Rodent effects on shrubs in a Mojave Desert shrub community

Steven Schuyler Vrooman

University of Nevada, Las Vegas

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RODENT EFFECTS ON SHRUBS IN A MOJAVE
DEsert shrub community

by

Steven Schuyler Vrooman
Bachelor of Science
New Mexico Tech
1995

A thesis submitted in partial fulfillment
of the degree requirements for the degree of

Master of Science

in

Biological Sciences

Department of Biological Sciences
University of Nevada, Las Vegas
May 1999
The Thesis prepared by

Steven Schuyler Vrooman

Entitled

Rodent Effects on Shrubs in a Mojave Desert Shrub Community

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Master of Science in Biological Sciences

Examination Committee Chair

Dean of the Graduate College

Examination Committee Member

Examination Committee Member

Graduate College Faculty Representative
ABSTRACT

Rodent Effects on Shrubs in a Mojave
Desert Shrub Community

by

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Dr. Lawrence R. Walker, Examination Committee Chair
Dr. Daniel B. Thompson, Examination Committee Chair
Associate Professors of Biological Sciences
University of Nevada, Las Vegas

The mounds created by many species of Dipodomys (kangaroo rats) are long-term modifications of the soil chemical and physical environment which have been shown to increase both the diversity and abundance of annuals in the deserts of the Southwestern United States. I characterized shrub distribution and soil parameters on and off rodent mounds in a Coleogyne ramosissima community in Lucky Strike Canyon near Las Vegas, Nevada and performed several experiments to investigate rodent effects on seedlings and seeds of C. ramosissima. Rodent mounds were found to be long-term modifications of the soil physical and chemical environment which support a higher diversity of shrub species than the surrounding environment. Both rodent foraging activities and mound building play a role in maintaining shrub diversity in the C. ramosissima community at Lucky Strike Canyon.
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CHAPTER 1

SHRUB AND SOIL CHARACTERISTICS ON RODENT MOUNDS IN A COLEOGYNE COMMUNITY

ABSTRACT

The mounds created by many species of Dipodomys (kangaroo rats) are long-term modifications of the soil physical and chemical environment which have been shown to increase both the diversity and abundance of annual plants in the deserts of the Southwestern United States. I characterized shrub distributions and examined variation in soil parameters on and off rodent mounds in a Mojave Desert plant community dominated by Coleogyne ramosissima in Lucky Strike Canyon in the Spring Mountains near Las Vegas, Nevada. Shrub cover, size, and diversity were higher on mounds than in the surrounding environment. Total soil nitrogen and organic matter were higher and soil bulk density was lower on mounds. Few differences were found between active and inactive rodent mounds, indicating that positive effects of mounds last for some time after abandonment. Rodent mound building in Lucky Strike Canyon causes a prolonged series of changes in soil physical and chemical parameters which are positive for the growth and recruitment of many plant species and may increase the diversity of shrub species in the Coleogyne community.
INTRODUCTION

Desert environments are characterized by low rainfall, large variations in temperature and infertile soil. These harsh environmental conditions may play a large role in determining plant distributions, especially compared with more temperate systems. Large-scale elevational and geographic variation in abiotic conditions may determine which plant species are found in a community, yet have little effect on the distribution and abundance of plants within that community. However, microhabitat variations in abiotic conditions occur on the scale of individual plants and can strongly affect plant establishment and growth.

Microhabitat variations in soil fertility can be influenced by the location of adult plants in the community. Many studies in deserts have documented a pattern of high soil fertility under shrubs compared with surrounding open areas (Charley and West, 1975; Garner and Steinberger, 1989; Schlesinger et al. 1996). The establishment of a shrub in an open area initiates a number of long-term changes in the local environment which may lead to the establishment of a “fertile island” under that shrub (Romney et al. 1978). The production of litter by the shrub, increased animal activity, and the entrapment of windblown litter all contribute to a pattern of high soil organic matter and nitrogen in the fertile island (Garner and Steinberger, 1989).

One of the factors responsible for the creation of fertile islands is the concentration of animal activity under shrubs. Most rodents in the family Heteromyidae are obligate desert granivores and are important components of the communities in which they live. Heteromyid rodents concentrate their activities under shrubs due to both the concentration of food in that microhabitat as well as protection from environmental extremes and predation (Jorgensen et al. 1995; Longland, 1994; Price and Reichman, 1987; Thompson, 1982). The concentration of rodent activity on the fertile island acts to localize rodent excretion and therefore nitrogen in this microhabitat.
Heteromyid rodents can also effect the distribution and abundance of soil nutrients by the creation of rodent mounds. Many species of the heteromyid genus *Dipodomys* (kangaroo rats) build large, conspicuous mounds which contain many tunnels and chambers and extend deep into the soil (Kenagy, 1973). The soils of mounds created by *Dipodomys spectabilis* have higher levels of nitrogen and organic matter as well as lower bulk density than adjacent non mound soils, all properties which may enhance plant establishment and growth (Mun and Whitford, 1990). These positive properties of mound soils may be a reason for the well documented increase in annual plant abundance and diversity on the mounds of *D. spectabilis* (Moroka et al. 1982; Moorhead et al. 1988; Mun and Whitford, 1990)

*Dipodomys spectabilis* mounds can have positive effects on shrubs as well. In a study in the Chihuahuan Desert of Southeastern Arizona, *Larrea tridentata* (creosotebush) on mounds showed an increase in growth, flowering, and fruiting compared with off-mound plants (Chew and Whitford, 1992). This positive effect of mounds on *Larrea* occurred even as the *Larrea* population not on rodent mounds was declining in size and vigor. The mounds, abandoned for 60 - 80 years, had a positive effect on Larrea even as shrubs not on rodent mounds were declining in size and vigor. These results suggest that *Dipodomys* mounds enhance shrub growth and reproduction and that the positive effects of mound soils may persist for some time after abandonment.

My initial observations in a *Coleogyne ramosissima* (blackbrush) community in the northern Mojave Desert indicated a pattern of high shrub diversity on rodent mounds compared with the surrounding off-mound environment. I examined the changes in mound soils brought about by rodent activity and their relationship with the fertile island effect. I also investigated whether patterns of shrub diversity on mounds could be attributed to long-term changes in mound soils brought about by rodent activity.
METHODS

Site description
This study was performed at the Mojave Experimental Research Plots (MERP) in the foothills of the Spring Mountains, 60 km northwest of Las Vegas, Nevada (Figure 1). This study is part of an ongoing series of experiments at MERP designed to study long-term trends in population dynamics and ecosystem processes in the Mojave Desert. These plots are located on an east-facing bajada of limestone derived erosional material. While MERP consists of multiple sites across a wide elevational and biotic gradient, this study was performed at MERP's Third Elevation Site at 1440 m elevation.

This site is dominated by Coleogyne ramosissima (blackbrush), which comprises about 85% of total shrub cover and is considered a distinct community in the Mojave Desert (Wallace and Romney, 1972). The topography of the site consists of a system of benches 20 - 100 meters wide and 200 - 400 meters long divided by a system of washes 2 - 5 m deep with steeply sloping sides. The soil surface on benches is usually covered by desert pavement and is underlain by hardpan caliche (CaCO₃) at 0.4 - 0.6 meters depth.

Lucky Strike Canyon receives an average annual rainfall of less than 20 cm. Summer thunderstorms are localized and short lived while winter storms are usually widespread and can last for several days. Winter temperatures often drop below -10 °C while summer highs can top 40 °C.

Plot selection
A large bench of the bajada at the southwest corner of the upper MERP site was chosen as the study location to minimize the effects of the washes that dissect the bajada. Using the MERP cornerpost as the focal point, three 1 ha study plots were laid out in an "L" shape pattern (Figure 1). Within each study plot, three 10 x 30 m mound sample
Figure 1 Site description
plots were laid out at randomly chosen points with their long axes running east to west. If two mound sample plots were less than 10 m from each other a new position was chosen randomly for one of them. The initial location selected for plot eight was in a wash so the plot was moved east onto the adjacent bench. The mound sample plots were numbered 1 - 9 from the northeast in a counter-clockwise direction.

All mound sample plots were censused for both active and inactive rodent mounds. Active mounds were classified as areas of disturbed, mounded soils with 1 or more holes leading into them. Inactive mounds were identified as areas of loose, slightly-mounded soils with a large percentage of the soil surface covered by either loose soil or large pieces of caliche. Inactive mounds did not have any visible holes leading into them. Two measurements were taken for each mound, one of the long axis and one perpendicular to the long axis at the widest point of the mound. The area of each mound was estimated from these two measurements by using the equation for an ellipse (radius 1 * radius 2 * π). The minimum long axis for a mound was 30 cm, smaller areas of disturbed soils were left out of this study.

Because sampling of mounds on plots 1-9 caused disturbance in much of the off-mound areas, 10 m x 30 m off-mound control plots were placed adjacent to each sample plot so that the two plots shared one 30 m boundary line. Most of the control plots were placed on the north side of a sample plot, but two were moved to the south due to their being within 10 m of another control or study plot. These plots were numbered 11 - 19 with control plot 11 being placed next to sample plot 1, control plot 12 next to sample plot 2, etc.

