

University of Nevada, Reno

Rodent Mediated Seed Dispersal of Joshua tree (*Yucca brevifolia*)

**A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in
Biology**

By

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Rodent Mediated Seed Dispersal of Joshua tree (*Yucca brevifolia*)

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Abstract. The Joshua tree is a charismatic and popular symbol of the Mojave Desert. Despite its popularity, we know little about the ecology of this species. The seed dispersal of Joshua tree, in particular, has not been thoroughly studied to this point. Here I examine the possible mechanisms acting to disperse Joshua tree seeds and their resulting fate. I hypothesized that Joshua tree seeds are cached by scatter-hoarding rodents and that other dispersal syndromes are unlikely. The majority of Joshua tree fruits monitored were taken directly from Joshua tree canopy by white-tailed antelope ground 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 between 1 cm and 3 cm in the field, and at 1 cm in a growth chamber. Seeds placed on the soil surface were unlikely to germinate. Anemochory is unlikely because the wind speeds required to move Joshua tree seeds and fruits across the soil surface were high (mean 43.6 km/h and 31.9 km/h respectively), and rodents are likely to remove seeds before abiotic burial. These data show that the most common fate of Joshua tree seeds is hoarding by rodents. Caches made by rodents are an effective means of dispersal for Joshua tree.

Key words: Joshua tree, *Yucca brevifolia*, white-tailed antelope ground squirrel, scatter-hoarding, Mojave Desert, seed dispersal

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INTRODUCTION

The mechanisms by which seeds are dispersed are not often quantified, even though plant recruitment can be closely tied to soil seed banks (Venable and Brown 1988, Eriksen and Ehrlén 1992, Chambers and McMahon 1994). There is an obvious and necessary link between seed dispersal and entrance into the seed bank. Ellner and Shmida (1981) hypothesized that desert annuals have evolved to reduce dispersal distance in order to avoid being dispersed to unsuitable sites. Given this constraint, the temporal heterogeneity of water availability will control recruitment (Noy-meir 1973, Freas and Kemp 1983), and selection should be against long range dispersal (Venable et al. 2008, Pueyo et al. 2008). Desert perennials, on the other hand, should be less dependent on a seed bank reservoir because they have the potential to produce seeds in both good and poor years for seedling recruitment. With reduced dependence on one seed crop, perennials can benefit from the advantages associated with successful seed dispersal such as distribution to suitable microsites for seedling survival, colonization of new habitats, and escape from competition with parents (Howe and Smallwood 1982, Schupp 1993).

The propagules of many perennials found in the arid lands of North America have morphological characteristics associated with frugivory, myrmecochory, and anemochory (van Rheed et al. 1999, Bronstein et al. 2007). Another dispersal syndrome, dispersal by scatter-hoarding rodents, has not been explored as closely (but see McAuliffe 1990 and Longland et al. 2001 for examples from the Sonoran and Great Basin Deserts). Seed dispersal by animal mutualists should be examined in arid environments because mutualisms have been hypothesized to facilitate survival and

increase species richness in extreme environments (Stachowicz 2001). While no obvious structures for dispersal (such as wings or elaiosomes) may be present on some large seeds, this does not mean that they lack an evolved dispersal syndrome. Many desert granivores rely on stored seeds during the dry seasons after seasonal periods of seed production. The short temporal window for seed harvest and the necessity of this food source to rodents for survival through period of low production have been hypothesized to favor the evolution of seed dispersal by scatter-hoarding rodents (Thompson 1982, Vander Wall 2001).

Seed dispersal by rodents has been shown to be important to perennial plants in several arid and semi-arid systems. McAuliffe (1990) found that most fallen seeds of velvet mesquite (*Prosopis velutina* Wooton) were scatter-hoarded by Merriam's kangaroo rats, and about half of all germinating mesquite seedlings were from rodent caches. Similarly, Reynolds (1954) found that mesquite seeds were mainly moved by Merriam's kangaroo rats in the Sonoran Desert. In the Great Basin Desert, Ord's kangaroo rats (*Dipodomys ordii*) scatter-hoard seeds of blackbrush (*Coleogyne ramosissima* Torrey) and Indian rice grass (*Achnatherum hymenoides* Barkworth)(Auger 2005). Rodent scatter-hoarding leading to effective seed dispersal has been shown in the less arid Sonoran Desert, Great Basin Desert and Sierra Nevada pine forests (McAuliffe 1990, Longland et al. 2001, Vander Wall 2008). These ecosystems have less temporal heterogeneity in the conditions required for successful seedling recruitment than those in the drier Mojave, but greater aridity should favor successful seed dispersal mutualisms if seeds are more likely to escape the harsh conditions that cause seed mortality by entering the seed bank. The Mojave Desert is the hottest and

driest in North America, and several studies have shown that rodent exclusion can alter the vegetation community (Reynolds 1950, Brown and Heske 1990, Kerley and Whitford 2009). However, few have actually documented the fate of seeds removed by granivores (Vander Wall et al. 2005).

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). While the pollination system of Joshua tree has been well studied (Godsoe et al. 2008, Smith et al. 2008), we know very little about its propagules post-maturation (e.g. seed set, seed fate, recruitment). What has been written about Joshua tree seed dispersal has been mostly speculation, from abiotic dispersal by rolling inside fruits (Trelease 1893), to wind dispersal (Webber 1953), to anachronistic dispersal by extinct megafauna (Laudermilk and Munz 1935, Lenz 2001). To date, there has been only one published study that experimentally tested the fate of Joshua tree seeds. Vander Wall et. al (2006) found that small piles of radioactive Joshua tree seeds were moved to small buried cache sites typical of rodents up to 56.6 m away from their source. This study made a strong case for rodent dispersal of Joshua trees. However, the identity of the animals moving the seeds was not determined.

In this study, I tested the hypothesis that rodents are the most likely disperser of Joshua tree seeds. This hypothesis generates five predictions. First, Joshua tree seeds cannot exit indehiscent fruits by abiotic means. Second, any fruits or seeds on the soil surface are likely to be found and taken by animal foragers. Third, scatter-hoarding rodents disperse seeds to likely sites for germination. Fourth, those seeds hoarded by

rodents are more likely to germinate and survive than those dispersed by other means. Finally, wind is not likely to disperse viable seeds to suitable germination sites.

METHODS

Study Sites

I used sites in the Piute Valley and the Ivanpah Valley to examine rodent interactions with Joshua trees. The Piute Valley site (674909, 3930163 UTM NAD83 zone 11 N) is located between the New York and Newberry Mountains in southern Nevada, USA and is easily accessible from the Nipton Road, which runs between Searchlight, NV and Nipton, CA. 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 with sparse creosote bush (*Larrea tridentata* Cov.). The Ivanpah Valley site (635815, 3906124 UTM NAD 83 zone 11N) is located on the east side of the Mojave National Preserve between the Ivanpah and New York mountains. This area was easily accessible from Las Vegas on the Nipton Road. The stands I used were dominated by Joshua tree and blackbrush.

I also used a pre-existing network of enclosures in the Pakoon basin to look at the role of wind in Joshua tree fruit dispersal (Esque 2004). The Pakoon Basin is located in the Parashant National Monument on the Arizona Strip, Mojave Co., AZ. This was the driest of the three sites I used for experiments. The Pakoon basin was dominated by creosote bush and burro bush (*Ambrosia dumosa* Gray) with sparse cover of Joshua tree.

Bagged Fruit Transects

In order to determine when and by what means Joshua tree fruits fall from infructescences, I monitored six transects of infructescences for fruit removal. I established three transects at the Piute Valley site and three at Ivanpah Valley (n = 30 trees per site). Each transect consisted of ten haphazardly selected trees, and no transect was less than 0.5 km from another. On each tree, I chose two infructescences of similar height and aspect. I covered one of these infructescences, chosen at random, with a mesh bag made of aluminum window screening. I cinched each mesh bag at the stem about 10 cm below the infructescence to restrict access by animals. These coverings may have provided some shelter from wind to the infructescence, but did not prevent Joshua tree branches from swaying. I visited transects bi-monthly, and recorded the number of fruits present. The difference in the numbers of fruits remaining attached to the tree after three months between bagged and unbagged infructescences was compared with a paired t-test.

