

Rodent mounds facilitate shrubs and shrubs inhibit seedlings in the Mojave Desert, USA



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ABSTRACT

The habitat immediately around long-lived desert shrubs often provides a favorable environment (“fertile island”) for annual plants and shrub seedling establishment. However, adult shrubs can also compete with shrub seedlings. Part of the fertile island effect is due to rodent burrowing and seed caching but less is known about the effect of rodent mounds on short- and long-term desert shrub demography. We demonstrate that the indirect influences of rodent mounds on soil fertility and permeability create conditions favorable for adult shrubs, enhancing shrub size, density, and local species diversity in a nearly monospecific community of *Coleogyne ramosissima* in the Mojave Desert, in the southwestern USA. Shrubs facilitate seedling establishment but shrub canopies and fertile islands are not favorable for seedling survival. Occasional success of seedlings growing in open areas on mounds (where seedling densities are lowest) appear to have the biggest effect on long-term shrub demography of the dominant shrub, *C. ramosissima*, and, by inference, on other species of shrubs that are found only on mounds.

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1. Introduction

Desert environments are regions of relatively low rainfall and infertile soils that typically feature pronounced local heterogeneity in the spatial distribution of limiting resources (MacMahon, 1999; Thompson et al., 2005). Biotic forces have a critical role in creating the spatial heterogeneity in arid ecosystems (Butterfield et al., 2010). Long-lived desert shrubs (>100 years) and mounds constructed by heteromyid rodents both contribute to that heterogeneity by ameliorating microclimates (McAuliffe, 1988), increasing water infiltration rates (Laundre, 1993) and increasing soil nutrients, mineralization rates and mycorrhizal inoculum (Mun and Whitford, 1990; Schlesinger et al., 1996; Titus et al., 2002; Davidson and Lightfoot, 2008). The production and capture of litter by the shrub and increased activity of animals drawn to the shrub canopy and rhizosphere concentrate organic matter and nutrients and create a zone of fertility (“fertile island”) in the low-resource desert matrix (Garner and Steinberger, 1989). In addition, shrubs can trap seeds, reduce drought, protect seedlings from herbivory, and stabilize substrates (Flores and Jurado, 2003). Granivorous heteromyid rodents concentrate their activities under the shrubs to maximize foraging and protection from both

environmental extremes and predation (Thompson, 1982; Price and Reichman, 1987; Jorgensen et al., 1995). Their activities of eating and caching seeds impact seed dispersal (Howe and Miriti, 2004) and seedling distributions (Longland et al., 2001) of many desert plants. Rodent burrowing and excretions, in turn, increase decomposition of organic matter and soil nitrogen levels, lower soil bulk density, and enhance desert shrub growth (Chew and Whitford, 1992) and annual plant diversity (Moorhead et al., 1988), gradually building mounds. The cumulative effects of shrubs and rodents thereby have potentially long-lasting effects on the structure and composition of desert plant communities.

The relationship between mounds and the fertile islands around shrubs appears to present a positive feedback loop, because shrubs attract rodents and rodent mounds are fertile habitats that promote shrub growth. However, shrubs and mounds can be unfavorable environments for shrub establishment and growth (McAuliffe, 1988; Miriti et al., 1998; Walker et al., 2001). Furthermore, there are likely to be different consequences of mound and shrub habitats for each life history stage of desert shrubs (Callaway and Walker, 1997). Therefore, the net effect of shrub environments and rodent mounds on shrub distributions is not clear (Flores and Jurado, 2003).

Initial observations of a *Coleogyne ramosissima* (blackbrush) shrub community in the northern Mojave Desert indicated a pattern of higher shrub diversity and density on rodent mounds compared to the surrounding off-mound environment (cf. Brown

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et al., 2004). This paper examines the indirect influences of rodent activities on desert shrub diversity and density through rodent mound effects on soil resources, *C. ramosissima* seedling dynamics, and shrub size. We address the following questions: 1) Does rodent mound building alter *C. ramosissima* seedling and adult shrub distribution and size relative to off-mound habitats? 2) Does rodent seed caching alter *C. ramosissima* seedling distribution relative to shrubs and mounds? and 3) Are other desert shrub species affected by rodent mound building?

