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Sweeney Granite Mountains Desert Research Center
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Science Newsletter

Prehistoric human settlement and lithic technology around Soda Lake

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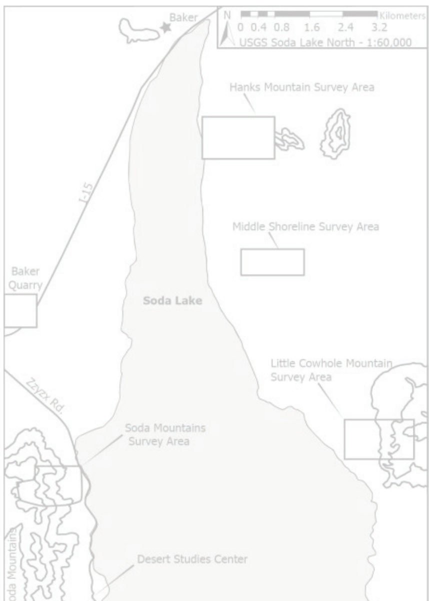

Figure 1. Map of Soda Lake that includes the five survey areas and other key features.

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Figure 2. East facing overview of the Soda Mountains survey area, with Zzyzx Road and Soda Lake in the background.

Long before the Mojave National Preserve became "the Preserve," archaeologists investigated the shorelines of its now dry playa lakes to find long lost remnants of past human activities. This work began in earnest during the 1930s, with archaeologists such as Elizabeth Campbell (*1, 2*) and Malcolm Rogers (*3*) finding terminal Pleistocene-early Holocene (TP-EH; ~13,800-9000 cal B.P.) age artifacts left by Native Americans along the ancient shorelines of today's Soda Lake. When Soda Lake filled to capacity and its borders breached by water, the overflow flowed northward into Silver Lake creating pluvial Lake Mojave (originally spelled Lake Mohave). Lake Mojave was some 300 km^2 at its late Pleistocene maximum (~21,900-19,750 cal B.P.), but with early Holocene warming and drying between 10,500 and 9600 cal B.P. Soda Lake's borders were no longer breached and Soda and Silver Lake became separate playa lakes (*4*). Humans were attracted to the shorelines of Lake Mojave, and later the shorelines of Soda and Silver Lake, because of the potable water, animals and edible plants (many associated with now dried up marshes), and sources of fine-grained volcanic (FGV) stone to make tools. Results of the ongoing archaeological research described here portray how TP-EH foragers organized their lithic (stone) technology and settlement strategies around Soda Lake.

The California State University, Fullerton (CSUF) Mojave Desert Archaeology Project (MDAP) began in 2009. Each summer since, Dr. Knell has led crews of student volunteers on systematic pedestrian (walking) surveys to identify, document, and record archaeological sites and analyze the stone artifacts at those sites. Five areas have been surveyed thus far (Figure 1). Only the Soda Mountains and Little Cowhole Mountain survey area data are completely analyzed and the results published; results from the other survey areas, and more recent research around Silver Lake, are forthcoming. What follows is a summary of Knell's current

Mountain), and even more recently surveyed areas around Silver Lake. Expanding the survey sample to include Soda and Silver Lake will facilitate broad understanding of TP-EH technological organization and settlement around all of Lake Mojave. Beyond survey work, other ongoing studies seek to: *1)* increase the sample of XRF-sourced lithic materials to better document mobility and land use strategies; and *2)* improve understanding of Lake Mojave's paleoenvironmental history through collaborative research with Dr. Matthew Kirby (CSUF Department of Geological Sciences). These and other planned studies hopefully will provide significant clues regarding past human lifeways around Lake Mojave, and develop context to more fully integrate Lake Mojave into regional discussions of TP-EH lifeways in the Mojave Desert and Great Basin.

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What can *Chorizanthe rigida* propagule morphology tell us about rainfall variability and geomorphology in desert ecosystems?

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Serotinous plants retain seeds and can delay seed dispersal for several months or even years (*1*). Desert serotinous species have different dispersal syndromes and many have seed release mechanisms triggered by rainfall. For instance, some plants, like *Oenothera deltoides,* that grows on sand dunes or *Eremothera boothii* that grows in sand washes, form lignified structures with capsules that release seeds in response to rainfall. Another interesting seed retention syndrome is that of the desert spineflower *Chorizanthe rigida*, a short desert annual whose lignified seed-retaining structures remain in the field for several years before releasing propagules with rainfall (Figure 1). *Chorizanthe rigida* is common in desert pavements and is distributed across the North American desert region (*2, 3, 4*). The objective of this article is to explore the ecological and evolutionary significance of seed retention in desert serotinous species with specific focus on

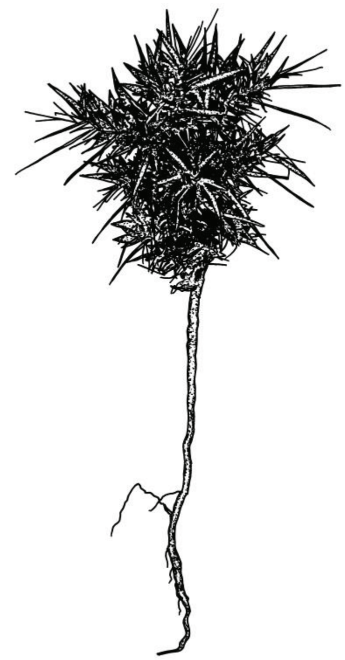

Figure 1. *Chorizanthe rigida* from the Mojave Desert.

