



Science Newsletter

Prehistoric human settlement and lithic technology around Soda Lake

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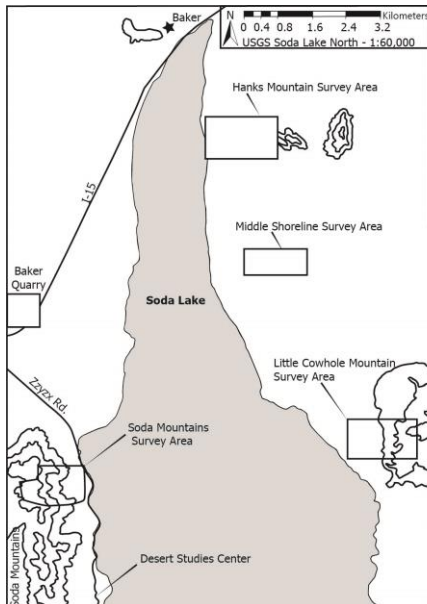


Figure 1. Map of Soda Lake that includes the five survey areas and other key features.

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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 km² 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

publications (5, 6) on the settlement and lithic technological strategies TP-EH foragers used in the Soda Mountains and Little Cowhole Mountain survey areas.

The Soda Mountains (~1000 m above sea level [asl]) enclose Soda Lake on the west (Figure 1), and has major outcrops of highly knappable black and green FGV stone (felsite) from exposed areas of the Soda Mountain formation (7, 8). Joesink-Mandeville et al. (9) previously surveyed a large area of the Soda Mountains (including the present study area) and discovered numerous felsite quarries and lithic workshops. Later, Semenza (10) excavated and analyzed a prominent felsite quarry (CA-SBR-5193) in the current study area. The MDAP survey updates the 30-year old record of sites discovered by Joesink-Mandeville et al. and provides new insights about the quarry and workshop activities at these sites. These insights come from 14 surface sites (excluding quarry SBR-5193) in the 0.83 km² survey area (Figures 1 & 2), and include: lithic scatters; bedrock quarries with tabular (blocky) seams, veins, and flake scars; and angular boulders with flake removals at the foot of slopes (Figure 3).

The Soda Mountains sites were assessed to establish which, if any, date to the TP-EH. Because the sites lacked temporally diagnostic artifacts, geologically dated alluvial fans along the eastern flank of the Soda Mountains (11) provided a rough dating method. Once the fan surfaces formed they were exposed to the present, implying that artifacts on each fan surface unit accumulated any time after the initial date of its formation and the present. The dated fan surfaces thus provide a means to obtain *terminus post quem* (limit after which) dates for the surface artifact scatters.

The alluvial fan in the Soda Mountains study area is the Johnny Fan, which has four fan surface age groups (11) and three archaeological sites (CA-SBR-16014, -15, and -16) (6). SBR-16014 has 95 chipped stone artifacts on a fan surface exposed since the Late Pleistocene (likely after 13,125 cal B.P. to present), and SBR-16015 has 10 chipped stone artifacts on a fan exposed since the Early Holocene (after 10,525 cal B.P. to present). SBR-16016 has more than 5,000



Figure 3. Close-up of a bedrock quarry with tabular (blocky) seams and scars from flake removals.

chipped stone artifacts in 44 spatially proximate lithic scatters or loci (each with 10 or more artifacts). Though these loci are on alluvial fan surfaces that formed at different times, 77.3% of the analyzed artifacts are on the Late Pleistocene to present fan surface. Knell et al. (6) concluded that most sites/loci and artifacts on the Johnny Fan were discarded before 5,000 cal B.P. based on: 1) the higher than expected percentage of sites/loci on the Late Pleistocene fan surface, 2) the region wide preference among TP-EH foragers to use FGV stones for bifaces, and 3) the significantly higher proportion of large, early stage felsite bifaces and large flake blanks on the Late Pleistocene fan surface. The 11 sites off of the Johnny Fan are undateable though, anecdotally, were likely created before 5,000 cal B.P.

The pre-5,000 cal B.P. date implies that the Soda Mountains were used most heavily from the terminal Pleistocene to Middle Holocene. The early part of this time frame corresponds to when TP-EH peoples made stemmed projectile points (broadly called Great Basin Stemmed [GBS] projectile points) like the Silver Lake and Lake Mojave styles, which are common to the Mojave Desert. The later part of this time frame corresponds to the indented or bifurcated Pinto point type, which was made from the Early to Middle Holocene (~10,200-7500 cal B.P.).

