



8-12-2011

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Recommended Citation

Megill, Laura; Walker, Lawrence R.; Vanier, Cheryl; and Johnson, Debra (2011) "Seed bank dynamics and habitat indicators of *Arctomecon californica*, a rare plant in a fragmented desert environment," *Western North American Naturalist*. Vol. 71 : No. 2 , Article 6.

Available at: <https://scholarsarchive.byu.edu/wnan/vol71/iss2/6>

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SEED BANK DYNAMICS AND HABITAT INDICATORS OF
ARCTOMECON CALIFORNICA, A RARE PLANT IN A
FRAGMENTED DESERT ENVIRONMENT

Laura McGill¹, Lawrence R. Walker^{1,2}, Cheryl Vanier¹, and Debra Johnson¹

ABSTRACT.—Protection of endangered desert plant species is frequently complicated by a lack of information about seeds, the most stress-resistant and populous life stage. We studied the relative locations of seeds and plants of a rare endangered herbaceous perennial, the Las Vegas bearpoppy (*Arctomecon californica*) in seven 1-ha sites randomly located within a 100-ha study area that was slated for development in Las Vegas, Nevada. We also measured the physical and biological attributes of the environment supporting the seeds and plants, including soil hardness, rock cover, cryptogamic crust cover, and associated vegetation.

Arctomecon californica seed density was 0.651 seeds · m⁻², and seeds were found throughout the top 4 cm of soil. Seed viability among sites ranged from 26% to 79%; however, no significant changes between depths were detected. The spatial distribution of the seed bank coincided with the current *A. californica* adult distribution only in sites with both a high plant density and high numbers of seeds. *Arctomecon californica* adults occupied open areas within the gypsum environment that supported significantly less vegetative cover than the surrounding area. We observed a positive association between *A. californica* adults and shadscale (*Atriplex confertifolia*) and a negative association with 7 other plant species among sites. Sites with an indurated abiotic crust hosted higher numbers of *A. californica* adults than sites with softer soils. However, rock cover, cryptogamic crust cover, and soil hardness were poor explanatory factors for characterizing *A. californica* presence. We suggest that land managers should incorporate seed bank census into monitoring programs due to the extreme year-to-year fluctuations in *A. californica* plant population densities.

RESUMEN.—A menudo la protección de especies de plantas desérticas en peligro de extinción se ve complicada por la falta de información sobre las semillas, la etapa de vida más abundante y resistente al estrés. Estudiamos la ubicación relativa de semillas y plantas de “Las Vegas bearpoppy” (*Arctomecon californica*), una planta perenne en peligro de extinción, en 7 sitios de 1 ha. localizados al azar dentro de un área de estudio de 100 ha que estaba destinada a la urbanización en Las Vegas, Nevada (E.U.A.). También medimos los atributos físicos y biológicos del ambiente que sostiene las semillas y plantas, tales como dureza del suelo, rocosidad, cobertura de costra cryptógama y vegetación asociada.

La densidad de semillas de *A. californica* fue 0.651 semillas · m⁻² y se observó en los 4 cm superiores del suelo. La viabilidad de las semillas varió del 26% al 79% entre los sitios; sin embargo, no detectamos cambios significativos entre profundidades. La distribución espacial del banco de semillas coincidió con la distribución actual de adultos de *A. californica*, sólo en sitios que tuvieron una alta densidad de plantas y altos números de semillas. Los adultos de *A. californica* ocuparon áreas abiertas dentro del ambiente de yeso que sostenía significativamente menos cobertura vegetal que las áreas circunvecinas. Observamos una asociación positiva entre los adultos de *A. californica* y el chamizo (*Atriplex confertifolia*) y una asociación negativa con siete otras especies de plantas entre sitios. Los sitios con una costra abiótica endurecida albergaron más adultos de *A. californica* que los sitios con suelos más blandos. No obstante, la cubierta rocosa, la costra cryptógama y la dureza del suelo fueron inadecuadas como factores para caracterizar la presencia de *A. californica*. Sugerimos que los manejadores de tierras deben incorporar censos de bancos de semillas en los programas de monitoreo, debido a las fluctuaciones extremas de un año a otro en la densidad poblacional de *A. californica*.

The survival of many desert plants relies on seed banks to buffer years of sparse or no recruitment due to highly stochastic yearly rainfall (Kemp 1989, Cabin and Marshall 2000). The spatial distribution and size of the soil seed bank are vital for effective population management of many rare plant species, but such information is often difficult to obtain (Adams et al. 2005, Satterthwaite et al. 2007). Currently, land managers must rely on adult plant populations

as a proxy for seed populations. Many short-lived desert plants produce huge numbers of seeds with the capability of long-term dormancy (Kemp 1989), so adult populations may be a poor indicator of seed presence in arid systems. Characteristics of the habitat may be more effective long-term indicators of seed presence in such cases. Habitat characterization has the additional benefits of identifying site factors that predict suitable but unoccupied habitat

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(Simberloff 1988, Hill and Keddy 1992, Wiser et al. 1998, but see Nilsson et al. 1988), further facilitating management decisions.