To provide a comparison with the mound measurements, false mounds were created on each off-mound control plot to represent the background, non-mound vegetation. Ten random points within each control plot were chosen to provide a focal point for each false mound and each was marked with a large nail. Mound areas were
divided into five size classes. Steel lumber strapping was made into circular hoops of area 0.22 m$^2$, 0.7 m$^2$, 1.51 m$^2$, 4.17 m$^2$, and 9.43 m$^2$, each representing the average of a size class. When the false mounds were censused, each one was randomly assigned to a size class. The edge of the appropriate hoop was placed at the nail with its long axis pointing west. This provided an easily repeatable way to delineate the boundaries of each false mound without permanently marking them.

Rodent Trapping

Rodent trapping was performed to identify the species present and to estimate their relative abundances. Three 5 X 5 trapping grids (5 m trap interval) were created on the north, south, and east sides of the three study plots. Each station consisted of a single Sherman live trap baited with a mixture of peanut butter and rolled oats. Traps were set in late afternoon and checked the following morning at 0630. Each rodent was identified as to species and sex, and marked with a permanent marker to measure recaptures. Trapping was performed for three consecutive nights during the new moon to minimize rodent avoidance of open spaces due to moonlight. The first trapping session was performed on July 6 - 8, 1997. The second session was performed from August 30 - September 1, 1997.

Soil Methods

Soils were collected from both mound and false mound sample plots in August, 1997. Sampling was concentrated on a line extending from the center of the mound sample plot in a northward direction and open soil samples were taken at least 10 cm outside the dripline of the nearest shrub. Soils were collected from both shrub and open sites or from whichever habitat was present. First the surface litter was removed, then a small trowel was used to remove the soil in a 5 x 5 x 10 cm hole. This sample was then
placed in an air-tight soil tin and stored in a cooler until all samples could be transported to the laboratory. At the same soil collection sites, measurements were made of surface compaction. I used an approximation of the Dynamic Cone Penetration Test (Capper and Cassie, 1978). A 2 kg weight was dropped from a height of 10 cm onto the end of a piece of 1/2 inch rebar held vertically at the surface of the soil. The depth to which the rebar penetrated was recorded as penetrance. This depth measurement was assumed to be inversely related to soil bulk density, but the exact relationship could not be calculated.

In the laboratory, all soils were passed through a 2 mm sieve. Gravimetric soil moisture content was determined on soils dried at 105 °C for 36 hours. Soil pH was measured with a glass electrode on a mixed sample of 5 g dry soil and 5 ml deionized H₂O (McLean, 1982). Organic matter content of soils was determined by a measurement of percent total weight lost after ignition at 550 °C for 4 hours. A 0.6 g sample of each soil was digested in a solution of sulfuric acid and a mercuric acid catalyst, and then analyzed colorimetrically for total Kjeldahl nitrogen using a salicylate procedure (Environmental Protection Agency 1984). Soil salinity was assessed by making saturation extracts of 10 g from each soil sample and by taking readings with an electrical conductivity bridge (Rhodes, 1982).

Shrub Measurements

The length, width, and height of all perennial shrubs greater than 15 cm in height and rooted within the border of each mound were measured on both sample and control plots and the species of each shrub was noted. Shrubs were excluded if their stems were clearly not growing out of disturbed mound soils even if some part of their canopies overlapped the mound area. This excluded shrub cover was assumed to be
Table 1 Numbers of individuals of each species captured in two trapping sessions, the first from July 6 - July 8, 1997, the second from August 30 - September 1, 1997. There was a total of three trapping nights in each session. Pelo = *Perognathus longimembris*, Chfo = *Chaetodipus formosus*, Peer = *Peromyscus eremicus*, Dime = *Dipodomys merriami*.

<table>
<thead>
<tr>
<th>Session</th>
<th>Date</th>
<th>Pelo</th>
<th>Chfo</th>
<th>Peer</th>
<th>Dime</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>July 6 - 8</td>
<td>16</td>
<td>7</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>2</td>
<td>Aug. 30 - Sep. 1</td>
<td>0</td>
<td>16</td>
<td>8</td>
<td>11</td>
</tr>
</tbody>
</table>
canceled out by the inclusion of shrubs on the mound whose canopies extended beyond
the borders of the mound. The length and width of each shrub were used to calculate
the area using the formula for the area of an ellipse. Each species’ cover was summed
and divided by the mound area to obtain the percentage total cover for the entire mound.
Density for all perennial vegetation was also determined, but due to the clonal nature of
_Ephedra nevadensis_ (Wallace and Romney, 1972), percent cover was used as a more
appropriate measure of proportional abundance on mounds.

Shrub analyses were performed with a non-parametric Wilcoxon rank-sum test
on JMP (SAS Institute, 1994) due to the non-normality of rare shrub measurements.
Percent cover for all species were square root - arcsin transformed prior to analysis. A
two-way, fixed factor analysis of variance (ANOVA) was used to analyze soil
parameters. Soil moisture, percent organic matter, and percent total nitrogen were also
arcsin-transformed prior to analysis. A sequential Bonferroni technique described by
Rice (1988) was used to adjust for multiple comparisons. All values for shrub and soil
analyses were reported as means with standard errors and significance was determined
at P < 0.05.

RESULTS

The overall mound density in the mound sample plots was 411 mounds/ha;
8.6% of the mound sample plot area (2,700 m²) was occupied by rodent mounds.
There were 111 mounds identified in this study and 56% of them were active. The
mean size of mounds in this study was 2.09 m² ± 0.23.

Two separate rodent trapping sessions were run, the first from July 6 - 8, and
the second from August 30 - September 1 (Table 1). During the first session,
_Perognathus longimembris_ was the most frequently captured, with 16 captures over the
three day period. _Chaetodipus formosus, Peromyscus eremicus, _and _Dipodomys_
Figure 2 Percent organic matter, percent total nitrogen, pH, and salinity of soils from four microhabitats (see methods). Data are means with standard errors. Means with a different letter indicate statistical significance (P < 0.05).
Figure 3  Percent moisture in summer, percent moisture in spring and penetrance (inversely related to bulk density) of soils from four microhabitats. Data are means with standard errors. Means with a different letter indicate statistical significance (P < 0.05).
merriami were also captured in moderate numbers. Individuals of Dipodomys microps, Onychomys torridus, and Sylvilagus auduboni were each captured once.

No P. longimembris were captured during the second trapping period, possibly due to that species being in torpor at that time (Table 1). Chaetodipus formosus was the most frequently captured species with 16 captures. Many individuals of D. merriami and P. eremicus were also captured, with 11 and 8 captures respectively. Onychomys torridus and Amnotherus leucurus were each captured twice during the second trapping period.

On the off-mound control plots, both salinity and penetrance were significantly higher (2-way, fixed-factor ANOVA) for soils under shrubs than in the open (Figures 2 and 3). The pH of soils under shrubs was slightly lower than in the open, but the difference was not significant. There were no significant differences in organic matter and total nitrogen between shrub and open soils off-mound. No significant difference in moisture levels in spring or summer was noted between shrub and open soils off-mound either (2-way, fixed-factor ANOVA).

The mound open and mound shrub habitats did not show any significant difference for any of the soil parameters measured (Figures 1 and 2). However many differences were found between mound soils and off-mound soils in nearly all the parameters measured (2-way, fixed-factor ANOVA, p = 0.05). Both mound shrub and open soils were significantly higher in total nitrogen and organic matter than off-mound shrub and open soils. Salinity in mound shrub and open soils was higher than in off-mound open soils and not significantly different than the off-mound shrub habitat. Soil moisture levels at the spring or summer sampling dates were not different between any habitats. Penetrance was higher for both mound shrub and open habitats than either off-mound habitat. The pH of mound shrub and open soils was not significantly different than off-mound shrub soil, but was significantly lower than off-mound open soil.
C. ramosissima comprised 85% of the total off-mound shrub cover (Table 2). Only C. ramosissima and E. nevadensis had measureable cover off-mound, although one Atriplex canescens was located in an off-mound plot. Total shrub cover was much higher on than off rodent mounds (Table 2). Both C. ramosissima and E. nevadensis had significantly higher percent cover on mounds than off, with the percent cover of E. nevadensis on mounds measuring almost 600 times more than off-mounds. The average volume of individual C. ramosissima was larger on mounds than off (Table 3). The average size of E. nevadensis on mounds tended to be larger than on off-mound sample plots, however the difference was not quite significant (1-way, fixed-factor ANOVA, p = 0.054).

Rare shrub species such as Grayia spinosa, Tetradyntia canescens, Menodora spinescens, and Lycium andersonii were found only on rodent mounds (Table 2). The difference in cover of G. spinosa between mounds and off-mounds was significant. T. canescens, M. spinescens, and L. andersonii were all so rare that their percent cover on mounds was not significantly different than 0. However, on average these rare species comprised about 20% of the total shrub cover on the mounds where they were found.

