



Science Newsletter

A Recent Sighting of a Banded Gila Monster, (*Heloderma suspectum cinctum*) in Mojave National Preserve, California

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Several college and university field courses are taught in Mojave National Preserve every year, often through the Desert Studies Center, a field station of the California State University, or the University of California Sweeney Granite Mountains Desert Research Center. This report of a recent sighting of banded Gila monster demonstrates that field classes can contribute valuable information on rare species in addition to providing student education.

The Gila monster, *Heloderma suspectum cinctum*, has rarely been sighted in California. Only 26 reported records have occurred over the past 153 years (1). There have been 11 reports from what is now Mojave National Preserve, 10 were from the Providence Mountains and one was sighted at Piute Springs, 55 kilometers to the northeast. All new sightings are important because they add



Figure 1. Gila monster habitat with the Granite Mountains in the background. May 2009. Photo by the author.

to the evidence that viable populations of banded Gila monsters persist in the Mojave Desert of southeastern California.

On May 2, 2009 a Gila monster was sighted crossing a gravel road in the Providence Mountains of the Mojave National Preserve in eastern San Bernardino County, California (34.55353°N 115. 35160°W). The adult lizard, measuring approximately 420 mm total length was observed at 1615 h and the air temperature was 24°C. The elevation was 1077 m. The annual precipitation prior to the sighting date was below normal. Nearby at Mitchell Caverns the annual precipitation has averaged below normal by 27.5% over

the past three years (2). This is noteworthy because DeLisle (3) suggested that the numerous Gila monster sightings in 1982 were due to "some combination of climatic conditions favoring surface activity." The meteorological data from nearby Mid Hills, CA showed that the total precipitation in the year prior to this Gila monster sighting was 14.42 cm. The five-year average precipitation was 20.36 cm prior to the sighting (4). Therefore the precipitation season at nearby Mid Hills, CA leading up to the May 2009 Gila monster sighting was drier than the average by 29.2%. These data do not seem to support DeLisle's hypothesis.

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This Science Newsletter:

The Mojave Desert is internationally known as a place to conduct scientific research on desert ecosystems. In fact Mojave National Preserve was designated in part to "retain and enhance opportunities for scientific research in undisturbed ecosystems" as stated in the California Desert Protection Act of 1994. Significant research is conducted through the Sweeney Granite Mountains Desert Research Center, part of the University of California Natural Reserve System, and the Desert Studies Center, operated by the California Desert Studies Consortium of California State Universities. Both are located in the Preserve.

The purpose of this newsletter is threefold. First, we would like to highlight some of the research being done by university scientists in the Preserve and to distribute this information to park staff and management. Second, this periodical will allow us to inform the public and research community about science being done by Preserve staff or funded through the National Park Service. And most importantly, we would like to build collaboration between scientists and resource managers so that scientists are made aware of the needs of managers and top quality science is brought to bear on the problems facing resource managers.

This newsletter is published twice per year, in the spring and fall. Copies are available in print at our Kelso Depot Visitor Center, Barstow Headquarters, Desert Studies Center, Sweeney Granite Mountains Desert Research Center, and electronically as pdf documents on the web¹. Articles range from non-technical news stories to highly technical research reports. All material in this newsletter has been peer-reviewed by subject-matter experts.

Debra Hughson, Science Advisor

¹<http://www.nps.gov/moja/naturescience/sciencenews.htm>

The terrain where the Gila monster was sighted consisted of gully eroded granite with medium-sized stones, rough gravel and coarse sand. The vegetation in the area was Mojave Desert scrub dominated by desert senna (*Senna armata*), cheesebush (*Hymenoclea salsola*), Mojave yucca (*Yucca schidigera*) and creosote bush (*Larrea tridentata*). Figures 1 and 2 show the topography, vegetation and substrate of the site.

The specimen was observed and photographed for approximately 30 minutes by the author, two assistants and 18 students from Cuesta Community College. The lizard hissed softly, stood its ground and faced its observers for a few moments before crossing back across the gravel road. It crawled under a parked vehicle and over the rocky terrain for a short distance before heading into a leafless desert senna bush where it was easily viewed until the end of the observation period. The Gila monster's dorsal pattern (Figure 3) appeared to be consistent with the description of the banded Gila monster, *Heloderma suspectum cinctum* (5), the subspecies

expected to occur at this locality, even though recent research found no support for recognition of Gila monster subspecies (6). Lovich and Beaman (1) noted that most sightings of Gila monsters in California occur in April and May. At Mitchell Caverns State Recreation Area, also in the Providence Mountains, May and June may be prime months for surface activity.

Prior to this sighting the last captured and photographed record of a Gila monster from this general area was in 1968 (Table 1). Voucher specimens or photographs are important to preclude the possibility that the specimen was a captive release or repeat sighting. This most recent sighting provides further evidence that Gila monsters survive in the eastern Mojave Desert of California. Further monitoring is required to verify the viability of the population.

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Figure 2. Gila monster showing rocky terrain. May 2, 2009. Photo by Andrea Reddick.



Figure 3. The Gila monster sighted in the Providence Mountains, San Bernardino County, California, May 2, 2009. Los Angeles County Museum Photographic Catalog (LACMPC) #1461. Photo by R. David Bowlus.

Table 1. Gila monster records in the Providence Mountains. From Lovich and Beaman (1).

