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Seed dispersal and seed fate in Joshua tree (*Yucca brevifolia*)

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ABSTRACT

Joshua tree (*Yucca brevifolia*) is a charismatic symbol of the Mojave Desert. Despite its familiarity, we know little about the reproduction of this species, including mechanisms of seed dispersal. Here we examine mechanisms of seed dispersal and resulting seed fate. We experimentally tracked fruit and seed removal and followed the fates of Joshua tree seeds using radioactive tracers. The majority of Joshua tree fruits monitored were taken directly from the tree canopy by white-tailed antelope squirrels, and seeds and fruits on the soil surface were quickly removed by animals. Rodents given seeds labeled with scandium-46 cached them between 0.1 cm and 4.1 cm deep. Seedling emergence was most common for seeds planted 1 cm deep, whereas seeds placed on the soil surface seldom germinated. Wind dispersal is unlikely because fruits and seeds lack adaptations for wind dispersal; wind speeds required to move Joshua tree seeds and fruits across the soil surface were higher than those typically found in the Mojave Desert. Further, rodents removed most seeds before abiotic burial was possible. We conclude that most Joshua tree seeds are dispersed by scatter hoarding by rodents, and that caches made by rodents are suitable sites for seedling emergence.

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1. Introduction

The propagules of many perennial plants found in North American deserts have morphological traits that indicate dispersal by wind or by ants, whereas seed dispersal by frugivorous animals appears to be uncommon (Bronstein et al., 2007; van Oudtshoorn and van Rooyen, 1999). Seed dispersal by scatter-hoarding rodents has not been explored thoroughly in deserts (but see Longland et al., 2001; McAuliffe, 1990), partly because traits that promote the harvest and storage of propagules by animals are not easily recognized. Attributes associated with dispersal by scatter-hoarding animals may encourage seedling survival in arid environments (Beck and Vander Wall, 2010). Seeds buried below the soil surface may escape from hot dry conditions that promote desiccation. Since many desert rodents eat and store seeds, it seems likely that many desert plants could be dispersed in this way. The short temporal window for seed harvest and the necessity of this food source to rodents for survival through periods of low production have been hypothesized to favor the evolution of seed dispersal by scatter-hoarding rodents (Thompson, 1982; Vander Wall, 2001).

Indeed, scatter-hoarding rodents have been identified as seed dispersers for several desert plant species. McAuliffe (1990) found that most fallen seeds of palo verde (*Cercidium microphyllum*) were scatter-hoarded by heteromyid rodents and about half of all palo verde seedlings were from rodent caches. Similarly, Reynolds (1954) found that velvet mesquite (*Prosopis julifora*) seeds were scatter hoarded by Merriam's kangaroo rats in the Sonoran Desert. In the Great Basin Desert, Ord's kangaroo rats (*Dipodomys ordii*) scatter-hoard seeds of Indian rice grass (*Achnatherum hymenoides*) (Longland et al., 2001). Several studies have shown that rodent exclusion can alter the vegetation community (Brown and Heske, 1990; Kerley and Whitford, 2009; Reynolds, 1950), although few studies have documented the fate of seeds handled by granivorous rodents (Vander Wall et al., 2005). Thus far, little has been published about dispersal by scatter-hoarding rodents in the drier Mojave Desert, but its arid environment may favor seed dispersal mutualisms if seeds stored in the soil are more likely to escape the harsh conditions that cause seed mortality.

Joshua tree (*Yucca brevifolia* Engelm.) is a long-lived perennial species endemic to the Mojave Desert that produces relatively large seeds in indehiscent fruits (Rowlands, 1978). Although the pollination system of Joshua tree has been very well studied

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(Godsoe et al., 2008; Pellmyr, 2003; Smith et al., 2008), we know very little about the fates of its propagules post-maturation (e.g., seed fate, seedling recruitment). What has been written about Joshua tree seed dispersal has been mostly speculation, from abiotic dispersal by rolling fruits (Trelease, 1893), to wind dispersal (Webber, 1953), to dispersal by extinct megafauna (Laudermilk and Munz, 1935; Lenz, 2001). To date, there has been only one published study that experimentally followed the fate of Joshua tree seeds. Vander Wall et al. (2006) found that Joshua tree seeds were scatter-hoarded by rodents up to 57 m from their source. This study made a strong case for rodent dispersal of Joshua trees, however, the identity of the species moving the seeds was not determined, and many questions concerning how rodents harvest seeds and how seedling recruitment occurs remain to be investigated.

In this study, we tested potential mechanisms for the dispersal of Joshua tree seeds and seed fate with a combination of field experiments. We hypothesize that rodents are dispersers of Joshua tree seeds and that dispersal by rodents increases the likelihood of successful seedling emergence.

2. Methods

2.1. Study sites

We used sites in Piute Valley and Ivanpah Valley to examine how rodents interact with Joshua tree fruits. The Piute Valley site (674909, 3930163 UTM NAD 83 zone 11N) is located between the New York and Newberry Mountains in southern Nevada, USA. It is located directly south of the Wee Thump Joshua tree wilderness, which contains some of the largest Joshua trees in Nevada. The area was dominated by Joshua trees and blackbrush (*Coleogyne ramosissima* Torr.) with sparse creosote bush (*Larrea tridentata* Cov.) cover. The Ivanpah Valley site (635815, 3906124 UTM NAD 83 zone 11N) is located on the east side of the Mojave National Preserve, CA between the Ivanpah and New York mountains. The stands we used were dominated by Joshua tree and blackbrush. Mojave Desert ecosystems experience extremely variable rainfall, although average rainfall is generally less than 14 cm/year. Mean monthly low temperatures can be below freezing in winter, and the mean monthly high is often greater than 45 °C in summer.