Tumble Fruit Trials

I evaluated the probability of movement of Joshua tree seeds through wind by allowing fruits to roll freely in 12 rodent-proof enclosures at the Pakoon Basin site. Each enclosure was a 20 m x 20 m square of wire mesh fencing buried to a depth of 30 cm or more (see Esque 2004). I set Sherman live traps in each enclosure for three consecutive days and nights prior to the start of any trials to remove any rodents present. I removed any rodents found inside the enclosures, inspected the enclosures for holes or tearing in fences, and fixed any holes found. I marked six Joshua tree fruits, collected locally, and set them 10 cm apart at the center of each enclosure. Fruits were allowed to roll freely, and I measured the distance each fruit had moved after each week. I noted the condition

of each fruit (whether any cracks were visible or seeds exposed from rolling friction) after each trial. I terminated all trials after the first week due to road damage from flash floods. In that time six of the enclosures had been interfered with by rodents, and all fruits in them had been eaten.

Wind Tunnel Data

I tested Joshua tree seeds and fruits in a wind tunnel to determine the wind speed required to push them along the ground surface. I used a portable open-bottomed tunnel of 15 cm x 15 cm x 240 cm (described in Belnap and Gillette 1997). The fan was powered by a diesel engine for which the throttle could be set once the desired wind speed was reached. I measured wind speed via a Pitot tube anemometer that recorded pressure changes as windspeed (Belnap and Gillette 1997). I took all measurements outside the USGS headquarters at Moab, UT and corrected for elevation and air pressure immediately prior to each trial.

I created two surfaces to look at minimal and moderate levels of microtopography. I made one surface of 60 mesh sand and one of landscape cobbles (3 cm – 8 cm along the shortest axis). The sand surface effectively mirrored minimal surface resistance. Fruits and seeds were placed against a 1 cm barrier (a cobble in this case) on the rocky substrate. I 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 constant wind speed that would move the seed or fruit was reached, the engine powering the fan to the wind tunnel was set at that speed and I recorded the wind speed at 10 cm above the substrate.

Fruit Removal Transects

To gauge the rate of removal of Joshua tree fruits from the soil surface, I laid out four transects at Piute Valley in July 2008. Each wandering transect consisted of 40 fruits set 5 m from each other. I set fruits haphazardly with regard to soil type and shrub cover. Each fruit was attached to the ground by a 7.5 cm piece of wire such that the fruit was unable to roll in the wind and no wire was visible above the soil. I visited each fruit transect daily until fewer than five fruits remained. I analyzed all data in R (package “survival”, Therneau 2009) and calculated a rate of removal through survival analyses.

Seed Removal Transects

I used a similar set of transects to determine the rate of removal of single seeds that might have fallen from a fruit or been knocked out by any other disturbance. I placed eight transects at Piute Valley and eight at Ivanpah Valley in July and August 2007. I placed 40 seeds in 200 m wandering transects such that seeds were 5 m from each other. At each site, I designated four transects for shrub cover, and placed seeds at least 10 cm underneath the nearest shrub cover. I used the remaining four transects at each site as no cover (or open) transects, and placed seeds at least 5 m from each other and at least 20 cm from the nearest shrub cover. All seeds were attached to a toothpick with thread of a color chosen to match the soil substrate. I pushed toothpicks wholly into the soil such that the toothpick was not visible and only the seed and thread protruded from the ground. I visited seed transects until fewer than 5 seeds remained per transect. As above, I analyzed all data in R (package “survival” Therneau 2009) and calculated rates of removal through survival analyses.

I trapped rodents prior to placing seed transects at both Piute Valley and the Ivanpah Valley. I laid traps on a 7 x 7 grid, and set trap stations 15 m apart with two Sherman live traps at each station. For bait, I used mixed bird seed. Traps were opened at dusk and left open until 10 am in an attempt to capture diurnal rodents. I set and checked trap grids for three nights at each location. I compiled a species list, but recaptured too few animals at either location to get reliable population estimates.

Enclosure Seed Caching Trials

I constructed two 10 m x 10 m enclosures at the Piute Valley site. Enclosures were constructed of wood and thick wire mesh (see Vander Wall 2000). I buried the wire mesh 50 cm below the ground to prevent rodents from tunneling in or out of the enclosures. Vegetation in the enclosures was Mojave Desert scrub (dominated by creosote bush and burro bush with a single Joshua tree in each enclosure). I buried a plastic bucket just outside of each enclosure to act as an artificial burrow and covered the top with plywood for shade. A PVC tube connected the bucket to the enclosure through a small buried hole in the hardware cloth fence. Each bucket consisted of three chambers separated by plywood with a 5 cm diameter circular hole between each chamber. I placed animals in the PVC tube entrance at the start of each trial, and they generally accepted the bucket as an artificial burrow.

I ran eight successful trials with white-tailed antelope ground squirrels (*Ammospermophilus leucurus*) and five with Merriam's kangaroo rats (*Dipodomys merriami*) between July and September 2008. In each trial, I released a single rodent into the artificial burrow, and placed 200 Joshua tree seeds labeled with scandium-46 at the base of the single Joshua tree inside the enclosure. Scandium-46 is a gamma emitter that

decays naturally to titanium, is biologically inert, and passes through the animals gut (see Vander Wall 2000). I gave rodents a minimum of 12 hr and a maximum of 48 hr to remove seeds. If a rodent did not remove seeds after 48 hr, I terminated the trial, released the rodent, and started a new trial. When a rodent removed at least half (100) of the available seeds, I sequestered the rodent in the burrow and surveyed the soil surface inside the enclosure with a Geiger counter to find any caches that had been made. I mapped each cache found, excavated any seeds, and recorded their depth, size (number of seeds), and microsite (under shrub cover or in the open). I also checked the artificial burrow for seeds. I removed all seeds and any feces found prior to the start of each new trial.

I used ten transects to determine the proportions of available vegetation cover within each enclosure. I laid the ten transect lines parallel to each other in a south to north orientation every meter starting at 0.5 m and ending at 9.5 m along the east-west wall of each enclosure. This resulted in 100 m of vegetation transect for a 100 m² area. On each transect, I took line intercept measurements (Elzinga et al 2001). I summarized percent vegetation cover by species as the total distance crossing a transect line divided by 100 m. I analyzed cache microsite preference by rodents relative to availability in R (package *adehabitat*, Calenge 2006) using a compositional analysis as recommended by Aebischer et al. (1994).

Unrestrained Seed Caching Trials

I conducted field trials using Joshua tree seeds labeled with scandium-46 to determine if white-tailed antelope ground squirrel behavior was affected by conditions in the enclosure in the Piute Valley. I placed seeds labeled with scandium-46 (150) at the

base of 25 different Joshua trees over the course of 18 days in August and September 2008. I placed seeds in a small pile in the path of a trailmaster motion sensor attached to a Canon 35 mm camera. I turned cameras on between 7 am and 9 am and removed labeled seeds before dusk in order to insure that only diurnal rodents could take them. I checked each camera once every two hours between noon and dusk. Once any seeds were removed, I surveyed the area within 25 m of the camera trap with a Geiger counter for any cached seeds. I recorded the number of seeds, depth to the top of the uppermost seed in the cache, distance to canopy cover, and distance from the seed source for each cache.

I recorded shrub cover from two 50 m vegetation transects. Transects were crossed at the original placement of seeds at each successful trial. I laid one transect directly east and west and one directly north and south. I collected data on vegetation cover similar to that recorded in the enclosures described above. I used a compositional analysis to analyze cache site preference for shrub cover with the three trials conducted outside the enclosures, as above.

Field Germination

In August 2007, I planted Joshua tree seeds to simulate rodent caches in order to discover the optimal depth below the soil surface a seed must be cached for seedling emergence. I placed two seeds in each cache, and buried caches at 0.1 cm, 1 cm, 2 cm, 3 cm, 4 cm, or 5 cm below the soil surface. I did not place seeds directly at the soil surface to discourage granivore interference. I arranged caches in groups of 36 with six caches of each depth randomly planted in a 6 x 6 grid. Each set of caches was inside a 70 cm x 70 cm enclosure of wire mesh, buried at least 10 cm into the soil to prevent seed removal by foraging rodents. I divided replicates (N=80 enclosures) equally into shade

and open groups. Those exclosures designated as shaded were beneath the canopy of creosote bush, while open exclosures were at least 2 m from the nearest shrub.

I checked exclosures intermittently between November 2007 and September 2008 for emergence and seedling survival. I recorded emergence if any Joshua tree leaves had broken through the soil, and considered seedlings alive as long as any green tissue was visible in the leaves. I analyzed these data with a linear mixed effects model with shrub cover and depth as fixed effects and exclosure treated as a random effect (R, package lme4, Bates et al. 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. I separated intact seeds from those that had been damaged by moth larvae, and I took five samples of 20 seeds each (randomly chosen from all seeds) to test viability. I placed seeds in Petri dishes with a piece of P6 filter paper and kept seeds moist for two weeks. After two weeks I recorded the number of seeds that germinated. I defined germination as the presence of a radicle.