<u>Location</u>	<u>Year</u>	<u>Comments</u>
Vulcan mine road	April 1968	Captured, died in L.A. Zoo 1990
Near Vulcan mine	1968-1982?	9 specimens, no photos
Near Mitchell Caverns	?	Reported by rangers, no photos
Vulcan mine road	May 2009	Many observers and numerous photos

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Acknowledgements

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Coevolution of Joshua trees and their Pollinators: A Short Review

Christopher Irwin Smith¹

The Joshua tree is an endemic yucca characteristic of the Mojave Desert. In this article Chris Smith summarizes recent research on the coevolution of Joshua tree and its pollinating moths.

Understanding how macroevolutionary patterns that take shape over epochs are produced by microevolutionary processes occurring over generations is the principal challenge for modern evolutionary biology. One of the most noticeable macroevolutionary patterns is the diversity of life on earth, and in particular the relatively enormous diversity of some groups compared to the rest of the living world. Flowering plants and herbivorous insects, for example, outnumber nearly all other organisms, both in terms of their sheer biomass and in their species diversity. The beetles (the insect order Coleoptera), for example, account for nearly one quarter of all described species (1), and may include millions more undescribed species (2). (The geneticist J. B. S. Haldane is said to have remarked that the creator has, “An inordinate fondness for beetles” (3)). Similarly, insect-pollinated species account for 90% of all land plants (4), or approximately 20% of all species on Earth. Work my collaborators and I have completed over the last ten years has focused on the pollination biology of the Joshua tree (*Yucca brevifolia*) as a way to understand the factors that have produced the diversity of plants and insects.

A commonly proposed explanation for the startling diversity of plants and insects is that coevolution – reciprocal evolutionary change in two interacting groups of organisms – has generated this diversity (5). There are a number of lines of evidence that support this idea. At a

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macroevolutionary level, plants with specialized defenses against insect herbivores - such as sticky sap or toxic compounds - have significantly greater species diversity than their more weakly defended relatives (6), and insect lineages that feed on flowering plants (the most diverse of all land plant lineages) contain more species than their close relatives that feed on less speciose groups of plants (3). Similarly, groups of plants with specialized pollinators are more diverse than those that rely on generalist pollinators (7). So it seems that groups of plants and insects that interact with one another often contain a large number of species. Finally, many plant / insect interactions demonstrate phenotype matching—that is, features of the plant’s and insect’s anatomy that are correlated in shape or sizes—that is suggestive of reciprocal adaptation. For example, Darwin’s Orchid, *Angraecum sesquipedale*, has a nectar spur an astonishing thirty centimeters long, and is pollinated by a hawk moth, *Xanthopan morgani praedicta*, with a proboscis just long enough to reach the nectar at the bottom of the tube (8). Similarly, the seed-eating camellia weevil, *Curculio camelliae*, has a rostrum (i.e., a snout) that is just long enough to penetrate the pericarp (i.e., the fruit) and reach the seeds of its host plant, the Japanese camellia, *Camellia japonica*. In different populations of the camellia, variation in the thickness of the pericarp is correlated with differences in length of the weevil’s rostrum (9).

While these findings are suggestive of coevolution between plants and insects, and indicate some connection between ecological interactions and species diversity, they stop short of showing that reciprocal natural selection is actually responsible for the diversity of plants and insects. To make a truly convincing case

that coevolution has contributed to the diversification of these groups it would be necessary to show that the plants affect the fitness of the insect, that these same insects affect the fitness of the plant, and that together these have caused the formation of new species. Clearly, testing all three of these ideas is a tall order, and finding one system where it is feasible to address each of these questions remains a much sought-after goal for research in coevolution. My collaborators and I are hopeful that we may be getting closer to this goal with our studies of the Joshua tree.

Natural History and Biogeography of Joshua Trees – Joshua trees are one of the most unusual and striking plants that occur in the Mojave National Preserve; their spiny, twisted silhouette and creamy white, musky-scented flowers seem to inspire strong reactions in anyone that sees them. The nineteenth century American explorer John C Frémont, perhaps the first European to ever see a Joshua tree, described them as, “the most repulsive tree in the vegetable kingdom,” whereas legend holds that early Mormon settlers imagined the trees as the prophet Joshua, pointing the way to the promised land (10). The early twentieth century botanist Susan McKelvey wrote of the Joshua tree that, “One would not be surprised to see a huge prehistoric monster standing by and feeding upon the fruit.” McKelvey described the tree’s flowers as, “curious rather than beautiful in appearance” (10), but her predecessor, William Trelease, considered them to be “the most attractive of all the Yuccas.” Trelease did admit however that scent of the flowers was “so oppressive as to render the flowers intolerable in a room,” but added on a more positive note that “the usual designation of fetid is not strictly accurate” (11).

This distinctive appearance has made the Joshua tree the iconic plant of the Mojave Desert. The trees occur across the Mojave in middle elevations between ~850 and ~1950 meters. Death Valley, the Amargosa Desert, and various low-elevation inland basins therefore create a natural barrier that divides the Joshua tree's range roughly in half, and populations on either side of this barrier differ noticeably in their growth form and foliage (Figure 1). Trees growing in the western half of the range are typically taller, have longer leaves, and do not begin to branch until they have grown to at least a meter in height. In contrast, eastern trees are typically smaller overall, branch closer to the ground, and have much shorter leaves on average (12, 13). Historically, taxonomists have recognized two varieties of Joshua tree on the basis of these differences (*Y. brevifolia brevifolia* in the west, and *Y. b. jaegeriana* in the east (10, 11)), and recently some have advocated splitting *Y. brevifolia* into two species (14).