Joshua tree flowers in mid-spring from Feb–March. Fruits form in early summer and seeds are mature in mid-summer (B. Waitman, unpub. data). Joshua trees form dens3 infructescences with clusters of 2–30 or more fruits. Fruits are 6–9 cm in length and 4–6 cm in diameter. Unlike many other species of *Yucca*, Joshua tree fruits have dry spongy flesh and are indehiscent. Joshua tree seeds are flat and round, 4–10 mm in diameter and nearly black with no external structures. Prior to this study, observations have been made of both ants and rodents removing Joshua tree seeds (Zembal and Gall, 1980, B. Waitman pers. obs.). However, ants are unlikely dispersers for this species. Joshua tree seeds lack elaiosomes and the only benefit ants may derive from these seeds is from eating the endosperm and damaging the seed.

2.2. Fruit harvest by animals

We monitored six transects to determine when and how Joshua tree fruits fall from infructesences. We established three transects in Piute Valley and three in Ivanpah Valley. Each transect consisted of ten haphazardly selected trees (3 transects or 30 trees per site), and we spaced transects more than 0.5 km apart. On each tree, we chose two infructescences of similar size, height and aspect. We covered one of these infructescences, chosen at random, with a mesh bag made of aluminum window screening. We cinched each mesh bag at the stem about 10 cm below the infructescence to restrict access by animals. The bags may have provided some shelter from wind to the infructescence, but did not prevent Joshua tree branches from swaying. The paired infructescence was not bagged. We visited transects bi-monthly, and recorded the number of fruits present. The difference in the proportion of fruits remaining attached to the tree after three months between bagged and unbagged infructescences was compared with a paired *t*-test.

2.3. Wind dispersal

We placed Joshua tree seeds and fruits in a wind tunnel to determine the wind speed required to move them along the ground surface. We used a portable, open-bottomed tunnel of 15 cm × 15 cm × 240 cm (described in Belnap and Gillette, 1997). We measured wind speed via a Pitot tube anemometer (Belnap and Gillette, 1997). We created two surfaces to look at minimal and moderate levels of microtopography. One surface consisted of 60 mesh sand (minimal surface resistance) and one of landscape cobbles (3–8 cm minimum diameter). For the rocky substrate, fruits and seeds were placed against a 1 cm barrier (i.e., a cobble). We placed one of six seeds or one of six fruits on the soil surface at the same spot underneath the wind tunnel for each trial. The wind speed was slowly increased until a seed moved a full length or a fruit rolled one full revolution. Once a wind speed that moved a seed or fruit was reached, we recorded the wind speed at 10 cm above the substrate. We took all measurements at the USGS field station in Moab, Utah, USA.

2.4. Fruit and seed removal

Joshua tree fruits may fall to the ground and become available to foraging animals. We wished to gauge the rate of removal of Joshua tree fruits from the ground surface. We established four fruit removal transects at Piute Valley in July 2008. Each transect consisted of 40 fruits set ≈5 m apart. We set fruits haphazardly with regard to soil type and shrub cover. Each fruit was tethered by a short wire such that the fruit was unable to roll in the wind and the wire was not visible. We surveyed each fruit transect daily until fewer than five fruits remained. We analyzed all data in R (package "survival", Therneau, 2009) and calculated rates of removal using survival analyses assuming a Weibull distribution and right censored data.

We used a similar set of transects to determine the rate of removal of single seeds that might have fallen or been knocked from a fruit. We placed eight transects at Piute Valley and eight transects at Ivanpah Valley in July and August 2007. To determine whether microsite influenced foraging rate, we designated four transects as shrub cover and four transects as open (no cover) at each site. We placed 40 seeds at ≈5 m intervals along each 200 m long transects. For the shrub cover, we placed seeds at least 10 cm beneath shrub canopy, and for the open transects, we placed seeds at least 20 cm from the nearest shrub cover. All seeds were tethered to a toothpick with a thread that matched the color of the substrate. We pushed toothpicks into the soil such that the toothpick was not visible. We surveyed transects until fewer than 5 seeds remained per transect. The explanatory variables tested for seed removal transects were site and presence of shrub cover. As above, we analyzed all data in R (Therneau, 2009) and calculated rates of removal using survival analyses assuming a Weibull distribution.

2.5. Rodent seed-caching

We constructed two 10 m × 10 m enclosures at the Piute Valley site to examine rodent removal of Joshua tree seeds. Enclosures

were constructed of wood and 12 mm wire mesh. The wire mesh extended ≈50 cm below ground to prevent rodents from tunneling in or out of the enclosures. The walls were ≈70 cm high topped with aluminum flashing to exclude climbing rodents. Vegetation in the enclosures was Mojave Desert scrub (dominated by creosote bush and burro bush) with a single Joshua tree in each enclosure. We buried a 20-L plastic bucket such that the lid was level with the ground surface just outside each enclosure to serve as an artificial burrow. Each bucket consisted of three chambers separated by plywood partitions with a 5-cm diameter circular hole between chambers. A 25-mm diameter PVC pipe connected the upper chamber to the interior of the enclosure through a small hole in the hardware cloth fence. We placed subjects in the PVC tube entrance at the start of each trial, and they generally accepted the bucket as an artificial burrow.

