measurable effect on the rodent fauna when the data were compared with those data for the nearby untreated Validation Site for the same time periods (Whitford, 1976). After shrub cover was reduced by a second treatment with dicamba, there

Table 1. *Changes in plant cover (%) following herbicide treatment in 1971 and 1972*

Species	1971 Pretreatment	1972 Treated area	1973 Treated area	1975 Treated area
Shrubs				
Larrea tridentata	9·5	2·8*	1·4*	1·9*
Prosopis glandulosa	2·6	2·0	0·4*	1·4*
Flourensia cernua	2·8	0·1*	<0·1*	0·2*
Lycium berlandieri	1·6	0·1*	<0·1*	<0·1*
Condalia lycioides	0·1	<0·1	<0·1	<0·1
Xanthocephalum sp.	<0·1	<0·1	<0·1	<0·1
Grasses				
Hilaria mutica	0·2	0·1	0·5	0·8
Muhlenbergia porteri	0·8	1·3*	4·3*	6·3*
Scleropogon brevifolius	<0·1	<0·1	<0·1	<0·1
Sporobolus flexulosus	<0·1	0·1	1·0	1·0
Erioneuron pulchellum	<0·1	<0·1	<0·1	0·4

* Cover percentage significantly different from pretreatment.

Table 2. *Comparison of plant cover (%) for two major shrubs and two major grasses on the herbicide treatment area, a control area 1 km to the south and the treatment area boundaries*

Species	1971 Pretreatment	1975 Herbicide treatment	1975 Treatment boundaries	1975 Control area
Shrubs				
Larrea tridentata	9·5	1·9	9·0	5·1
Flourensia cernua	2·8	0·2	4·4	5·3
Grasses				
Muhlenbergia porteri	0·8	6·3	2·2	2·8
Sporobolus flexuosus	0·1	1·0	0·5	0·9

Mean cover values underlined by the same solid line are not significantly different at the 5 per cent probability level.

was an influx of *D. ordii* into the area (Table 3). Because density of *D. ordii* on the treated area in 1973 was considerably higher than that recorded on the untreated Validation Site in 1974, we trapped the treated area and the untreated control. Comparison of data for 1974 and 1975 demonstrated that the high density of *D. ordii* persisted on the treated area but that *D. merriami* was the dominant species on the control area (Table 3). Although density of *D. merriami* was reduced on the treated area, the total density of the two species of *Dipodomys* on the treated area appeared to be greater than was that on the untreated. The number of recaptures was considerably lower on the treated than on the untreated area; if minimal estimates were used, the densities in July 1974 were 21 *D. ordii* and six *D. merriami*.

Rodents other than *Dipodomys* exhibited no consistent pattern (Table 3). The data from 1975 suggest that several species which appear to be typical minor components of Chihuahuan Desert shrub communities (Whitford, 1976), such as *Neotoma* spp. and *Peromyscus maniculatus*, did not become established on the treated site possibly due to the reduction in shrub cover but there are insufficient data to test this idea.

Table 3. *Rodent densities (number.ha^{-1}) on the treated site (T) and adjacent control site (C)*

	1971 July Pre-treatment	1972 July T	1973 July T	1974 April T	1974 April C	1974 July T	1974 July C	1975 July T	1975 July C
Dipodomys merriami	12·8	22·9	16·8	21·2	12·2	10·7	16·1	10·5	19·6
Dipodomys ordii	0·6*	0	12·4	22·5	3·6	57·2	7·6	28·8	2·4*
Dipodomys spectabilis	0	0	0	0·6*	0·6	0	0	0	0
Perognathus flavus	1·2*	0	2·6*	18·2*	5·1	50·0*	25·3	5·2	5·8*
Perognathus penicillatus	0	0·7	0·6*	0	0	0	0	0	0
Onychomys torridus	1·2*	0·7	2·1	0·6*	0	0	0	0	1·7*
Peromyscus maniculatus	0	2·1	0·6*	0	1·8	0	0	0	1·7*
Neotoma albigula	0·6*	0	0	0	0	0	0	0	0·6*
Neotoma micropus	0	0	0·6*	1·2*	0	0	0	0	0·6*
Reithrodontomys megalotis	0	0	0	1·2*	0	0	0	0	0·6*

Density estimates are calculated by Lincoln Index except where * indicates minimum estimate of total number of individuals trapped during the 4 day period

The other species that was consistently present was *Perognathus flavus*, but there was no consistent pattern in the abundance of this species (Table 3). Whitford (1976) discussed the erratic population responses of this species and found no consistent relationship between food and climate and numbers. Therefore, no conclusions can be drawn regarding the effects of habitat manipulation on *P. flavus*.