Few significant differences (1-way, fixed-factor ANOVA) were found between active and inactive mounds in either total cover, individual shrub species cover, or soil parameters (Tables 4 and 5). Penetrance on active mounds was significantly higher (1-way, fixed-factor ANOVA, p = 0.002), indicating that the soil density of active mounds was lower than inactive mounds.
Table 2 Mean and standard error of percent cover of perennial shrub species on rodent mounds and at randomly chosen locations off of rodent mounds. Means are reported for 111 mound and 90 off-mound samples. Statistical significance determined by 1-way, fixed-factor ANOVA on JMP (* p < 0.05, ** p < 0.01, *** p < 0.001).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mounds Mean</th>
<th>Mounds SE</th>
<th>Off-mounds Mean</th>
<th>Off-mounds SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total cover</td>
<td>62.191***</td>
<td>0.111</td>
<td>4.501</td>
<td>0.138</td>
</tr>
<tr>
<td>Coleogyne ramosissima</td>
<td>32.773***</td>
<td>0.144</td>
<td>3.809</td>
<td>0.178</td>
</tr>
<tr>
<td>Ephedra nevadensis</td>
<td>8.878***</td>
<td>0.067</td>
<td>0.015</td>
<td>0.083</td>
</tr>
<tr>
<td>Grayia spinosa</td>
<td>0.329***</td>
<td>0.030</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tetradyemia canescens</td>
<td>0.018</td>
<td>0.004</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Menodora spinescens</td>
<td>0.014</td>
<td>0.004</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lycium andersonii</td>
<td>0.010</td>
<td>0.004</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3: Mean and standard error of the aboveground volume (m³) for the two most abundant shrub species on and off rodent mounds. Data are means for 111 mounds and 90 off-mounds. Statistical significance determined by a 1-way, fixed-factor ANOVA on JMP (* p < 0.05, ** p < 0.01, *** p < 0.001).

<table>
<thead>
<tr>
<th>Species</th>
<th>Mounds Mean</th>
<th>Mounds SE</th>
<th>Off-mounds Mean</th>
<th>Off-mounds SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coleogyne ramosissima</td>
<td>0.387*</td>
<td>0.293</td>
<td>0.226</td>
<td>0.244</td>
</tr>
<tr>
<td>Ephedra nevadensis</td>
<td>0.170</td>
<td>0.193</td>
<td>0.117</td>
<td>0.227</td>
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Table 4  Percent cover of shrub species for active and inactive mounds. Data are means for 62 active mound samples and 49 inactive mound samples. Statistical significance determined by a 1-way, fixed-factor ANOVA on JMP (* p < 0.05, ** p < 0.01, *** p < 0.001).

<table>
<thead>
<tr>
<th>Species</th>
<th>Active mounds</th>
<th>Inactive mounds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Total cover</td>
<td>62.223</td>
<td>0.285</td>
</tr>
<tr>
<td>Coleogyne ramosissima</td>
<td>32.694</td>
<td>0.396</td>
</tr>
<tr>
<td>Ephedra nevadensis</td>
<td>7.392</td>
<td>0.160</td>
</tr>
<tr>
<td>Grayia spinosa</td>
<td>0.444</td>
<td>0.029</td>
</tr>
<tr>
<td>Tetradyhia canescens</td>
<td>0.015</td>
<td>0.008</td>
</tr>
<tr>
<td>Menodora spinescens</td>
<td>0.029</td>
<td>0.010</td>
</tr>
<tr>
<td>Lycium andersonii</td>
<td>0.013</td>
<td>0.008</td>
</tr>
</tbody>
</table>
Table 5 Mean and standard error for salinity, pH, percent organic matter, percent total nitrogen, percent moisture in spring, percent moisture in summer, and penetrance values of 60 active mound soil samples and 38 inactive mound soil samples. Statistical significance determined by a 1-way, fixed-factor ANOVA on JMP (* p < 0.05, ** p < 0.01, *** p < 0.001).

<table>
<thead>
<tr>
<th>Species</th>
<th>Active mounds</th>
<th>Inactive mounds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MEAN</td>
<td>SE</td>
</tr>
<tr>
<td>pH</td>
<td>7.840</td>
<td>0.018</td>
</tr>
<tr>
<td>salinity</td>
<td>0.866</td>
<td>0.026</td>
</tr>
<tr>
<td>% organic matter</td>
<td>6.571</td>
<td>0.004</td>
</tr>
<tr>
<td>% nitrogen</td>
<td>2.191</td>
<td>0.000</td>
</tr>
<tr>
<td>% moisture (summer)</td>
<td>0.407</td>
<td>0.001</td>
</tr>
<tr>
<td>% moisture (spring)</td>
<td>3.282</td>
<td>0.001</td>
</tr>
<tr>
<td>penetrance</td>
<td>8.667**</td>
<td>0.433</td>
</tr>
</tbody>
</table>
DISCUSSION

Rodent mounds covered 8.6% of the mound sample plots. Other studies have found Dipodomys spectabilis mounds to make up 2% of the total environment in a semi-desert grassland in southern New Mexico (Moroka et al. 1982). The high percentage of area covered by mounds at my site could be due to the inclusion of mounds from several rodent species, as I measured all the mounds in a size range of 0.2 m² to 10.1 m² in this study. Most of the mounds (80%) were in the middle three size classes (with means of 0.7 m², 1.51 m², and 4.17 m² respectively) and many were probably created by D. merriami. The smaller mounds could have been made by smaller rodent species common at the site such as P. longimembris, C. formosus, or P. eremicus. All of these rodent species are granivorous.

There have been many studies which have documented a pattern of high soil fertility under shrubs compared with open areas in Southwestern U.S. deserts, creating what is known as the fertile island effect (Charley and West, 1977; Schlesinger et al. 1996; Walker et al., in review). While the amount of organic matter under shrubs was slightly higher, there was no significant difference between soil total nitrogen and organic matter between shrubs and open areas off mounds. A paper on the effects of fertile islands on the growth of Ambrosia dumosa seedlings by Walker et al., (in review) found a pattern of high soil fertility under C. ramosissima at MERP at a similar elevation. The lack of a strong fertile island effect between shrubs and open areas off mounds in this study could be due to my sampling methodology. Open soil samples taken from a shrub were sometimes only 10 cm from the dripline. While this was always outside the pattern of shrub litter evident under the canopy of adult shrubs, this could still be within the zone of influence of the shrub effect on soils.

There was some evidence of shrub effects on soil at my site. Penetrance under shrubs was much higher, indicating a lower soil bulk density. The pH of shrub soils
was slightly lower, possibly due to organic acids from the decomposition of shrub litter (Schlesinger, 1997). The salinity of shrub soils was significantly higher, which may be due to an increase in rodent activity under shrubs (Bowers, 1982; Price and Waser, 1985; Thompson, 1987). There was, however, no difference in soil moisture in either the spring or summer soil sampling date between shrub and open areas off mound.

Mound soils were different than off-mound soils in nearly all the parameters measured. Mound shrub and open soils had about twice as much organic matter and total nitrogen as off-mound shrub and open sites. A similar pattern in soil fertility was also reported by Moorhead et al. (1988), although the difference between mound and open soils in their study was not as large as the pattern I observed. A study by Mun and Whitford (1990) also found total nitrogen higher on mounds. The higher levels of nitrogen and organic matter on mounds could be due either to rodent activity or the greater cover of shrubs on mounds, however there was no difference between open and shrub mound soils. This may indicate that the production of litter by shrubs on mounds had only a slight effect on the soils beneath them. Rodent excretion could be one factor responsible for the fertility of mound soils. Another rodent activity responsible for the fertility of mound soils could be the constant turnover of mound soils by the rodent occupants. This could have the effect of "tilling in" litter from both shrubs and the abundant annual plants on mounds (Moroka et al. 1982; Moorhead et al. 1988; Mun and Whitford, 1990). The increase in organic matter due to this turnover of soil could increase microbial decomposition and the availability of nitrogen in mound soils. The turnover of soil would also blur the difference between mound shrub and open soils, and could explain the lack of any difference between these two habitats.

Soil moisture one week after a rain event of about 1 cm (Table 3; percent moisture in spring) did not differ between mounds and off mounds. Soil moisture measurements in the summer (dry season) showed slightly higher percent moisture off
mounds, but the difference was not significant. In a detailed study of the water dynamics of rodent mounds, Mun and Whitford (1990) took soil moisture measurements on and off mounds every three days from January to September at their Chihuahuan Desert site. Their results indicated that mound soils dried faster than off-mound soils. The faster drying rates of mound soils could be due to the physical structure of mound soils such as low soil bulk density and the presence of tunnels into the mounds. These characteristics could increase evaporation from the soil surface, and the large plant cover could increase water loss to the atmosphere through transpiration. The lack of a difference in soil moisture on and off mounds in my study could reflect differences between a Mojave Desert and a Chihuahuan Desert site or could be simply due to my moisture measurements being taken in uniformly wet and dry periods. Even though mound soils may dry faster, they may be more favorable sites for plant growth. Mun and Whitford (1990) found irrigation of off-mound soils to have little effect on the growth of annuals, probably due to nitrogen limitation. Rodent mounds in their study had high levels of available nitrate which allowed annual plants to take advantage of rain events and allowed for both higher numbers and diversity of annuals even though mound soils dried faster than off-mound soils.