We ran eight successful scatter-hoarding trials with white-tailed antelope squirrels (*Ammospermophilus leucurus*) and five with Merriam's kangaroo (*Dipodomys merriami*) rats in which animals removed and buried Joshua tree seeds between July and September 2008. In each trial we released a single rodent into the artificial burrow and placed 200 Joshua tree seeds labeled with scandium-46 at the base of the Joshua tree inside the enclosure. Scandium-46 is a gamma-emitting radionuclide with a half-life of 84.5 days, decays to non-toxic titanium, and is not sequestered by animals or plants (Vander Wall, 2000). We allowed rodents up to 48 h to remove seeds. We considered a trial complete if a rodent removed at least half (100) of the available seeds, even if less than 48 h had elapsed. We then sequestered the rodent in the nest bucket and surveyed the enclosure with a Geiger counter to find any caches that the subject had made. To determine whether rodents preferentially cache seeds in certain microsites we excavated caches, recorded their depth, number of seeds per cache, and microsite (under shrub or in the open), and mapped cache sites. We also checked the artificial burrow for seeds. We removed all seeds and feces prior to the start of the next trial.

We determined the vegetation cover within each enclosure using line intercept transects. We established ten transect lines parallel to each other 1 m apart starting at 0.5 m and ending at 9.5 m. This resulted in 100 m of vegetation transect for a 100 m^2 area. On each transect, we took line intercept measurements (Elzinga et al., 2001). We estimated percent vegetation cover for each plant species as the proportion of the transect line that intercepted the species multiplied by 100. We analyzed cache microsite selection by rodents relative to availability (i.e., cover) in R (package adehabitat, Calenge, 2006) using compositional analysis as recommended by Aebischer et al. (1993).

We also conducted open field trials using Joshua tree seeds labeled with scandium-46 to determine if the seed-caching behavior of white-tailed antelope squirrels was affected by the enclosures. We placed 150 labeled seeds per trial at the base of 25 different Joshua trees over the course of 18 days in August and September 2008. A Trailmaster motion-sensing Canon 35 mm camera was stationed at each pile of seeds. We turned cameras on between 7 and 9 am and removed labeled seeds before dusk in order to ensure that only diurnal rodents (i.e., white-tailed antelope squirrels) could harvest them. Once rodents removed seeds, we surveyed the area within 25 m of the station with a Geiger counter using the same procedures described for the enclosures.

We estimated shrub cover along four 25-m transects along cardinal directions at the site of each successful trial ($n = 3$). We collected data on vegetation cover in the same manner as described above for enclosures. We used compositional analysis to determine whether rodents preferred cache microsites relative to shrub cover.

2.6. Seed germination

In August 2007 in Piute Valley, we planted Joshua tree seeds to simulate rodent caches in order to discover the optimal depth at which seeds must be cached to maximize seedling emergence. All seeds were collected on site in Piute Valley in 2007. We placed two seeds in each cache, and buried seeds at 0.1 cm, 1 cm, 2 cm, 3 cm, 4 cm, or 5 cm below the soil surface. We did not place seeds on the soil surface because ants may have removed them. We randomly assigned depth treatments to positions in a 6 × 6 grid with six replicates of each depth treatment. We planted these sets of caches inside 70 × 70 cm wire mesh exclosures that extended 10 cm into the soil to prevent entry by foraging rodents. We divided replicates ($N = 80$ exclosures) equally into shade and open treatments. Shaded exclsoures were beneath the canopy of creosote bush, while open exclosures were >2 m from the nearest shrub. Only intact, healthy-looking seeds were used. To test for viability, we placed five replicates of 20 seeds (randomly chosen from stock seeds) in Petri dishes with a piece of P6 filter paper and kept them moist. After two weeks, we recorded the number of seeds that had germinated (i.e., emergence of a radicle).

We checked exclosures intermittently between November 2007 and September 2008 for seedling emergence and survival. We defined emergence as leaves penetrating through the soil surface, and considered seedlings alive as long as any green tissue was visible. We analyzed these data with a linear mixed effects model with shrub cover and depth as fixed effects and exclosure as a random effect (R, package lme4, Bates, 2008). Joshua tree fruits were collected from the Piute Valley site in July 2007 and stored in a paper bag in a climate-controlled warehouse until use.

We also used a growth chamber (Forma Scientific diurnal growth chamber) to determine the emergence of seeds from typical cache depths under optimal moisture conditions in artificially created soil (3 parts gravel, 3 parts sand, 2 parts clay, 1 part organic matter). We buried Joshua tree seeds at 0, 1, 4, 7, or 10 cm deep with caches sizes of one, five, or 10 seeds. We placed two caches of a treatment in a 10 cm × 10 cm plastic pot. We replicated each combination five times (150 total caches) and randomly distributed treatment pots in the growth chamber. The growth chamber had three shelves, and we placed pots next to each other with 32 pots on each shelf in a 4 x 8 grid, though only 11 pots were on the bottom shelf. Each pot was watered once every three days with 200 ml of water. We set the growth chamber at 25 °C during a 12 h day period and 15 °C during a 12 h night period, and each pot was watered from 30 June 2008 to 15 October 2008. We kept two vents at the front of the growth chamber open to maintain a low humidity at the soil surface to inhibit mold formation.