Perhaps the most interesting thing about Joshua trees, however, is their pollination biology. Like all yuccas, Joshua trees are pollinated exclusively by yucca moths – a group of drab grey moths in the family Prodoxidae. The moths in turn reproduce solely by laying their eggs in the developing flowers. The female yucca moth has a unique set of tentacle-like appendages that grow out of her external mouthparts, and that are not equivalent to structures in any other group of insects. The moths use these 'tentacles' to grasp tiny balls of pollen as they move between flowers on the yucca plant. When the moth reaches an unfertilized flower, she first positions herself on the pistil (the female part of the flower), and then cuts into the pistil with her ovipositor, a specialized, blade-like organ at the tip of her abdomen that delivers her eggs (Figure 2). The moth deposits several eggs directly onto the undeveloped ovules (the part of the flower that will eventually develop into seeds). After

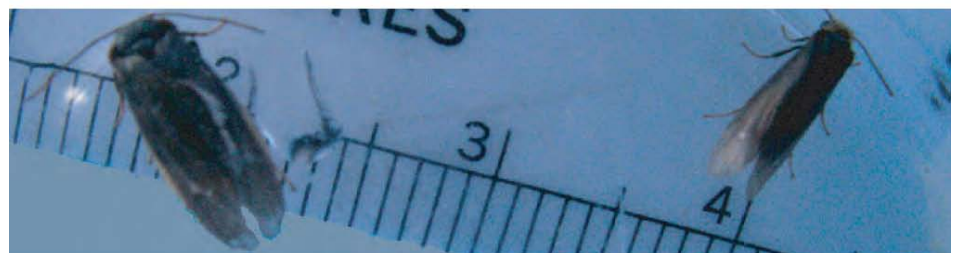
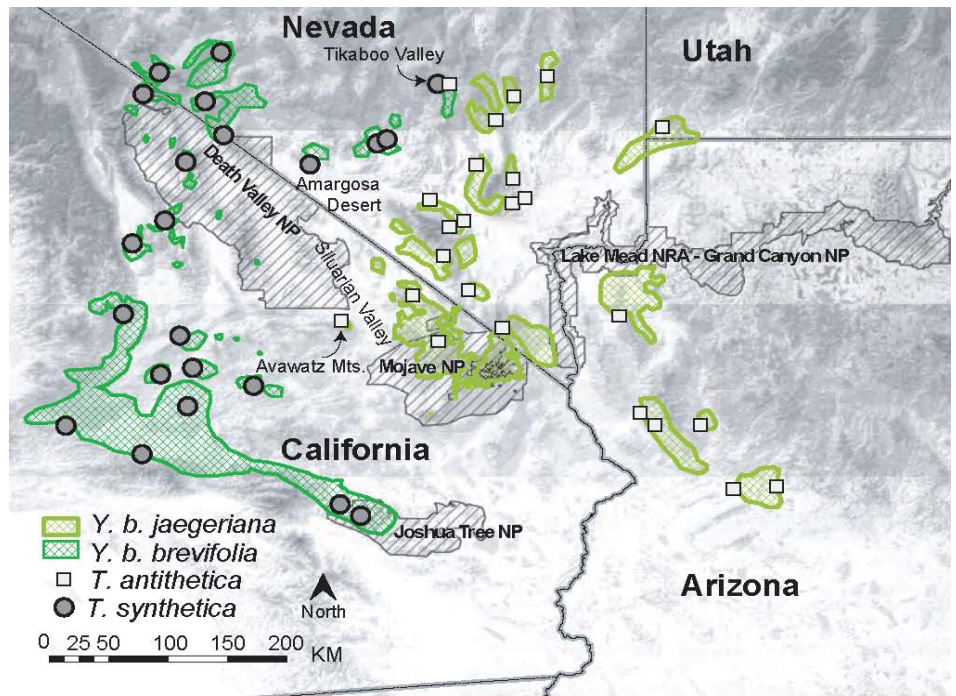


Figure 1. Distribution and morphology of Joshua trees (*Yucca brevifolia*) and their pollinators (*Tegeticula* spp). Top Panel: Range map of the Joshua tree. Dark green shows the range of the western variety (*Y. brevifolia brevifolia*), lighter green the range of the eastern variety (*Y. brevifolia jaegeriana*). Collection localities for the pollinating moths are shown as grey circles (*T. synthetica*) and white squares (*T. antithetica*). Location of particular populations and geographic features mentioned in the text are indicated. Center panel: The Joshua tree's pollinators, *T. synthetica* (left) and *T. antithetica* (right). Scale is in centimeters. Photo: J. B. Yoder. Bottom panel: The two Joshua tree varieties, *Y. b. brevifolia* (left) and *Y. b. jaegeriana* (right) growing side-by-side in Tikaboo Valley, NV. For consistency of presentation, the image is reversed from its original orientation. Photo: J. B. Yoder.

laying her eggs, in order to ensure that the ovules will develop into the mature seeds that her caterpillars will feed on, she climbs to the top of the pistil and pollinates the flower using her tentacles to spread pollen directly onto the stigma. Needless to say, this deliberate, purposeful pollination is a far-cry from the almost accidental nature by which honey bees pollinate flowers, so much so that Charles Darwin described the yucca-yucca moth interaction as, “The most remarkable fertilization system ever described” (15).

It was recently discovered that the Joshua tree is –in fact– pollinated by two different species of yucca moth, *Tegeticula synthetica*, and *T. antithetica* (16). These two species are genetically distinct (16-18), and differ in overall body size and the in length of the female moths’ ovipositors (16) (Figure 3). Intriguingly, the distribution of the two moth species also shows an east-west split, with Death Valley and the Amargosa Desert forming the primary dividing line (17) (Figure 1). Furthermore, the distribution of the two moth species matches exactly the distribution of the two tree varieties described by previous taxonomic studies (12, 17) (Figure 1).