Growth Chamber Seed Germination

I used a growth chamber (Forma Scientific diurnal growth chamber) to determine the emergence of seeds from typical cache depths under optimal moisture conditions. I used an artificially created soil (3 parts gravel, 3 parts sand, 2 parts clay, 1 part organic matter). Joshua tree seeds were buried at 0 cm, 1 cm, 4 cm, 7 cm, or 10 cm below the soil surface with caches sizes of one, five, or ten seeds. I replicated each combination five times (N=75) and randomly distributed pots in the growth chamber. The growth chamber had three shelves, and I 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. I placed two caches of each type in

a 10 cm x 10 cm plastic pot. All pots were watered once every three days with 200 ml of water, but humidity was low enough for soil to dry out between watering. I set the growth chamber at 25° C during a 12 hour day period and 15° C during a 12 hr night period, and each pot was watered from 30 June 2008 to 15 October 2008. I kept two vents at the front of the growth chamber open to prevent high humidity and possible mold formation on emergent seedlings. Opening the vents also helped to maintain a low humidity at the soil surface.

I checked these caches periodically from June 2008 to September 2008 for emergence and survival. I recorded emergence when leaves broke through the soil surface, or seeds germinated in the case of seeds on the surface. I considered a seedling alive if any leaf tissue was green. I 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, I excavated all caches to see if seeds had germinated. Joshua tree fruits were collected from the Piute Valley site in July 2008 and stored in a paper bag in a climate controlled warehouse until use. I separated intact seeds from those that had been damaged by moth larvae, and I took five samples of 20 seeds each (randomly chosen from all seeds) to test viability. I placed seeds in Petri dishes with a piece of P6 filter paper and kept seeds moist for two weeks. After two weeks I recorded the number of seeds that germinated. I defined germination as the presence of a radicle.

RESULTS

Removal of Joshua tree fruits from the canopy

The Joshua tree infructescences I monitored produced a mean of 13.5 ± 1.1 fruits at Piute Valley and 10.1 ± 0.7 fruits at Ivanpah Valley ($t = 2.61$, $df = 58$, $P = 0.010$). Joshua tree fruits began disappearing from infructescences shortly after mesh bags were closed on 21-24 May 2007 (Fig. 1, 2). Transects were monitored until fewer than 20 % of fruits remained on covered infructescences or September 2007. This 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 rate was 0.11 ± 0.01 fruits/infructescence/day at Piute Valley and 0.29 ± 0.04 fruits/infructescence/day at Ivanpah Valley.

The mesh bags were removed on 18 September 2007. At that time some of the mesh bags had been chewed through at the Ivanpah Valley site, and some branches holding bagged infructescences had blown off as a result of damage to the Joshua tree from weevils at Piute Valley. When I took down each transect, 18 of the original 30 bags were intact (with transects pooled by site). Intact bags lost no fruits, and 72.3 ± 0.1 % (196/280 across all transects) of fruits remained attached to the infructescence at Piute Valley and 86.3 ± 0.1 % (165/185 across all transects) remained attached at Ivanpah Valley. The remaining fruits had all fallen and collected at the bottom of the mesh bag. Significantly more fruits were found detached or gone when infructescences were unbagged and available to animals ($t = 8.819$, $df = 40$, $P < 0.0001$ at Piute Valley, $t = 3.557$, $df = 46$, $P = 0.002$ at Ivanpah Valley, Fig. 3) than had fallen off the infructescences inside bags.

Wind as a possible dispersal mode

Tumble fruit trials were all terminated after one week due to extreme road damage from flash floods that prevented access to the enclosures. In that time, 44.4 % (32/72) of all fruits were eaten by rodents that broke into six of the enclosures. In each case, Merriam's kangaroo rats were trapped in the enclosures after fruits were eaten, and these animals were the most likely culprits. Of the remaining 40 fruits, only 7 had changed position after one week. Those fruits that were not eaten (n = 40) moved a mean of 10.5 cm (range 0 to 206 cm) in one week. No uneaten fruits showed any visible signs of damage from movement.

In the wind tunnel, joshua tree fruits were moved by lower wind speeds than seeds (31.9 ± 2.6 km/h and 43.6 ± 2.6 km/h respectively at 10 cm) on the sandy, low resistance, substrate. 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 and $t = 2.69$, $df = 10$, $P = 0.019$ for fruits). Wind speeds averaged 87.6 ± 5.5 km/h and 73.6 ± 4.8 km/h respectively for movement of seeds and fruits (Fig. 4) on the rocky substrate. It is important to note that these values were taken at 10 cm above the ground, and that these wind speeds would be much greater if measured at the 1.8 m height typical of weather stations.

Removal of propagules from the soil surface

The four fruit removal transects were monitored for 13 to 16 days. In that time a mean of $91.3 \pm 0.7\%$ of fruits were removed from each transect. There was no difference between transects in rate of removal ($\chi^2 = 2.16$, $P = 0.54$). The weibull distribution gave

the best fit, and the mean half-life for fruits at Piute Valley was 2.9 ± 0.25 days (N=4, Fig. 5).

I monitored seed removal transects for 20.9 ± 1.8 days (N=14) until fewer than 10 seeds remained, except for two transects from which only 60% (24/40) and 72.5 % (29/40) of seeds were removed during this study. The mean removal from each transect over the entire monitoring period was $85.6 \pm 2.1\%$. Only site significantly affected the fit of each survival function ($Z = 34.34$, $P < 0.0001$). The mean half life estimated by survival analysis ($\chi^2 = 18.98$, $P < 0.0001$) was 12.6 ± 0.9 days (N=16) for all transects with a mean of 10.6 ± 0.73 days (n=8) in the Ivanpah Valley (Fig. 6) and 14.6 ± 1.29 days (n=8) at Piute Valley (Fig.7). There was no difference in removal rate between seeds placed under shrub cover and those placed in the open ($Z = 0.773$, $P = 0.44$).

The rodent trapping done concurrently with seed removal transects indicated low populations for all rodents. Only eight individuals were caught at Piute Valley over three days, and only 17 were captured in the Ivanpah Valley (Table 1). No white-tailed antelope ground squirrels were captured when traps were left open in the morning, and the two species common to both sites were Merriam's kangaroo rats and little pocket mice (*Perognathus longimembris*).

Rodent treatment of Joshua tree seeds

A total of 16 white-tailed antelope ground squirrels were placed in the enclosures, only eight of which made caches. Those squirrels that did not make any caches either ignored seeds entirely, ate all seeds, or disappeared from the enclosure (possibly removed by the abundant red-tailed hawks in the study area). The eight animals that did store seeds made a total of 32 caches with a mean cache depth of $1.21 \text{ cm} \pm 0.31 \text{ cm}$ and a mean

cache size of 3.4 ± 1.5 seeds (Table. 2). The mean nearest neighbor distance was $1.45 \text{ m} \pm 0.73 \text{ m}$ and mean distance from the source was $2.39 \text{ m} \pm 0.38 \text{ m}$. Similarly, five Merriam's kangaroo rats were placed in the enclosure, and all five cached seeds.

Merriam's kangaroo rats cached a mean of 6.4 ± 1.4 seeds per cache $1.7 \pm 0.5 \text{ cm}$ below the surface (Table 2). The nearest neighbor distance was $1.89 \pm 0.63 \text{ m}$ and Merriam's kangaroo rats cached seeds a mean distance of $3.73 \text{ m} \pm 0.42 \text{ m}$ from the seed source.

The two enclosures had a similar amount of shrub cover, 21.5 % and 27.8 %.

Rodents appeared to be caching at random with respect to shrub cover. Compositional analyses of both white-tailed antelope ground squirrel and Merriam's kangaroo rat cache locations were both not significant for preference with respect to shrub cover microsite ($\Lambda = 0.99$, $df = 1$, $P = 0.947$ for white-tailed antelope ground squirrels and $\Lambda = 0.849$, $df = 1$, $P = 0.365$ for Merriam's kangaroo rats).

A total of 23 camera traps with labeled seeds were set outside enclosures, but only three stations had any seeds removed. This may have been due to a fence effect whereby abundant raptors perched along nearby fences depressed rodent populations. The three successful trials all photographed white-tailed antelope ground squirrels removing Joshua tree seeds. Caches were generally shallower (mean depth $1.1 \text{ cm} \pm 0.4 \text{ cm}$, Table 2) and smaller (mean 2.8 ± 0.4 seeds, Table 2) than those made by ground squirrels inside the enclosures. Caches made by white-tailed antelope ground squirrels in trials using camera traps had mean distance of $11.48 \text{ m} \pm 2.62 \text{ m}$ 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 $3.36 \text{ m} \pm 1.39 \text{ m}$, and this was not different from that found inside enclosures ($t = 1.36$, $df = 9$, $P = 0.224$). These white-tailed antelope ground squirrels

were also caching effectively at random with respect to shrub cover ($\Lambda = 0.470$, $df = 1$, $P = 0.132$).