We checked these caches periodically from June 2008 to September 2008 for seedling emergence and survival. We recorded emergence when leaves broke through the soil surface, or seeds germinated in the case of seeds on the surface. We analyzed results with a linear mixed effects model with cache depth and cache size as fixed effects and the pot as a random effect for each cache. At the conclusion of this study, we excavated all caches to see if seeds had germinated. Seed viability was tested at the beginning of the study as described for the germination experiment.

3. Results

3.1. Removal of Joshua tree fruits from tree canopy

The Joshua trees we monitored produced a mean of 13.5 ± 1.1 fruits/infructescence at Piute Valley and 10.1 ± 0.7 fruits/infructescence at Ivanpah Valley ($t = 2.61$, df = 58, $P = 0.010$). Joshua tree fruits began disappearing from paired uncovered infructescences

shortly after we installed mesh bags on 21–24 May. We monitored transects until fewer than 20% of fruits remained on uncovered infructescences, which took 86 days at Piute Valley and 50 days at Ivanpah Valley. Fruits were removed significantly faster at Ivanpah Valley than Piute Valley ($t = 3.15$, df = 52, $P = 0.002$). Removal rates were 0.11 ± 0.01 fruits/infructescence/day at Piute Valley and 0.29 ± 0.04 fruits/infructescence/day at Ivanpah Valley.

We removed mesh bags on 18 September. At that time, rodents had entered 12 of the 30 mesh bags at Ivanpah Valley. We found white-tailed antelope squirrels inside two of the bags along with the shattered remains of Joshua tree fruits. Simultaneously at the Piute Valley site, some bagged infructescences had blown off as a result of damage to the peduncle from weevil infestation. When we terminated the fruit removal study, 18 of the original 30 bags were intact at each site. Since transects within sites showed similar rates of removal, hereafter all statistics are given for pooled data with 30 monitored infructesences at each site. Intact bags lost no fruits, and $72.3 \pm 0.1\%$ (196/280) of fruits remained attached to the infructescence at Piute Valley and $86.3 \pm 0.1\%$ (165/185) remained attached at Ivanpah Valley. Detached infructescences still had $22.5 \pm 5.9\%$ (75/288) of fruits at Piute Valley and $10.7 \pm 4.0\%$ (32/310) at Ivanpah valley. Significantly more fruits had been removed when infructescences were unbagged and available to animals than had fallen off the infructescences inside bags ($t = 8.819$, df = 40, $P < 0.0001$ at Piute Valley; $t = 3.557$, df = 46, $P = 0.002$ at Ivanpah Valley, Fig. 1).

3.2. Wind as a possible dispersal mode

In the wind tunnel, Joshua tree fruits were moved by lower wind speeds than seeds on the sandy, low resistance, substrate (31.9 ± 2.6 km/h and 43.6 ± 2.6 km/h, respectively). As expected, both seeds and fruits were moved by lower sustained wind speeds on the sand substrate than on the rock substrate ($t = 6.77$, df = 10, $P < 0.0001$ for seeds; $t = 2.69$, df = 10, $P = 0.019$ for fruits). Wind speeds sufficient to move seeds and fruits on the rocky substrate averaged 87.6 ± 5.5 km/h and 73.6 ± 4.8 km/h, respectively. Note that these values were recorded at 10 cm above the ground, and that corresponding wind speeds would have been much greater if measured at the standard 1.8 m height of weather stations.

No weather data are available for our study sites, but data from other weather stations at similar elevations within Joshua tree habitat throughout the Mojave Desert (e.g., Christmas Tree Pass, NV; Red Rock, NV; Lost Horse, CA; and Yucca Valley, CA at 1.8 m) suggest that comparable wind speeds are uncommon. In 2007, for example, 24.5%–53.5% of observations were over 30 km/h, but only 0%–1.3% of all wind speed observations were greater than 70 km/h.

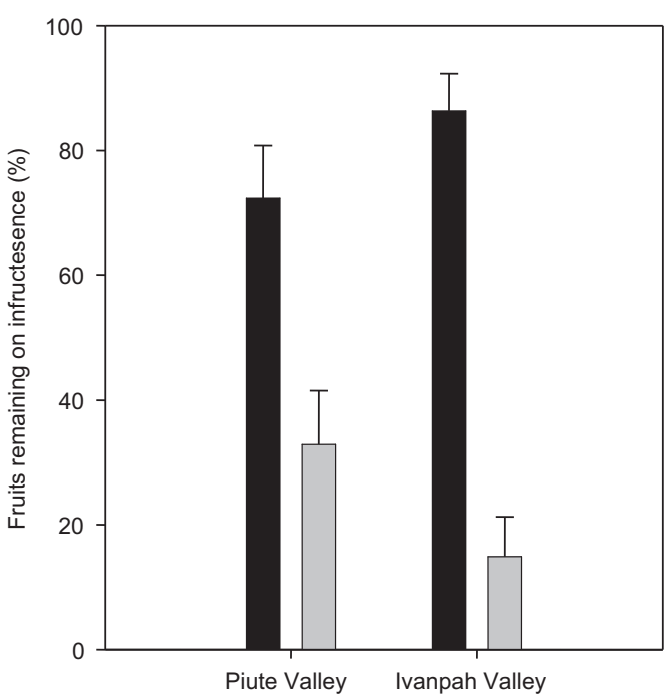

Fig. 1. Proportion of Joshua tree fruits remaining attached to infructescences in September 2007 after a 3-month monitoring period. Black bars are for infructescences restricted from animal access, gray bars are infructescences available to animals. Error bars are ±1 SE.

