

2016

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Recommended Citation

Borchert, Mark I. 8784318 (2016) "Rodent Removal of Fallen Joshua Tree (*Yucca brevifolia*) Fruits," *Bulletin of the Southern California Academy of Sciences*: Vol. 115: Iss. 3.

Available at: <http://scholar.oxy.edu/scas/vol115/iss3/2>

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Cover Page Footnote

Acknowledgements I wish to thank Lesley DeFalco and Stephen Vander Wall for commenting on the draft manuscript. I thank the two anonymous reviewers of the manuscript for their helpful suggestions and edits.

Rodent Removal of Fallen Joshua Tree (*Yucca brevifolia*) Fruits

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Abstract.—Joshua trees (*Yucca brevifolia*) produce large, indehiscent fruits that contain numerous large seeds. Seed dispersal in this species depends on rodents to dismantle fruits and extract the seeds which they disperse tens of meters from the source. Using camera trapping and fruits tied to bobbins, I show that white-tailed antelope squirrels (*Ammospermophilus leucurus*) and kangaroo rats (*Dipodomys* spp.) moved intact, fallen fruits 6 to 7 m from trees before opening them. Pocket mice (*Chaetodipus fallax* and *Perognathus longimembris*) and pinyon mice (*Peromyscus trueii*) dismantled fruits and harvested loose seeds but did not appear to move them although they readily harvested loose seeds. Mobilizing fruits may be an important, overlooked step in the seed dispersal process, especially if the fruits are indehiscent. Fruit-carrying behavior of rodents described in this study adds to the dispersal distance of Joshua tree seeds.

Joshua tree is an iconic, widespread arborescent succulent of the Mojave Desert. In the late Pleistocene Joshua trees were distributed over southeastern California, southern Nevada, southeastern Arizona, and into much of northern Mexico (Cole et al. 2011). As temperatures warmed during the Holocene, its distribution receded from Mexico, southeastern Arizona and southern California into a considerably smaller patchwork of disjunct areas (Cole et al. 2011; Barrows and Murphy-Mariscal 2012). As climate continues to warm into the 21st Century, modeling suggests that Joshua tree likely will disappear in the southern part of its distribution and perhaps expand north into Nevada (Cole et al. 2011).

The ability of Joshua tree to expand its range in response to the anticipated rapid warming may be limited by seed dispersal that would effectively move it to suitable, unoccupied habitats (Lenz 2001; Cole et al. 2011). Lenz (2001) hypothesized that beginning in the middle Miocene (15.1–11.2 mya) mammals such as gomphotheres, mastadons and mammoths likely were long distance dispersers of Joshua tree seeds. Indeed, he suggested its large, multi-seeded fruit may have evolved in response to consumption by these large mammals. However, following the extinction of megaherbivores in the late Pleistocene, Joshua tree seed dispersal now depends entirely on the more limited dispersal (< 100 m) of rodents in the Sciuridae, Heteromyidae and Cricetidae (Vander Wall et al. 2006; Waitman et al. 2012). Whether extinct megaherbivores dispersed Joshua tree seeds is open to question (Waitman et al. 2012) but it is clear that the role of rodent seed dispersal in relationship to present-day climate warming deserves careful examination.

Joshua trees produce seeds in large, non-fleshy, indehiscent fruits. Seed release and dispersal depends exclusively on rodents breaking into fruits and extracting seeds (Vander Wall et al. 2006; Waitman et al. 2012), although Vander Wall et al. (2006) also noted that rodents dragged some fruits away from the source plant before opening them. Preliminary camera trapping of fallen fruits in 2013 revealed that both white-tailed antelope squirrels and kangaroo rats moved unopened fruits from beneath trees, but it was unclear how many fruits were taken, or how far they moved them. If rodents carry fruits from the source, it would increase the total distance

rodents disperse Joshua tree seeds. The goals of this study were: (1) to determine which rodent species moved fruits from beneath trees and (2) to quantify the distances fruits were carried by rodents in two contrasting Joshua tree habitats.

