Who’s Your Mommy: Estimated Seed Dispersal Distance of Joshua trees Through Pedigree Reconstruction

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ABSTRACT

Joshua trees, *Yucca brevifolia* and *Yucca jaegeriana*, are keystone species of the Mojave desert. This region is especially impacted by climate change, and evidence suggests that the current range of *Y. brevifolia* and *Y. jaegeriana* has already been affected. One key element to modeling and understanding plant range and future survival is seed dispersal distance. Current research has determined average seed dispersal using radioactively marked seeds, but does not account for other factors which may impact seedling survival and thus true dispersal distance. In this study, microsatellite data were used with FRANz 1.2.3 to construct a wild pedigree. This pedigree was used to determine distance between parents and offspring of *Y. brevifolia* and *Y. jaegeriana* (n=716) in Tikaboo Valley, Nevada in order to estimate seed dispersal distance (SDD). SDD was found to be significantly greater than the distance seen in the literature to this point. Additionally, there is some evidence suggesting long distance dispersal events. As the Mojave desert is threatened by global warming and development of green energy, this data provides potential insight which further study might use to project migration patterns and survival of Joshua trees going forward.

INTRODUCTION

As the world continues to be impacted by climate change, deserts and semi-arid regions are especially impacted. In the Southwestern United States, projections have predicted an increase in average temperatures, severe heat waves, and lower levels of precipitation (IPCC 2022). As climate changes, the area plant species are able to inhabit shifts as well (Corlett and Wescott 2013). If unable to migrate at the necessary rate, these species are expected to go extinct (Corlett and Westcott 2013). Understanding seed dispersal of a species is therefore a key part in understanding the speed with which an organism may migrate (Thuiller et al 2007, Johnson et al 2019).

The Mojave Desert is an area of particular interest when considering the impacts of climate change. Deserts have been impacted more by climate change, becoming disproportionately drier and warmer (Zhou et al 2015, IPCC 2022). Projections expect these trends to continue, leading to a dryer and warmer Southwest, with the Mojave Desert expected to be one of the most severe cases of this in the United States (Dominguez et al 2010, Diffenbaugh et al 2008). Additionally, the Mojave desert is in the midst of a legal struggle between green energy development at the cost of habitat destruction (Smith 2023). Joshua trees (*Yucca brevifolia* and *Yucca jaegeriana*) are at the center of this turmoil, with efforts to grant protections as endangered species being contested by business groups (Sahagún 2020a, Sahagún 2020b, Sahagún 2022, Moore 2021, Smith 2023)

Joshua trees (*Yucca brevifolia*) are an iconic, keystone species of the Mojave Desert. Reductions in the range of *Y. brevifolia* have been attributed to climate change, with recent range records supporting these models (Cole et al 2011, Barrows and Murphy-Mariscal 2012). Other models predict expansion into new territory that will become viable as increases in CO_2 levels

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will increase freezing tolerance (Dole et al 2003). However, all of these models operate on assumptions of Joshua tree seed dispersal distance (SDD) which warrant further study. Previous research of Joshua trees suggests multiple species of rodents are responsible for dispersing seeds, with seeds an average SDD of 30 meters (Vander Wall et al 2006). This was accomplished through the use of radioactively marked seeds, and later scanning of nearby areas with geiger counters to find where individual seeds had been deposited (Vander Wall et al 2006). Further study found abiotic dispersal through wind unlikely and determined rodents cached seeds at a depth consistent with an experimentally determined optimal depth (Waitman et al 2012).

This existing research doesn't consider all of the factors which will impact the survivability of the seeds, and as such the true dispersal of *Y. brevifolia* may differ from current estimations. Vander Wall et al (2006) observed some events of secondary dispersal which they were unable to account for in their tracking analysis due to limitations with seed tracking methods. Additionally, tracking seed dispersal alone does not account for effective SDD of plants which germinated and survived (Gelmi-Candusso et al 2019). Genetic data can be used through parentage analysis to determine parent-offspring pairs (Harrison et al 2013). The use of microsatellites to construct these pairs has been found effective in primate-dispersed plant species compared to other methods of determining SDD, despite potential noise in the data due to paternal relationships caused by pollination rather than seed dispersal (Gelmi-Candusso et al 2019).

This study will use microsatellite data from Joshua trees in Tikaboo Valley to reconstruct a pedigree between sampled trees. This is a sympatric zone in which both *Y. jaegerina* and *Y. brevifolia* and their hybrids can be studied (Royer et al 2020, Smith et al 2021). From there, GPS coordinates of each sampled Joshua tree will be used to infer Joshua tree SDD.

METHODS

Existing coordinate and microsatellite data across 10 loci from 716 Joshua trees in Tikaboo Valley was provided by the Smith lab (Flatz et al 2011). A maximum likelihood pedigree was constructed in FRANz 1.2.3 (Almudevar 2003), and parental relationships with LOD scores greater than 3 were selected for analysis. Duplicate genotypes were removed from the dataset to minimize the presence of clones, and samples which caused FRANz runs to fail were removed, leaving 697 Joshua trees for analysis. Coordinate data was not factored into the pedigree construction, and all comparisons were made between individuals with at least 6 typed loci. Using R version 4.2.1 in RStudio 2022.07.1, distance was calculated and maps were generated using the R package geosphere (R Core Team 2022, RStudio Team 2020, Hijmans 2022, Kahle and Wickham 2013, Wickham et al 2019). These resulting SDD values were compared with those from the literature using a one-sample Wilcoxon signed rank test.