2. Study site and methods

2.1. Study site

This study was conducted in 1996–1998 in Lucky Strike Canyon on the eastern slopes (bajada) of the Spring Mountains, 60 km northwest of Las Vegas, NV at 1440 m a.s.l. Our site was characterized by a series of relatively flat ($<10^\circ$ slope) benches averaging 20–100 m wide and 200–400 m long and divided by 2–5 m deep gullies with steeply sloping sides ($30\text{--}90^\circ$ slope). The bench soils typically contain a hardpan caliche (CaCO_3) layer 0.4–0.6 m deep overlain by a surface desert pavement. The desert shrub community is dominated by *C. ramosissima*, which comprises about 80% of total shrub cover and is a common vegetation type in the Mojave Desert (Wallace and Romney, 1972). *C. ramosissima* is dispersed by scatter-hoarding rodents that are also seed predators (Meyer and Pendleton, 2005; Vander Wall, 2010). Lucky Strike Canyon received an average annual rainfall of 10.5 cm between 1989 and 1997 (Corn Creek, Desert National Wildlife Range), mostly as winter storms. Air temperatures typically range from -10° to $+40^\circ\text{C}$.

2.2. Sampling design

At our site, we established three adjacent, rectangular 1 ha study areas, within which we placed three 10×30 m plots along randomly chosen points on several east–west axes. Plots were at least 10 m from any adjacent plots and did not include gully habitats. Within each plot, we counted all rodent mounds (mounded, loose soil with pieces of caliche present) that were at least 30 cm on their long axis and determined if the mounds were active (at least one rodent hole or tunnel present) or inactive (no rodent holes). The area of each mound ($n = 111$) was determined by measuring the longest and shortest perpendicular radii and using the area of an ellipse ($r_1 * r_2 * \pi$). Off-mound control plots, also 10×30 m, were placed adjacent to each sample plot such that the two plots shared one 30 m boundary line. In each control plot, ten random points were chosen to provide a focal point for off-mound habitats ($n = 90$), randomly assigned areas of 0.22 m², 0.7 m², 1.51 m², 4.17 m², or 9.43 m² to represent averages of 5 actual mound size classes.

The species, length, width, and height of all perennial shrubs >15 cm in height and rooted within the border of each mound were measured on both mound and off-mound plots. Shrub area was calculated based on the area of an ellipse and then divided by mound area to obtain percent cover for each species on and off mounds. Shrub volume was estimated by area times height.

In August 1997, soil samples were taken from the top 10 cm of mineral soil from both the mound and control habitats and placed in an air-tight container kept at 5°C . To optimize finding both shrub and open habitats on mounds, we sampled all large mounds (>2 m²; $n = 29$) and $n = 29$ smaller mounds chosen at random. At each mound, we sampled, when possible, both under the shrub (from ≥ 10 cm inside the drip line of the largest *C. ramosissima* shrub in each habitat) and in the open (≥ 10 cm from the drip line of the nearest shrub). Because not all mounds had shrubs or open areas, sample sizes differed for mound shrub (MS; $n = 53$) and

mound open (MO; $n = 45$). A similar number of control sampling sites ($n = 58$) resulted in $n = 20$ samples for off mound shrub (OMS) and $n = 52$ samples from off mound open (OMO) habitats. Soil permeability was measured at each soil sample site by the depth in centimeters that a metal rod entered the soil when hit by a 2 kg mass (cf. the Dynamic Cone Penetration Test; Capper and Cassie, 1978). In the lab, soils were sieved (2 mm mesh); gravimetric moisture was determined on soils dried at 105°C for 36 h; pH was measured in a 1:1 solution; and organic matter was determined by loss of mass after ignition at 550°C for 4 h. 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 determination of total Kjeldahl nitrogen using a salicylate procedure (Environmental Protection Agency, 1984). Soil salinity was assessed with an electrical conductivity bridge.

Rodent species richness and relative abundances were estimated during two, three-night trapping sessions (6–8 July and 30 August – 1 September 1997) using Sherman live traps baited with peanut butter and rolled oats. Three 5×5 trapping grids (5 m trap interval; $n = 75$ traps) were placed around the plots. Trapping was done during the new moon to minimize rodent avoidance of open spaces due to moonlight.

All *C. ramosissima* seedlings within the borders of each mound and sampling plot, under shrubs and in the open, were censused in October 1996 and February 1998. Individual seedlings were not marked but plots were revisited bimonthly, persistent dead stems were monitored, and plots were carefully checked for evidence of new recruitment. No recruitment of seedlings was observed in the 16 month period, likely due to the near absence of precipitation during the study period (infrequent pulses of recruitment are typical of the study area). We included only live seedlings ($n = 420$) to calculate density calculations, but dead seedlings were included when determining if a live seedling was growing from a seed cluster or alone. These seedling clusters presumably represent evidence of caching by granivorous rodents (Pendleton et al. 1993; Beck and Vander Wall, 2010). Mean cluster density in each habitat was calculated to determine if there was a habitat preference for rodent caching of *C. ramosissima* seeds.