Over the past seven years, my colleagues and I have visited every publicly accessible population of Joshua trees to collect moths and flowers and to make measurements of the trees. All populations of *Y. b. brevifolia* are pollinated by *T. synthetica*, and all populations of *Y. b. jaegeriana* are pollinated by *T. antithetica*. Our surveys of the moth and tree populations also revealed two exceptions to the general rule that Death Valley and the Amargosa Desert separate the two varieties. The two tree varieties come into contact north of the Amargosa Desert in Tikaboo Valley – an 80 km long basin between the Pahranaagat and Groom Mountains – and both moth species co-occur in a narrow contact zone within this valley. There is

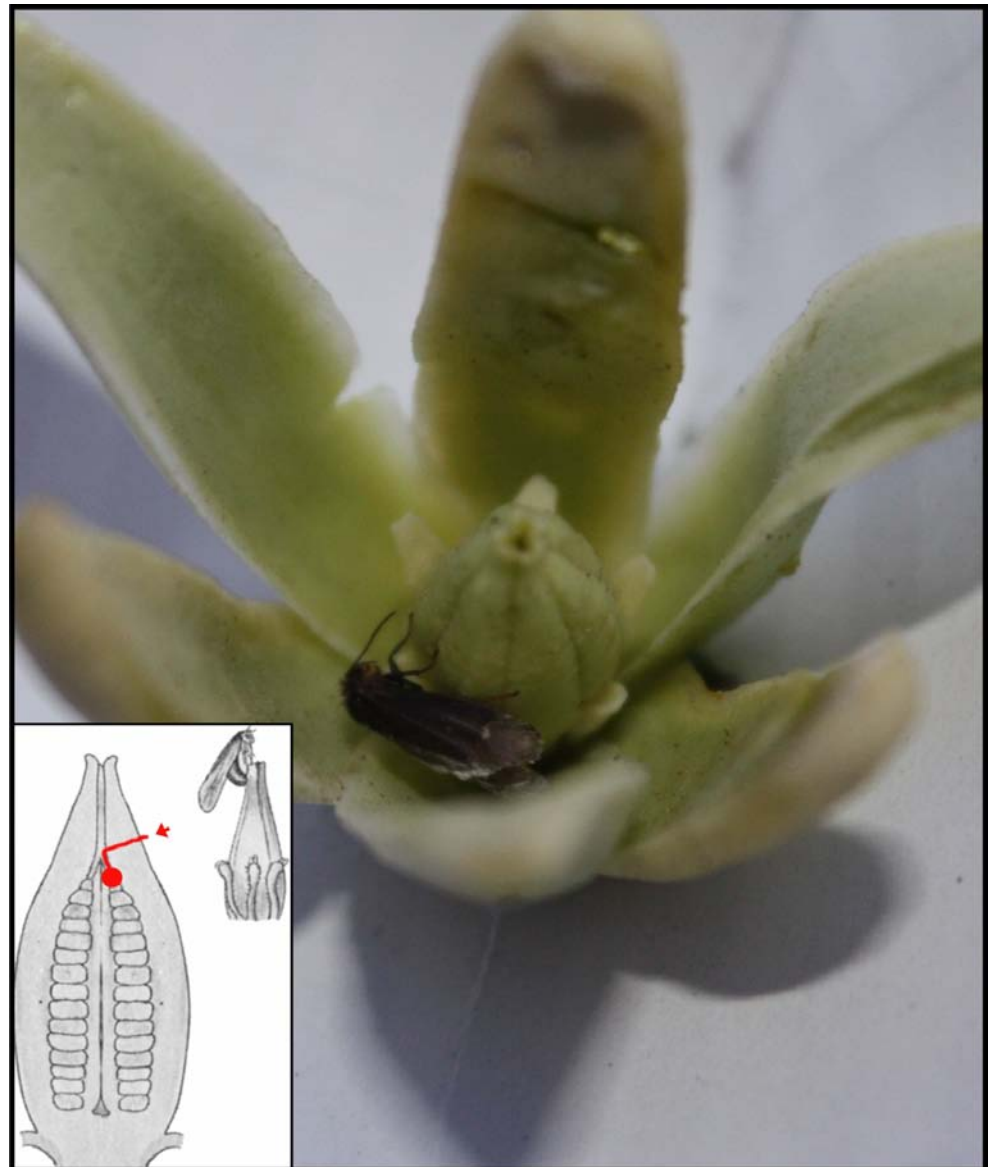


Figure 2. *T. antithetica* on a flower of *Y. b. jaegeriana*. (Photo: C. I. Smith). Inset: Schematic of oviposition behavior by yucca moths on *Y. brevifolia* (11). Moths perch with their forelegs on the stigma, and force the ovipositor through the styler wall, and down the styler canal. Cross section of the pistil shows the path of oviposition.

also a population of *Y. b. jaegeriana* and *T. antithetica* along the ridgeline of the Avawatz Mountains, just west of Silurian Valley at the southern end of Death Valley (Figure 1). This population probably was established by dispersal from the nearby Kingston Mountains.