Discussion

The slight recovery of shrub canopy after treatment with herbicide represents the growth response of shrubs which were not completely killed. The increases in grass cover were due primarily to the moist growing conditions in 1972–74 which resulted in similar increases on the treated and untreated areas.

The increase in cover of bush muhly, *M. porteri*, appeared to be the result of release from competition or inhibition by creosotebush, *Larrea tridentata*. The normal growth habit of *M. porteri* is as a clump of grass within the stems of the creosotebush which apparently serves as a nurse plant. The advantages which accrue to young *M. porteri* when becoming established under creosotebush (such as protection from large grazing herbivores) might be balanced by competition for water and nutrients with *L. tridentata*, or perhaps by the effect of growth inhibitory compounds released by creosotebush. Regardless of the mechanism of inhibition, killing of creosotebush resulted in significant increase in growth rate of *M. porteri* when compared to the cover changes on the control plots.

In their study of desert rodents in sand dune habitats, Brown & Lieberman (1973) found considerable overlap in seed size selection and habitat utilization in *D. merriami* and *D. ordii*. Schroder & Rosenzweig (1975) reported competition coefficients determined from overlap in habitat utilization ranging from 0·85 to 0·98 for these two species. Such high habitat overlap suggests that habitat perturbation should not favor one species more than the other. In addition, Schroder & Rosenzweig considered *D. ordii* and *D. merriami* as likely competitors because of their similar size and morphology.

In a study of habitat, diet, microenvironment and physiology of these species in southern New Mexico, Gaby (1972) found that *D. merriami* inhabited rockier soils and made shallower burrows than did *D. ordii*. He found dietary overlap based on weight and on importance value, but showed the diets to be quite different. *Dipodomys ordii* was less tolerant of high temperatures, whereas *D. merriami* had a higher metabolic rate at low ambient temperatures. Based on these data, Gaby (1972) concluded that *D. ordii* and *D. merriami* were well separated ecologically and were not competing even though they occurred together on 10 of the 24 sites studied in Dona Ana County, New Mexico.

In studies on the nearby Jornada Validation Site, we frequently caught *D. merriami* and *D. ordii* at the same trap station. This suggests that there is considerable habitat overlap (Whitford, 1976) but the features of the habitat that favor one or the other are not clear.

The data from this study document shifts in relative abundance of *D. ordii* and *D. merriami* following reduction in shrub cover and concomitant increases in grass cover. *Dipodomys ordii* initially appeared in 1973 when grass cover was increasing in all areas of the Jornada. This increase in grass cover corresponds to that reported by Schroder & Rosenzweig in 1972 and 1973 for their study area near Socorro, New Mexico.

Whitford (1976) reported that populations of *D. ordii* remained at approximately one per hectare during 1972 and increased to five per hectare in 1973, whereas densities of *D. merriami* ranged between 30 and 40 per hectare in 1972 and 1973. The replacement of *D. merriami* by *D. ordii* as the most abundant species on the treated site in 1973 and in subsequent years probably is the result of the change in habitat structure. Because the soil structure was the same on the treated and untreated areas, the differences in abundance cannot be attributed to soils as suggested by Davis & Robertson (1944). Also, because stems and root systems of dead shrubs remained intact, burrow sites were not unlike those in areas supporting live shrubs. Schroder & Rosenzweig (1975) thought *D. merriami* and *D. ordii* might avoid competition by utilizing different portions of the same habitat, and suggested that grassier habitats favored *D. ordii*. Their hypothesis is supported by the results of this study because the increased grass and reduction of shrub cover on the treated area favored *D. ordii* while on the shrub-dominated control area *D. merriami* was the most abundant species and *D. ordii* occurred at much lower density.

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