Emergence from Caches

Of the 5760 seeds planted in the field, only 183 seedlings emerged from 133 (133/2880 = 4.6 % of possible emergence) artificial caches between August 2007 and September 2008 (Fig. 8). Significantly more seedlings emerged under shrubs than in the open ($Z = 0.39$, $P < 0.001$, Fig.9). However, cache depth had only a marginally significant effect on emergence when individual enclosure was treated as covariates ($Z = 1.73$, $P = 0.083$). Most seedlings emerged from caches made 1-3 cm below the surface, while only 3 caches emerged from 0.1 cm below the surface. The seeds I used to test seed viability were almost all viable; 99 of 100 seeds had a radicle emerge in two weeks of moisture (19.8 ± 0.2 seeds per dish).

In the growth chamber, 36 % (27 of 75) of pots had seedlings emerge (or seeds germinate if on the soil surface). Similar to results from field plantings, those seeds planted at 1 cm were most likely to emerge (Fig. 9). There was not a significant effect of cache size on seedling emergence ($Z = 1.84$, $P = 0.065$), but cache depth did have a significant effect on emergence ($Z = 4.49$, $P < 0.0001$). No seedlings emerged from caches deeper than 4 cm, though seeds did germinate in the soil.

Emergent seedlings were watered until the completion of this experiment. At completion (116 days), most seedlings (17/19 = 89.5 %) that germinated at the surface had died while seedlings from buried caches mostly survived (Fig. 9). Cache size had no effect on the proportion of possible seedlings surviving ($Z = 0.84$, $P = 0.397$), but cache depth had a significant effect on survival ($Z = 2.91$, $P = 0.003$, Fig 10). An excavation of

each cache once the experiment was concluded revealed that 33 % (5/15) of caches buried at 10 cm and 6.6 % (1/15) at 7 cm had no evidence of seeds with radicle protrusion, and showed no signs of having germinated (all other caches had at least some root mass). The seed used to test viability were also mostly viable in this study, 93 of 100 seeds had an emergent radicle (18.6 ± 0.4 seeds per Petri dish).

DISCUSSION

These results show that Joshua tree seeds are dispersed by scatter-hoarding rodents. The majority of protected fruits did not fall from infructescences over the three month monitoring period, while fruits available to animals were mostly removed by the end of the same period. When I removed the mesh bags from the infructescences that I monitored, I found white-tailed antelope ground squirrels trapped in two of the mesh bags with the shattered remains of Joshua tree seed coats. While published field observations of granivory of Joshua tree, Zembal and Gall (1980) observed white-tailed antelope ground squirrels and Mojave ground squirrels (*Spermophilus mohavensis*) removing seeds from the canopy on multiple visits. It appears that ground squirrels, and possibly other rodents, will take fruits directly from the Joshua tree canopy, and it is rare to find intact fruits still present in the canopy late in the summer or early in fall (pers. obs).

Fruits that do fall are unlikely to be carried by wind as some have hypothesized (Trelease 1893, Lenz 2001). The short time period when I left fruits to roll freely resulted in almost no dispersal. However, I do not have a record of the wind speed that these fruits experienced and wind conditions may have been mild. The wind speeds required to move Joshua tree seeds and fruits as observed in a wind tunnel suggest that neither Joshua tree

seeds nor fruits are well adapted to anemochory. While the wind speeds required to move Joshua tree fruits and seeds across a uniform sand surface (31 km/h) are common in the Mojave, those required to move Joshua tree seeds and fruits from a 1 cm obstacle were quite high and unlikely to occur (Fig. 4). Seeds or fruits would encounter numerous rocks or shrubs if they were to be blown across the landscape, and it is unlikely that these perturbations would be enough to puncture the thick pericarp of the fruit to release the seeds.

While the majority of Joshua tree fruits monitored appeared to have been removed from the canopy, some fell to the ground. These fruits were rapidly taken by rodents. Several camera traps revealed white-tailed antelope ground squirrels and Merriam's kangaroo rats taking fruits within several days. In this study, fruits on the soil surface had a half life of 2.9 days, and more than 95 % would be removed within 15 days (5 half lives at 2.9 days = 14.5 days). These data suggest that rodents can take fruits faster than wind will move them. The same is true of Joshua tree seeds on the soil surface. Joshua tree fruits are indehiscent, but some seeds can be released due to incomplete removal by rodents. While animals take seeds at a much slower rate than fruits, loose seeds were still removed by granivores when found.

When rodents take seeds, they are either eaten or cached (Price and Jenkins 1986). Both white-tailed antelope ground squirrels and Merriam's kangaroo rats made caches with Joshua tree seeds inside the enclosures. However, it appears that the caching behavior of white-tailed antelope ground squirrels in this study was affected by the enclosures. White-tailed antelope ground squirrels made caches of a similar depth, size, and nearest neighbor distance in enclosure trials and in field trials. However, white-tailed

antelope ground squirrels outside the enclosure made more caches with fewer available seeds and placed caches much further from the source. This change in behavior was most likely due to the effects of being enclosed in a much smaller area than observed home ranges for white-tailed antelope ground squirrels (Allred and Beck 1963). A better estimate of common dispersal distance can be taken from the three trials conducted outside of the enclosures. White-tailed antelope ground squirrels in the field moved seeds an average distance of 21 m. However, this was probably an underestimate of dispersal distance because I did only a cursory search beyond 25 m from the source. All five of the Merriam's kangaroo rats tested here cached profusely. They also dug new burrows, cached seeds in larders and scattered caches inside the enclosures, and cached all seeds within 12 hr of the start of each trial. No further trials were run outside the enclosures with this species. Merriam's kangaroo rats have been observed to remove Joshua tree seeds outside the enclosures (Vander Wall et al 2006), and scatter hoarding is typical behavior for this rodent (Daly et al. 1992, Jenkins et al. 1995).

Seeds which have been cached and are not disturbed before germination have a much greater chance of emerging than those left on the soil surface. In both field trials and laboratory studies, a much smaller fraction of seeds left on the soil surface or only buried beneath a 0.1 cm layer of sand emerged compared with those that were buried deeper. Presumably, soil water evaporates too quickly on or near the soil surface for seeds to imbibe and retain enough water for germination. It is important to note that no seeds were planted directly on the soil surface in field trials, and "surface" caches were covered with a thin layer of soil less than 1 mm thick. Had these seeds been distributed directly on the soil surface, they would likely not have experienced the necessary

conditions for germination. Similarly, seeds buried both in the field and laboratory were most likely to produce emergent seedlings from 1-3 cm, these depths are very similar to the depths of caches made by rodents in this study (Table 2). Germination trials in the laboratory with Joshua tree seeds commonly yield greater than 90 % germination, and seeds have no apparent dormancy (seeds taken directly from fruits collected from the canopy once fruits had dried germinated readily). The low germination recorded in this study cannot be attributed to low seed viability.

These results corroborate the conclusions of the only other study to look at Joshua tree seed fate. Vander Wall et al. (2006) found that seeds left on the soil surface were removed by animals that made caches with means of 2.6 to 8.3 seeds at a range of 0.7 cm to 1.95 cm deep, and are then moved to smaller and shallower secondary caches (range 2.2 to 3.9 seeds at 0.5 cm to 0.85 cm below the surface). The initial cache depths are similar to those made by Merriam's kangaroo rats in this study (Table 2), while the secondary caches are closer in character to those made by white-tailed antelope ground squirrels. It is not clear that primary and secondary caching behavior is always similar within these species. Vander Wall et al. (2006) also observed that cached seeds moved several times before losing track of them (seeds may or may not have been eaten) and found that seeds were moved an average distance of 56.6 m. By moving seeds several times, rodents can engage in a type of relay dispersal that vastly increases the distance a seed may travel before its ultimate fate of germination or mortality.

Joshua tree fruits are most likely first available to climbing rodents (such as white-tailed antelope ground squirrels), but fruits do fall due to abiotic factors such as wind. Once on the soil surface, fruits are taken quickly by ground-foraging rodents such

as Merriam's kangaroo rats. At least in this study, Merriam's kangaroo rats cached a greater percentage of seeds (rather than eating them) in enclosures than did white-tailed antelope ground squirrels and may disperse a larger proportion of the Joshua tree seeds they encounter. Vander Wall et al. (2006) found that Joshua tree seedlings were more likely to emerge from under shrub cover than in the open. There was no evidence in this study that rodents are preferentially placing caches under shrub cover (where Joshua tree seedlings were more likely to emerge from caches).