Arctomecon californica Torrey and Fremont (Papaveraceae: Las Vegas bearpoppy) is an ideal case study to test the relative effectiveness of adult populations compared to habitat variables in predicting seed presence. The species is considered critically endangered by the state of Nevada, and approximately 30 out of 91 populations have been extirpated due to rapid urban expansion in the Las Vegas Valley, Nevada (Mistretta et al. 1996). *Arctomecon californica* is a short-lived perennial plant and is considered extinct at a site where live plants are absent, opening the way for land development. Understanding the seed bank dynamics and habitat-based indicators for *A. californica* success is the only workable approach for managing this species. Efforts to increase the *A. californica* population through restoration have been largely unsuccessful (Science Applications International Corporation 2001), and plant salvaging (Winkel 2004) remains difficult. Previous work on this species has yielded general descriptions of biological and physical characteristics of habitat for the plants (Meyer 1987, Mistretta et al. 1996, Sheldon-Thompson and Smith 1997, Hickerson and Wolf 1998, Drohan and Merkler 2009), but seeds, which may represent the most critical life stage, have been largely ignored.

Like many species in arid habitats, *A. californica* appears to depend heavily on a long-lived seed bank in order to persist through years that do not provide appropriate conditions for germination. Germination occurs *en masse* during late winter months (Meyer 1987, 1996) when rainfall is sufficient, producing extreme year-to-year fluctuations in *A. californica* plant population densities (Meyer 1987). Successful recruitment has been observed in locations where adult plants have been absent for several years (Welsh et al. 1987). Recent soil seed bank analyses in areas occupied by *A. californica* in Lake Mead National Recreational Area (hereafter LMNRA) have yielded conflicting results regarding the size of the seed bank (see Science Applications International Corporation 2001, Megill 2007). Ambiguity surrounding the spatial distribution of the seed bank has resulted in expensive mitigation measures, including soil reclamation, seed collecting, and fencing barriers to aid recoloniza-

tion of disturbed areas (G. Marrs-Smith, Las Vegas Conservation Transfer Area Manager for the Bureau of Land Management, personal communication). Information about the size and spatial extent of the seed bank is critical to future management decisions regarding this species.

The purpose of this study was to characterize the abundance and dispersion of *A. californica* seeds and seedlings and their link to adult plants, associated plant species, and other biotic and abiotic indicators within a highly impacted area of Las Vegas Valley. The results can provide valuable insight for future management decisions by allowing identification of habitat that is likely to host seeds but does not currently support plants. This approach can reveal the actual size of the population, once seeds are included, and assist land managers in prescribing more targeted and defensible mitigation procedures. More broadly, this study provides a revealing test case for the assumptions regarding seed bank distribution that are frequently overlooked in making decisions about rare and endangered plants in arid environments.

METHODS

Study Species

Arctomecon californica is a rare, short-lived, herbaceous perennial plant that is endemic to the Mojave Desert of southern Nevada and northern Arizona. Plants flower from March to June, 1–2 years after establishment, and are generally self-incompatible (Meyer 1987). Plants live approximately 4–5 years (Meyer 1987).

Study Area

The study was conducted in north Las Vegas, Nevada (36°17'59.3160"N, 115°9'9.4320"W; 675 m asl), in the Mojave Desert (Fig. 1). The study area was selected because it was severely fragmented from past urban expansion (Hickerson and Wolf 1998), illegal dumping, and unauthorized recreational vehicle usage (G. Marrs-Smith, Las Vegas Conservation Transfer Area Manager for Bureau of Land Management, personal communication). The study area is an ancient gypsic marsh remnant covered by Quaternary alluvium and eolian deposits (Haynes 1967, Drohan and Merkler 2009). Gypsum outcrops are embedded within non-gypsum soils commonly referred to as "badlands" (Mistretta et al. 1996). The climate is characterized by

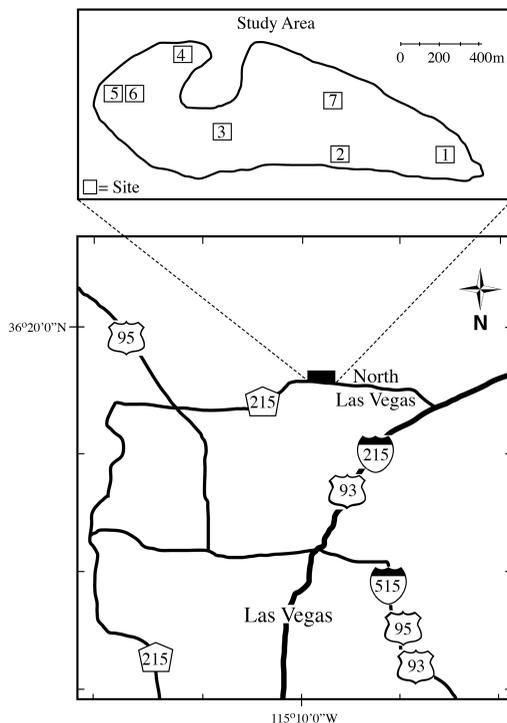


Fig. 1. Maps of Las Vegas, Nevada, depicting the 100-ha study area and the study sites.

extreme daily fluctuations, strong seasonal winds, and unpredictable precipitation. Temperature extremes range from -1°C to 49°C , with a mean annual precipitation of 114 mm (range 20–145 mm; NCDC 2007).