To assess how TP-EH foragers organized lithic technology without adding artifacts to the existing collections, Knell (5) developed a field protocol that allows for the relatively quick recordation of key chipped stone artifact attributes that simultaneously has enough analytical vigor to infer important aspects of the lithic technology. In this method four main variables are recorded for each artifact: 1) lithic raw material type (FGV, CCS [cryptocrystalline silicate; chalcedony, chert, and jasper], obsidian), 2) artifact type or technological type (e.g., biface thinning flake, core reduction flake, retouched flake, unused biface), 3) presence/absence of dorsal cortex (outer rind of stone), and 4) weight (recorded in grams using a portable scale) to estimate artifact size. Each core (nucleus from which flakes and flake blanks were struck) and tool was described in detail. Of an estimated (conservatively) 20,000 lithic artifacts in the Soda Mountains study area, 2,073 from the 14 sites were analyzed in the field.

The vast majority (90.2%) of analyzed chipped stone artifacts are debitage (byproducts of tool manufacture), with cores and tools (8.2% and 1.5%, respectively) in low proportion. Virtually all were made from directly procured Soda Mountain formation felsite obtained from exposed outcrops and boulders (Figure 3). The three non-felsite artifacts (two CCS, one FGV) are from unknown

sources. The 32 tools include bifaces (worked on two faces) and unifaces (one face worked). Twenty-three bifaces are percussion flaked and ovate, with expanding margins (Figure 4C) or converging edges that formed a point (Figure 4D). These bifaces are large in size (average 180.1 gm) and frequently have exterior cortex. Most (95%) broke during early stage manufacture as knappers created a sinuous bifacial edge (Stage 2) or began the thinning procedures (Stage 3). These and other factors indicate the 23 bifaces are unused, early stage manufacture rejects. Another early stage (Stage 2) biface was used as a tool. The 8 unifacial tools—3 utilized flakes, 2 end scrapers, 2 retouched flakes, and a multipurpose tool—presumably were used for cutting and scraping activities.

The 170 cores were sources for removing large flakes (i.e., flake blanks) to make various bifacial and unifacial tools. Most (86.5%) are multidirectional cores, which have flake removals from multiple platforms and directions (Figure 5). Biface cores were the second most common (8.2%) type, and have flake detachment scars reflecting intent to create flake blanks rather than thin bifacial cutting tools. A small number of flake cores (large flakes with intentional flake removals from both sides) and unidirectional cores (blade-like flake removals from a single platform) also were identified. Most cores retained exterior cortex and were large (average 420.3 gm).

Among the 1,871 analyzed debitage specimens are 471 flakes diagnostic of biface manufacture or core reduction to create flake blanks. The 44 specimens diagnostic of biface manufacture include flakes to thin the biface, and alternate flakes to create a sinuous bifacial edge from flat/tabular stones like Soda Mountains felsite (Figure 3). The 427 core rejuvenation and percussion core reduction flakes are, respectively, byproducts of maintaining the face of the core and establishing trajectories for removing flake blanks. As a group, these flakes are large. Overall, the debitage are byproducts of early stage manufacture, blank production, and/or testing raw material quality.

To summarize, the Soda Mountains survey area has 14 felsite quarry and workshop sites where knappers during the TP-EH and Early-to-Middle

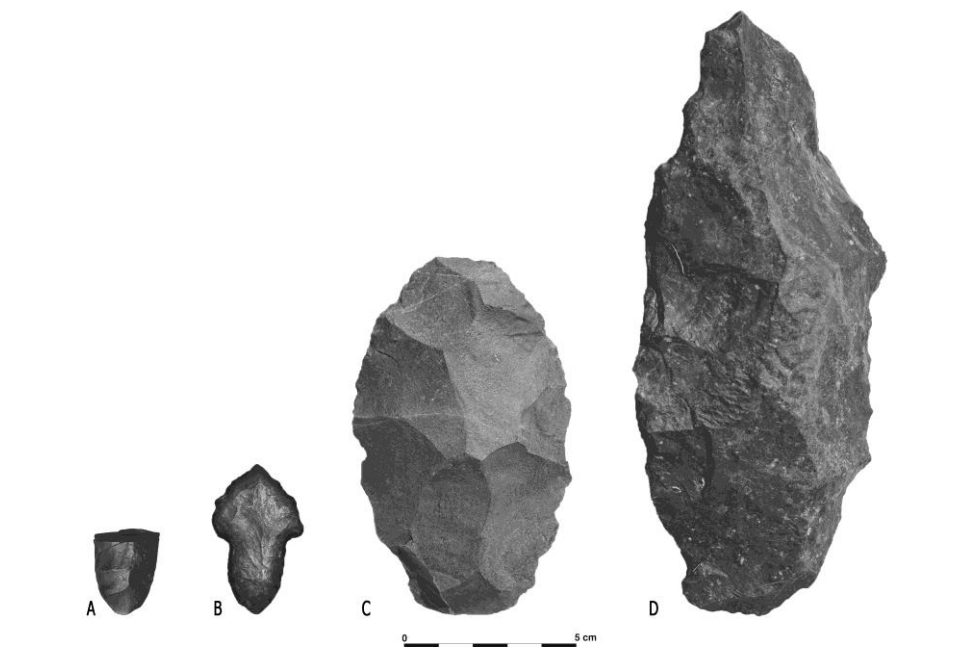


Figure 4. Selected bifacial implements: (A) Lake Mojave projectile point base, Little Cowhole Mountain survey area; (B) Lake Mojave projectile point, Little Cowhole Mountain survey area; (C) early stage unfinished biface, Soda Mountains survey area; (D) biface core, Soda Mountains survey area. Used with permission from Knell et al. 2014: Figure 3.