Scatter-hoarding by rodents is likely the most common fate of Joshua tree seeds once they leave indehiscent fruits. However, two long term studies of Joshua tree populations did not observe any seedling recruitment (Comanor and Clark 2000, Gilliland et al. 2006). This seems inconsistent with what appears to be a common interaction necessary for seedling recruit. This inconsistency may be explained by environmental conditions. Rodent scatter-hoarding as a dispersal syndrome is dependent on the seed crop being large enough to satiate the ability of the population of rodents to find and consume caches (Kelly 1994, Vander Wall 2001). Rainfall is extremely variable in the Mojave Desert (Hererford et al. 2006), and perennial phenology is closely keyed into rainfall (Beatley 1975, 1976). In this study only 4.6 % of caches had emergent seedlings, and of those only 2.4% had seedlings that survived through the 2008 summer. The year that these seeds were planted (2007) had relatively high rainfall (rain gauges near germination sites recorded > 20 cm of precipitation), and there were still very few seedlings produced. Joshua tree recruitment is dependent on both a larger seed crop than rodents can consume (determined by winter rainfall) and the proper conditions for germination, emergence and survival (influenced by summer rainfall). The rainfall and

temperature conditions required for a good recruitment year are probably episodic and may require several years of adequate rainfall if seedlings are to survive. Future research should be aimed at determining the moisture and temperature conditions required for survival of Joshua tree seedlings.

Wind is an unlikely disperser for Joshua tree seeds. It took an inordinate amount of wind to move both seeds and fruits along sand and cobble surfaces, microtopography that is common in Joshua tree habitat. While these wind conditions are unlikely, it is possible that heavy winds could move Joshua tree fruits short distances. However, those fruits and seeds left on the soil surface are unlikely to remain on the surface for long enough to be buried by abiotic means before being taken by animals. Other species of yucca such as weak-leaf yucca (*Yucca filamentosa*) and whipple's yucca (*Yucca whipplei* Torrey) have evolved to be dispersed by wind. These species of yucca have dehiscent fruits, winged seeds, and small seed masses that make seed dispersal by wind a more probable mechanism (McKelvey 1938). These characteristics are absent in the Joshua tree which has indehiscent fruits, relatively large rounded seeds, and no wing structure. Because of the high wind speeds required to move Joshua tree seeds and fruits, it seems unlikely that wind has played a role in shaping the morphology of seeds and fruits.

Endozoochory is certainly an unlikely dispersal mechanism for Joshua trees today, because there are no extant large mammals that occupy Joshua tree habitat save wild horses, burrows, and cows in limited areas. It has been suggested that Joshua trees may once have been dispersed by the Shasta Ground Sloth (Lenz 2001), a now extinct giant ground sloth that was concurrent with Joshua trees during the Pleistocene. While seed fragments have been found in the fossilized dung of ground sloths (Hansen 1978),

we cannot know whether these seeds were viable or if ground sloths functioned as seed predators. Joshua tree seeds have a thin seed coat, which is easily shredded and discarded by rodents, and may not survive passage through the gut of a large herbivore. Producing large indehiscent fruits is consistent with dispersal by frugivory, but there are too little data to evaluate this hypothesis. Mast seeding is consistent with a number of other hypotheses including the avoidance of predation and increased probability of seed dispersal by hoarding animals (Kelly 1994, Vander Wall 2001, Enders 2009). There is evidence from fossilized woodrat middens that *Neotoma lepida* collected Joshua tree seeds over the last 12,000 years and as long ago as 43,000 thousand years BP (Spaulding, 1983, Betancourt et al. 1990). Rodents have had a long evolutionary history with and consequently a great probability of exerting selection pressure on the seed traits of Joshua trees. Further, rodents have been observed to remove and scatter-hoard seeds from both bird and large mammal dung (Vander Wall and Longland 2004). If seeds could survive the passage through the ground sloth gut, they may later have been taken by rodents. This interaction may have served to broaden the seed shadow of Joshua tree dispersal. While this hypothesis is plausible, it cannot be evaluated in the absence of data.

An understanding of Joshua tree seed dispersal is necessary to predict the likely changes in range for this Mojave endemic as the climate warms. A recent model predicts that Joshua tree habitat will shift north and upward in elevation (Dole et al. 2003). From data collected in this study, it does not appear that Joshua trees will be limited by the availability of dispersers. Both white-tailed antelope ground squirrels and Merriam's kangaroo rats have broad ranges, and a host of other scatter-hoarding rodents (e.g. *Chaetodipus formosus*, *Dipodomys microps*, *Dipodomys deserti*) not tested in this study

are broadly distributed across the arid lands of North America (Smith and Reichman 1984, Hollander and Vander Wall 2004). However, it is still unclear whether Joshua trees would be able to disperse to new habitat as a result of climate change; there are still questions of recruitment limitation through seedling mortality, and we do not know how long it takes for a Joshua tree to reach fruiting age. These questions must be answered before we can accurately predict how a warming climate will affect this species.

It is probable that many other large-seeded perennials in the Mojave Desert are also dispersed, to some extent, by scatter-hoarding rodents. Other species of *Yucca* in the Mojave Desert including the Mojave yucca (*Yucca schidigera* Ortgies) and banana yucca (*Yucca baccata* Torrey) have indehiscent fruit and similarly shaped seeds (though slightly smaller in the case of Mojave yucca). It is unclear whether rodents prefer these seeds, though I can see no reason why they would not. Seeds of both blackbrush and desert almond (*Prunus fasciculata* Torrey) labeled with scandium 46 were found in similar caches as those found in this study (S. Vander Wall pers. com., M. Beck pers.com.), and this was likely due to rodent food hoarding. Similarly, seeds of catclaw acacia (*Acacia greggii* Gray) were found mixed in with target seeds in camera trap trials with labeled Joshua tree seeds in this study. Rodents will hoard any items that they perceive as food, and this includes many types of seeds. Burial in caches beneath the soil surface conferred a significant advantage in this hot dry environment where seeds on the soil surface are likely to dry out before germinating. Given the relative advantage of being dispersed (determined here as greater probability of emergence), it seems likely that rodents have applied diffuse selection pressure on many perennial species towards larger seeds and a coevolving dispersal syndrome.

The relationship between Joshua trees and scatter-hoarding rodents is a mutualistic one. This relationship may be context dependent (Bronstein 1994). Small seed crop size along with an overabundance of rodents may shift this interaction from mutualism to predation on seeds by rodents. Further research should address the relationship between seed crop size, rodent population size, and the role of seed predators on dispersal quality.

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Table 1. Individual rodent captures over three days at two sites associated with seed removal transects.

Site	<i>Dipodomys merriami</i>	<i>Dipodomys microps</i>	<i>Chaetodipus. formosus</i>	<i>Perognathus longimembris</i>	<i>Neotoma lepida</i>
Piute Valley	3	0	4	1	0
Ivanpah Valley	4	4	0	8	1

Table 2. Characteristics of white-tailed antelope ground squirrel's caches from camera trap trials and ground squirrel and kangaroo rat caches from inside enclosures at Piute Valley. All means are pooled across all caches found. Values in parentheses are one standard error.

	<i>A. leucurus</i> Field	<i>A. leucurus</i> Enclosure	<i>D. merriami</i> Enclosure
Trials	3	8	5
Caches Found	39	32	46
Caches/Subject	13.0 (7.1)	3.3 (1.1)	9.2 (1.7)
Cache Depth (cm)	1.08 (0.44)	1.20 (0.31)	1.72 (0.54)
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