Sampling Design

Seven 1-ha sites were randomly placed within a 100-ha area during December 2005–May 2006. Each site consisted of a $99 \times 99\text{-m}$ area divided into 2178 contiguous quadrats ($1.5 \times 3\text{ m}$). A random subset of at least 954 of the quadrats (Table 1; different sample sizes were produced by variable terrain) within each site was selected for soil sampling prior to seed dispersal. One randomly located 9-cm-diameter soil core (0–2-cm and 2–4-cm depths) was extracted per selected quadrat using a metal teaspoon, a centimeter ruler, and a soil core guide to minimize contamination between sampling depths. We sieved soils from each depth (Hubbard sieves $<60\text{ mm}$), and *A. californica* seeds (black in color), which were quite obvious within the gypsum soils,

were recovered, enumerated, and tested for viability (tetrazolium test; Peters 2000). Within each site, we chose 220 quadrats (irrespective of soil core selection) for measurement of several habitat variables: cover of associated plants by species (cm^2), gypsum soil surface strength, cover of surface rock, and cover of cryptogamic crust (biological crust). Surface rock and cryptogamic crust cover was estimated within quadrats and assigned to one of the following categories: 0%–25%, 25%–50%, 50%–75%, or 75%–100% (Sutherland 2004). Gypsum soil surface strength was determined using a portable penetrometer (Soiltest CL-700A) at 3 random locations within the quadrat to obtain a quadrat mean. All live *A. californica* plants were counted and assigned Cartesian (x, y) coordinates (0.1-m precision). From 31 March to 1 April 2007, we completely excavated one active ant mound per site at 2-cm intervals down to an underground depth of 16 cm. We sieved each ant mound for *A. californica* seeds.

Data Analysis

The data included a large proportion of zeros but did not follow a Poisson distribution. For this reason, the structure and complexity of the data made formal statistical testing tenuous, so a resampling approach was employed to compare effects in many cases. Bootstrapping (resampling data with replacement) was used to compute confidence intervals for most analyses (Efron and Tibshirani 1998) because of the small, uneven sample sizes and dramatically nonnormal distributions that were observed for most measured variables. Confidence intervals derived from bootstrapping were calculated on a quantile basis, because uncertainty was frequently asymmetrical. Due to the small number of seeds observed, we included both viable and nonviable seeds in our analyses unless otherwise noted. We assessed significance by nonoverlapping 95% confidence intervals and set α at 0.05. All analyses were performed in R (R Development Core Team 2006).

We estimated soil seed density within sites ($n = 7, 99 \times 99\text{ m}$) and depths (0–2 cm and 2–4 cm) by bootstrapping the number of seeds from individual soil cores while seed viability was at the individual seed level. To test for randomness of seed dispersion within each site, we used a chi-square test to compare the observed seed dispersion by quadrat ($1.5 \times 3\text{ m}$)

to a Poisson distribution within each site. We tested seed presence for association within and among transects using Spearman's rank correlation to look for systematic trends in seed distribution across the sites. The low density of seeds precluded any analysis of the relationships between the number of seeds present in the soil seed bank and habitat indicators.

Dispersion of seedlings and adults was determined by the same procedure as seed dispersion. We used a chi-square test to compare the observed distribution of seedlings and adults by quadrat to a Poisson distribution within each site. To test for spatial association between adults and seeds/seedlings within each site, we compared the mean of the shortest distance from each seed/seedling to the nearest adult to the 95% confidence interval derived from the means of 10,000 jackknife samples, which represented the distance between random points that did not contain seeds/seedlings and the nearest adults.

To determine other plant species' associations with *A. californica* adults (low sample size precluded this analysis for seeds), we attempted principal components analysis (PCA) with all plant species included; however, factor loadings were not easily interpretable. Likewise, graphical analysis suggested complex curvilinear relationships among species. Therefore, each plant species was analyzed alone with subsequent Bonferroni adjustment to control the family-wise error rate. Sites were divided into 2 groups: those with relatively large *A. californica* populations (Sites 1 and 4; >200 plants) and those with small populations (Sites 2, 3, 5, 6, and 7; ≤ 25 plants). For each plant species, a bootstrapped 95% confidence interval was used to compare proportional areas covered based on calculated area from plant measurements. In the same way, within sites, the representation of a species within quadrats that did not contain *A. californica* was compared to representation in quadrats that contained *A. californica*.

Few *A. californica* adults were coincident with sites chosen for cryptogamic crust cover, rock cover, and soil surface strength measurements, so we used 3 separate statistical approaches to examine habitat characteristics. First, contingency tables tested for associations between cryptogamic crust (presence/absence) and rock cover quartiles with *A. californica* plant

presence/absence within a quadrat for each site. Second, within each site, we bootstrapped the measurements for quadrats with no *A. californica* 10,000 times to form resampled data sets (n = number of quadrats with *A. californica* adults within the site). We compared quadrats with and without plants by using the resulting 95% confidence intervals. Third, we used a Spearman's rank correlation to relate the total number of *A. californica* adults in a site to site-wide mean cryptogamic crust cover, rock cover, and soil penetrability derived from category midpoints. Site-level associations among habitat variables, number of seeds, number of adults, associated plant species cover, plant diversity (measured by the Simpson index: $1/\sum p_i^2$), total plant cover (cm^2), and seed densities were tested using a Spearman's rank correlation (a conservative test).