In addition to clustering, we measured whether seedlings were on or off a mound, the distance and direction from the nearest shrub canopy, and the species of that shrub. The distance from a shrub was combined into one of three classes: ≥ 10 cm inside the shrub canopy edge (drip line), within 10 cm of each side of the drip line, and ≥ 10 cm outside the drip line. Direction (aspect) was converted to the cosine in degrees (range: -1 to $+1$) and pooled by 45° increments (22.5° on either side of six cardinal points) for presentation and analysis. Seedling mortality was calculated as the difference in seedling numbers between the two sample dates because there was no recruitment.

2.3. Statistical analyses

Shrub cover 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 values for all species were arcsine-transformed prior to analysis. A two-way analysis of variance (ANOVA) was used to analyze soil variables with shrub (shrub or open) and mound (on or off-mound) as fixed factors. Soil moisture, percent organic matter, and percent total nitrogen were arcsine-transformed prior to analysis. To analyze seedling survival we used logistic regression. The estimate of a logistic regression coefficient, B, is used to calculate the odds ratio ($=e^B$) a multiplicative factor. The odds ratio is the multiplicative increase (>1) or decrease (<1) in the probability of survival associated with every one-unit change in the independent variable,

or for a qualitative category, the change from on-mound to off-mound. All seedling density analyses were performed with a two-way ANOVA, with shrub or open and mound type (on or off-mound) as fixed factors. Post-hoc analyses of pairwise differences in means were made with a Tukey–Kramer Honestly Significant Difference test in JMP. All values for shrub and soil analyses were reported as means with standard errors and significance was determined at $P < 0.05$.

3. Results

Mound density was 411 mounds ha^{-1} or 8.6% of the mound plot area (2700 m^2). Mean mound size was $2.09 \pm 0.23 \text{ m}^2$ (range: 0.12–14.13 m^2); 56% of the mounds were active.

Seven species of shrubs were found and *C. ramosissima* dominated with 78% of total shrub cover on mounds and nearly 100% off mounds (Table 1). *Ephedra nevadensis* was the second most common species. Four species found exclusively on mounds (*Grayia spinosa*, *Tetradymia canescens*, *Menodora spinescens*, and *Lycium andersonii*) constituted about 20% of mound shrub cover. A single *Atriplex canescens* shrub was found off-mound. Total shrub cover was 15 times higher on than off rodent mounds. *C. ramosissima* shrub density was higher ($P < 0.001$) on mounds ($1.95 \pm 0.41 \text{ shrubs m}^{-2}$) than off ($0.79 \pm 0.29 \text{ shrubs m}^{-2}$) and mean volume of individual *C. ramosissima* shrubs was higher ($P < 0.05$) on mounds ($0.39 \pm 0.29 \text{ m}^3$) than off ($0.23 \pm 0.24 \text{ m}^3$).

Mound soils differed from off-mound soils ($P < 0.001$) because they had lower pH, higher salinity, organic matter, and nitrogen, and were more permeable (Fig. 1). Overall, soils under shrubs differed from soils in open habitats in only two parameters: shrub soils had higher salinity ($P < 0.001$) and more permeability ($P = 0.02$) than open habitats (Fig. 1). Although there were no significant interactions between on or off mound and shrub or open habitats for any soil variables the shrub effects on salinity and permeability were greatest in off mound habitats (Fig. 1). There was no difference in soil moisture due to shrub or mound location (Vrooman, 1999). Permeability was the only soil variable that differed ($P < 0.01$) between active and inactive mounds and it was higher on active ($8.67 \pm 0.40 \text{ cm}$) than on inactive ($6.54 \pm 0.52 \text{ cm}$) mounds.

Seven species of rodents and one lagomorph were captured during the two trapping sessions, with *Perognathus longimembris* dominating the first session ($n = 16$; both session total = 16), and *Chaetodipus formosus* dominating the second session ($n = 16$; total = 23). *Peromyscus eremicus* and *Dipodomys merriami* were also common ($n = 13$ and 19, respectively). Four less common species were *Onychomys torridus* ($n = 3$), *Amnospermophilus leucurus* ($n = 2$), *Dipodomys microps* ($n = 1$), and *Sylvilagus auduboni* ($n = 1$).