Figure 5. Close-up of a massive Soda Mountain formation felsite core and large flake that refits.

Holocene produced large, early-to-middle stage bifaces and large flake blanks from big bifacial, multidirectional and unidirectional cores. Many bifaces broke or were rejected during early stage production, with many others roughed-out and transported for reduction and use elsewhere. The lack of finished biface tools suggests the

unfinished bifaces were not intended for use at the quarry/workshop, but transported elsewhere for modification into projectile points and thinned biface tools. The paucity of unifacial flake tools suggests that activities requiring tools likely were incidental to the primary biface/flake blank production strategy.

Little Cowhole Mountain is a low elevation (500 m asl), isolated mountain on the east shoreline of Soda Lake. The 1.29 km² survey area extended from the TP-EH shorelines at the 285.5 and 287 m contour intervals (4) into the western edge of Little Cowhole Mountain (Figures 1 & 6). The area above the 287 m contour was devoid of artifacts; below this, survey revealed approximately 4,000 chipped stone artifacts arrayed in three spatially separated, northwest-southeast trending bands (areas of concentrated artifacts). The artifact bands directly correspond to ancient shorelines (6). The highest elevation and oldest band—the A-band—is located at or slightly above the 287 m contour or A-shoreline. Just below the A-shoreline/A-band is the B-band, with the C-band associated with the B-shoreline or 285.5 m contour interval. Multiple lines of evidence (dated shorelines, temporally diagnostic artifacts, technological strategies, and degree of patina/weathering) indicate that the bands are time transgressive, with the A-band artifacts discarded earlier than the C-band artifacts and the B-band temporally between these (6). TP-EH foragers thus gradually shifted their areas of habitation to lower elevation contours as Lake Mojave drained through time.

During the survey 1,060 of the roughly 4,000 lithic artifacts were analyzed using the same methods as in the Soda Mountains. The Little Cowhole chipped stone is mostly debitage (94.8%); tools (4.4%) and cores (0.8%) are less common. CCS (58.1%) and FGV (40.0%) are the most common lithic materials, with trace amounts of obsidian (1.6%) and 'other' materials (quartz and quartzite; .3%).

Where the lithic materials came from is unknown in most cases, though several FGV and obsidian specimens were identified to source area using energy dispersive x-ray fluorescence (XRF). This technique matches the composition of key elements from known lithic sources to archaeological specimens. A preliminary XRF study indicates that two artifacts are from sources nonlocal (more than a 40 km radius) to Lake Mojave: a biface tool of Goldstone Variety 1 dacite procured from Ft. Irwin (70-80 km northwest of Lake Mojave), and a nondiagnostic concave-base projectile point fragment of Shoshone Mountain obsidian (140 km north of



Figure 6. Pin flagged artifacts along the A-shoreline/A-band, with part of Little Cowhole Mountain in the background.

Lake Mojave in western Nevada). The other 16 obsidian artifacts also are nonlocal since the nearest obsidian source is more than 40 km from Lake Mojave. Among the locally procured lithic materials are 25 Baker Quarry rhyolite specimens (Figure 1) and 358 green and black felsite artifacts (presumably) from the Soda Mountain formation. Some of the black Soda Mountains felsite may actually be nonlocal Goldstone dacite. The Little Cowhole lithic assemblage thus includes artifacts from local and non-local sources.

The 47 tools include 17 bifaces and 30 unifacial flake tools. Among the bifaces are eight projectile points, five unfinished bifaces, one tool fragment, and edge segments from three bifaces. Three projectile points are TP-EH age GBS specimens: a Lake Mojave point base (Figure 4A), a complete Lake Mojave point (Figure 4B), and the tip of an indeterminate GBS point. The other projectile point fragments are not temporally diagnostic. The unfinished bifaces are all made from FGV and discarded during manufacture Stages 2 (initial edging), 3 (primary thinning), and 4 (secondary thinning). Most of the unifacial tools are scrapers, retouched flakes and utilized flakes, with a few single spur graters and multipurpose tools. The majority of flake tools are made of CCS. The projectile points presumably were hunting weaponry (also possibly for cutting), and

the bifacial and unifacial tools likely for cutting and scraping tasks.