Mound soils had a much higher penetrance value which indicated that mound soils had a lower bulk density. Mun and Whitford (1990) found that soil bulk density was much lower on mounds than for off-mound soils. Mounds, especially active ones, protrude 10 or 20 cm above the surrounding ground surface. They have a number of chambers and tunnels in them as well. Tunneling and the continual reworking of the soil on the mound surface, could both be expected to lower the density of mound soils. Chew and Whitford (1992) found mound soils were much deeper than non-mound soils in the surrounding areas, where an impermeable layer of caliche (on average about 30 cm under the surface) was usually present. While mound depth was not measured in
this study, the average depth of the caliche layer at this site was between 40 and 60 cm when measured by Lei (1995). One of the prominent characteristics of the surface of the soil on both active and inactive mounds was the large pieces of caliche found on the surface of the mounds. It is likely that mound-building rodents actively deepen the soil under mounds by burrowing into the caliche layer and bringing these pieces to the surface.

Mounds had a much higher percent cover than off-mound plots which was largely due to the increase in *C. ramosissima* cover on mounds. *E. nevadensis* had a much higher percent cover on mounds; the clonal nature of *E. nevadensis* could allow this species to spread rapidly into the favorable mound habitat. Mounds also had a much higher number of shrub species than off-mound areas. In fact, no individuals of *G. spinosa, L. andersonii, M. spinescens,* or *T. canescens* were found on the off-mound plots. The average size of individual *C. ramosissima* was larger on mounds and the average size of *E. nevadensis* was marginally larger on mounds as well, indicating a positive effect of mounds on shrub vigor. This pattern of increased shrub vigor on mounds was also noted by Chew and Whitford (1990), who observed a positive effect of rodent mounds on the growth, flowering and fruiting of *L. tridentata,* the dominant shrub in this community.

Several studies have noted a high diversity and abundance of annuals on mounds in the Chihuahuan desert (Moroka *et al.* 1982; Moorhead *et al.* 1988; Mun and Whitford, 1990), this has been attributed to both high nitrogen levels and soil physical properties (such as low bulk density) of mound soils (Mun and Whitford, 1990). These same patterns were found in soils at my site. These results suggest that mounds could be a more favorable site for shrub growth than the off-mound environment, resulting in both greater cover and diversity of shrubs on mounds.
If the positive soil characteristics of mounds are responsible for the increase in shrub diversity, these mounds may be older than the shrubs growing on them. However, I was not able to obtain a direct measurement of the age of shrubs or mounds in my study. A study along the Colorado River in Arizona found that many individuals of *L. andersonii*, *E. nevadensis*, and *A. dumosa* had survived for more than 100 years and could possibly have lifespans of several hundred years (Bowers *et al.* 1995). My site in the Mojave Desert, while higher in elevation, receives similar amounts of rainfall, and shrubs at my site could be of equivalent age. If the mound soil characteristics, including soil depth, that promote shrub growth also promote longevity, it is possible that the increased longevity of adults of less common shrub species on mounds, in conjunction with a low survivorship of adult shrubs of these species off mounds, could contribute to the pattern of shrub diversity at my site. However, due to the difficulty in measuring adult mortality in such long-lived shrub species, I did not address this possible mechanism behind increased shrub diversity on rodent mounds.

I found few differences between active and inactive mounds in either shrub species composition or soil characteristics. The only difference between active and inactive mound soils was in penetrance which could be expected to increase with recent rodent activity. Chew and Whitford (1992) found that *D. spectabilis* mounds, which they estimated to have been abandoned for 50 - 60 years, still had positive effects on the growth and flowering of *L. tridentata*. A study by Jones (1986) found that survival to maturity in *D. spectabilis* was increased if that rodent obtained the maternal mound and its associated protection and food supply. The survival of dispersing small rodents at my site should be increased if they reinhabit old mounds rather than build new ones. The high shrub cover, low soil bulk density, and deeper soils would make reinhabiting an inactive mound less of a caloric expenditure than initiating a mound in compacted soil. The rodent mounds at Lucky Strike Canyon probably go through cycles of activity.
and abandonment, with mound soil characteristics remaining stable through long periods of abandonment and each cycle of activity contributing to the fertility of mounds soils.

The long-term soil changes initiated by rodent mound building appear responsible for the high diversity and cover of shrubs on mounds, however, the exact mechanisms are unclear. Some of the increase in shrub cover on mounds can be attributed to the larger size of *C. ramosissima* and *E. nevadensis* on mounds; the soil characteristics of mounds have a positive effect on shrub growth and vigor. Another possible explanation for the increase in shrub cover and diversity could be that mound soils are positive sites for shrub recruitment. The soil characteristics of rodent mounds may foster the establishment and growth of shrub seedlings of many species, this would result in a high number of shrub adults on mounds. This could explain the large differences in shrub cover and diversity between mounds and off-mounds in the *C. ramosissima* community at this site.

The guild of mound-building, granivorous rodents exert a strong effect on shrub abundance and distribution in the *C. ramosissima* community at Lucky Strike Canyon. This effect is positive, rodent activity promotes the diversity and vigor of shrubs, but indirect, as the rodent effect on shrubs is mediated through changes in the soil. While the end result of rodent mound building on shrub diversity is clear, the exact mechanisms responsible for these patterns will require more investigation.
CHAPTER 2

MECHANISMS RESPONSIBLE FOR ENHANCING SHRUB DIVERSITY ON RODENT MOUNDS IN A COLEOGYNE COMMUNITY

ABSTRACT

The mounds created by several species of Dipodomys (kangaroo rats) in the Coleogyne ramosissima community at Lucky Strike Canyon have been found to be long-term modifications of the soil physical and chemical environment and may be partially responsible for the high diversity of shrub species on rodent mounds at this site. I performed experiments to determine the effects of rodent foraging and caching on C. ramosissima seeds as well as to determine the effects of rodent mound soil on C. ramosissima seedlings. The net effect of rodent foraging and caching was to reduce the density of seeds and therefore seedlings on rodent mounds. Rodent mound building contributed to the mortality of C. ramosissima seedlings on mounds, possibly by promoting both light and water stress in seedlings. Rodent activities were found to play a large role in maintaining shrub diversity in the C. ramosissima community.

INTRODUCTION

In a study of the Coleogyne ramosissima community at Lucky Strike Canyon 60 km northwest of Las Vegas, Nevada, I noted a pattern of high shrub cover and diversity
on rodent mounds created by several species of granivorous desert rodents (Chapter 1). Long-term soil changes in soil characteristics initiated and maintained by mound building appear to be responsible for this pattern, however, the exact mechanisms remain uncertain. Mound soils had a positive effect on the growth and vigor of adult *Coleogyne ramosissima* and *Ephedra nevadensis*, this could explain some of the increase in shrub cover on mounds. However, this enhancement of adult shrub growth does not provide a mechanism for the increase in shrub diversity on rodent mounds.

One possible mechanism for the increase in cover and diversity on mounds could be that mounds are positive sites for the recruitment of many shrub species. If the soil characteristics of rodent mounds are favorable for the establishment and growth of shrub seedlings, the greater number of shrub seedlings on mounds would lead to a greater number of shrub adults on mounds as well. However, preliminary measurements of a cohort of *C. ramosissima* seedlings show that seedlings are no more numerous on mounds than off-mounds, despite a much higher cover of adult *C. ramosissima* on mounds. This may indicate that mounds are actually poor sites for the recruitment of shrub seedlings. If rodent mounds are poor habitats only for *C. ramosissima* recruitment, however, space not occupied by *C. ramosissima* might be utilized by seedlings of other shrub species.

Desert rodents can be very important components of the communities in which they live. The amount of yearly net primary production (NPP) rodents consume may be less than 10% of the total, yet this may actually mean consumption of 80-90% of the yearly seed crop of some plant species (Chew and Chew, 1970; Soholt, 1973). Most rodents of the family Heteromyidae are obligate desert granivores found in the deserts of the southwestern U.S. By concentrating their consumption on just one stage of the life cycle of plants, they can have effects on plant communities that are out of proportion to the amount of plant biomass they consume.
Several studies in the Chihuahuan Desert have shown shifts in the abundance of annual plant species due to the experimental removal of granivorous rodents. Large-seeded winter annuals are preferred by rodent granivores, in the absence of predation large-seeded annuals are competitively dominant and suppress the local diversity of other annual species (Samson et al. 1992; Guo et al. 1995; Davidson et al. 1985). In an experiment by Brown and Heske (1990), long-term removal of three species of Dipodomys (kangaroo rats) caused a shift in the vegetation type from desert shrub to grassland. They concluded that these three species were a keystone guild in this system as shown by the large changes that resulted from their exclusion. These experiments show that foraging by desert granivores can increase the abundance and diversity of annuals.