Mean seedling density of *C. ramosissima* seedlings did not differ on ($2.42 \pm 0.61 \text{ seedlings m}^{-2}$) or off (2.23 ± 0.74) mounds, in

contrast to adult *C. ramosissima* shrubs. However, *C. ramosissima* seedling densities were higher ($P < 0.001$) under shrubs than in the open both on and off mounds in October 1996 (Fig. 2A). Clusters of seedlings were more common ($P < 0.05$) under shrubs off mounds ($2.66 \pm 0.51 \text{ m}^{-2}$) than under shrubs on mounds (1.05 ± 0.28), in the open off mounds (0.49 ± 0.43) or in the open on mounds (0.30 ± 0.41). Over half (57%) of the seedlings alive in October 1996 died by February 1998 (Fig. 2B) and mortality was affected by both mound and shrub environments. Mortality was higher ($P < 0.0001$; Fig. 2) on mounds (70%) than off mounds (29%). The logistic regression of seedling survival revealed significant effects of all independent variables (Table 2). Occurrence on a mound affected seedling survival with survival increasing by a factor of 4.9 in moving from on-mound to off-mound locations. There was a strong effect of aspect on seedlings because their probability of survival increased by a factor of 2.01 (doubling) in moving from a location south of a shrub to one north of a shrub; a one-unit change in the cosine of aspect (Table 2; Fig. 3). Seedling survival was also higher ($P < 0.013$) in the open ($\geq 10 \text{ cm}$ from a shrub). The probability of survival increased by a factor of 1.57 for seedlings located in the drip line area compared to seedlings located $\geq 10 \text{ cm}$ beneath the shrub (see methods) and the probability of survival increased again by a factor of 1.57 for seedlings located in the open compared to seedlings located within 10 cm of the shrub drip line (Table 2; Fig. 3).

4. Discussion

Our study suggests that the influence of rodents on desert shrub distributions can be both indirect through the influence of rodent mounds on soil conditions, shrub size, and seedling survival, and direct, through rodent dispersal of seeds. Higher densities and cover of adult *C. ramosissima* shrubs and higher diversity and cover of other shrub species on than off mounds appears to result from the favorable growing conditions (fertile islands) provided by the mounds. The dominant *C. ramosissima* shrubs in our study area were ten-fold denser and had 1.7-fold more volume on than off mounds. Increased shrub vigor on mounds was also noted by Chew and Whitford (1992) for growth, flowering, and fruiting of *Larrea tridentata* in the Sonoran Desert. Shrub community diversity and cover were also higher on than off rodent mounds, and four of the five less common shrub species were not found in off-mound habitats (Table 1). Rodent mounds were patches of high shrub diversity in a largely monospecific community, and, by necessity, the primary location of interspecific shrub interactions. Given that rodent mounds covered 8.6% of our study plots, a value within the range of values for a semi-arid grassland in southern New Mexico (Moraka et al., 1982), rodent mounds can be inferred to be an important factor facilitating and structuring shrub species diversity in this region of the Mojave Desert. The positive effects of fertile islands on seedling densities around adult shrubs are offset to some degree by negative effects of adult shrubs on seedling survival. Nevertheless, we illustrate how both mounds and existing shrubs are critical determinants of the distribution of desert shrubs, through their influence on shrub seedlings and adults.

Both rodent mounds and shrubs augment spatial heterogeneity of soil conditions in deserts, although there is more known about shrubs than mounds, particularly about how the presence of shrubs often increases soil fertility (Schlesinger et al., 1996; Titus et al., 2002; Thompson et al., 2005). The effects of rodent mounds on soil properties were more pronounced than shrub effects in this study. We found that rodent mounds improved soil fertility, particularly by increasing nitrogen and organic matter, as found by Moorhead et al. (1988) and Mun and Whitford (1990). Rodent activities involve excretions and soil turnover and these activities

Table 1
Mean percent cover of shrub species by habitat.

Species	% Cover in habitat			
	Mounds		Off-mounds	
	Mean	SE	Mean	SE
<i>Coleogyne ramosissima</i>	32.773***	0.144	3.809	0.178
<i>Ephedra nevadensis</i>	8.878***	0.067	0.015	0.083
<i>Grayia spinosa</i>	0.329***	0.030	0	0
<i>Tetradymia canescens</i>	0.018*	0.004	0	0
<i>Menodora spinescens</i>	0.014*	0.004	0	0
<i>Lycium andersonii</i>	0.010	0.004	0	0

$n = 98$ (mounds); $n = 72$ (off-mounds). * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; SE = standard error.