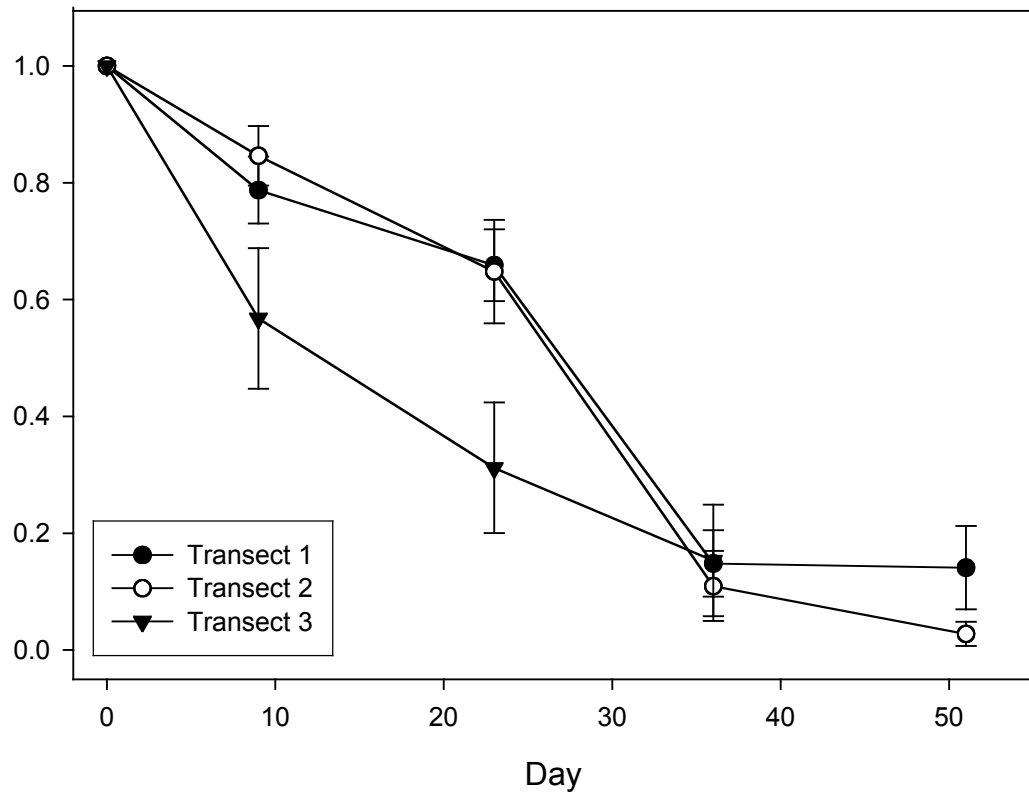


Figure 1. Mean proportion of fruits remaining on each monitored infructescence in the Ivanpah Valley, monitoring was terminated after 52 days. Error bars are ± 1 SE.

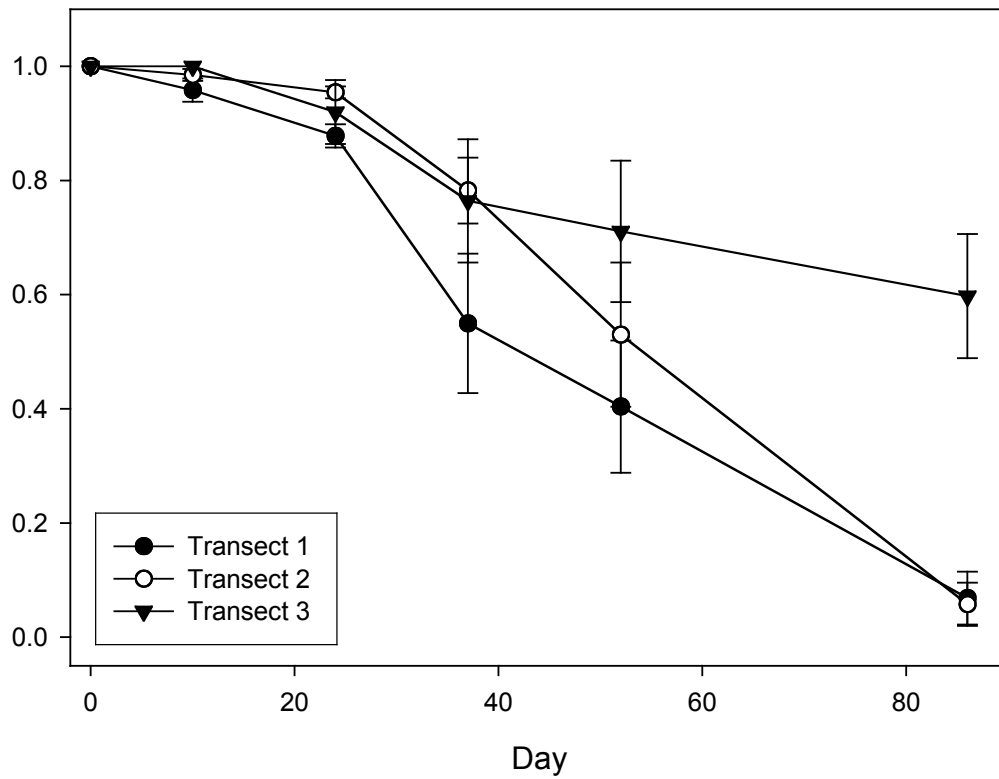


Figure 2. Mean proportion of fruits remaining on each monitored infructescence at Piute Valley, monitoring was terminated after 86 days. Error bars are ± 1 SE.

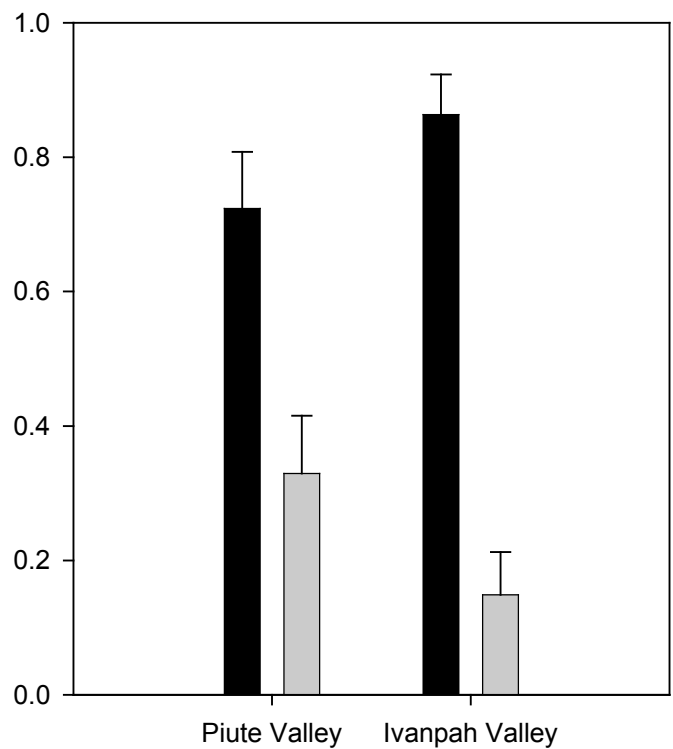


Figure 3. The number of fruits remaining attached to infructescences in September 2007 after a 3 month monitoring period. Black bars are for infructescences restricted from animal access, gray bars are infructescences available to animals. Error bars are ± 1 SE.

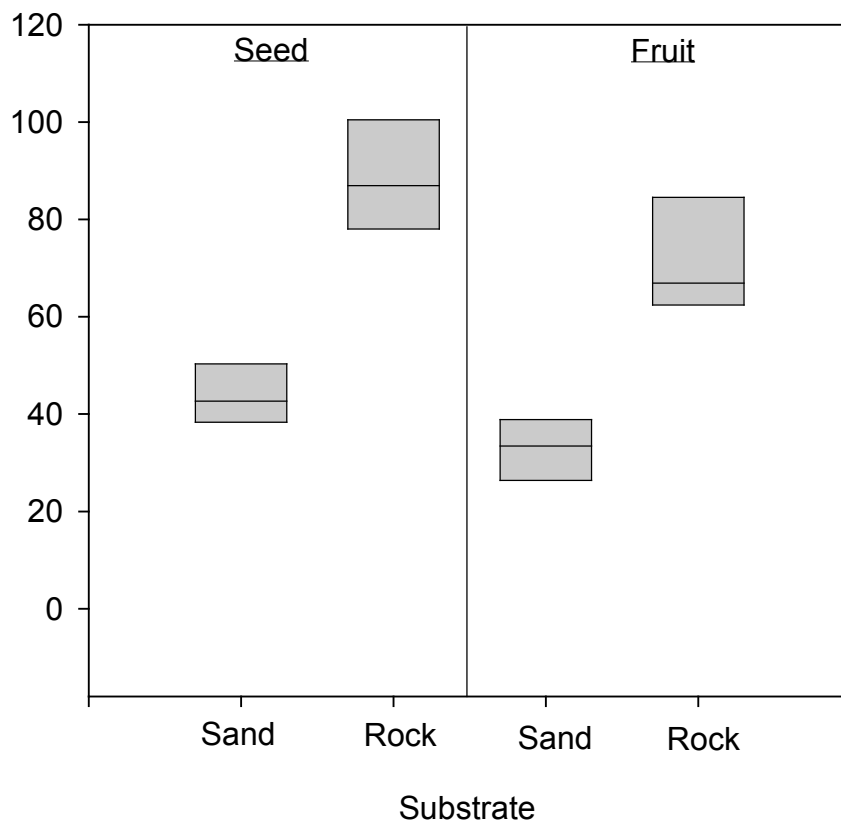


Figure 4. Sustained wind speeds required to move Joshua tree propagules one seed (or fruit length) on either a sand substrate (43.6 ± 2.6 km/h and 31.9 ± 2.6 km/h for seed and fruit respectively) or a rock substrate (87.6 ± 5.5 km/h and 73.6 ± 4.8 km/h for seed and fruit respectively). Bars are 90% confidence intervals.