A number of studies have found that Heteromyid desert rodents concentrate much of their foraging activities under the canopies of shrubs (Jorgensen et al. 1995; Longland, 1994; Thompson, 1982). This could be due to a greater predation risk for rodents associated with open habitats (Reichman and Price). Rodents may also concentrate their activities under shrubs due to the greater densities of seeds in this microhabitat. Several studies have documented a many-fold increase in seed density in soils under shrubs compared with open soils (Hassan and West, 1986; Nelson and Chew, 1977; Price and Reichman, 1987; Reichman, 1984). If C. ramosissima seeds are palatable to rodent granivores and these granivores concentrate their foraging activities under shrubs, rodent foraging could drastically reduce the density of C. ramosissima seeds under shrubs. This could be a mechanism behind the low numbers of C. ramosissima seedlings on rodent mounds, as mounds have a much higher cover of shrubs than the surrounding environment (Chapter 1).

The low numbers of C. ramosissima seedlings on rodent mounds could also be due to high levels of seedling mortality on mounds. A study by Mun and Whitford
(1990) performed measurements of soil water potential every three days for eight months and found that mound soils dried much more rapidly after rainfall than off-mound soils. They attributed this to high rates of evaporation and infiltration due to the low bulk density of mound soil as well as loss due to transpiration by the greater plant biomass on mounds. If rodent mounds in Lucky Strike Canyon dry faster than off-mound soils this could have a negative effect on the survivorship of *C. ramosissima* seedlings.

To investigate the mechanisms controlling shrub diversity on rodent mounds in the *C. ramosissima* community I performed a series of experiments to address the effects of rodent activities on the fate of seeds and seedlings in this community. I hypothesized that the low numbers of seedlings on mounds was due to either the foraging of seeds by rodents, high seedling mortality on mounds, or a combination of these two mechanisms.

**METHODS**

**Site description**

This study was performed at the Mojave Experimental Research Plots (MERP) in the foothills of the Spring Range, 60 km northwest of Las Vegas, NV (Figure 1). This study is part of an ongoing series of experiments at MERP designed to study long term trends in population dynamics and ecosystem processes in the Mojave Desert. While MERP consists of multiple sites across a wide elevational and biotic gradient, this study was performed at the MERP’s Third Elevation Site at 1440 m elevation.

This site is dominated by *Coleogyne ramosissima* Torr. (blackbrush), which comprises about 85% of total shrub cover and is considered a distinct community in the Mojave Desert (Wallace and Romney, 1972). The topography of the site consists of a system of benches 20 - 100 meters wide and 200 - 400 meters long divided by a system
Figure 4  Centimeters of rainfall per year, 1989-1997. From Corn Creek, Desert National Wildlife Range.
of washes 2 - 5 m deep with steeply sloping sides. The soil surface on benches is usually covered by desert pavement and is underlain by hardpan caliche (CaCO₃) at 1 - 2 meters depth.

Lucky Strike Canyon receives an average annual rainfall of less than 15 cm. Precipitation measurements taken at Corn Creek (Figure 4), the headquarters of The Desert National Wildlife Range, show a wide variation in precipitation from year to year (National Climatic Data Center, 1989-1997). Corn Creek is about 11 km from the MERP Upper Site. Summer thunderstorms are localized and short lived while winter storms are usually widespread and can last for several days. Winter temperatures often drop below -10 °C while summer highs can top 40 °C.

Study Species

*Coleogyne ramosissima* (blackbrush) is a small shrub which is found in both the Mojave Desert and on the Colorado Plateau. In the Mojave, *Coleogyne* is the dominant shrub in a community which is found between the *Larrea tridentata - Ambrosia dumosa* community which exists at lower elevations and the *Pinus monophylla - Juniperus osteosperma* woodlands above (Shreeve, 1942). *C. ramosissima* communities are usually found on coarse, non-saline soils underlain by caliche at 40 - 60 cm depth (Bowns, 1973). The lower elevational limit of *Coleogyne* in the northern Mojave Desert appears to be limited by soil moisture (Lei and Walker, 1997). In the *C. ramosissima* community, *C. ramosissima* often forms almost pure stands which are found growing with little other vegetation (Bowns, 1973).

*C. ramosissima* is a mast seeding species which does not produce successive large crops even when precipitation is adequate (Pendleton et al. 1993). It may be possible that the lack of successive seed crops from year to year helps keep the
populations of seed predators at low levels due to a lack of food in non-crop years. This effect may be magnified in the *C. ramosissima* community by the scarcity of other shrub species. When a mast seeding event does occur, the large numbers of seeds produced quickly satiates the populations of seed predators and allows many seeds to avoid predation. *C. ramosissima* produces large seeds which are quite palatable to rodent granivores (personal observations) and many seedlings emerge from scatterhoarded caches made by species of the family Heteromyidae (Pendleton *et al.* 1993).

Plot selection

A large bench at the southwest corner of the upper MERP site was chosen as the study location. A large bench was chosen to minimize the effects of the bench edges and washes. Using the MERP corner post as the focal point, three 1 ha study plots were laid out in an "L" shape pattern (Figure 1). Within each study plot, three 10 x 30 m mound sample plots were laid out at randomly chosen points with their long axes running east to west. If two mound sample plots were less than 10 m from each other a new position was chosen randomly for one of them. Plot eight was initially selected as being in a wash, and was moved east onto the adjacent bench. The mound sample plots were numbered 1 - 9 from the northeast in a counter-clockwise direction.

All mound sample plots were censused for both active and inactive rodent mounds. Active mounds were classified as areas of disturbed, mounded soils up to 30 cm high with 1 or more holes leading into them. Inactive mounds were identified as areas of loose, slightly-mounded soils with a large percentage of the soil surface covered by either loose soil or large pieces of caliche. Inactive mounds did not have any visible holes leading into them. Two measurements were taken for each mound, one of the long axis and one perpendicular to the long axis at the widest point of the mound. The area of each mound was estimated from these two measurements by using the equation

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for an ellipse \((r_1 r_2 \pi)\). The minimum long axis for a mound was 30 cm, smaller areas of disturbed soils were left out of this study.

Off-mound control plots, also 10 m x 30 m, were placed adjacent to each sample plot so that the two plots shared one 30 m boundary line. Most of the control plots were placed on the north side of a sample plot, but two were moved to the south due to their being within 10 m of another control or study plot. These plots were numbered 11 - 19 with control plot 11 being placed next to sample plot 1, control plot 12 next to sample plot 2, etc.

To provide a comparison with the mound measurements, false mounds were placed on each off-mound control plot to represent the background, non-mound vegetation. Ten random points within each control plot were chosen to provide a focal point for each false mound. Mound areas were divided into five size classes. Steel lumber strapping was made into circular hoops of area 0.22 m\(^2\), 0.7 m\(^2\), 1.51 m\(^2\), 4.17 m\(^2\), and 9.43 m\(^2\), each representing the average of a size class. When the false mounds were censused, each one was randomly assigned to a size class. The edge of the appropriate hoop was placed at the nail with its long axis pointing west. This provided an easily repeatable way to delineate the boundaries of each false mound without permanently marking them.

Shrub Measurements

The length, width, and height of all perennial shrubs > 15 cm in height and rooted within the border of each mound were measured on both sample and control plots and the species of each shrub was noted. Shrubs were excluded if their stems were clearly not growing out of disturbed mound soils even if some part of their canopies overlapped the mound area. This excluded shrub cover was assumed to be canceled out by the inclusion of shrubs on the mound whose canopies extended beyond it's borders.
The length and width of each shrub were used to calculate the area using the formula for the area of an ellipse. Each species' cover was summed and divided by the mound area to obtain the percentage total cover for the entire mound. Density for all perennial vegetation was also determined, but due to the clonal nature of *Ephedra nevadensis* (Wallace and Romney, 1972), percent cover was used as a more appropriate measure of proportional abundance on mounds.

*C. ramosissima* Seedling Measurements

All *C. ramosissima* seedlings within the borders of each mound were censused on both the sample and control plots. I included only live seedlings (n = 420) in my density calculations, however I also censused a large number of dead *C. ramosissima* seedlings as well. Seedling characteristics measured included mound or off mound, distance and direction from the nearest shrub canopy, and the species of that shrub. They were also marked as to whether they were in a clump or alone. Seedlings on mound and off mound plots were sampled in October of 1996 and recensused in February of 1998 to obtain a measure of mortality.