Phenotype Matching and Coevolution Between Joshua Trees and their Pollinators – The intimacy of the relationship between Joshua trees and their pollinators would seem to offer an ideal opportunity for reciprocal evolutionary change. Since the moths

spend most of their time on the flowers of the Joshua tree, and considering how different the two tree varieties are in their overall growth form, it seems reasonable to wonder whether the trees might have different flowers as well. Work I completed with William Godsoe and Jeremy Yoder, two graduate students at the University of Idaho, suggests that, indeed, the flowers are quite different. In fact, statistically the two tree varieties differ much more in floral anatomy than in growth form (12). This difference is particularly noticeable in the pistils – the female part of the flower. Flowers of the

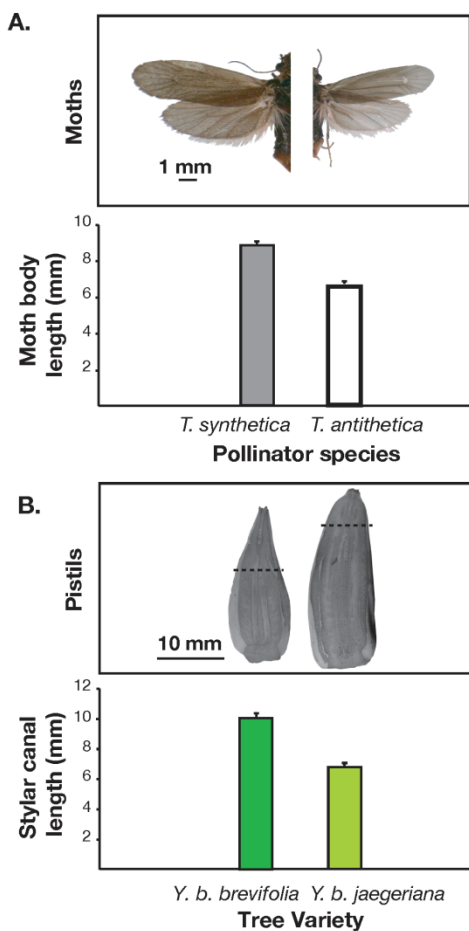


Figure 3. Phenotype matching in Joshua trees and their pollinators. A: Pinned and spread specimens of *T. synthetica* (left) and *T. antithetica* (right), and average body size in each species. **B:** Floral pistils from *Y. b. brevifolia* (left) and *Y. b. jaegeriana* (right), and average length of the stylar canal in each variety. Dotted lines on each pistil represent the lowest extent of the stylar canal. Error bars represent 95% confidence intervals; differences in stylar canal length and moth body size are statistically significant ($P < 0.001$). Figure modified from (12).

western variety, *Y. b. brevifolia*, have relatively slender pistils with a long narrow style, giving them a shape something like a wine bottle. On the other hand, the pistils of the eastern tree variety, *Y. b. jaegeriana*, are thicker, with a very short style, so that they look something like a milk bottle (Figure 3). Preliminary work also seems to indicate that the flowers of each variety also differ in their scent profiles, containing different mixtures of aromatic compounds that have been described as “mushroomy” and “like a fine blue cheese,” respectively (19). Whether or not these odors are

actually ‘fetid’ remains a matter of personal opinion.

Interestingly, the biggest difference of all between the two tree varieties turns out to be the length of the stylar canal, a hollow tube through which germinated pollen grains grow to reach the unfertilized egg (12). The eastern trees have a relatively short stylar canal, whereas that of the western trees is significantly longer. This tube is also the path through which the female yucca moth inserts her ovipositor (Figure 2) (11), and –amazingly– the length of the stylar canal in each tree variety matches exactly the body length of their respective pollinators (12) (Figure 3).

It is clearly tempting to conclude that the differences in the body size and ovipositor length of the two moth species must be adaptations to their respective host species. Perhaps a larger body and longer ovipositor helps *T. synthetica* reach the ovules of its long-styled host? The evidence for this is intriguing, but so far it is incomplete. In Tikaboo Valley, the one site where both tree types co-occur, the female moths of each species visit both tree types more or less indiscriminately (18). So, it is possible to track the success of female moths from both species when they visit trees of each variety. By collecting caterpillars from the fruit of each tree type, and then using DNA fingerprinting techniques to genotype them, we have been able to determine how often *T. synthetica* caterpillars emerge from *Y. b. jaegeriana* trees, how often *T. antithetica* caterpillars emerge from *Y. b. brevifolia* trees, and how many offspring each female moth produces from each flower. The results show that although both moths visit both tree types in the contact zone, *T. synthetica* never successfully produces offspring from flowers of its non native host, and that *T. antithetica* produces many fewer larvae when laying eggs on *Y. b. brevifolia* than on its native host (18) (Figure 4).

These results are compelling, but it is not clear that the lower success of each moth species when visiting a foreign host is due to mismatches between the moth’s ovipositor and the floral style. Differences between the two tree varieties other than the length of the styles –differences in plant secondary chemistry, for example– could also explain the fewer number of larvae produced when moths visit foreign hosts. This spring I will be setting up some additional experiments, and looking specifically at how variation in style length within tree varieties affects moth oviposition success.

Can coevolution cause the formation of new species?