Materials and Methods

Study Area

The study was conducted in two 7.61-ha areas located approximately 6 km north northeast of Big Bear City, California. Both areas occupy gently sloping (average $< 5^\circ$) topography in the high desert of the San Bernardino Mountains at an elevation of 1800 m. The Cactus Flats (CF) site ($34^\circ 19'73''\text{N}$, $116^\circ 48'85''\text{W}$) has no documented occurrence of fire since 1910 when records first began (fire history maps, Supervisor's Office, San Bernardino National Forest), although a wildfire burned to the southwest edge of the study area in 1946. The Lone Valley site (LV) ($34^\circ 17'84''\text{N}$, $116^\circ 47'49''\text{W}$) is located 3.5 km SSE of CF. There are no documented fires for this area since record keeping began (1910).

The study area has a cold desert climate which is characterized by cold, snowy winters and warm, dry summers. Average annual precipitation (1985 - 2014) based on a spatial interpolation of regional climate stations (PRISM Climate Group, Oregon State University, Website <http://prism.oregonstate.edu> created 6 July 2015) is 313 ± 145 mm SD, most of which falls as snow from November to April. The study area also experiences occasional ephemeral summer and fall rainfall events. Both years of the study occurred during a prolonged drought with 136 mm of precipitation recorded in 2013 (43% of the average) and 255 mm (81% of the average) in 2014.

Vegetation Sampling

At 26 points randomly located at each site, I recorded the vegetation cover and composition using 10-m line transects. From each point I oriented a 10-m tape in a random direction. Every 0.5 m on the transect tape I recorded the following variables that intercepted a point: rock, bare ground, herbs and forbs, litter, coarse woody debris, live or dead shrubs, and live or dead trees. The number of intercepts of each variable on the transect was divided by 20 to calculate percent cover for each transect.

Camera Trapping

I camera-trapped the study areas to identify the species that removed fallen Joshua tree fruits. In each study area, I located 10 camera-trapping stations in a 2×5 grid with spacing of ≥ 90 m between stations. At CF, fruits and seeds were photographed beginning 19 September 2013 and in 2014 beginning 15 July. At LV fruits and seeds were photographed beginning 26 October 2013 and beginning 21 August 2014.

At each station, I attached a BirdCam 2.0 camera (EBSCO Industries, Calera, Alabama USA) to the bole of a Joshua tree ~ 35 cm above the ground. Approximately 75 cm from the lens I placed 5 Joshua tree fruits on the ground and programmed cameras to take a photograph every 1.05 minutes beginning at sunset (~ 1845 hours) for an average of 681 photos in the 12-hrs of dark. Cameras flashed automatically every 1.05 minutes during the night. At sunrise (~ 0630), I replaced missing or partially opened fruits with new ones so that cameras photographed 5 fruits at 1.05-min intervals for 12 hours during the day. For each 12-hour period I recorded the proportion of fruits removed from the camera field or opened within the camera's field of view. I camera-trapped each station for 3 days (72 hours), but I only analyzed the first 12-hr day or

night period when animals removed fruits or seeds from the station. If animals failed to remove fruits or seeds from stations in the 72-hour period, the station was recorded as “not visited”.

I carried out the same 72-hour protocol using Joshua tree seeds that I extracted from fruits collected at CF in 2013. In two side-by-side circular plastic dishes (1.5 cm × 9.0 cm), I placed ~39.2 grams of seeds (to simulate the average number of seeds in 5 fruits) uninfested by yucca moth larvae (*Tegeticula synthetica*) (Borchert and DeFalco 2016). Seeds were neither counted nor weighed after deployment.

Once seeds or fruits were discovered, rodents usually removed them in a rapid series of visits. Trapping showed the average interval between visits (\pm SD) was 7 ± 5.4 minutes ($n = 19$). A species was designated the harvester if there was at least one photograph of the animal in the series of visits, and the time between visits did not exceed 15 minutes. In other words, if there was no photograph of the animal, or if the interval between consecutive visits exceeded 15 minutes, the sequence of visits was not analyzed. The little pocket mouse (*Perognathus longimembris*) could not be distinguished from the San Diego pocket mouse (*Chaetodipus fallax*) in the photographs so they were combined and are referred to as “pocket mice”. Similarly, Merriam’s kangaroo rat (*Dipodomys merriami*) and the Pacific kangaroo rat (*D. agilis*) were combined and are referred to as “kangaroo rats”. Live trapping, however, showed that Merriam’s kangaroo rat was by far the most abundant kangaroo rat species (Borchert and DeFalco 2016).