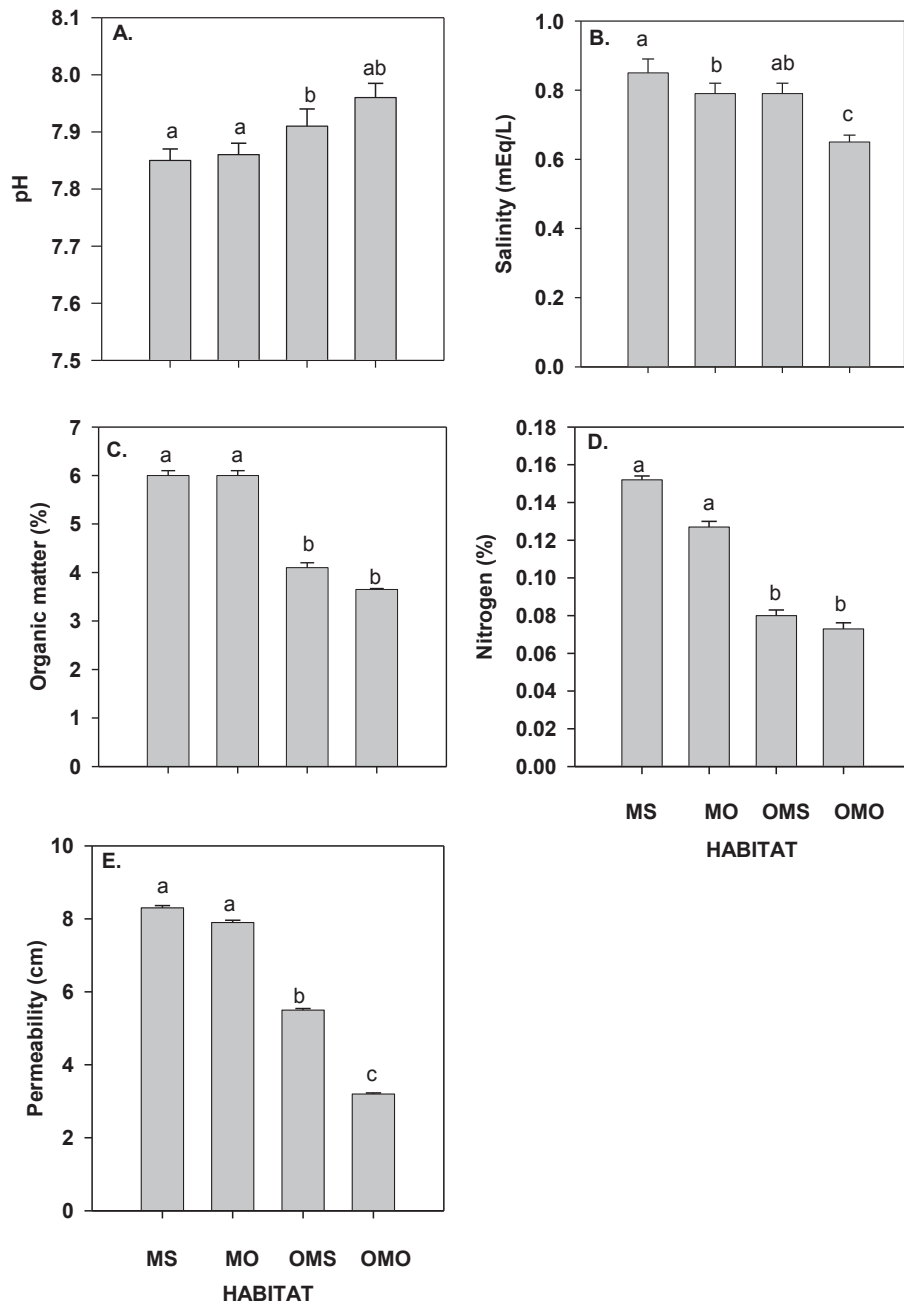


Fig. 1. Soil parameters by habitat (MS = mound shrub, MO = mound open, OMS = off-mound shrub, OMO = off-mound open). Bars represent means \pm 1 S.E. and columns with different letters are significantly different ($P < 0.05$); $n = 53$ (MS), 45 (MO), 20 (OMS), and 52 (OMO).

may increase organic input, especially through litter burial (Moraka et al., 1982) and microbial decomposition (Ayarbe and Kieft, 2000; Titus et al., 2002). The turnover of soils throughout a rodent mound may help explain the lack of a strong shrub effect on the fertility of mound soils, although shrub effects were also not pronounced off mounds. However, strong effects of *C. ramosissima* shrubs on soil fertility (and subsequent growth of *Ambrosia dumosa* seedlings) were found in a study in the same area (Walker et al., 2001), suggesting that our samples, which sometimes were within 10 cm of the drip line and litter of shrubs (due to dense shrub cover on mounds), may have still been within the zone of influence of the shrub effect on soils. We also found higher pH under off-mound shrubs than on both shrub and open habitats on mounds,

suggesting that mounds accumulate more organic acids than do open habitats from the decomposition of shrub litter (Thompson et al., 2005) or from root activity. The higher salinity on than off mounds could result from the differential sorting of soil nutrients under shrubs (Schlesinger et al., 1996).