RESULTS

The maximum likelihood pedigree resulted in 83 parent-offspring relationships. Of these, 34 had LOD scores greater than 3. The mean distance of these was 520 ± 1797 m, with a median distance of 47.5 m. This group is significantly different from the 30.0 m mean reported in Vander Wall et al (2006); (one-sample Wilcoxon signed rank test $V=469$, $p < 0.05$).

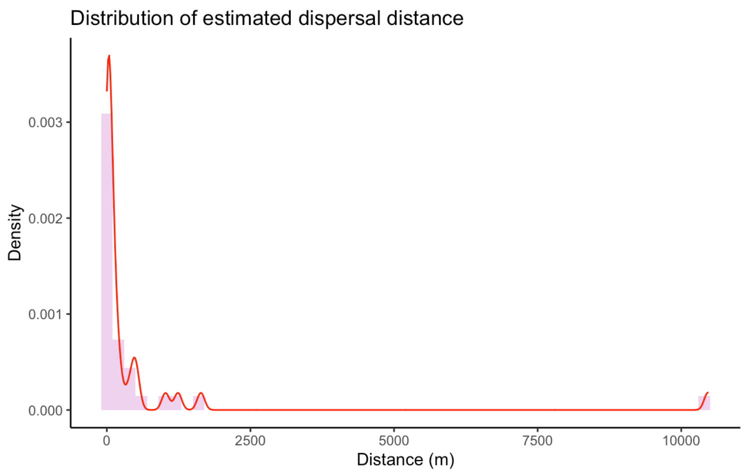

Figure 1. Distribution of distance between inferred parent-offspring pairs of *Y. brevifolia* (n = 34). The red line represents density distribution, and pink bars are a histogram with a bin width of 200 meters.

DISCUSSION

The inferred seed dispersal distance (mean = 520 ± 1797 m, median = 47.5m, Figure 1) is significantly larger than was seen in Vander Wall et al (2006). Vander Wall et al (2006) suggests that seeds may germinate in not just primary, but also secondary or tertiary caches, which would mean that true dispersal distance is greater than the 30 meter average distance that was determined using only the primary caches. The greater averages in our data may be partially caused by seed dispersal to secondary or tertiary caches, though it is difficult to speak to the extent by which this may increase the dispersal range, given practical difficulties in studying these secondary and tertiary caches (Vander Wall et al 2006). This greater seed dispersal distance would suggest greater capacity to migrate north to avoid climate change, though further study is needed to accurately project future range.

Additionally, there were multiple parent-offspring relationships which may be indicative of long distance dispersal (LDD) events, one of which was over 10 km in distance from each other (Figure 1). It is unclear if this data is a result of seed dispersal, pollination, or erroneous pedigree inferences.

Wild pedigrees constructed using genetic data can mismatch individuals with candidate parents, though they typically are more prone to miss relationships that are present in the data than infer a false relationship (Riester et al 2009, Pemberton 2008). Additionally, some of the error which has been observed in FRANz is a result of not knowing the direction of a paternal relationship (Riester et al 2009). This is less relevant in the context of determining SDD, as the direction of parental relationships does not affect the distance, though being more certain of this direction may prove useful in future study if attempting to observe directions of migration.

Given this data is from the nuclear genome, paternal and maternal parentage cannot be directly inferred in the absence of plastid data, though this has still been able to provide reliable estimates of SDD when compared to other methods in the past (Gelmi-Candusso et al 2019). Though the impact of pollinators on this data overall should be considered, pollination is not likely the cause of the long distance parentages that have been inferred. *Tegeticula yuccasella*, the yucca moth pollinator of *Yucca filamentosa*, have been found to transfer pollen in a range of 0 to 50 m, frequently depositing self-pollen (Marr et al 2000). However, Marr et al (2000) was conducted through analysis of transfer of paint between flowers that were being observed, and may not account for rare instances of long distance pollination.

If there are LDD events occurring in *Y. brevifolia*, further study will be needed to determine details of this mechanism of dispersal. Testing in wind tunnels has shown dispersal through wind to be highly unlikely, and consumption of Joshua tree fruits by birds has suggested seeds are left undisturbed (Waitman et al 2012, Lenz 2001). There are documented observations of native mule deer and other introduced animals such as horses, burros, and cattle eating Joshua tree fruits, but this is likely more common in *Y. jaegeriana*, as the height of *Y. brevifolia* has been suggested as an obstacle for these animals (Lenz 2001). Further research may make comparisons across *Y. brevifolia* and *Y. jaegeriana* through STRUCTURE with microsatellite data used in this study (Pritchard et al 2000, Falush et al 2003, Falush et al 2007, Hubisz et al 2009).

As Joshua trees continue to face pressures from climate change and land development, the speed at which they can migrate is essential for their survival outlook and projections of future range (Corlett and Wescott 2013). This study suggests the effective SDD of Joshua trees is greater than the SDD that was previously understood, and that there may be long distance dispersal events which warrant further research.

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