RESULTS

Soil Seed Bank

Seeds were rare and scattered throughout the soil column. Of the 114 seeds found within 9164 soil cores extending down 4 cm from the surface, 38 seeds were viable, which translates to a density of 0.651 viable seeds per m^2 or 6510 viable seeds per 100 ha. Soil seed density varied by site, but at no site were there significantly more or fewer seeds in the 0–2 cm depth increment than in the 2–4 cm depth increment (Fig. 2). Overall, 60% of the seeds were found within the top 2 cm of the surface and 40% at the 2–4 cm depth. The proportion of viable seeds did not significantly change with depth within a site, but viability among sites ranged from 26% to 79%.

The dispersion of seeds across the site varied, with little evidence for biotic or abiotic factors in the environment serving to increase seed density. Seeds were spatially clumped in 2 sites (site 1: $\chi^2_1 = 8.9$, $P = 0.003$; site 2: $\chi^2_1 = 8.9$, $P = 0.003$) but were indistinguishable from a random distribution ($\chi^2_1 < 3.0$, $P > 0.05$) in the other sites. No *A. californica* seeds were found in any of the 7 excavated ant mounds. We observed no significant association between seed densities and soil penetrance ($\rho = 0.56$, $P = 0.194$, $n = 7$), mean cryptobiotic crust ($\rho = -0.21$, $P = 0.658$, $n = 7$), or rock cover ($\rho = 0.19$, $P = 0.676$, $n = 7$) among sites.

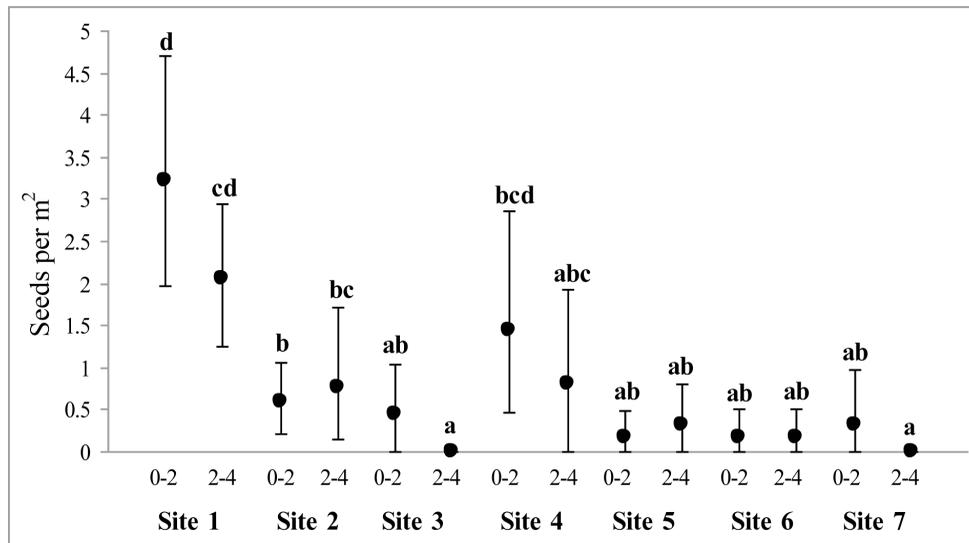


Fig. 2. Mean number of *Arctomecon californica* seeds per m² (viable and nonviable) with 95% confidence intervals. The “0–2” and “2–4” labels refer to the depth (cm) at which the sample was removed. Identical letters denote groups with overlapping confidence intervals.

TABLE 1. Sample sizes for *Arctomecon californica* seed and plant censuses by site and depth. Differences in sample sizes among sites were due to terrain features.

| Site | Depth (cm) | Cores | Seeds | Viable seeds | Viable seeds per m ² | Seedlings | Juveniles | Adults | Total plants | Plants per m ² |
|------|------------|-------|-------|--------------|---------------------------------|-----------|-----------|--------|--------------|---------------------------|
| 1 | 0–2 | 2141 | 44 | 13 | 1.23 | 513 | 138 | 61 | 713 | 0.073 |
| | 2–4 | | 28 | 4 | | | | | | |
| 2 | 0–2 | 2084 | 8 | 1 | 0.53 | 10 | 0 | 0 | 10 | 0.001 |
| | 2–4 | | 10 | 6 | | | | | | |
| 3 | 0–2 | 1056 | 3 | 0 | 0.00 | 1 | 3 | 1 | 5 | 0.001 |
| | 2–4 | | 0 | 0 | | | | | | |
| 4 | 0–2 | 987 | 9 | 8 | 1.59 | 147 | 97 | 14 | 258 | 0.026 |
| | 2–4 | | 5 | 2 | | | | | | |
| 5 | 0–2 | 980 | 1 | 0 | 0.32 | 12 | 4 | 0 | 16 | 0.002 |
| | 2–4 | | 2 | 2 | | | | | | |
| 6 | 0–2 | 954 | 1 | 1 | 0.16 | 17 | 4 | 3 | 24 | 0.002 |
| | 2–4 | | 1 | 0 | | | | | | |
| 7 | 0–2 | 968 | 2 | 1 | 0.16 | 0 | 0 | 0 | 0 | 0.000 |
| | 2–4 | | 0 | 0 | | | | | | |