Rodent Foraging Experiments

A number of experiments were performed in the fall of 1997 to investigate rodent seed and microhabitat preference. To avoid disturbance to my established plots, these experiments were performed on two benches separate from but adjacent to the study plots. Because of the possibility that moonlight could affect foraging patterns and intensity (Longland, 1994), I attempted to limit trials to nights during which the moon was less than one-quarter full. One experiment was performed on a night with the moon 75 percent full, this allowed me to test the effect of the phase of the moon on rodent foraging activity at my site. Seeds of *C. ramosissima, Grayia spinosa, Lycium andersonii, and E. nevadensis* were available from commercial seed suppliers.
(Comstock Seed, Reno, NV). Seeds of *Tetradymia canescens* and *Menodora spinescens* were unavailable from commercial sources.

Rodent foraging was measured by burying about 0.5 g of seeds 8 cm deep in a small slit in the soil made by a metal spatula. The spatula technique minimized surface soil disturbance, so that rodents were limited to finding seeds by smell. Each site was marked with a vinyl flag in close proximity to the buried seeds. Seeds were set out in the late afternoon and each site was checked in the early morning. A site was marked visited if there was evidence of rodent digging or "scrapes" at the site. In most cases, the sign of rodent scrapes indicated that the seeds had been removed as well.

**Rodent Seed Preference**

A total of 10 seed preference experiments were performed in the fall of 1997. Two experimenters walked randomly chosen north-south lines parallel to and at least 15 m from each other. One experimenter was chosen at random to plant *C. ramosissima*, the other experimenter buried the seeds of another species. Every ten meters, the nearest clump of 3 or more shrubs (off-mound) was chosen and a clump of seeds was buried.

These experiments lasted for several months over which time environmental conditions such as weather and temperature could be expected to vary widely, perhaps adversely effecting rodent foraging. *C. ramosissima* seeds were chosen as the standard against which rodent preference for *E. nevadensis*, *L. andersonii*, and *G. spinosa* were measured. All trials between a particular shrub species and *C. ramosissima* were combined and analyzed with logistic regression with species as the independent variable and foraged or not (0 or 1) as a binary dependent variable.

**Rodent Habitat Preference**

Four experiments to determine the habitat preference of foraging rodents were performed in the fall of 1997. Two experimenters walked along a randomly chosen
north-south line at least 15 m from each other. Every 10 m, the nearest mound greater than 1.5 m² was located and Coleogyne seeds were buried and marked as described above. A minimum distance of 5 m between burial sites was chosen to minimize the same rodent finding two sites one immediately after another. Because of this minimum distance, I could not choose two sites on the same mound and I chose to use the mound shrub habitat, which made up about 60% of the total mound area. The other three habitats used in this experiment were off-mound open, off-mound single shrub, and off-mound shrub clump (a group of three or more C. ramosissima adults). I ran a logistic regression with habitat, date of experiment, and percent full moon as the variables to determine if any of these factors had an effect on the intensity of rodent foraging on buried C. ramosissima seeds.

Rodent Caching

The first seedling census was performed in October 1996. Many of the C. ramosissima seedlings measured in this study were found to be growing in clumps of two or more seedlings arising from the ground less than 1 cm apart. Dead seedlings were included when identifying a live seedling as growing from a clump or not. Dead seedlings were identified by their distinctive size and branching pattern, which were very similar to the growth pattern of live C. ramosissima seedlings. C. ramosissima is known to be cached by rodents (Pendleton et al. 1993) and I made the assumption that clumps of seedlings had been cached by granivorous rodents. To estimate rodent caching, I calculated mean clump density in each habitat to determine where rodents had cached C. ramosissima seeds.

Seedling Mortality

I performed the first seedling census in October of 1996 and recensused in February of 1998 to determine seedling mortality. Each seedling was assigned a value
for each of four habitat variables, mound type, distance from shrub, aspect, and clump type. Mound type indicated whether a seedling was growing on a mound or off. The variable distance from shrub was transformed into three distance classes. Class one indicated that the seedling was growing 10 cm or more under the canopy of a shrub, distance class two indicated a location from 5 cm inside to 5 cm outside the dripline of a shrub, and class three meant that the seedling was 10 cm or more outside the dripline of the nearest shrub. Distance class one and two were equivalent to the shrub habitat, distance class three was equivalent to the open habitat. A seedling's aspect indicated on which side of the nearest shrub it was growing. I took this measurement and transformed it by taking the cosine of the aspect in degrees. North was assigned a value of 1, East and West a value of 0, South a value of -1 and so on. The variable clump type referred to whether a seedling was in a clump or alone. I ran a logistic regression with the independent variables mentioned above to determine the effect of each of these on seedling mortality.

Statistical Analyses

All seedling density analyses were performed with a two-way fixed factor ANOVA on JMP (SAS Institute, 1994), with distance and mound type as the class variables. Post-hoc analyses of pairwise differences in means were made with a Tukey-Kramer Honestly Significant Difference test on JMP. Shrub analyses were performed with a non-parametric Wilcoxon rank-sum test on JMP (SAS Institute, 1994) due to the non-normality of rare shrub measurements. Percent cover for C. ramosissimawas arcsin-transformed prior to analysis.

To analyze rodent seed preference, rodent foraging preference and seedling mortality I used logistic regression, a multivariate technique which allows for a binary dependent variable to be used in an analysis much like multiple regression. To remove
independent variables with insignificant effects, I used a backwards stepwise selection technique, which begins with all the independent variables in the model. Then at each step, the likelihood ratio statistic is computed for each variable and the most insignificant variable dropped from the model. At the next step, the likelihood ratio statistic is computed for the remaining variables and the most insignificant variable dropped again, until only variables with a significant effect on the dependent variable are left in the model.

For each model I obtained both $G_M$ and $R^2_L$ which are analogous to the F statistic and $R^2$ (in linear regression) respectively. I also report the logistic regression coefficients and the standardized coefficients for each model. The logistic regression coefficient can be interpreted as the change in the dependent variable which is associated with a one-unit change in the independent variable. However, due to the independent variables having different units, it is very hard to compare their relative effects on the dependent variable. Therefore I ran each analysis on SAS as well, which reports standardized coefficients for each independent variable. These measure how many standard deviations of change in the dependent variable result from a one unit change in each independent variable, and the relative contributions of each variable to the $R^2_L$ statistic can be obtained.

RESULTS

Initial Measurements

The mean percent cover of *C. ramosissima* on mounds was 32.7% while the average for all off-mound habitats was 3.8%, this difference was highly significant ($p = 0.001$). The average density of adult *C. ramosissima* on mounds was significantly higher than off-mounds ($p = 0.001$); mean shrub density on mounds was 1.95 shrubs/m² while off-mounds it was 0.79 shrubs/m². The density of *C. ramosissima*
Figure 5 Mean and standard error of *Coleogyne ramosissima* seedling clump density in the mound open, mound shrub, off-mound open, and off-mound shrub microhabitats at the first seedling census in October, 1996 (see methods). Different letters represent significant differences by Tukey HSD test (n = 301).
seedlings on mounds in the fall of 1996 was 2.42 seedlings/m² while off mounds it was 2.23 seedlings/m², this difference was not significant.

Rodent Seed Preference

Rodents detected and dug up 63 percent of the buried seed caches in the ten experiments. I performed three logistic regressions with the independent variable species. In the test of seed preference between C. ramosissima and G. spinosa, the probability that the contribution of the seed species was due to random chance was 0.62, as measured by the reduction in log-likelihood when the variable was included in the model. In the test of seed preference between C. ramosissima and E. nevadensis, the probability that the contribution of the seed species was due to random chance was 0.63, as measured by the reduction in log-likelihood when the variable was included in the model. In the test of seed preference between C. ramosissima and L. andersonii, the probability that the contribution of the seed species was due to random chance was 0.91, as measured by the reduction in log-likelihood when the variable was included in the model. The species of the seed made a significant reduction in log-likelihood in none of these three tests. I conclude that rodent seed preference was equal for all four species.

Rodent Habitat Preference

Rodents detected and dug up 65 percent of the buried C. ramosissima seed caches in the four experiments. I performed a logistic regression with three independent variables: habitat, date, and percent full moon. The dependent variable was foraged or not; a value of 1 indicated that the cache was found and dug up and a value of 0 indicated not dug up. The probability that the contribution of the variables date and habitat was due to random chance was 0.95 and 0.55 respectively, as measured by the reduction in log-likelihood when the variable was included in the model. Therefore the
Figure 6  Mean and standard error of Coleogyne ramosissima seedling density at the first census in October 1996 in each of the four microhabitats sampled. Different letters represent significant differences by Tukey HSD test (n=420).
Table 6 Logistic Regression of seedling mortality on three independent habitat variables. The habitat variables used include mound type (on or off a rodent mound), aspect of the seedling, and the distance class of the seedling (the distance from the nearest adult shrub). Coefficient, standard error, p (based on likelihood ratio), and standardized coefficient are reported for each independent variable (n = 420).