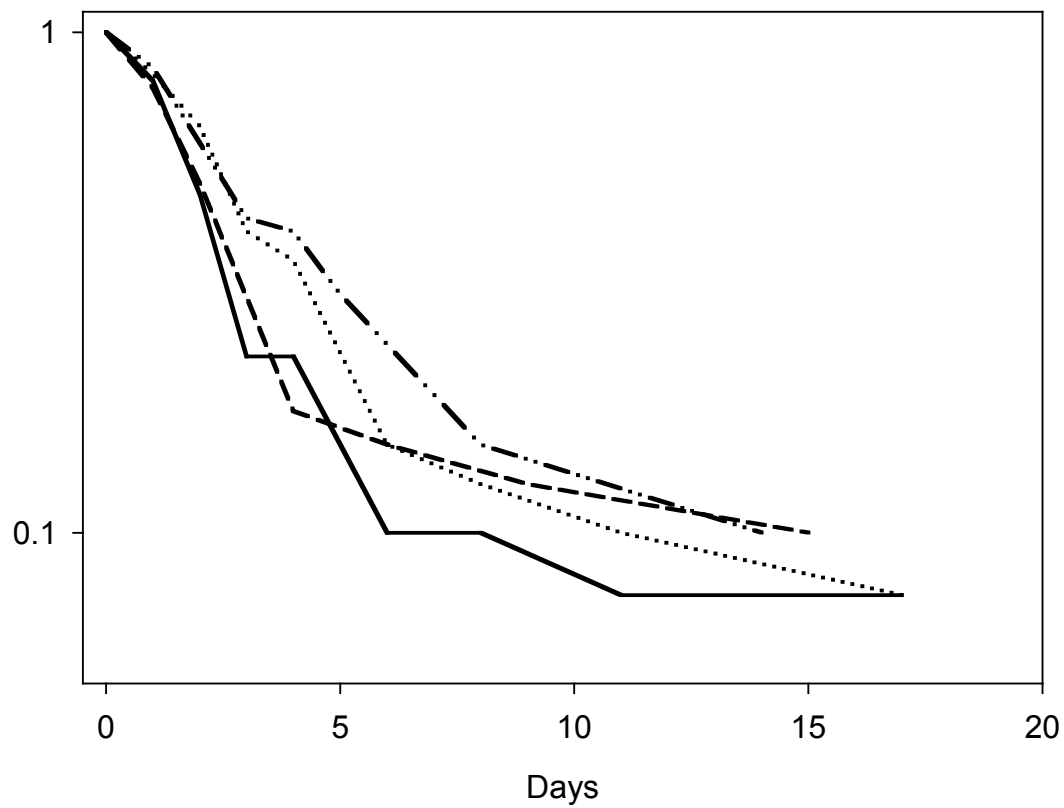


Figure 5. Removal of single fruits from the soil surface from four transects plotted on a log scale against time in days at Piute Valley.

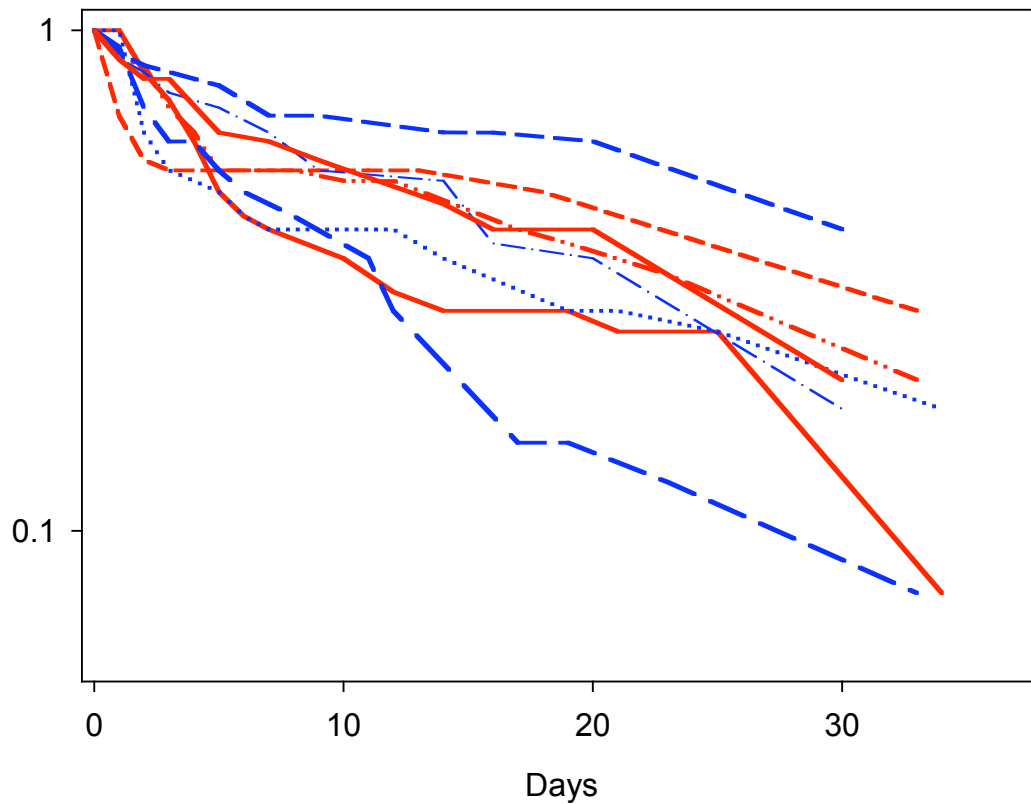


Figure 6. Removal of single seeds from the soil surface by animals plotted on a log scale against the time in days at Piute Valley. Transects with seeds left under shrubs are in blue and transects with seeds placed in the open are in red.

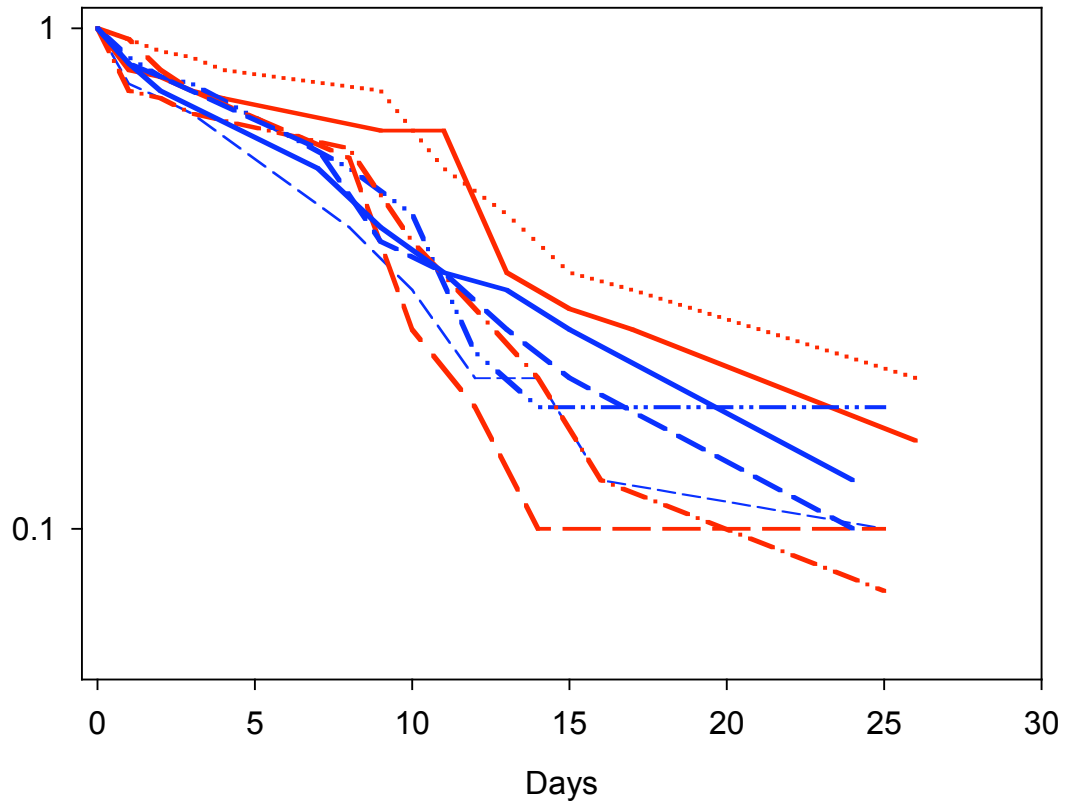


Figure 7. Removal of single seeds from the soil surface by animals plotted on a log scale against the time in days at Ivanpah Valley. Transects with seeds left under shrubs are in blue and transects with seeds placed in the open are in red.