Ultimately, if we want to understand whether coevolution between species is responsible for the diversity of plants and insects, we need to understand how it affects the rate at which new species are formed. On the one hand, considering that the behavior of the moths completely determines whether cross-pollination occurs, it seems to make sense that the

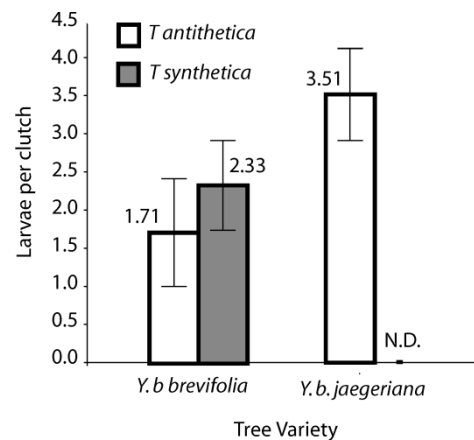


Figure 4. Average clutch sizes of female yucca moths ovipositing onto each variety of Joshua tree. Clutch size data are based on caterpillars reared from fruits collected in the Tikaboo Valley contact zone. Average clutch sizes were estimated using mitochondrial DNA sequences and microsatellite DNA to assign individual larvae to matriline and determine the number of offspring produced by each female on each fruit. Error bars represent 95% confidence intervals; *T. antithetica* females produce significantly fewer larvae on *Y. b. brevifolia* than on *Y. b. jaegeriana* ($p = 0.0014$). *T. synthetica* larvae were never reared from eastern trees. Figure modified from (18).

moths could cause reproductive isolation between yucca species. Indeed, the different rates at which the two moth species oviposit on the two tree types described above mirrors patterns of gene flow between the two tree varieties (18). On the other hand, understanding what caused the two tree types to become differentiated in the first place is not easy. Adaptation to different environments could also have caused the trees to develop different growth patterns and floral shapes, and simple geographic isolation is probably the most common means by which new species originate.

In the case of the Joshua tree, we can say that the climate that the two tree varieties experience are not meaningfully different (20). Similarly although populations of Joshua tree in the eastern and western Mojave have been geographically separated for several million years, the differences between the pollinators associated with these populations evolved much more recently (17). Having eliminated these two alternative hypotheses, coevolution remains a plausible explanation.

Understanding whether and how interactions between species may promote species diversity remains a central question for evolutionary biologists. Although our understanding of the interaction between Joshua trees and their pollinators is still incomplete, a pattern seems to be emerging that suggests reciprocal adaptation has played a direct role in promoting reproductive isolation. We may soon have a very clear idea of how this system has evolved, and the specific factors that have played the largest role in their evolutionary history.

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Demographic Studies of Joshua Trees in Mojave Desert National Parks: Demography With Emphasis on Germination and Recruitment

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A collaborative effort between the U.S. Geological Survey and the National Park Service is establishing long-term Joshua tree monitoring plots in the Mojave Desert. But where are the seedlings?

The study of population change with regard to reproduction, seed dispersal, and germination, establishment, growth, and survival/mortality is known as demography. Demographic studies provide managers with information to assess future trends on the density, distribution, health, and population changes of importance or value, including Joshua trees (*Yucca brevifolia*). Demographic research provides the potential to understand the combined impacts of climate change and land-use practices and determine if strategies for protecting important species are likely to succeed or fall short of management goals and will identify factors that have the potential to de-stabilize populations outside the realm of natural variation so that management strategies can be developed to circumvent challenges for key species, processes, and ecosystems. The National Park Service and US Geological Survey are collaborating to collect demographic information about the demographics of Joshua tree in the Mojave Desert.

Joshua trees are widespread across the Mojave Desert (1) and occur in five National Park Service administrative units (Figure 1,). As the tallest and most massive plant in the low- and mid-

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Mojave Desert National Parks Joshua Tree Study Areas

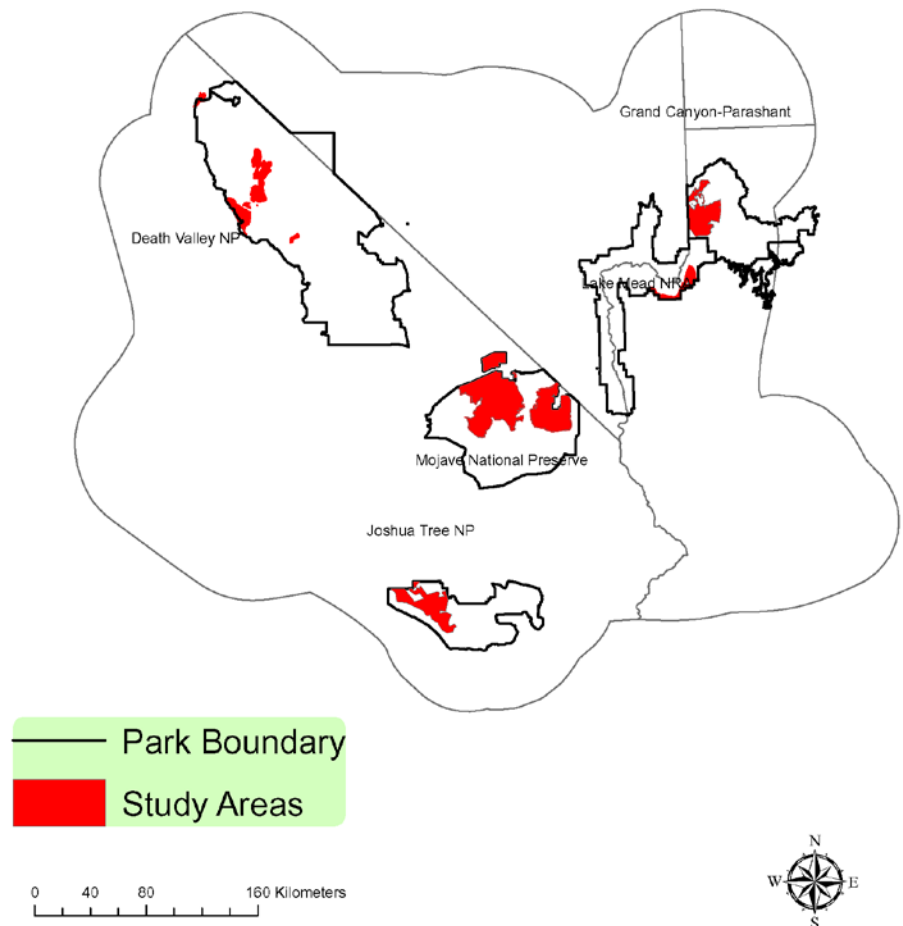


Figure 1. National Park units and the areas surveyed for Joshua trees within each park.

elevations of the Mojave Desert, the Joshua tree is a keystone species providing food, shelter and structure to wildlife. Recently the persistence and population status of Joshua trees has come into question primarily due to increased wildfires (2, 3) and concerns about how climate variation will affect Joshua trees (4, 5).