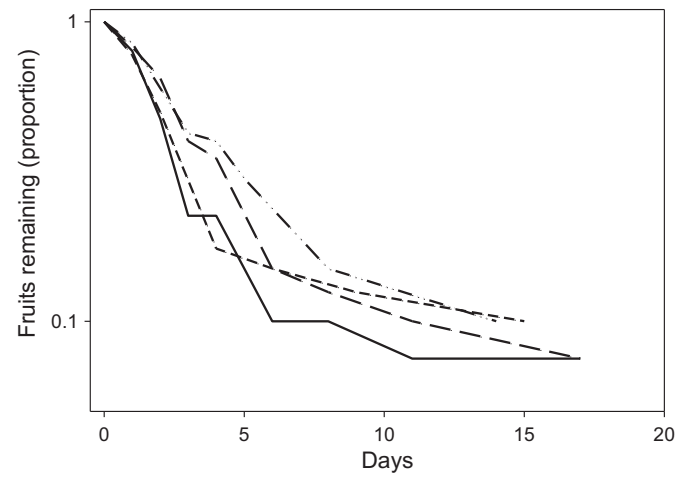

Fig. 2. Removal of single Joshua tree fruits from the soil surface along four transects plotted on a log scale against time in days at Piute Valley.

3.3. Removal of fruits and seeds from the soil surface

We monitored the four fruit removal transects until five or fewer fruits remained (13–16 days). During this time, a mean of $91.3 \pm 0.7\%$ of fruits were removed. There was no difference between transects in rate of removal ($\chi^2 = 2.16$, $P = 0.54$, df = 3). The mean half-life for fruit removal from four transects at Piute Valley was 2.9 ± 0.25 days (Fig. 2). Half-lives were calculated by survival analyses as the mean time for half of a set of seeds to be removed.

We monitored seed removal transects for 20.9 ± 1.8 days until fewer than 10 seeds remained per transect, except for two transects from which only 60% (24/40) and 72.5 % (29/40) of seeds were removed during this study after 65 days. Only site significantly affected the fit of each survival function ($Z = 34.34$, $P < 0.0001$). The

Table 1
Characteristics of white-tailed antelope squirrel (*Ammospermophilus leucurus*) caches of Joshua tree seeds in open field and enclosure trials and Merriam kangaroo rat (*Dipodomys merriami*) caches in enclosure trials. Means are pooled across all caches found. Values in parentheses are one standard error.

	A. leucurus field	*A. leucurus* enclosure	*D. merriami* enclosure
Trials	3	8	5
Caches found	39	32	46
Caches/subject	13.0 (7.1)	4.0 (1.1)	9.2 (1.7)
Cache depth (mm)	10.8 (4.4)	12.0 (3.1)	17.2 (5.4)
Seeds/cache	2.8 (0.4)	3.4 (1.5)	6.4 (1.4)
Nearest neighbor distance (m)	3.37 (1.39)	1.45 (0.73)	1.89 (0.63)
Distance from source (m)	21.27 (2.82)	2.39 (0.37)	3.72 (0.42)
Shrub/open microsite	16/23	10/22	10/36

mean half-life estimated by survival analysis was 10.6 ± 0.73 days in the Ivanpah Valley and 14.6 ± 1.29 days at Piute Valley ($\chi^2 = 18.98$, $n = 16$, $P < 0.0001$). There was no significant difference in removal rate between seeds placed under shrubs and those placed in the open ($Z = 0.773$, $P = 0.44$).

3.4. Rodent treatment of Joshua tree seeds

We placed 16 white-tailed antelope squirrels in the enclosures, but only eight made caches. Those squirrels that did not make caches either ignored seeds, ate all seeds, or disappeared from the enclosure (possibly removed by red-tailed hawks abundant in the study area). The eight animals that did store seeds made a total of 32 caches with a mean depth of 12 ± 3 mm and a mean size of 3.4 ± 1.5 seeds (Table 1). The mean nearest neighbor distance was 1.5 m ± 0.7 m and mean distance from the source was 2.4 m ± 0.4 m. The five Merriam's kangaroo rats that we placed in the enclosure all cached seeds ($n = 46$). Merriam's kangaroo rats cached a mean of 6.4 ± 1.4 seeds per cache 17 ± 5 mm deep (Table 1). The nearest neighbor distance was 1.9 ± 0.6 m, and Merriam's kangaroo rats cached seeds a mean of 3.7 ± 0.4 m from the seed source.

The two enclosures had a similar shrub cover, 22% and 28%. Compositional analyses of both white-tailed antelope squirrel and Merriam's kangaroo rat cache locations with regard to shrub cover were not significant ($\Lambda = 0.99$, df = 1, $P = 0.947$ for white-tailed antelope squirrels; $\Lambda = 0.849$, df = 1, $P = 0.365$ for Merriam's kangaroo rats), suggesting that these rodents cache at random with respect to shrub cover.