Arctomecon californica Plants

Arctomecon californica plants were rarer than seeds, and they were arranged more systematically in some cases (Table 1). Plant density varied by site, ranging from 0 to 0.07 plants per m² (Table 1). Seedling density followed a similar pattern (Table 1). We found that *A. californica* adults were significantly more clumped than would be expected in a randomly dispersed population at all but the 2 most sparsely populated sites (site 1: $\chi^2_2 = 307.3$, $P < 0.001$;

site 2: $\chi^2_1 = 2.5$, $P = 0.115$; site 3: $\chi^2_1 = 3.3$, $P = 0.069$; site 4: $\chi^2_2 = 157.6$, $P < 0.001$; site 5: $\chi^2_1 = 11.4$, $P < 0.001$; site 6: $\chi^2_1 = 16.0$, $P < 0.001$). Seedlings were significantly clumped in the 2 most heavily populated sites (site 1: $\chi^2_3 = 1021.5$, $P < 0.001$; site 4: $\chi^2_2 = 56.4$, $P < 0.001$). Seeds of *A. californica* were located significantly closer to *A. californica* adults ($\bar{x} = 5.6$ m) than to points without seeds ($\bar{x} = 10.0$ m) in the most heavily populated site, site 1 (95% CI 7.8–13.6), but at no others. Seedlings were located significantly closer to plants than



Fig. 3. The number of *Arctomecon californica* seedlings compared to the number of adult plants at each site.

TABLE 2. Plant species percent cover for sites with abundant *Arctomecon californica* adults (Sites 1 and 4) compared to sites with few or no *A. californica* adults (Sites 2, 3, 5, 6, and 7). Means and bootstrapped (1000 samples) 95% confidence intervals (in parentheses) are provided. Bolded values denote significant differences between groups of sites as inferred by nonoverlapping confidence intervals and are the larger value in each significant comparison.

| Plant species | Sites with abundant <i>A. californica</i> (% cover) | Sites with few to no <i>A. californica</i> (% cover) |
|-------------------------------|--|---|
| <i>Acacia greggii</i> | 0.0031 (0, 0.0093) | 0.0753 (0, 0.2247) |
| <i>Ambrosia dumosa</i> | 1.4260 (1.0739, 1.8433) | 3.8047 (3.4576, 4.1791) |
| <i>Atriplex canescens</i> | 1.0602 (0.8493, 1.2749) | 1.4878 (1.2816, 1.7058) |
| <i>Atriplex confertifolia</i> | 0.0382 (0.0156, 0.0644) | 0.0000 (0, 0) |
| <i>Ephedra torreyana</i> | 0.8276 (0.3969, 1.5084) | 0.8240 (0.6340, 1.0289) |
| <i>Eriogonum inflatum</i> | 0.0000 (0, 0) | 0.0491 (0.0236, 0.0811) |
| <i>Gutierrezia sarothrae</i> | 0.0029 (0, 0.0084) | 0.0551 (0.0224, 0.0947) |
| <i>Krameria parvifolia</i> | 0.7096 (0.4804, 1.0064) | 0.8067 (0.5964, 1.0256) |
| <i>Larrea tridentata</i> | 0.9973 (0.3200, 1.8411) | 0.7113 (0.4164, 1.0378) |
| <i>Lepidium fremontii</i> | 0.0033 (0, 0.0089) | 0.0482 (0.0189, 0.0836) |
| <i>Menodora spinescens</i> | 0.2753 (0.1420, 0.4456) | 0.2738 (0.1882, 0.3647) |
| <i>Phacelia pulchella</i> | 0.0029 (0, 0.0087) | 0.0033 (0, 0.0076) |
| <i>Prosopis glandulosa</i> | 0.0004 (0, 0.0009) | 0.2029 (0.0064, 0.4878) |
| <i>Sphaeralcea ambigua</i> | 0.0327 (0.0053, 0.0687) | 0.0342 (0.0091, 0.0664) |
| <i>Xylorhiza tortifolia</i> | 0.0009 (0, 0.0024) | 0.0451 (0.0160, 0.0580) |

to randomly chosen points in all sites, and no seedlings were found outside of quadrats containing adult plants (data not shown). We detected no significant correlation ($\rho = 0.55$, $P = 0.205$, $n = 7$) between the number of adults in a site and the number of seeds, although there was a general positive trend (Table 1). There was a perfect rank correlation between the number of adults in a site and the number of seedlings ($\rho = 1$, $P = 0.0028$, $n = 6$; Fig. 3).