Fruit Spool-and-Line Method

In the proximal end of fruits 6.0-8.0 cm in length, I drilled a 0.8-mm diameter hole to a depth of 5 cm. In this opening I inserted a 0.8 g bobbin (Danfield, Lancashire UK). At each study site, I established a grid of 52 points (4 × 13) with 35-m spacing between points. I placed a fruit under a Joshua tree (> 1.5 m in height) nearest each point and tied the bobbin thread to a slender bamboo stake pushed into the soil. Some fruits were moved but not eaten. These I revisited daily until they were eaten, or moved and then eaten. Only fruits moved > 1.0 m were considered mobilized outside the Joshua tree canopy. After a fruit was moved, I measured the distance and compass direction to the point where it was taken.

Between 29 July and 31 July 2014 at CF I censused the 52 spool-and-line fruits just before 0630 and again at 1845 and recorded which fruits were moved at night and during the day. In this way, I compared the distances fruits were moved by nocturnal and diurnal rodents.

Statistical Analysis

I used the Mann-Whitney U test to compare differences in cover between the two sites and distances fruits were moved between sites in each of the two years. T-tests were used to compare the average number of fruits taken per station at the two sites.

Results

Vegetation

Vegetation differed between the two sites. Both sites had a similar cover of Joshua trees, but CF cover was dominated by live shrubs (*Lycium andersonii*, *Purshia tridentata* var. *glandulosa*) and bare ground (Table 1). In contrast, pinyon pine (*Pinus monophylla*) cover at LV averaged 23.5% whereas pinyons were absent in the transects at CF. The understory of LV was dominated by herb cover, collapsed dead shrubs and downed Joshua trees (Table 1). Due to the low cover of live shrubs, the understory of LV was considerably more open than CF.

Table 1. Plant species cover, herbaceous cover, bare ground cover, dead shrub cover and litter cover for Cactus Flats and Lone Valley. Values are mean cover ± 1 SD. Cover comparisons were made using Mann-Whitney U for 26 transects at each site.

Plant species	Cactus Flats	Lone Valley	Statistical significance
<i>Yucca brevifolia</i>	8.1 (9.8)	11.1 (17.0)	$P = 0.95$
<i>Pinus monophylla</i>	0.0	23.5 (20.4)	$P < 0.001$
<i>Lycium andersonii</i>	12.7 (10.9)	0.0	$P < 0.001$
<i>Purshia tridentata</i> var. <i>glandulosa</i>	10.0 (13.0)	3.1 (6.2)	$P = 0.053$
<i>Artemisia tridentata</i>	2.7 (6.7)	1.9 (4.9)	$P = 0.91$
<i>Fremontodendron californicum</i>	4.2 (12.7)	0.0	$P = 0.08$
Herbaceous	0.8 (2.7)	18.1 (15.8)	$P < 0.001$
Litter	0.0	7.7 (11.4)	$P < 0.001$
Dead shrubs	11.2 (14.8)	18.5 (11.2)	$P < 0.02$
Bare ground	45.0 (19.2)	26.1 (21.7)	$P < 0.001$

Camera Trapping

There were 80 photographs of animals at fruit stations and 407 photographs at seed stations. White-tailed antelope squirrels comprised the highest percentage (61.3%) of photographs at fruit stations followed by kangaroo rats (16.3%) (Table 2). Kangaroo rats dominated photographs at seed stations (45.5%) followed by white-tailed antelope squirrels (16.5%). Western scrub jays (*Aphelacoma californica*) visited seed stations at LV in both years (Table 2). Although jays were active at CF, they were not photographed at seed stations in either year.

Fruit Removal and Fruit Movements

Of the total 208 fruits placed under trees (2 sites × 2 years × 52 trees per site), 147 (70.7%) were moved and subsequently opened, 29 (13.9%) had cut threads and the fruit was missing, 20 (9.6%) fruits were missing but the bobbin remained, 5 (2.4%) remained unopened at stations, 4 (1.9%) were moved but not opened, and 3 (1.4%) were taken into woodrat nests.

Of the 147 fruits that were moved and opened, 101 (68.7%) were taken beyond the canopy (> 1.0 m) (Fig. 1). Fruit transport distances did not differ significantly between the two sites in 2013 ($Z = -1.03$, $p = 0.30$) or in 2014 ($Z = 1.64$, $p = 0.10$) (Table 3) even though the understory was more open at LV than at CF (Table 1). Of the 101 fruits moved > 1.0 m, 10 (9.9%) were

Table 2. Number of photographs by species for each site and each year.