In the open field trials, we set 23 cameras, but only three stations had any seeds removed. These three trials all photographed white-tailed antelope squirrels. Caches were slightly shallower (Table 1) than those made by white-tailed antelope squirrels inside the enclosures. Caches made by white-tailed antelope squirrels in trials using camera traps had mean distance of 21.3 ± 2.8 m from the source, a significantly greater distance than those found inside the enclosure ($t = 10.55$, df = 9, $P < 0.0001$). The nearest neighbor distance was 3.4 ± 1.4 m, and this was not different from that found inside enclosures ($t = 1.36$, df = 9, $P = 0.224$). These white-tailed antelope squirrels cached randomly with respect to shrub cover ($\Lambda = 0.470$, df = 1, $P = 0.132$).

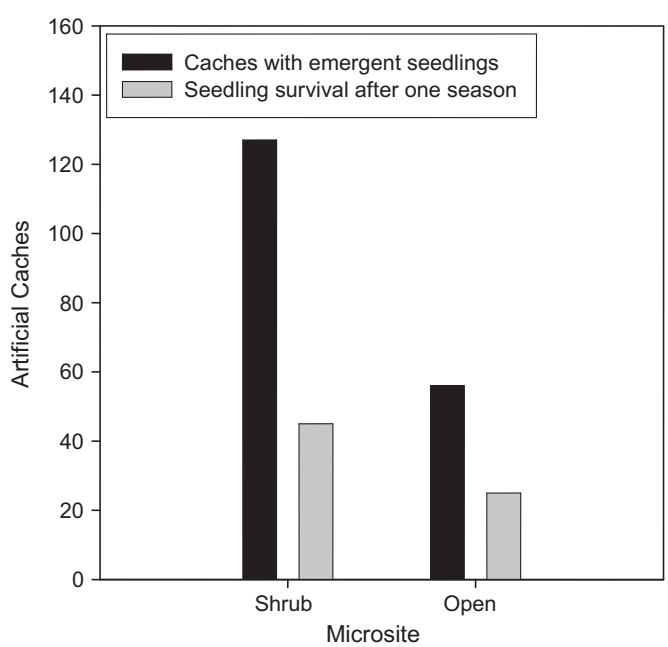

Fig. 3. The absolute number of Joshua tree seedlings emerging (black bars, $n = 183$) from seeds buried either under shrub cover or in the open, and number surviving after one season (gray bars, $n = 70$). Each bar represents all seedlings that emerged or survived regardless of depth.

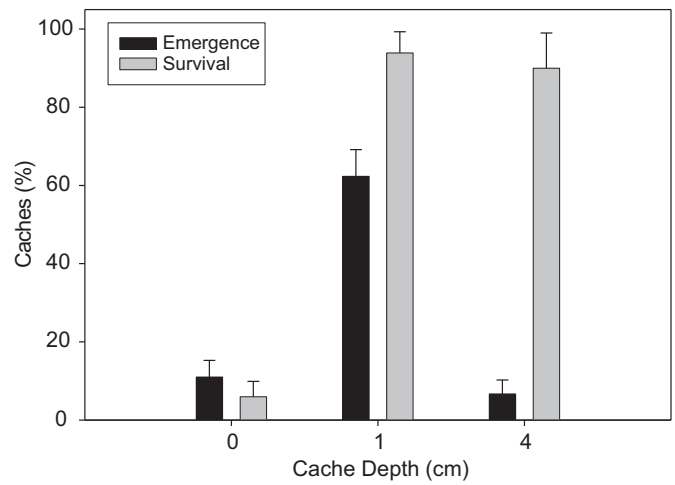

Fig. 4. Mean proportion of caches with Joshua tree seedlings emerging from pots at three depths (0 cm, 1 cm, and 4 cm, black bars), and mean proportion of caches surviving through the end of the study period (gray bars). Note that no seedlings emerged from caches buried at 7 cm or 10 cm. Error bars are ±1 SE.

3.5. Seedling emergence from caches

Of the 2880 artificial cache sites in the field, only 133 (4.6%) produced seedlings between August 2007 and September 2008. Only 183 of 5760 seeds produced seedlings (3.2%). This was despite the fact that 99% of seeds germinated in the viability test. Significantly more seedlings emerged under shrubs than in the open (96/1440 = 6.7% under shrub cover vs. 37/1440 = 2.6% in the open, $Z = 0.39$, $P < 0.001$, Fig. 3). Cache depth did not have a significant effect on emergence in the field ($Z = 1.73$, $P = 0.083$). Most seedlings emerged from seeds buried 1–4 cm deep (116/133 = 87%); only 2 seedlings emerged from seeds buried 0.1 cm deep.

In the growth chamber, 36% (27 of 75) of pots produced seedlings. Cache depth had a strong effect on emergence ($Z = 4.49$, $P < 0.0001$); seeds planted 1 cm deep had the highest rate of emergence (Fig. 4). Cache size marginally affected seedling emergence ($Z = 1.84$, $P = 0.065$). No seedlings emerged from caches deeper than 4 cm, although upon excavating seeds we found that some had germinated but the seedling had died before emerging.