Habitat Variables

We observed largely negative associations between *A. californica* and other plant species.

Seven associated plant species had lower cover in sites supporting large populations of *A. californica* plants compared to sites with small populations (Table 2). *Atriplex confertifolia* was positively associated with *Arctomecon californica* on Site 4 only. Overall, plant species cover and plant diversity (Simpson index) were not significantly correlated with the number of *A. californica* adults on a site-wide basis (Spearman's rank correlation; $P > 0.05$). Within sites, quadrats with *A. californica* plants had significantly less overall vegetative cover than quadrats without *A. californica* plants (Table 3).

TABLE 3. Mean total vegetative percent cover based on quadrats lacking *Arctomecon californica* adults compared to quadrats with at least one *A. californica* adult. Means and bootstrapped (1000 samples) 95% confidence intervals (in parentheses) are provided for each site. Bolded values denote significant differences between quadrats with and without *A. californica* plants and are the larger value in each significant comparison. The subsample of quadrats in Table 1 for which vegetative data were recorded was used in this analysis (nd = no data collected).

| Site | Quadrats lacking <i>A. californica</i> plants | | Quadrats with <i>A. californica</i> plants | |
|------|--|----------|---|----------|
| | % cover | <i>n</i> | % cover | <i>n</i> |
| 1 | 4.97 (3.08, 7.35) | 160 | 1.90 (0.89, 3.15) | 23 |
| 2 | 6.16 (4.66, 7.88) | 183 | nd | |
| 3 | 10.68 (8.62, 13.00) | 181 | nd | |
| 4 | 6.62 (4.82, 8.74) | 161 | 9.30 (0.07, 20.62) | 5 |
| 5 | 7.39 (5.84, 9.23) | 184 | 0.08 (0.06, 0.09) | 2 |
| 6 | 10.02 (8.36, 11.72) | 176 | 3.60 (0.86, 6.70) | 7 |
| 7 | 9.36 (7.67, 11.17) | 184 | 0 (0, 0) | |
| All | 7.95 (7.25, 8.67) | 1229 | 3.12 (1.47, 5.18) | 37 |

Site-level differences in soil hardness were related to *A. californica* presence, but finer-scale variations in soil hardness added no additional information. A site's soil surface strength and the number of *A. californica* adults were positively related ($\rho = 0.76$, $P = 0.046$). This pattern was largely determined by the extreme cases: sites with the hardest soils (site 1 = $1.81 \text{ kg} \cdot \text{cm}^{-2}$, 95% CI 1.69–1.93; $n = 713$ adults; and site 4 = $1.74 \text{ kg} \cdot \text{cm}^{-2}$, 95% CI 1.61–1.87; $n = 258$ adults) had more *A. californica* adults than sites with softer soils (e.g., site 7 = $1.35 \text{ kg} \cdot \text{cm}^{-2}$, 95% CI 1.27–1.43; $n = 0$ adults). Quadrat-level analysis yielded no evidence that soil penetrability differed between quadrats containing *A. californica* adults and those without *A. californica* adults within any of the sites or overall (Table 4).

We found little evidence that rock and cryptogamic crust cover can help characterize *A. californica* habitat. We observed no linear or nonlinear correlation ($\rho = -0.11$, $P = 0.082$) between the mean amount of surface rock cover at a site and the number of *A. californica* adults overall. Within sites, rock cover of quadrats with *A. californica* adults did not significantly

differ from that of quadrats without *A. californica* adults (Table 4). We found no evidence for a relationship between cryptogamic crust cover and *A. californica* adults within sites (Table 4). Furthermore, there was not a significant relationship between the mean amount of crust cover at a site and the number of *A. californica* plants ($\rho = -0.64$, $P = 0.139$).

DISCUSSION

Seeds play a crucial role in population persistence in arid and semiarid environments (Cabin et al. 2000), but they are the most difficult segment of the population to quantify (Bigwood and Inouye 1988). Intensity of sampling in soil seed banks should ideally be a function of seed density (Bigwood and Inouye 1988). With more than 9000 cores, this study included one of the most intensive samples of a single perennial plant species' seed bank in the literature for arid or semiarid habitats (sensu Page et al. 2006). Even so, because of the low densities of *A. californica* seeds in the sampled sites ($0.65 \text{ seeds} \cdot \text{m}^{-2}$), few seeds were located irrespective of adult *A. californica* plants. It is clear that very rare species may require extraordinary sampling intensity of the soil seed bank to obtain reliable estimates of seed density and dispersion. This study has demonstrated that, for species with sporadic germination, multiyear monitoring is not just recommended but essential if a biologically realistic assessment of soil seed bank dynamics is the goal.