An additional effect of rodent mounds was increased permeability, probably due to both increased root exudates and the increased activity of rodents (Jorgensen et al., 1995), including burrowing (Mun and Whitford, 1990), and the removal of a compact caliche layer from 40 to 60 cm deep in the soil profile (Lei, 1995). Mound soils with high plant cover and soil permeability can dry out faster than off mound soils (Mun and Whitford, 1990), although we found no soil moisture differences, perhaps because

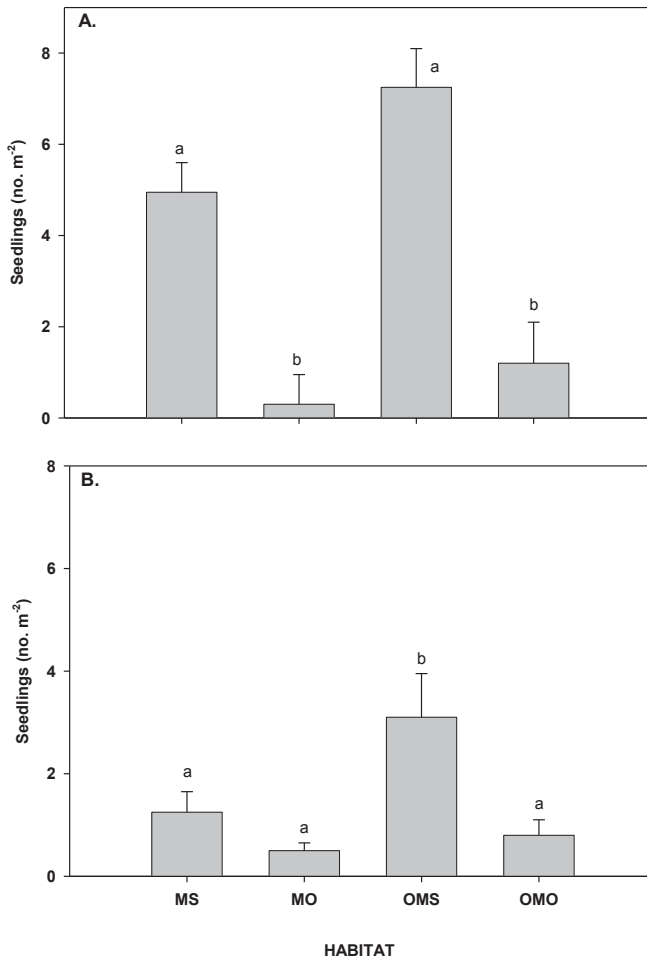


Fig. 2. *Coleogyne ramosissima* seedling density (no. m⁻²) by habitat (MS = mound shrub, MO = mound open, OMS = off-mound shrub, OMO = off-mound open) in A) October 1996, and B) February 1998. Bars represent means \pm 1 S.E. and columns with different letters are significantly different ($P < 0.05$); $n = 201$ sampled sites.

our measurements were not extensive enough to detect differences under the highly variable desert conditions. Alternatively, increased water retention in the organic soils on mounds, increased infiltration of precipitation, or reduced transpiration under the denser shrub on mounds offset any increases in water loss from mound soils (Rostagno, 1989).

The pattern of higher shrub diversity and cover on rodent mounds can be explained by three non-exclusive hypotheses or scenarios. First, several studies have noted higher diversity and cover of annuals on mounds in the Chihuahuan Desert (Moorhead et al., 1988; Mun and Whitford, 1990), and attributed the differences to higher soil nitrogen and higher soil aeration (from increased permeability) on than off mounds. The higher resource

Table 2

Logistic regression of *Coleogyne ramosissima* seedling mortality on mound type (on or off), aspect of seedling location relative to adult shrub (cosine of degrees), and distance of seedling from adult shrub.