Cache size had no effect on the proportion of seedlings surviving ($Z = 0.84$, $P = 0.397$), but cache depth had a significant effect on survival ($Z = 2.91$, $P = 0.003$, Fig. 4). Most seedlings (17/19 = 89.5%) from seeds placed on the ground surface had died by day 116 whereas most seedlings from buried seeds survived. Excavation of cache sites after the experiment was concluded revealed that 33% (5/15) of seeds buried at 10 cm and 6.6% (1/15) of those at 7 cm showed no signs of having germinated. Seed viability tests revealed that 93% of seeds were viable (18.6 ± 0.4 seeds per sample).

4. Discussion

Our results show that Joshua tree seeds are harvested by rodents directly from fruits in the tree canopy. White-tailed antelope squirrels, the only scansorial rodent commonly encountered at our sites, were the most commonly observed harvesters of Joshua tree seeds. In their eagerness to gather Joshua tree seeds, these squirrels

repeatedly broke into our wire mesh exclosures. Zembal and Gall (1980) also reported white-tailed antelope squirrels removing seeds from Joshua tree fruits. Although most Joshua tree fruits appeared to have been removed from the canopy, some fell or were knocked from the infructesences. Once on the soil surface, fruits were taken quickly by ground-foraging rodents. Both white-tailed antelope squirrels and Merriam's kangaroo rats were photographed opening fruits on the ground. This happened quickly, with >95% of fruits removed within 15 days. Individual seeds probably fall infrequently, but these are also gathered quickly by rodents (Fig. 2).

During our caching trials, both white-tailed antelope squirrels and Merriam's kangaroo rats cached Joshua tree seeds. White-tailed antelope ground squirrels made caches of a similar depth and size in enclosure trials and in open field trials. However, outside the enclosure, these squirrels made proportionately more caches and placed caches much further from the source. This change in behavior was probably due to an enclosure effect. The three open field trials may provide a better estimate of common dispersal distances, however, even the 21 m observed in the field trials was likely an underestimate because we made only a cursory search beyond 25 m from the source. These results are consistent with other studies on white-tailed antelope squirrels; these rodents were found to be one of the most effective dispersers of singleleaf pinon pine (*Pinus monophylla*) seeds (Hollander and Vander Wall, 2004). All five of the Merriam's kangaroo rats we tested cached extensively. They also dug new burrows and constructed small larders. No Merriam kangaroo rats visited our bait stations outside the enclosures, but this species is thought to have removed and cached Joshua tree seeds in another study (Vander Wall et al., 2006), and scatter hoarding is a typical behavior for this rodent (Daly et al., 1992; Jenkins et al., 1995).

Wind is an alternative means of seed dispersal, but it is unlikely to disperse Joshua tree seeds effectively. Joshua tree fruits are indehiscent so seeds are not exposed to the wind. The wind tunnel study suggests that fruits that do fall are unlikely to be carried far by wind as some have hypothesized (Trelease, 1893, Lenz, 2001). It took very strong winds to move seeds and fruits along both sand and cobble surfaces. These soil surfaces span the range of microtopography that is common in Joshua tree habitat. In any event, fruits and seeds on the soil surface are likely to be gathered by rodents (Fig. 1). Individual fruits that we positioned on the soil surface to monitor movement by the wind (study not described here), were dismantled or removed by rodents before we could measure any displacement due to the wind.

The scatter hoarding behavior exhibited by white -tailed antelope squirrels and Merriam's kangaroo rats is indicative of directed dispersal. Seeds that have been buried in soil have a much greater chance of establishing seedlings than those left on the soil surface. In both field trials and laboratory studies, only a small fraction of seeds left on the soil surface or buried 0.1 cm deep produced a seedling compared to those that were buried deeper. Presumably, soil water evaporates too quickly near the soil surface for seeds to imbibe enough water for successful germination (e.g., Zheng et al., 2010). Buried seeds, both in the field and laboratory, were most likely to produce emergent seedlings when 1–3 cm deep, depths similar to the caches rodents made in this study. Seeds taken directly from mature fruits exhibited germination rates of ≈95%. We cannot explain the low germination of seeds buried in the field observed in this study, but it cannot be attributed to low seed viability. Potential explanations include seed predation, seed dormancy, or drought conditions that prevented emergence. A later visit to these field sites revealed that a small fraction of seeds emerged the following year (T. Esque, pers. obs.).

Scatter-hoarding by rodents is a common fate of Joshua tree seeds, but seedling establishment from caches appears to be infrequent. Comanor and Clark (2000) and Gilliland et al. (2006) conducted long-term studies of Joshua tree populations but did not observe any seedling establishment. This result seems inconsistent with what appears to be a common interaction necessary for seedling recruitment. This inconsistency may be explained by variation in Joshua tree seed production. Scatter-hoarding as a dispersal syndrome is often dependent on masting, the production of large seed crops may be sufficient to satiate the appetite of granivorous animals (Kelly, 1994; Vander Wall, 2002). If scatter-hoarding rodents are satiated, the remaining seeds that have been hoarded are available to germinate. The quality of seed dispersal may thus be dependent on the overabundance of seed production. Rainfall is extremely variable in the Mojave Desert (Hereford et al., 2006), and perennial phenology is closely keyed to rainfall (Beatley, 1975, 1976). The year that these seeds were planted (2007) had relatively high rainfall (rain gauges near germination sites recorded >200 mm of precipitation), yet there were few seedlings produced. The rainfall and temperature conditions that favor seedling survival probably occur infrequently, making recruitment episodic. The relationship between Joshua trees and scatter-hoarding rodents is a mutualistic one; however, the relationship may be context dependent (Bronstein, 1994). Small seed crop size along with an overabundance of rodents may shift this interaction from mutualism toward seed predation by rodents.