Arctomecon californica seeds were rare, even though *A. californica* is known to have a high estimated reproductive output (4098 ± 757 seeds per plant) for a perennial species (Meyer 1987, Megill 2007). There are several plausible explanations for this result. (1) Our sampling period corresponded with a low point in *A. californica* seed populations in the study area because of a mass germination event during spring 2005, just prior to sampling (G. Marrs-Smith, Las Vegas Conservation Transfer Area Manager for Bureau of Land Management, personal communication). The large number of seedlings in this study supports this supposition (Table 1). (2) The study area is severely fragmented due to urban expansion, which has encroached on and extirpated extant *A. californica* populations (Hickerson and Wolf 1998, Mistretta et al. 1996). Habitat

TABLE 4. Habitat-based indicators for each site, including size of *Arctomecon californica* population, means, 95% confidence intervals, significant differences between sites (denoted by letters if any nonoverlapping confidence intervals were observed), and points sampled (number of quadrats with *A. californica*, number of quadrats without *A. californica*).

| Site | Mean soil penetrability (kg · cm ⁻²) | 95% CI | Mean rock cover (%) | 95% CI | Mean cryptogamic crust cover (%) | 95% CI | Points sampled |
|------|--|----------------|---------------------|-------------------|----------------------------------|----------------|----------------|
| 1 | 1.68 | (1.54, 2.13) a | 62.28 | (56.03, 74.27) b | 0.00 | (0, 0) a | 30, 183 |
| 2 | | | | | | | 0, 213 |
| 3 | 0.42 | (0.25, 2.83) a | 37.50 | (0.50, 87.50) ab | 0.00 | (0, 3.50) ab | 1, 156 |
| 4 | 1.57 | (1.41, 2.13) a | 24.06 | (19.00, 32.94) a | 0.20 | (0.03, 1.25) b | 18, 142 |
| 5 | 1.75 | (0.50, 3.50) a | 15.50 | (3.00, 62.50) ab | 1.25 | (0, 9.00) ab | 1, 95 |
| 6 | 1.81 | (0.89, 2.83) a | 46.83 | (22.83, 62.50) ab | 0.67 | (0, 1.50) ab | 3, 154 |
| 7 | | | | | | | 0, 186 |

fragmentation both directly reduces plant populations and “increases isolation between extant populations,” thus indirectly altering biotic interactions (e.g., pollinator diversity, behavior) that can lead to the reduction of future reproductive output (Wilcock and Neiland 2002, Lienert 2004, Picó 2004). Hickerson and Wolf (1998) reported that an *A. californica* population in fragmented habitat near the subpopulations in this study had significantly lower reproductive success than subpopulations in unfragmented habitat, potentially due to fewer and less diverse pollinators. Seed production within our study area may have been hindered by a lack of pollinators, thereby lowering the number of seeds to be dispersed relative to the number of plants. (3) Our results may underestimate the soil seed bank because we did not intensively sample around parent plants but randomly across the site. (4) There is also the possibility that an unidentified secondary disperser may be removing the *A. californica* seeds within these subpopulations. Granivory trials and demographic studies in the future may elucidate key dispersers or factors that influence the spatial distribution of seeds within the soil seed bank. This type of information clearly would aid in designating suitable and potential habitat and would help managers design defensible mitigation measures. Collectively, all of the above possibilities offer plausible explanations for the low density of seeds detected.

Ambiguity surrounding the spatial distribution of the soil seed bank has hindered management decisions regarding *A. californica*. For example, development proceeds in areas that do not support live *A. californica* plants consistently across years. Additionally, a small-scale soil seed bank study conducted by Science Applications International Corporation

(2001) in LMNRA concluded that the soil was “depauperate” of *A. californica* seeds and suggested that the species lacks a soil seed bank. However, Megill (2007) substantiated the presence of a soil seed bank and presented 4 lines of evidence of its persistent nature. The current study also supports Megill’s (2007) conclusions that *A. californica* does maintain a residual soil seed bank. Therefore, *A. californica* populations should not be assumed extinct simply because no established aboveground plants are present.

We examined the spatial distribution of the soil seed bank in relation to aboveground *A. californica* plants in order to determine if adult plant populations are reliable indicators for the spatial distribution of the soil seed bank. Typically, primary dispersal would tend to clump seeds around the parent plant (Levin 1981). Megill (2007) and Megill (unpublished data) reported that seeds of *A. californica* travel 0.5 m on average from the parent plant in the prevailing wind direction during primary dispersal and that these seeds tend to form significantly clumped deposits approximately 60–100 cm away from the parent plant. In our study, we found that seeds were closer to adults only in the site with a reasonably large sample of both seeds and plants ($\bar{x} = 5.6$ m; Table 1). It is possible that the biological interpretation of this result was hindered by low statistical power resulting from the small sample size of either seeds or plants, as we found that seedlings were very close to adult plants at all sites. Therefore, our data suggest that the presence of adult plants in relatively high densities (0.006 plants · m⁻²) may indicate the presence of a soil seed bank, possibly because the plants serve as seed sinks (Aguilar and Sala 1997, Bullock and Moy 2004). Although, as the density of an aridland species

declines, adult plants become a less reasonable proxy for predicting soil seed banks.