Variable	B	SE	P	Odds ratio
Mound type	1.59	0.24	0.001	4.90
Aspect	0.70	0.17	0.001	2.01
Distance	0.45	0.18	0.013	1.57

B = coefficient; SE = standard error, P is based on likelihood ratio; Odds Ratio is e^B; $n = 420$ seedlings.

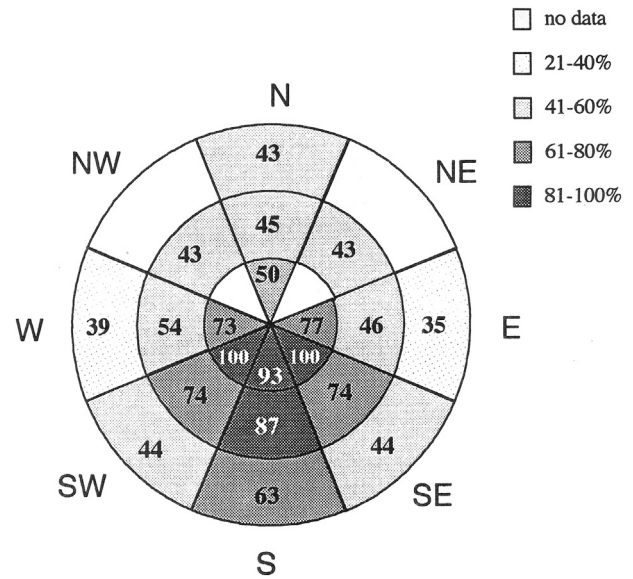


Fig. 3. *Coleogyne ramosissima* seedling mortality (%) by aspect and distance from the nearest adult shrub for both mound and off mound habitats combined; $n = 420$ seedlings. Distances included ≥ 10 cm inside the shrub canopy (inner ring), within 10 cm of each side of the drip line (middle ring), and ≥ 10 cm outside the drip line (outer ring).

availability on compared to off mounds may favor shrub growth (Chew and Whitford, 1992) and increase soil resource combinations that can be exploited by different shrub species. Protection from herbivores by the denser shrub cover on mounds could also potentially promote diversity. Second, more favorable recruitment of seedlings on than off mounds may explain the higher shrub diversity and cover. Although we found highest seedling densities under off-mound shrubs, on-mound open habitats represent a combination of high seed accumulation and high rodent activity (presumably including caching). Caches can facilitate seed germination and seedling establishment (Longland et al., 2001) and seeds in caches outside of shrub canopies are least likely to be rediscovered (Muñoz and Bonal, 2011), perhaps favoring germination in open mound habitats. Third, high shrub diversity and cover on mounds may be due to higher plant longevity on compared to off mounds. The remarkable longevity of many desert shrubs (often

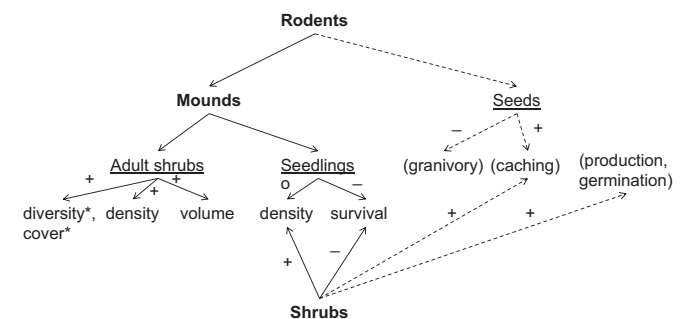


Fig. 4. Effects of rodents on *Coleogyne ramosissima* shrub density and volume, seedling density and survival, and granivory (positive, negative, or neutral) in this study. Additionally, rodent mound effects on adult shrub community diversity and cover are indicated with asterisks (*C. ramosissima* plus six other shrubs in the same habitat: *Ephedra nevadensis*, *Grayia spinosa*, *Tetradymia canescens*, *Menodora spinescens*, *Lycium andersonii*, and *Atriplex canescens*, in descending order of cover). *Coleogyne ramosissima* shrub effects on *C. ramosissima* seedling density and survival are also indicated. Dotted lines and parentheses indicate hypothesized relationships that were not measured in this study but are inferred from other studies.

several hundred years; Bowers et al., 1995; Webb, 1996) could be promoted by mound conditions. Favorable growth, coupled with low survivorship of adult shrubs of less common species off mounds, might contribute to higher diversity and cover on mounds. Mortality of these long-lived shrubs could not be measured in our short-term study, but recent improvements in ageing techniques (S.G. Kitchen, pers. comm.) could help elucidate shrub demography on rodent mounds.