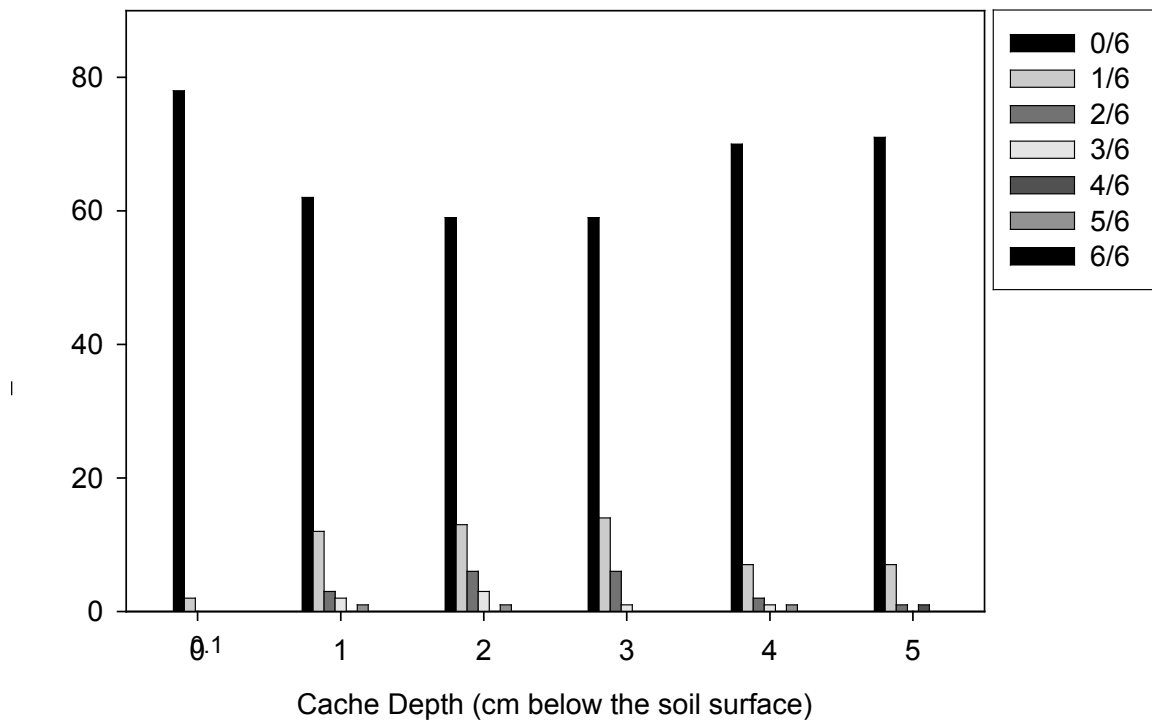


Figure 8. The frequency of seedling emergence from caches (y- axis) as a function of cache depth (x-axis). Shaded bars represent the possible outcomes of seedlings emerging from the six caches in each enclosure.

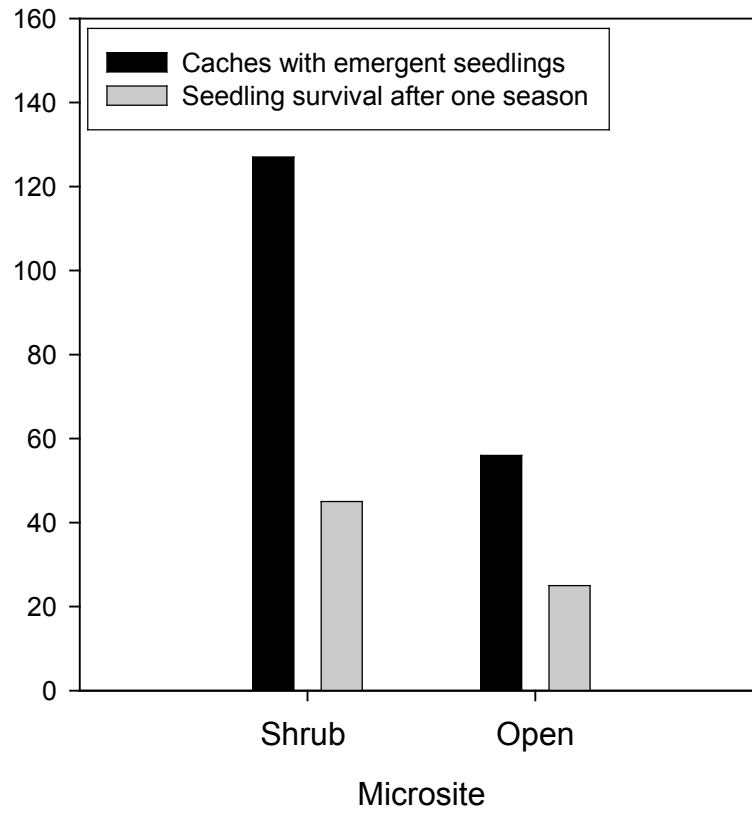


Figure 9. The number of seedlings emerging (black bars, $n = 183$) from seeds buried either under shrub cover or in the open, and the number surviving after one season (gray bars, $n = 70$).

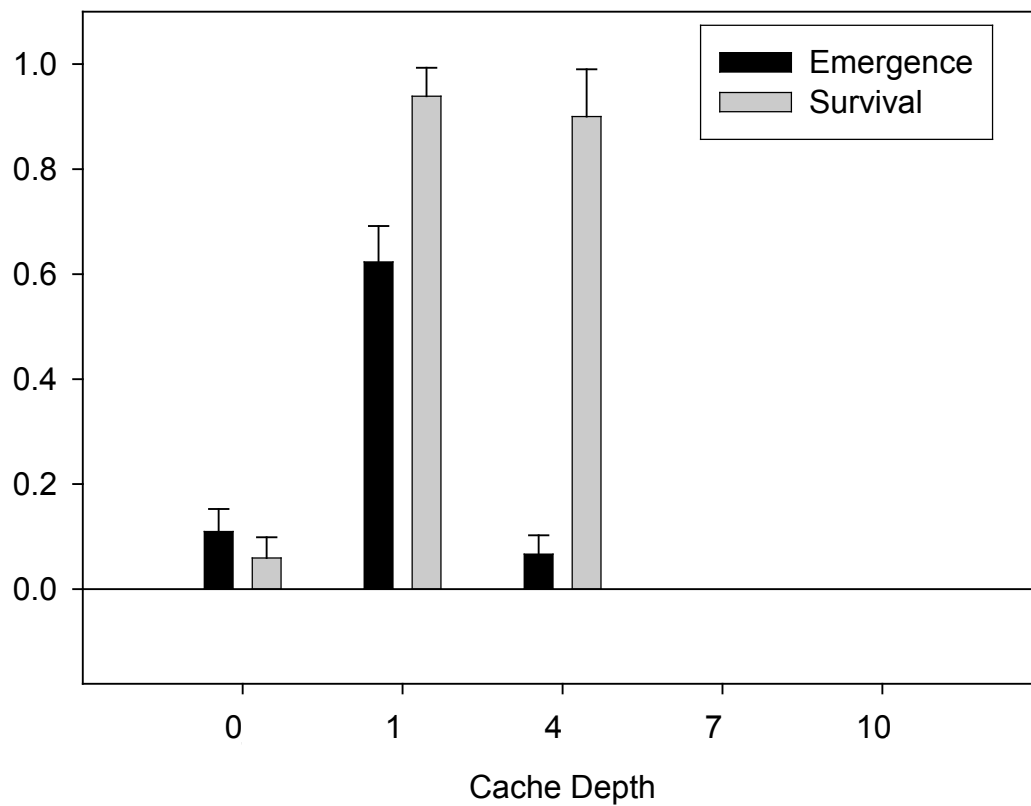


Figure 10. The mean proportion of caches with seedlings emerging from pots at three depths (0 cm, 1 cm, and 4 cm, black bars), and the mean proportion of caches surviving through the end of the study period (gray bars). No seedlings emerged from caches buried at 7 cm or 10 cm. Error bars are ± 1 SE.