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C. rigida. Deserts are characterized by low and unpredictable rainfall (*5, 6*). However, desert rainfall is not completely random; desert regions have different seasonal precipitation patterns. In North America, the Mojave Desert has mostly winter precipitation while the Sonoran Desert has a bi-seasonal rainfall distribution pattern with both winter and summer rainfall (*7*). The interaction of rainfall and temperature imposes important challenges to plants: summer rainfall occurs in the hot season of the year when evaporation rates are very high while, in contrast, low temperatures during the long cool season result in low evaporation rates, allowing moisture to last longer in the soil. Moreover, the interaction between rainfall and temperature with the different soil and ground surface desert features results in soil moisture pulses of varying duration and infiltration depth (8).

Desert annuals spend most of their life as seeds (*i.e.* from a year to even several years), germinating and growing when moisture is available (*9*). These ephemeral plants display different strategies that allow them to cope with varying degrees of environmental variability and unpredictability (*10, 11*). For instance, long days and rising temperatures indicate the beginning of the summer, and even if there is available water, winter annuals will not germinate until days shorten and temperatures drop, signaling the beginning of the cool season (*12*). Furthermore, not all of the seeds of an individual's cohort will germinate at the same time, a strategy that allows them to spread the risk of germination between years as a "bet-hedging" strategy (*10, 11, 13*). It has been suggested that delaying seed dispersal and timing of seed release allows desert annuals to cope with environmental variability as well (*1, 2*). In our research, we addressed two questions related to seed retention in the rigid spineflower: How does *C. rigida* avoid releasing seeds in response to a summer rain, a false cue that would prove fatal for seedlings? Does delayed seed dispersal allow *C. rigida* to cope with a highly unpredictable desert environment?

Figure 2. *Chorizanthe rigida* grows in the spring time (top) and its lignified skeletons remain in the field for several years retaining seeds and releasing them to rainfall (bottom).

Chorizanthe rigida (rigid spineflower, Polygonaceae) is a winter desert annual germinating during the cool season and setting seed at the end of the spring (Figure 2). Its tiny flowers produce an achene that matures inside an involucre composed of three spiny bracts. The propagules of *C. rigida* are formed by the involucre containing the achene (Figure 3). The seed germinates inside the involucre and seedlings emerge in the winter season (*3, 4*). These plants become lignified at the end of its life cycle with the erect, short (2-10 cm), and spiny skeleton remaining in the field for several years (Figure 2). *C. rigida* is distributed from Baja California's Central Desert (lat. 29°N) to the Great Basin in Nevada (lat. 40°N) and is common in the Mojave and Sonoran deserts (Figure 4). Because of its broad distribution range, *C. rigida* experiences both different seasonal and within-season rainfall patterns that vary in their predictability, an ideal system to study the adaptations of serotinous species to different levels of environmental variability and unpredictability.

Chorizanthe rigida has an interesting dispersal mechanism: the involucres are attached to the plant by a pedicel that when wet, softens, allowing raindrops to detach them. The remaining attached involucres are retained when both their pedicels and the plant dry again after the rainfall event occurs. Since the base of the pedicel controls detachment of the involucre, we measured both the involucre base area and the force needed to cause detachment to investigate if *C. rigida* could prevent releasing propagules to a false summer rain cue. We sampled *C. rigida* populations occurring at sites that had either mostly winter rainfall or a bi-seasonal rainfall regime. We found that propagules of plants from sites with both summer and winter rainfall had involucre bases double the size of those from strict winter rain deserts. We also found that bases with a larger area required more force to detach than those of smaller involucres. Our results show that different biomechanical ecotypes have evolved as a response to different seasonal rainfall patterns allowing *C. rigida* to avoid dispersing seeds to a false summer rainfall cue (*14*).

Rainfall in deserts is erratic; a germination-causing rain may or may not be followed by subsequent rainfall events (*6*). To cope with unpredictability, many desert annuals have evolved bet-hedging strategies such as soil seed banking (*10, 13*). A less explored bet-hedging trait is seed size. In a randomly varying environment, plants should produce a variable cohort of seed sizes, with many small seeds that have high survival probabilities in a favorable season and some large seeds that have higher survival probabilities in an unfavorable year that would allow them to achieve long–term persistence (14). Given that *C. rigida* retains its entire seed cohort in its tissues, it is an excellent system to investigate bet-hedging theory predictions regarding within-individual seed size variation. We collected plants from sites varying in winter rainfall unpredictability and performed morphometric measurements on the propagules. Our results showed that there is higher seed size

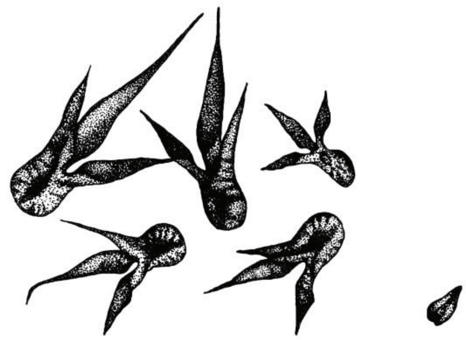

Figure 3. *Chorizanthe rigida* propagules formed by the involucres (left) containing an achene (right).

variation in *C. rigida* individuals from sites with more unpredictable rainfall. By producing many small seeds and some larger seeds *C. rigida* may display a bet-hedging strategy as seeds of different size have different probabilities of surviving and getting established (Figure 3).