	Cactus Flats				Lone Valley			
	2013		2014		2013		2014	
	Fruits	Seeds	Fruits	Seeds	Fruits	Seeds	Fruits	Seeds
White-tailed antelope squirrel	15	18	12	30	15	16	7	3
Kangaroo rats	3	81	7	90	3	14	0	0
Pocket mice	2	25	0	8	2	20	0	4
Pinyon mouse	3	3	4	1	3	18	1	54
Merriam’s chipmunk	0	0	2	0	0	0	0	0
California ground squirrel	0	0	1	1	0	0	0	0
Western scrub jay	0	0	0	0	0	2	0	19

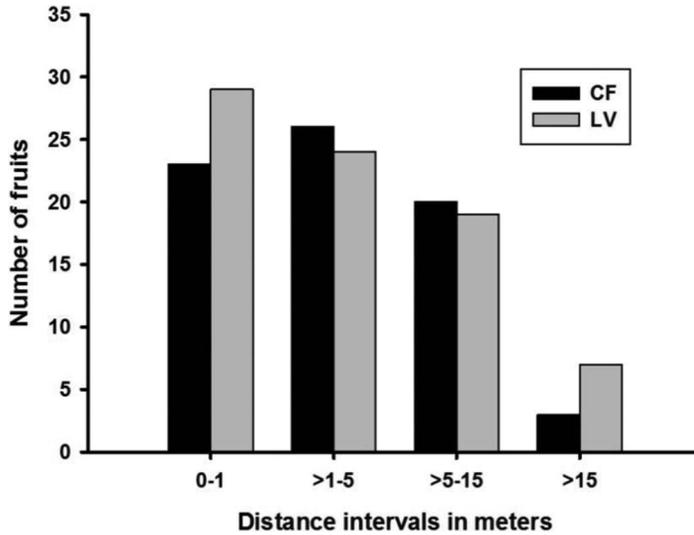


Fig. 1. The number of spool-and-line fruits dispersed by distance intervals at each site. Distances were pooled for 2013 and 2014. CF is Cactus Flats and LV is Lone Valley.

taken beyond 15 m (Fig. 1): the maximum distance a fruit was moved was 46.9 m, and the mean maximum distance was 21.2 m ($n = 4$).

At CF in 2014 the mean (\pm SD) distance fruits were moved by white-tailed antelope squirrels during the day ($8.3 \text{ m} \pm 7.8 \text{ m}$, $n = 7$) did not differ significantly ($Z = 0.95$, $p = 0.36$) from the mean distance of those moved at night by kangaroo rats ($4.5 \text{ m} \pm 3.4$, $n = 11$). The maximum distance a fruit was carried in the day was 25 m while the maximum distance at night was 11.3 m.

White-Tailed Antelope Squirrels

White-tailed antelope squirrels removed the highest percentages of fruits in late morning (0900-1200) and early afternoon (1200-1500) (Fig. 2). In 2013 at CF they moved 22% of the 50 fruits from 6 stations, and at LV 76% of fruits from 8 stations (Table 4). The average number of fruits taken per station at LV was significantly higher ($t = 2.59$, $df = 11$, $p < 0.001$) than the average number taken at CF in 2013 (Table 4). In 2014 at CF, white-tailed antelope squirrels moved 42% of the 50 fruits from 5 stations, and 52% were moved from 6 stations at LV. The average number of fruits taken per station did not differ significantly ($t = 0.03$, $df = 9$, $p = 0.97$) between the two sites (Table 4). In the two years, five fruits were dismantled by white-tailed antelope squirrels at CF while just one was opened at LV.

Table 3. Fruit dispersal distances ($> 1.0 \text{ m}$) at CF and LV for 2013 and 2014. Values are means \pm 1 SD (sample sizes).