These results corroborate the conclusions of the only other study to look at Joshua tree seed fate. Many of the caches made in this study by Merriams' kangaroo rats and white-tailed antelope squirrels resembled those found by Vander Wall et al. (2006). That study also observed that rodents excavated and recached some seeds several times. Although our results and those of Vander Wall et al. (2006) found that Joshua tree seedlings were more likely to emerge from under shrub cover than in the open, we found no evidence that rodents preferentially placed caches under shrub cover. Vander Wall et al. (2006) found that cache sites were fluid in nature, with marked seeds showing up in new locations as they were pilfered or recached. This pilfering and recaching behavior likely means that some seeds can be dispersed further than an animal's home range as seeds are stolen and buried anew, sometimes further from their source.

Wallen and Ludwig (1978) and Janzen (1986) have suggested that *Yucca baccata* and *Yucca decipiens* may have been dispersed by herbivores or extinct megafauna. Likewise, Lenz (2001) suggested that Joshua trees may have been dispersed by the Shasta ground sloth (*Nothrotheriops shastens*), an extinct giant sloth that co-occurred with Joshua trees during the Pleistocene. Cole et al. (2011) also supported the notion that in the past the Shasta ground sloth was a disperser of Joshua tree seeds and that current dispersal is constrained by the extinction of the sloth. Support for this idea comes from seed fragments in the fossilized faeces of extinct sloths (Laudermilk and Munz, 1935). Although the hypothesis that Joshua tree was dispersed by extinct megafauna is impossible to test, we see several weaknesses in the argument. First, Joshua tree seeds have a thin seed coat and would likely have been damaged by sloths or other herbivores during digestion. Laudermilk and Munz (1935), referring to Joshua tree seed in sloth dung, stated that "the flat black testa [of seeds] has been split in each instance and all indication of the contents lost", indicating that the seeds had been damaged. Second, Joshua tree does not produce the types of fruits and seeds that one would expect from a plant that is dispersed by large, terrestrial mammals (e.g., Herrera, 1989). Most Joshua tree pods are borne well out of reach of terrestrial animals, 4–20 m above the ground. Pods only occasionally fall at maturity, so it is difficult to understand how herbivores would

consume them efficiently. Finally, although the Pleistocene megafauna is mostly gone, Joshua tree is still effectively dispersed, albeit slowly (Cole et al., 2011). A possible analog for North American Pleistocene megafauna, the horse (*Equus calabus*), does not seem to be an effective disperser; it is absent from most of the range of Joshua tree and when we offered Joshua tree seed pods to horses (either whole or broken up and mixed with oats) they refused to eat them. It is clear that seed-caching rodents are responsible for seed dispersal today, and we suspect that they were an important, if not the sole, means of dispersal in the past.

There are 35 species of yuccas in North America. About half of these species, including Mojave yucca (*Yucca schidigera*), banana yucca (*Y. baccata*), and 15 other species (section Sarcoparpa) have indehiscent fruit and relatively large (8–10 mm), thick (3 mm), wingless seeds, similar to those of Joshua tree (section *Clistocarpa*). Seeds of these species typically weigh $\approx$100 mg. Although seed dispersal has never been studied in these species, it is likely that these large-seeded yuccas are also dispersed by scatter-hoarding rodents. Vander Wall et al. (2006), for example, found seeds of Mojave yucca mixed with Joshua tree seed in caches. The other yucca species, Whipple's yucca (*Yucca whipplei*, section *Hesperoyucca*) and 16 species in section *Chaenocarpa*, such as soaptree yucca (*Yucca elata*) and Spanish bayonet (*Yucca filamentosa)*, have thin-walled, dehiscent fruits, and small (5–6 mm), thin ($\approx$1 mm), winged seeds. Seeds of these species typically weight $\approx$15 mg. A number of authors have suggested that these species are wind dispersed (Dodd and Linhart, 1994; Huth and Pellmyr, 2000; Massey and Hamrick, 1998). The wind-dispersed taxa appear to be ancestral (e.g., Powell, 1984), suggesting that rodent-dispersed yuccas evolved from a wind-dispersed ancestor.

Our results indicate that the arid environment of the Mojave Desert may play an important role in the maintenance of the Joshua tree-rodent interaction. Joshua tree seeds that escape the hot dry surface conditions are far more likely to germinate and survive. It is unclear whether this is cause or consequence of the relationship with rodents as seed dispersers. While this study shows that rodents can act as effective dispersal agents, more work is necessary to determine the context under which rodent-dispersed seeds are most successful. Potential effects include rodent population density, masting events, temperature, and the timing of seasonal rainfall. The conditions that promote Joshua tree seedling survival are virtually unknown. Understanding these influences on the life cycle of Joshua tree is especially important given current expectations of migration due to climate change (Cole et al., 2011).

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