<table>
<thead>
<tr>
<th>Independent Variable</th>
<th>B</th>
<th>Standard Error</th>
<th>p</th>
<th>Standardized Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mound type</td>
<td>1.59</td>
<td>0.24</td>
<td>0.0001</td>
<td>0.40</td>
</tr>
<tr>
<td>Aspect</td>
<td>0.70</td>
<td>0.17</td>
<td>0.0001</td>
<td>0.27</td>
</tr>
<tr>
<td>Distance class</td>
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<td>0.18</td>
<td>0.013</td>
<td>0.23</td>
</tr>
</tbody>
</table>
**Figure 7** Mean and standard deviation of percent mortality of seedlings on mound and off-mound habitats (averaged across open and shrub habitats) (n=420).
variables date and habitat were excluded from the model. The reduction in the log likelihood when the variable percent of full moon was included in the model was significant \(p = 0.003\). Therefore the only variable which caused a significant reduction in log likelihood was percent of full moon on the night of the experiment. However, only a small amount of variation in whether a cache of seeds was recovered or not was explained by the percent of full moon at \(R^2_L = 0.014\). Overall, rodent foraging activity was distributed equally across habitat types and time.

Seed Caching

The mean number of seedling clumps per square meter of habitat was 1.05 for mound shrub, 0.30 for mound open, and 0.49 for off mound open (Figure 5). None of these means were significantly different from each other. The off-mound shrub habitat, however, had 2.66 clumps/m² which was significantly higher than the mean for the other three habitats.

First Census - October 1996

The average density for all habitats was 3.8 seedlings/m². There were significantly more seedlings under shrubs in both mound and off mound habitats than in either the mound open or off-mound open habitats (Figure 6). At 7.18 seedlings/m², the off mound shrub habitat had a slightly higher density of seedlings than the mound shrub habitat with 4.95 seedlings/m², but the difference was not significant. The same pattern was found between the off-mound open and mound open habitats, with 1.19 and 0.33 seedlings/m² respectively, but again the difference was not significant.

Seedling Mortality

Overall, 57 percent of the live seedlings measured at the first census died by the time of the second census. To investigate which habitat factors could be responsible for
this mortality, the independent variables mound type, distance class, aspect, and clump type were entered into a logistic regression and a backwards stepwise selection was applied. The significance of the likelihood ratio for the variable clump type was 0.89, and this variable was dropped from the model. Each of the remaining independent variables were retained in the model due to a significant likelihood ratio statistic for each variable. The prediction model obtained was logit (y) = -3.34 + 1.59(mound type) + 0.45(distance) + 0.70(aspect). The $R^2_L$ for the entire model was 0.16 indicating that the model explained a moderate amount in the variation in whether a seedling died or not. The standardized coefficients for the independent variables showed that mound type was the most important predictor (Table 6, Figure 7). Surprisingly, the aspect of a seedling explained slightly more of the variation in mortality than the distance from the nearest adult shrub (Table 6, Figure 8). The aspect which suffered from the most mortality was South, seedling mortality decreased uniformly as the aspect of the seedling approached the northerly direction.

Final Census - February 1998

The final density of *C. ramosissima* seedlings showed a considerable reduction in density in all habitats (Figure 9). The mound shrub habitat, as shown in the logistic regression, suffered the worst seedling mortality, as the mean density of seedlings in this habitat went from 4.95 to 1.24 seedlings/m². The mound open habitat retained the lowest mean density with 0.21 seedlings/m², however this was not significantly different from either the mound shrub or off-mound open habitats. The off-mound shrub habitat also suffered a high level of mortality, with a change in mean density from 7.18 to 3.06 seedlings/m². However, the density in this habitat remained significantly higher than in the other three habitats. The final mean seedling density on mounds, 0.73
Figure 8 Percent mortality of *C. ramosissima* seedlings by aspect and distance from the nearest adult shrub for both mound and off mound habitats. Means for SW - SE and NW - NE were combined due to low numbers of seedlings at those aspects. The inner most ring represents distance class 1 (under shrub) the middle ring distance class 2 (the dripline), and the outer ring distance class 3 (in the open); (n=420).
Figure 9  Mean and standard error of *Coleogyne ramosissima* seedling density at the second census in February, 1998 in each of the four microhabitats sampled. Different letters represent significant differences by Tukey HSD test (n=420).
seedlings/m², was significantly less than off mounds with a mean seedling density of 1.94 seedlings/m² (p = 0.003).

DISCUSSION

Adult *C. ramosissima* had a much higher percent cover on rodent mounds than in the off-mound areas sampled. The mean size of *C. ramosissima* was larger on mounds than off (Chapter 1). Since seeds are initially produced by adult shrubs, the much higher cover of *C. ramosissima* on mounds should lead to a higher number of seeds in this habitat. Although seeds could be dispersed by abiotic forces such as wind into the open, *C. ramosissima* seeds are heavy, at 0.1 g per seed, and they do not have any structural adaptations for wind dispersal. Much of the initial seed production, therefore, may fall and remain under the parent shrub canopies in the mound shrub and off-mound shrub habitats. The lack of any difference in seedling densities between mound and off mound plots in the first census suggested that either a significant amount of mortality of seeds or seedlings had occurred on mounds or that seeds had dispersed away from their parent shrubs.

Rodent Seed Foraging

Rodents recovered 63 percent of all buried caches in the ten seed preference experiments. No preference for *E. nevadensis*, *G. spinosa*, or *L. andersonii* over *C. ramosissima* was detected; *C. ramosissima* was not preferred over any species either. Populations of *E. nevadensis*, *G. spinosa*, and *L. andersonii* were found concentrated on rodent mounds (Chapter 1). Seeds from these species should be produced mainly in the mound shrub habitat. If rodents show a marked dislike for the seeds of any of these species, these seeds could remain in the mound shrub habitat and grown there. This could provide a mechanism for the occurrence of rare shrub species on rodent mounds.
However, rodents showed no distaste for any one shrub species’ seeds, and this possible mechanism for the enhancement of shrub species diversity on mounds must be rejected.

Rodents recovered 65 percent of all buried caches in the four seed foraging experiments. In a similar experiment on the comparative foraging success of rodents versus ants on seeds both buried and placed on the surface, Reichman (1979) found that rodents found 100 percent of caches of seedlings buried 1.5 cm deep within 24 hours in the Chihuahuan Desert. In this study seeds were buried much deeper, from 8 to 10 cm deep, and left overnight for a maximum of 12 hours of foraging. These differences may account for the lower percentage of seeds recovered by rodents in this study.

The only significant predictor of whether a cache of buried seeds was found or not was the percent full moon on the night of the trial. This was a poor predictor, however, accounting for only a small amount of the variation in cache discovery. Habitat had no effect on cache discovery, indicating that as a whole the rodent community foraged for buried *C. ramosissima* seeds equally on mounds, off mounds in the open, off mounds under large clumps of shrubs, and off mounds under single *C. ramosissima*. When the results from the previous two experiments are examined together, they reveal that the nocturnal granivorous rodent community at Lucky Strike Canyon showed few patterns in foraging behavior in regards to either seed preference or microhabitat foraging preference.

**Rodent Caching**

The densities of *C. ramosissima* seed caches were not significantly different between the mound shrub and mound open and off mound open habitats. The density of caches in the off mound shrub habitat, however, was significantly higher than the other three habitats. This pattern could be due to a greater amount of rodent foraging in
the habitats with fewer caches, a greater amount of rodent caching in the off mound shrub habitat, or a combination of the two. Because rodent foraging intensity was equal between all habitats in my foraging experiments, I assumed that the pattern of seed caches in each microhabitat was created primarily by differential caching. There was evidence of rodent caching in each habitat in this study. The most likely explanation for the presence of caches in the mound open and off-mound open habitats is that rodents had removed seeds from underneath adult *C. ramosissima* and cached them in the open. The effect of rodent caching alone would be to both move seeds into the mound open and off mound open habitats, as well as to concentrate them off mound under shrubs, as determined by the pattern of cached *C. ramosissima* seedlings.

The net effect of the foraging and caching activities of granivorous rodents on the distribution of seeds in the *C. ramosissima* community is difficult to determine. Rodents foraged at a high intensity and found, on average, over 60 percent of all seed caches buried in these experiments. Over longer periods of time, rodents could be expected to find a larger proportion of buried seeds. Neither rodent seed or habitat preference appears to create a particular pattern of seeds in any habitat. If, as I assume, the abiotic dispersal of seeds is minimal, the net effect of rodent foraging and caching in the *C. ramosissima* community may be to create a more homogenous distribution of seeds among all habitats.

First Seedling Census

The presence of *Coleogyne* seedlings at MERP was first noticed in 1995, and at that time they were 2 - 4 cm tall. Examination of precipitation patterns (Figure 4) indicated an unusual amount of rainfall in 1992, this may be when this cohort of seeds was produced. *C. ramosissima* seeds require cold stratification to germinate (Pendleton
et al. 1995), these seeds would have germinated in 1993 and are estimated to be three years old at the time of the first seedling census in October, 1996.