Site	Year	Distance (m)
Cactus Flats	2013	6.1 ± 4.82 (32)
	2014	4.8 ± 4.7 (19)
Lone Valley	2013	7.6 ± 5.9 (34)
	2014	6.8 ± 6.2 (14)

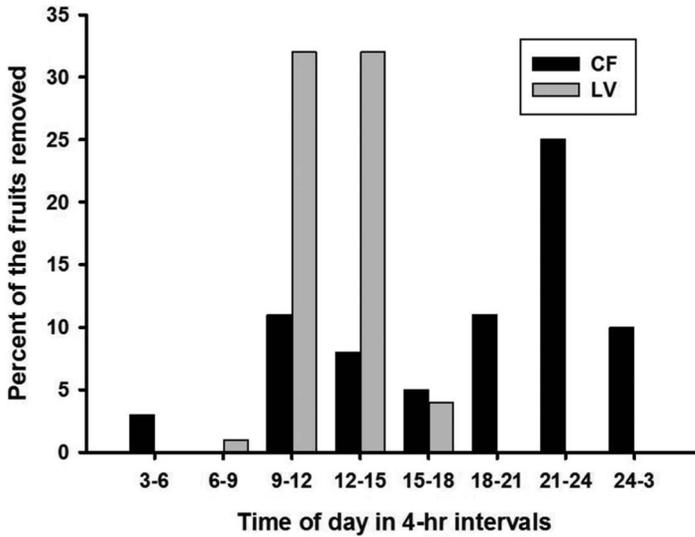


Fig. 2. Percent of the fruits removed at the two sites in four-hour intervals over 24 hours. Values are for the two years combined. CF is Cactus Flats and LV is Lone Valley.

In the two years at both sites, white-tailed antelope squirrels visited a total of 8 seed stations, far fewer than the 25 stations visited for fruits. In 2013 at CF squirrels left 25–75% of the seeds in dishes, although they removed nearly all the seeds in 2014. At LV they collected all the seeds in both years. Nocturnal rodents invariably collected the small number of seeds not taken by white-tailed antelope squirrels during the day.

Kangaroo Rats

Kangaroo rats visited stations between 1800 and 0600 hours and removed the highest percentage of fruits just before midnight (Fig. 2). At CF kangaroo rats removed 41% of the 50 fruits from 5 stations in 2013, and 59% of the fruits from 8 stations in 2014 (Table 4). In contrast, they only harvested fruits at LV in 2013 and were not photographed removing fruits or seeds at LV in 2014.

Table 4. Fruit removal from camera-trapping stations by white-tailed antelope squirrels and kangaroo rats. Fruits removed per station are means ± 1 SD with sample sizes in parentheses. The percentages in parentheses are for 50 fruits (5 fruits × 10 stations). CF is Cactus Flats and LV is Lone Valley.

Site	Year	Stations visited	# Fruits taken (%)	# Fruits removed per station
White-tailed antelope squirrels				
CF	2013	6	11 (22%)	1.8 ± 0.9 (6)
	2014	5	21 (42%)	4.2 ± 1.6 (5)
LV	2013	8	38 (76%)	4.4 ± 0.8 (8)
	2014	6	26 (52%)	4.2 ± 1.3 (6)
Kangaroo rats				
CF	2013	5	17 (34%)	3.2 ± 1.3 (5)
	2014	6	24 (48%)	4.4 ± 1.3 (6)

At CF kangaroo rats collected seeds at 5 stations in 2013 and at 8 stations in 2014. They collected nearly all of the seeds after multiple visits. Pinyon mice, and sometimes pocket mice, harvested the few seeds not taken by kangaroo rats. In 2013 at LV, kangaroo rats gathered seeds from 2 stations; seeds not taken by kangaroo rats were collected by pinyon mice at LV.

Pocket Mice and Pinyon Mice

Pocket mice dismantled 7 fruits at 2 stations at LV in 2014, and three fruits were removed. Pinyon mice opened 7 fruits at 2 stations at CF and removed 3 fruits. They collected seeds from 5 stations at LV and from 3 stations at CF in the two years. Like pocket mice, pinyon mice harvested more seeds than fruits. In the two years, they took seeds from two stations at CF and from 7 stations at LV.

A pair of western scrub jays was present at each site in both years. At LV they visited 4 stations in two years and removed all the seeds from two stations, one in 2013 and one in 2014 (Table 2). At each site they carried one spool-and-line fruit a short distance (< 3 m). A California ground squirrel (*Otospermophilus beecheyi*) briefly visited seed dishes at one CF station in 2014.