An example of how fire and climate variation have affected Joshua trees follows. In 1998 the Mojave Desert experienced a wet El Niño cycle that resulted in an abundance of the invasive annual grasses such as red brome (*Bromus madritensis*). In 1999 the 6,000 ha Juniper Fire Complex burned large expanses of Joshua Tree National Park and subsequent monitoring of Joshua

trees indicated that ~68% died of exposure to fires (3). Wildfire immediately reduced survivorship of all Joshua trees <1 m tall, and in the following years reduced the survival of reproducing adults (3). Other researchers have found similarly high mortality related to fires (2). Most Mojave Desert fires result from increased standing biomass of non-native annual plants (6). After the 1999 fire in Joshua Tree National Park a very dry La Niña event occurred in 2002 and resulted in another 9 % of Joshua trees dying from drought – even on unburned sites (3). Although mortality due to climate variability/change during the study was substantially lower than losses due to fire, extended drought can cause mortality of even the largest Joshua trees. Wildfire immediately reduced survivorship of all Joshua trees <1 m tall, and subsequently reduced the survival of reproducing adults (3). Drought exacerbated these losses with particularly large losses of the smaller size classes (3, 7).

The fires also remove cover of perennial plants over large burned expanses reducing the availability of cover for Joshua tree germination and establishment sites (8). Gross changes in vegetation cover may also affect the distribution of rodent species (9) that can be important to Joshua tree seed dispersal (10-12). If climate shifts toward hotter and drier conditions in this region, then it seems likely that mortality will be accentuated, which would cause significant concern for the persistence of Joshua tree populations.

All of the observations described above led resource managers and researchers to consider the capacity for Joshua tree populations to sustain such losses over the long term. In 2007 the National Park Service and USGS initiated a research project designed to establish permanent demographic study plots for Joshua trees on National Park Service lands across the Mojave Desert; identify and quantify seed dispersal mechanisms; and to

conduct experiments on germination and establishment under natural conditions. Here, we provide preliminary information about this ongoing project. Information regarding Joshua tree seed dispersal is available in a recently completed thesis (12) and will not be reported here.

Study Area – Joshua tree populations were surveyed in five National Park Service administrative units within the Mojave Desert Inventory and Monitoring Network (MOJN), including Joshua Tree National Park (JOTR), Death Valley National Park (DEVA), Mojave National Preserve (MOJA), Lake Mead National Recreation Area (LAME), and Grand Canyon / Parashant National Monument (PARA) (Figure 1). In DEVA, Joshua trees are widely dispersed in several small and isolated stands in the remote northeastern parts of the park: Lee Flat, Hidden Valley, White Top Mountain and the Cottonwood Mountains, and Cowhorn Valley near Loretta Mine Road. JOTR has large relatively well-connected stands north of the Little San Bernardino Mountains, west of the Hexie Mountains and south of Queen Mountain. LAME Joshua trees are located near Mead View on Grapevine Mesa and along the southern border of the park north of Golden Rule Peak. In MOJA, the population is split by the Mid Hills and New York Mountains with one group in the Lanfair Valley and the other surrounding Cima Dome and Ivanpah Mountains and in the Ivanpah and Shadow Valleys. Finally, PARA has a single widely dispersed stand west of the Grand Wash Cliffs and southeast of the Virgin Mountains in the Pakoon Basin. We used a sixth study area on BLM administered lands near Searchlight, Nevada, within the current range of the Joshua tree for manipulative experiments on seed dispersal, germination, and establishment.

Demographic Study Plots – Demographic plots were established in 2007 when field crews verified the distribution of Joshua

trees within the five parks. Fifty random plots were established within the range of Joshua trees in each park except in LAME, where 20 plots were used because of its more restricted distribution of the species. Each plot had at least one Joshua tree and when randomly selected sites were found to be without Joshua trees they were abandoned – without trees to measure the plots would not contribute to the study. Each 0.25 ha plot (50 m x 50 m) was searched entirely for Joshua trees of all sizes by two people walking in opposite directions and searching under every shrub and bunchgrass, especially searching for small plants. Initial demographic and growth measurements included height, greatest width and perpendicular width, stem diameter, presence of cloning, flowering state and history, number of leaf rosettes (i.e., terminal branch buds), and associated shrubs and grasses species for Joshua trees less than one meter tall (for cover site analysis). Individual Joshua trees were mapped on each plot.