Seedling Mortality

There was a high level of mortality, 57 percent, of *C. ramosissima* seedlings between October, 1996, and February, 1998. The habitat variable I measured which accounted for the most variation in whether a seedling lived or died was mound type. As shown in Figure 7, 71 percent of the seedlings on mounds died while only 29 percent of the seedlings in the off mound habitats died. Aspect was the second most important variable in the logistic regression model. Eighty-one percent of the seedlings on the south of a shrub died while only 45 percent of the seedlings on the north side died, the seedlings with aspects in between these two extremes suffered intermediate levels of mortality (Figure 8).

The most likely explanation for the pattern of mortality due to mound type is drought stress. Although soil moisture measurements taken in both the spring and summer showed little difference between mound and off-mound habitats (Chapter 1), a study by Mun and Whitford (1990) found mound soils dried much faster than off mound soils, a pattern which I believe is similar on mounds at my site. The first seedling census was taken at the beginning of a long period during which Lucky Strike Canyon received very little rainfall. This drought did not break until late in the fall of 1997. If off mound soils dried slower than mound soils, seedlings off mounds might have been better able to survive the drought.

The pattern of seedling mortality related to seedling aspect may be due to drought stress as well. During the winter and early spring, which are the wet seasons in the Mojave, the sun is low in the southern sky. On noon of January 21st (winter solstice) the sun only reaches 30 degrees above the horizon at the latitude of Las Vegas.
(McCullagh, 1978). At this time the sun is casting a long shadow on the north side of the shrub while the south side is receiving full sunlight. The north side of a shrub is exposed to much less solar radiation than the south side during the winter and early spring and may remain at a lower temperature as well. The temperature at the ground surface plays an important role in determining the amount of evaporation from the soil (Buckman, 1969). Areas receiving less solar radiation would experience less evaporation from the soil surface and retain a greater amount of soil moisture. Seedlings growing on the north side of a shrub, and to a lesser extent the east and west sides as well, would have water for a longer time in the springtime, possibly allowing them to survive through the summer drought better than seedlings on the south side of a shrub.

Another variable which helped explain some of the variation in mortality was distance from shrub. Seedlings growing underneath the canopy of shrubs suffered the most mortality, seedlings at the dripline an intermediate level of mortality, and seedlings in the open the lowest amount of mortality. I expected the opposite result, as adult shrubs often act as nurse plants to seedlings due to higher levels of nutrients and the amelioration of surface temperatures in this microhabitat (Franco and Nobel, 1989). In an experiment at Lucky Strike Canyon by Walker et al. (in review), they performed a number of manipulations of the shrub environment around Ambrosia dumosa seedlings. Surprisingly, in a comparison between A. dumosa seedlings in the open with and without an excised shrub canopy placed on top of them to provide shade, they found that seedlings without a canopy survived longer. From their results they hypothesized that, other things being similar, a seedling under the canopy of an adult shrub suffers from a lack of light, which could cause the seedling to weaken and die. Their results agree with a study on the recruitment of woody species under Prosopsis glandulosa (mesquite) which found that seedlings were unable to take advantage of the high nutrients under shrubs due to light stress (Franco-Pizana et al. 1996). The pattern of
mortality due to distance from shrub in this study may result from the effects of light limitation on *C. ramosissima* seedlings under shrub canopies.

**Final Seedling Census**

By February 1998, there had been a large reduction in the density of *C. ramosissima* seedlings in all habitats. This mortality was most noticeable in the mound shrub habitat, in which the density of seedlings had become indistinguishable from the density in the mound open and off mound open habitats. There was a high level of mortality in the off-mound shrub habitat as well, however the density in this habitat remained significantly higher than in the other three habitats in this study. This is most likely the result of both large amount of seed caching by rodents and a lack of the effects of rodent mound building on seedlings in this microhabitat. The net effect of rodent mound building on seedlings of *C. ramosissima* was to increase seedling mortality on mounds. One probable mechanism for this increase in mortality was drought stress due to the faster drying rate of mound soils. Another was the large cover of shrubs on mounds (Chapter 1), which could have subjected seedlings on mounds to light stress as well.

**Conclusions**

Both rodent foraging and caching of seeds as well as seedling mortality on mounds were responsible for the final pattern of *C. ramosissima* seedlings in different habitats. One effect of rodent foraging and caching of seeds was to homogenize the final distribution of seeds in all habitats before seed germination. However, I rejected the hypothesis that the concentration of rodent activities under shrubs was the mechanism responsible for the lower than expected numbers of *C. ramosissima* seedlings on mounds, as I found no evidence for any difference in rodent foraging intensity between habitats. The mechanism which appeared to have the greatest effect
on the density of *C. ramosissima* seedlings on mounds was the high level of seedling mortality on rodent mounds due to both drought stress and light stress on mounds. The effect of rodent mounds on *C. ramosissima* seedling survivorship in the future depends on several factors. The amount of drought stress seedlings experience on mounds will depend highly on the future precipitation patterns at Lucky Strike Canyon; it is quite probable that a drought will occur again at this site and more seedlings will die. At some future date, seedling leaf area will increase enough so that seedlings will not suffer from light stress under shrubs any more, however, *C. ramosissima* seedlings in this study grew very slowly, and they could take decades to become large enough to no longer be susceptible to light stress under shrubs. Due to these factors, the negative effects of rodent mounds on seedling survivorship will most likely continue for some time.

There are several mechanisms which could be responsible for the large cover and diversity of shrubs on rodent mounds. In an earlier experiment at this site I proposed that mounds could be positive sites for shrub recruitment and that this could provide a mechanism for the increase in shrub diversity on mounds (Chapter 1). Mounds appear to have a negative effect on the survivorship of *C. ramosissima* seedlings in this community. This does not mean, however, that mounds would exhibit the same effect on seedlings of other species. In my intensive search of the entire ground surface of the mound and off-mound sample plots for seedlings I could positively identify only two *G. spinosa* seedlings growing on a rodent mound. Therefore, I was not able to follow a population of seedlings of less common shrub species through time to determine the effect of rodent mounds on the recruitment of species other than *C. ramosissima*. However, the lack of any adult shrubs of *G. spinosa*, *L. andersonii*, *Menodora spinescens* or *Tetradymia canescens* growing off mounds strongly suggests that rodent mounds provide a positive habitat for the recruitment and growth of seedlings of these
species, at least compared with the off-mound habitat in this community (Figure 10, arrow 2).

Another mechanism for the increase in diversity of shrub species on mounds involves the negative effect of rodent mounds on the survivorship of *C. ramosissima* seedlings (Figure 10, arrow 1). Rodent mound building had a positive effect on the growth and vigor of adult shrubs on mounds (Figure 10, arrows 3 and 4) resulting in a high shrub cover on mounds (Chapter 1). This positive effect on shrubs may also result in a negative effect on *C. ramosissima* seedling survival, possibly due to light stress from the shade under shrub canopies (Figure 10, arrow 5). This negative effect on *C. ramosissima* seedlings may result in a positive effect on the seedlings of less common shrub species (Figure 10, arrow 6), as few *C. ramosissima* seedlings survive on mounds and space which could be occupied by *C. ramosissima* may be left open for other species to recruit into.

I hypothesize that the changes in soil conditions initiated by rodent mound building may promote the diversity of shrubs in several ways. First, mound soils are positive for the growth of many shrub species (Chapter 1) and may also promote the growth and establishment of seedlings of less common shrub species (Figure 10, arrows 3 and 4). Second, mounds have a negative effect on the survivorship of *C. ramosissima* seedlings, which may reduce competition for seedlings of other shrub species (Figure 10, arrow 6).

The net effect of rodent activity is to increase the diversity of shrubs in the *C. ramosissima* community at Lucky Strike Canyon. The primary mechanism for this increase is indirect, as the rodent effect on shrubs is mediated through the rodent effect on soil due to mound building. However, the rodent effect on *C. ramosissima* varied with the life stage of the shrub studied; there was an positive effect on shrub adults resulting in increased size on mounds and there was a negative effect on seedlings.
leading to high seedling mortality on mounds. One question for future research at this site is at which age do *C. ramosissima* seedlings start to benefit from increased growth due to mound soils more than they suffer from the negative effects of rodent mounds.

Rodents in desert systems have been found to have many effects on plant distribution and abundance. Rodent foraging can play a role in maintaining annual diversity; rodent preference for large-seeded annuals keeps populations of these competitively dominant species in check and maintains a high diversity of annuals in both the Chihuahuan and Sonoran Deserts (Samson *et al.* 1992; Guo *et al.* 1995; Davidson *et al.* 1985). A guild of three species of heteromyid rodents was found to play a keystone role in a Chihuahuan Desert shrub habitat (Brown and Heske, 1990), as the removal of these rodents led to a change in the community from desert shrub to grassland. My study may be the first, however, to find a positive effect of rodent activity on the diversity and abundance of long-lived species such as shrubs in desert systems.
Figure 10 Model of the effects of rodent mound building on shrub establishment and persistence. Other shrub adults included in the model represent less common shrub species such as *Ephedra nevadensis*, *Grayia spinosa*, *Tetradymia canescens*, *Menodora spinescens*, and *Lycium andersonii*. 

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