Discussion

White-tailed antelope squirrels moved fallen Joshua tree fruits at both sites in both years and visited more fruits (63%) than seed stations (20%). Similarly, in southern Nevada, white-tailed antelope squirrels visited just 13% of the 23 stations supplied with Joshua tree seeds (Waitman et al. 2012). Although fruits collected at CF in 2013 were large (averaging 4.3 cm in diameter and 6.6 cm in length) and weighed 14 g (dry), white-tailed antelope squirrels (100-110 g) easily carried them from the stations. Moreover, because the average fruit contained 95 undamaged seeds, they efficiently moved numerous seeds in a single visit, as opposed to the multiple visits required to carry loose seeds (Table 2). Because shrub cover was low at LV compared to CF, I expected fruits to be moved greater distances but there was no significant difference in mean distance between the two sites. At CF, rodents carried fruits through dense shrubs stems (especially *Lycium*) into openings and through additional shrub patches before opening them. As a result, threads often traced highly circuitous routes. At LV rodents frequently hid fruits next to downed Joshua tree stems near the location of deployment. Fruits carried greater distances often were taken in straight lines.

In addition to collecting fallen fruits, white-tailed antelope squirrels are agile climbers (Zemba and Gall 1980; Waitman et al. 2012, Borchert and DeFalco 2016). In both years at CF squirrels removed or opened 24 - 28% of canopy fruits (Borchert and DeFalco 2016). For example, in 2014 I placed a sample of spool-and-line fruits in eight trees. Camera trapping showed white-tailed antelope squirrels climbed trees and dismantled fruits but they also carried the spool-and-line fruits to the ground, where they dispersed them in the same way they dispersed fallen fruits in this study (unpublished data).

The results of this and other studies suggest white-tailed antelope squirrels are likely keystone seed dispersers in deserts of the arid West because it is a relatively large rodent, is an excellent climber, possesses cheek pouches for seed storage, and scatterhoards seeds (Beck and Vander Wall 2010). Furthermore, it is widely distributed across eight states (Belk and Smith 1991), and is relatively abundant (Clark 2010; Borchert and DeFalco 2016). In southern Nevada, Bradley (1968) found seeds of 11 shrubs and six forbs and grasses in the cheek pouches of white-tailed antelope squirrels including *Y. brevifolia*, *Y. baccata* and *Y. schidigera*. Squirrels also collected and dispersed fallen *Pinus monophylla* seeds (Hollander and Vander Wall 2004) and the fruits of *Prunus andersonii* (Beck and Vander Wall 2010). White-tailed antelope squirrels

removed 75% of the fruits in the canopies of *P. andersonii* as well as the seeds and fruits of *Y. brevifolia* (Zembal and Gall 1980; Waitman et al. 2012; Borchert and DeFalco 2016). At CF I camera-trapped squirrels removing both seeds and fruits of *Fremontodendron californica* from beneath shrubs. In 2015 at LV, they were camera-trapped removing and opening fruits of *Opuntia phaeacantha* (0.5-1 m in height). White-tailed antelope squirrels likely climb other desert shrub and tree species to obtain fruits and seeds.

Although Merriam's kangaroo rats, the most common kangaroo rat species on the two sites (Borchert and DeFalco 2016), are considerably smaller (40-50 g) than white-tailed antelope squirrels, they also carried fruits, sometimes tens of meters. Kangaroo rats are well-known seed dispersers (Longland 1994; Jenkins et al. 1995; Jenkins and Breck 1998; Longland et al. 2001, Waitman et al. 2012; Longland and Ostoja 2013) but carrying large fruits has not been described for this species. I photographed this species removing fruits at CF in both years but not at LV where they gathered seeds in one (2013) of the two years. Still, the maximum length of camera trapping a station was only 72-hours, so fruit mobilization by kangaroo rats also may have occurred at LV but was not photographed. They readily collected loose seeds from dishes and typically visited stations multiple times (Table 2) until all but a few seeds remained.

Because nearly all kangaroo rat species do not climb, fruit removal by these species is likely confined to years of high fruit production when they fall to the ground (Borchert and DeFalco 2016). Nevertheless, even in years of low fruit production, white-tailed antelope squirrels consume or disperse canopy fruits before they reach the ground. Therefore, in low production years non-climbing rodents only have access to seeds in unopened fruits on the ground abandoned by white-tailed antelope squirrels or to seeds left in dismantled fruits. Pinyon mice and pocket mice removed small numbers of fruits and were likely more important in dispersing seeds than fruits.