Desert pavement surfaces are covered with packed rocks of different sizes depending on their age and parent material. Soils underlying desert pavements are very fine and have relatively high salt content because they have low water infiltration (*16*). Desert pavements are surrounded by shrub mounds that have contrasting hydrological and micro-topographical conditions. Shrub-mounds have sandy soils with good water infiltration and higher nutrient availability from litter decomposition (*17*). Many desert annuals prosper under nurse shrubs that provide shade and higher nutrient and moisture

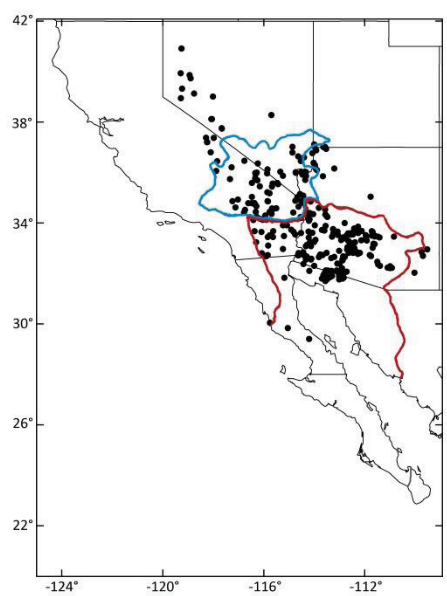

Figure 4. *Chorizanthe rigida* is distributed from the Mojave (blue) to the Sonoran (red) deserts.

Figure 5. *Chorizanthe rigida* on the desert pavements at the end of the growing season at the Clark Mountains Wilderness Area in the Mojave Desert National Preserve.

availability (*18, 19*). In contrast to the predictions of the nurse plant model, the rigid spineflower is associated with the apparently harsh environment of desert pavements. We characterized the micro-topographical surface and soil conditions of desert pavements and shrub mounds in order to analyze the microhabitat distribution of *C. rigida*. We found that *C. rigida* was distributed in the rough edges of desert pavements or in desert pavements formed by large rocks (Figure 5). In contrast to nurse-shrub associated desert annuals whose seeds get dispersed by wind or animals into the shrub mounds at the end of the growing season, *C. rigida* retains its seeds and synchronizes seed releases with winter rainfall. By doing this, the propagules of *C. rigida* are dispersed by runoff to desert pavement surfaces, germinating immediately after rains at a time when there is available moisture in the soil. Timing seed release lets *C. rigida* establish in desert pavements which provide stable conditions necessary for long-term persistence of the dead seed-retaining skeletons until the next rain event occurs (*20*).

Despite the extreme variability and unpredictability of desert ecosystems, seed retention and timing of seed release to seasonal rain cues allows *C. rigida* to thrive during brief windows of opportunity. Seed size variation in individual plants may allow *C. rigida* to cope with desert rainfall unpredictabitility, and to persist through harsh years.

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The natural history and behavior of the sand wasp *Steniolia nigripes* (Hymenoptera: Crabronidae)

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Sand wasps (Crabronidae: Bembicinae) demonstrate an array of interesting behavioral and morphological traits (*1, 2, 3*), but many of the approximately 1,700 species have not been investigated in depth. I studied a population of *Steniolia nigripes* located at the Granite Mountains in the Mojave Desert, California, from 2008 to 2013. I present information on the distribution and habitat of these wasps, as well as seasonal patterns in population size and location. I also discuss the response of *Steniolia nigripes* to environmental variation. In addition, I describe the behavior of wasps of both sexes, including foraging, prey selection, aggression, and space use. This paper represents the first truly comprehensive description of *S. nigripes* natural history and behavior.

Solitary wasps have long been of special interest to behavioral biologists, including the foundational ethologist Niko Tinbergen. Many solitary wasps are large, brightly colored, and fascinating to observe. Although they do not cooperate in nest-building as social species do, solitary wasps often aggregate in large numbers. These features have attracted naturalists to the study of solitary wasps for well over a century (*4, 5*).The sand wasps (Crabronidae: Bembicinae) are an appealing group of wasps with great variation in their behavior and extensive species diversity (*6*). Indeed, the Bembicinae are the second largest subfamily of the sphecid wasps, containing over 80 genera and more than 1,700 species (*4, 5*). This diversity of species and the corresponding diversity of behavior present in the Bembicinae

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