Granivory may have contributed to the lack of association between aboveground plants and the spatial distribution of seeds we observed within the other 6 sites in our study area. Granivores can impact seed survivorship and seedling recruitment by consuming considerable proportions of seeds from some plant species (Reichman 1979, Crist and MacMahon 1992). The impact on rare plants can be quite severe if most of the seed crop is lost to predators. Recent work has revealed that *A. californica* seeds do not persist for long periods of time on the soil surface, apparently because of ant harvesting (Megill 2007). Granivory experiments in nearby LMNRA suggested that approximately 40% of *A. californica* seeds that reached the surface were dispersed and/or consumed by ants and rodents (Megill 2007). In our study, 7 excavated *Pogonomyrmex* sp. (harvester ant) nests yielded no *A. californica* seeds. These results are surprising because ant nests were sufficiently close to *A. californica* adults (mean distance: 10.0 ± 3.1 m) for foraging and seed harvesting (Crist and MacMahon 1992). However, it is possible that the very low densities of *A. californica* seeds within these fragmented sites preclude use of the seeds as a major food source for some or all granivores. Although we observed no evidence of granivory within our fragmented subpopulations, our observation may not apply to populations where *A. californica* seeds are more abundant.

If adult plants are not always reliable indicators of the spatial distribution of the soil seed bank across the landscape, then habitat variables should be integrated to be of maximal value to those vested in conserving rare species (Wiser et al. 1998). One of the strongest indicators of present and potential habitat for *A. californica* may be the abundance or scarcity of plant cover provided by other vascular species. Land managers could rely on the occurrence of positively associated species such as *Atriplex confertifolia* (this study, Meyer 1986, Nelson and Welsh 1993), as well as the scarcity of other plant species that were negatively correlated with *Arctomecon californica* (Table 2). However, we suggest that land managers exercise caution, because positively and negatively associated species may be subject to the same constraints (i.e., pressures from habitat fragmentation) as the study species.

Additionally, areas with low vegetative cover and high soil surface strength supported significantly higher densities of adult *A. californica* plants. Our results substantiate those of Nelson and Welsh (1993) and Mistretta et al. (1996), which showed that *A. californica* inhabits open areas within the creosote and salt-bush plant community typical of the Mojave Desert, perhaps because these regional dominants cannot establish on the abiotic crusts found in the open areas (Meyer et al. 1992, Romão and Escudero 2005). Meyer et al. (1992) suggested that only in instances where a thin layer of alluvium over the crust is present would the necessary buffer for successful establishment be provided for the dominant species. Therefore, we propose that the frequent presence of *A. californica* adults on gypsum-laced soils may be the consequence of minimal competition for resources, as Palacio et al. (2007) suggested for other endemic gypsum-tolerant species. Unfortunately, experimental tests of competitive interactions between *A. californica* and other species are currently impractical due to the difficulty of cultivating *A. californica* plants.

We suggest that land managers exercise caution when disturbing *A. californica* habitat because of the likely longevity of the soil seed bank, the relatively short lifespan of plants, and the rarity of recruitment years. Our results especially apply in areas lacking baseline data for the targeted species, because current mitigation measures such as soil banking may prove ineffective, as suggested by Scoles-Sciulla and DeFalco (2009). The resultant study discovered that seed reserves become diluted during the reclamation process due to the mixing of the upper and lower soil layers, which decreases seedling emergence by as much as 79% (Scoles-Sciulla and DeFalco 2009). Additionally, due to the extremely patchy nature of seeds in arid and semiarid environments (Reichman 1984, Coffin and Lauenroth 1989), surface soil extracted for reclamation may be devoid of seeds (Science Applications International Corporation 2001). Furthermore, seed reserves can be lost due to soil storage and replacement (Bellairs and Bell 1993, Koch and Ward 1994).

Conclusions

Arctomecon californica maintains a residual soil seed bank that likely overlaps generations and provides a buffer against catastrophic

events. The inclusion of seeds within the seed bank reveals the presence of a substantially larger population than previously believed. In instances of heavily populated sites, the soil seed bank is proximal to established plants. Areas with hard, gypsum-laced soils and low vegetative cover may be of particular interest, as these are the most likely sites for future establishment of *A. californica*. In conjunction with the above habitat indicators, the presence and absence of certain vascular plant species may narrow possible sites. More importantly, areas that fall within the known range of *A. californica* (including historical, active, and dormant sites) should be considered *A. californica* habitat.

We suggest that seed bank sampling of rare plants should occur across multiple years of reproduction, including exceptionally prolific years. In this way, seed fate pathways can be traced to elucidate key abiotic and biotic factors that influence seed bank dynamics such as dispersal limitation (Quinn et al. 1994), granivory (Reichman 1984, Crist and MacMahon 1992), and establishment restrictions (Martínez-Duro et al. 2009). Only in this way can the relative importance of seed production, primary and secondary dispersal, mortality, and germination best inform appropriate conservation action.

ACKNOWLEDGMENTS

We thank E. Powell for helpful discussions about *A. californica* and J. Chambers, C. Cross, and S. Meyer for their insightful reviews of the manuscript. Essential field assistance was provided by B. Bovary, R. Estacio, L. Fitzhenry, T. Milleret, T. Patel, M. Razaq, N. Rennie, C. Rhodus, H. Sanders, P. Sotolongo, and T. White. For technical and logistic support, we thank the Bureau of Land Management, Las Vegas Field Office. Funding for this project was provided under the Southern Nevada Public Lands Management Act.

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Received 6 July 2010
Accepted 11 February 2011