Fruit removal by kangaroo rats and white-tailed antelope squirrels increases the known dispersal distance of Joshua tree seeds. The weighted average distance of primary dispersal by rodents in southern Nevada was 13.7 m, and the weighted averaged distance of secondary dispersal was 12.1 m, summing to 25.8 m (Vander Wall et al. 2006). In this study the weighted average fruit movement distance for the two sites was 6.4 m which, when added to 25.8 m for seed dispersal sums to 32.2 m, an increase of almost 25%. In this study the mean maximum distance for fruits was 21.2 m, which when summed with Vander Wall et al.'s (2006) estimate of maximum primary seed dispersal of 30.0 m totals 51.2 m, or a 41% increase over estimate when only seed dispersal is considered. Nevertheless, 51.2 m does not include the mean maximum distance for secondary seed dispersal.

Fruit movement in this study demonstrates how a thorough examination of disperser behavior may reveal unobserved steps in the dispersal process, steps that increase seed dispersal distances. For example, seed dispersal by agoutis (*Dasyprocta* sp.) illustrates how dispersal distances can increase once its foraging behavior was fully examined. In central Amazonia agoutis cached single Brazil nuts (*Bertholletia excelsa*) within 10 m of the source (Tuck Haugaasen et al. 2010). However, a second study of Brazil nut dispersal (Tuck Haugaasen et al. 2012) showed agoutis carried unopened fruits an average of 20.8 m before they scatterhoarded nuts another 4 m. Fruit and seed dispersal together averaged 29.2 m. Thus, studies that rely only on marked seeds may underestimate dispersal distances, especially for plant species with indehiscent fruits (Tuck Haugaasen et al. 2012). In the Sonoran and Mojave deserts of California at least 22 plant species are serotinous like *Y. brevifolia* (Martinez-Berdeja and Ezcurra 2015) suggesting that other species may benefit from the fruit-carrying behavior of *Ammospermophilus* and *Dipodomys*.

If fruit mobilization is a widespread phenomenon in Joshua trees, seed dispersal distances for this arborescent succulent may be greater if, in addition to fruit displacement, seeds are

re-cached multiple times. Repeated re-caching increases dispersal distances because the cumulative distance from the source increases with each successive re-cache (Vander Wall and Joyner 1999, Roth and Vander Wall 2005, Perea et al. 2011, Jansen et al. 2012, Wang et al. 2014). Jansen et al. (2010) followed the dispersal of a large-seeded palm (*Astrocaryum standleyanum*) by Central American agoutis (*Dasyprocta punctata*). After caching and re-caching palm seeds numerous times (up to 36), agoutis moved 33% of the seed > 100 m and some seeds up to 900 m. Vander Wall et al. (2006) recorded secondary caching of Joshua tree seeds, but tertiary or quaternary caching could further increase seed dispersal distances.

Several researchers have suggested the limited seed dispersal of Joshua tree as a major impediment to its migration in response to climate change (Cole et al. 2011; Barrows and Murphy-Mariscal 2012). Nevertheless, it is important to note that the expansion of a species outside its current range in response to climate change depends on factors besides seed dispersal including: seed availability (Kroiss et al. 2015), abundance of germination microsites (Kroiss et al. 2015), interspecific plant competition (Urban et al. 2013; Tomiolo et al. 2015), interactions with obligate pollinators (Blatrix et al. 2013), disturbance (Serra-Diaz et al. 2015; Springer et al. 2015) and landscape heterogeneity (Chardon et al. 2015; Serra-Diaz et al. 2016).

California scrub jays are well-documented long distance dispersers of the acorns of California oaks (Pesendorfer et al. 2016) and were present at both sites. In this study scrub jays dispersed small numbers (< 3) of fruits short distances (< 2 m) although the threat may have discouraged them from flying far. They also were photographed collecting loose seeds at LV. Nevertheless, even when fruits were abundant, I did not observe them opening fruits to extract seeds. The role of scrub jays in the dispersal of Joshua trees remains unresolved. Even if they did not open fruits, it is possible that they collect and disperse seeds from partially open fruits attached to the panicle or dismantled fruits on the ground.

Acknowledgements

I wish to thank Lesley DeFalco and Stephen Vander Wall for commenting on the draft manuscript. I thank the two anonymous reviewers of the manuscript for their helpful suggestions and edits.

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