In several experiments at our study site with seeds of four of the six common shrubs (*C. ramosissima*, *G. spinosa*, *L. andersonii*, and *E. nevadensis*), rodents detected and dug up 65% of seeds buried for 12 h, but showed no preference by seed species or by habitat (Vrooman, 1999). Reichman (1979) found 100% retrieval of seeds buried for 24 h in the Chihuahuan Desert. Rodent foraging may therefore not be critical for explaining the distribution of adult shrubs. However, secondary dispersal by rodents (see Vander Wall et al., 2005) resulted in caching of *C. ramosissima* seeds preferentially under *C. ramosissima* shrubs off mounds, based on where clusters of seedlings were found. The evidence that desert rodents remove and consume or cache a majority of seeds that are produced (Pendleton et al. 1993; Beck and Vander Wall, 2010) supports the suggestion that groups of seedlings represent seed caches rather than passive dispersal into the same microhabitat. Rodent caching also can promote seed germination and establishment (Longland et al., 2001), particularly with heavy-seeded plants such as *C. ramosissima* (S. Meyer, pers. comm.), thereby influencing shrub demographics.

Recruitment in desert shrubs is episodic and depends on seed and seedling responses to environmental filters that are both biotic (e.g., rodent dispersal) and abiotic (e.g., desiccation). *C. ramosissima* seedling densities in this study were determined by rodent seed dispersal (mostly to shrubs and off mounds), mound conditions (higher mortality on mounds than off mounds), and shrub microhabitats (highest mortality under shrubs, particularly on the south side). Seedlings benefit from the shade (Valiente-Banuet and Ezcurra, 1991) and nutrients (Titus et al., 2002) under shrubs but can, particularly in dry years, suffer from competition for water with shrubs (Tielborger and Kadmon, 2000; Walker et al., 2001). Highest mortality on the south side of a shrub can be a reflection of such competition (Brittingham and Walker, 2000). The higher seedling mortality on mounds was independent of dispersal or shrub microhabitat and contrasts with the positive soil effects of mounds on adult shrubs. Therefore, although *C. ramosissima* shrubs maintain higher levels of soil moisture than other shrubs (Walker et al., 2001) and the 1997 growing season was moderately wet (Vrooman, 1999), higher mortality under shrubs on than off mounds suggests that desiccation was a factor limiting *C. ramosissima* seedling survival during this study.

Our results show that rodent mounds provide favorable soil conditions for desert shrubs and promote higher shrub diversity on than off mounds (Fig. 4). The dominant *C. ramosissima* grows larger on than off mounds. In the episodic mast years for *C. ramosissima*, rodents preferentially cache seeds under shrubs off mounds. Due to higher seedling mortality on the likely drier conditions on mounds, seedling densities were highest under shrubs off mounds by the end of our study. However, higher seedling mortality under shrubs than in open habitats suggests that long-term shrub recruitment and survival will occur from the occasional seedling that survives the rigors of the establishment phase in open habitats, particularly on mounds which provide better soil conditions. A similar conclusion was reached by Miriti et al. (2001) that open-grown *Ambrosia* shrubs were ultimately most critical to the long-term spatial dynamics of shrubs in the northwestern Sonoran Desert. Presumably, higher shrub densities on than off mounds also favor higher propagule pressure close to the ultimately favorable open

mound environments. We did not find enough seedlings of other shrubs to explain their fidelity to mounds, but suggest that the same long-term benefits of mounds apply, particularly for those shrubs found only on mounds. Therefore, we have the lowest seedling densities in the habitat (mound open) where shrubs are most likely to survive, in part because nutrients are relatively high and competition likely minimal. In a nearby study, Walker et al. (2001) found highest survival of out-planted *Ambrosia* seedlings in fertile soils where shrubs had been removed, followed by naturally open habitats; lowest survival was under existing shrubs. Our mound open habitats provide an approximate parallel to the shrub removal habitat in that paper.

In conclusion, our results highlight the role of desert rodents in determining patterns of perennial shrub demography. The fertile habitats provided by rodent mounds led to increases in shrub size, density, and diversity in our study in the northern Mojave Desert. The dominant shrub, *C. ramosissima*, was the only shrub found in off mound habitats and the only shrub with seedlings present. Establishment of *C. ramosissima* seedlings was preferentially under shrubs but the shrub canopy and the fertile rodent mounds were not favorable for seedling survival. Therefore, we propose that shrub seedlings that manage to establish in open habitats on the fertile rodent mounds are most likely to influence long-term shrub demography of both *C. ramosissima* and the other mound-limited shrubs.

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