From 2007 to the present, 3385 Joshua trees were measured within the five parks. JOTR has the highest density of plants per plot, and LAME has the lowest (Table 1). Figure 2 represents a histogram of all the Joshua trees that were measured across five parks. Each bar in the graph represents the number of trees found in each height class. This composite graph of Joshua trees representing all the parks is fundamentally similar to the relative size distribution of other long-lived plants, such as the Giant Sequoia tree (13), where there are large numbers of plants in the smallest size classes, moderate numbers of middle-sized plants, followed by greatly reduced numbers of the largest and oldest plants. Fluctuations in the abundance of long-lived plants in the smallest size classes are to be expected, but the pattern and timing of the variation can provide insights into factors that affect future stands of such plants. The

difference in the smallest size classes of Joshua trees are interesting because it may provide a glimpse of how Joshua trees respond to environmental variation in the much harsher Mojave Desert conditions. Such differences in the size distributions of Joshua trees are even more pronounced when the data are singled out for each park, and this is the focus of ongoing analyses.

Focal Trees on Demographic Plots – We randomly selected six focal plots from among the demographic plots at each park to revisit once per year and measure overall height, growth of branches, the addition of new leaves, evidence of flowering/fruitletting, and number of branch terminations. Within each of these focal plots, one tree was randomly selected within each of six height classifications <1 m, >1 to 2 m, >2 to 3 m, >3 to 4 m, and ≥4 m tall. When trees of all size classes were not available within a focal plot, we expanded the search to include the nearest tree of required size and collected a GPS datum on the location of those trees. All these trees were measured once; we have only partially re-measured the focal plots of Joshua trees. We plan to visit these focal trees annually during the late-reproductive season (May – June) to measure the previous year's growth.

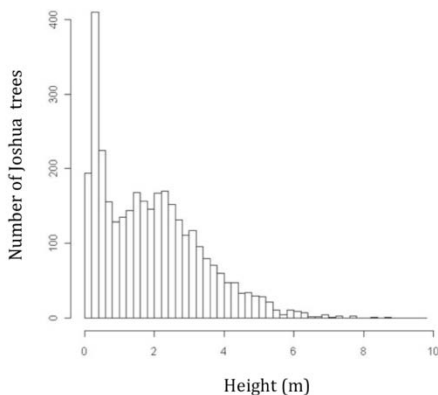


Figure 2. Histogram of Joshua tree size classes in 20 cm increments. Data represent plots located in all of 5 National Park study units combined.

Table 1. Percent vegetation cover in unburned and burned habitats by height class

Park Unit	Number of Plots (N)	Mean Density of Joshua Trees/0.25 ha	Range
All	221	NA	1-85
DEVA	50	15.5 (14.2)	1-85
JOTR	50	23.8 (18.9)	1-28
LAME	20	7.7 (4.9)	2-21
MOJA	50	20.9 (16.0)	1-63
PARA	50	9.3 (7.1)	1-32

Demographic measurements of these trees in relation to climate conditions and other environmental data can shed light on the reproductive health of the meta-populations and help identify areas to focus future research and (or) intensive management. Although results of our analysis of growth rates are incomplete, our initial observations noted a higher incidence of leaf-rosette division in the absence of flowering than we expected (i.e., when the flower buds die the branch typically sprouts laterally to create a 'fork' for continued growth). The work on focal trees has reinforced our observation that the germination and establishment are very rare in most locations within MOJN.

Germination and Establishment of Joshua Trees – Joshua trees do not flower or produce seed regularly, and upon flowering they depend on the yucca moth for pollination (14). Instead, Joshua trees produce flowers and seed infrequently and this pattern, known as masting, is an adaptation to avoid seed predators (15). Masting only creates fresh seed available for germination every few years, and the longevity of viable seed in the soil seed bank is unknown. Even though we reported what appears to be a robust sample of Joshua trees in the smallest size classes (Figure 2), we never saw a seedling Joshua tree (5 or fewer leaves, but still in the smallest size class – Figure 3) in 3 years of sampling in parks. We hypothesize that 1) we missed the timing of seedlings because we were between masting events, 2) environmental conditions (precipitation and temperature) were not conducive to producing seedlings during our study, 3) they died before detection, or 4) seed predation overwhelmed

opportunities for germination.

To test these hypotheses, we began planting Joshua tree seeds experimentally beginning in August 2007. We planted and followed the fates of 5760 seeds to understand seedling germination and survival. Exclosures were placed in pairs with one in the open and the other under the canopy of a creosote bush. Exclosures were 0.5 m x 0.5 m and approximately 0.1 m tall providing ample room to grow for several years. From December 2008 to the present, seedling height and health status have been measured monthly and cages have been checked for new germination, growth, and survival of the seedlings.

Laboratory observations indicate that the seeds we used had greater than 90% germinability at the time of planting. Of the 5760 seeds planted in 2007, 130 (2.3%) germinated and 22 (16.9%) of the germinants survived to two years of age. This experiment indicates that although potential germinability was quite high, actual germination of plants, even though they were protected from vertebrate predators, can be quite low. No doubt this is dependent on soil moisture, temperature and also seed predation from invertebrates is likely. We have more recently planted additional cohorts of seeds to fill in data gaps on the germination and establishment success of Joshua trees in a variety of conditions.

Considerations – This research project has begun to provide information required to understand the life history of the Joshua tree throughout a large portion of its range. Like other long-lived

desert organisms, the earliest stages of life history cycles can elude biologists (e.g., desert tortoise, (16)). We predicted that a thorough survey aimed at finding the smallest size-classes of Joshua trees with an increased sample size could be more successful than previous attempts where long-term data were collected on smaller cohorts of Joshua trees (e.g., 17, 18). However locating Joshua tree seedlings in situ has continued to elude us, except during controlled experiments where seeds were sown and tracked. We believe this indicates that recruitment has been quite rare for several years in most of the Mojave Desert. However, the establishment of these permanently marked plots will provide opportunities to capture recruitment should it occur in the future.

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