The 1,005 debitage specimens include flakes diagnostic of biface production and/or resharpening/repair, and reducing cores to make flake blanks. The 261 biface thinning, biface shaping (pressure flakes) and alternate flakes account for 89.4% of the technologically diagnostic artifacts, signifying that biface manufacture and resharpening/repair were integral to the technological strategy. The high proportion of CCS pressure flakes suggests that many late manufacture stage CCS bifacial implements were finished, resharpened, and/or repaired in the study area. The four small obsidian biface thinning flakes indicate that TP-EH foragers finished or resharpened/repared completed obsidian bifacial implements along the shoreline.

Four multidirectional cores (flake removals from multiple platforms and directions) and four unidirectional cores (blade-like flakes removed in a single direction) were identified, along with 31 flakes from reducing cores and rejuvenating their faces. Flake blank production was thus part of the technological strategy.

To summarize, the Little Cowhole shoreline functioned as an occasionally reoccupied

habitation zone by TP-EH foragers, who gradually shifted their settlements to lower elevations as Lake Mojave dried over time. These foragers transported and discarded artifacts acquired from sources local (Soda Mountain formation felsite and Baker Quarry rhyolite) and nonlocal (dacite and obsidian from the north) to Lake Mojave. While camped along the shorelines, TP-EH foragers produced and maintained/repared later stage CCS bifaces and projectile points, created and used CCS unifacial flake tools, as well as produced middle-to-late stage FGV bifaces and some FGV flake tools. Many cutting, scraping, and incising tools were discarded, along with some of the hunting weaponry.

To understand the range of TP-EH lithic technological organization strategies around Soda Lake, patterns of lithic raw material procurement, tool production, tool use, and discard are compared between the survey areas. Because site function influences lithic technological strategies, emphasis is placed on establishing that the Soda Mountains study area was part of a larger quarry/workshop complex and the Little Cowhole shoreline a habitation zone.

The modes of procuring lithic material differ between the study areas. Knappers directly quarried black and green felsite from exposed outcrops in the Soda Mountains, the byproducts of which were found at 14 quarry and workshop sites. The Little Cowhole survey area has lithic materials from local (Baker Quarry rhyolite, Soda Mountains felsite) and nonlocal (Goldstone dacite, Shoshone Mountain obsidian) sources, as is expected where foragers repeatedly camped or coalesced after forays around and away from Lake Mojave.

The XRF-sourced artifacts provide tentative clues regarding the mobility strategies TP-EH foragers made before arriving at Lake Mojave. Both the Goldstone dacite and Shoshone Mountain obsidian indicate a general southward pattern of movement to Lake Mojave. Unpublished XRF data from the Campbell's Lake Mojave collections corroborate this pattern.

The production and modification of bifaces was

central to the technological strategy in each survey area. However, differences in scale are apparent, with abundant early stage production debris in the Soda Mountains and late stage production and finishing debris in the Little Cowhole area. The Soda Mountains biface thinning flakes are significantly larger than those in the Little Cowhole area, suggesting that large flakes were removed from large bifaces.

Correspondingly, most all of the Soda Mountains bifaces are early stage manufacture rejects as knappers sought to initially shape (Stage 2) and thin (Stage 3) the bifaces. By contrast, the Little Cowhole bifaces were finished implements like broken projectile points (which were not present in the Soda Mountains), or unfinished bifaces that were discarded during primary and secondary thinning procedures (Stages 3 and 4, respectively) and reflect the middle-to-late stages of manufacture. Thus, the main difference is the Soda Mountains has considerably more early stage bifaces and production debris than the Little Cowhole area. This implies that the Soda Mountains was a quarry/workshop area, and the many finished tools and late stage bifaces along the Little Cowhole shorelines remnants of campsites.

Differences are also apparent in the emphasis on producing flake blanks (flakes that can be modified into bifacial or unifacial tools), with the Soda Mountains having considerably more and larger flake blanks than the Little Cowhole area. The Soda Mountains has 21 times more cores and significantly larger cores and core reduction flakes than the Little Cowhole area. The Soda Mountains lack of finished tools and low frequency of biface thinning flakes suggests that knappers usually transported unmodified or minimally modified flake blanks to other locations for manufacture into bifacial or unifacial tools.

The survey areas differ in the types of tools and activities requiring tools. The Soda Mountains has comparatively few finished tools, but considerable tool production debris in the form of large flakes, unfinished bifaces, and cores—a pattern expected if biface and flake blank production were primary activities, and activities requiring tools were ancillary to the production focus. The Little Cowhole area has few cores and unfinished bifaces, but many finished flake tools

and projectile points as is anticipated at habitation areas. While camped along the Little Cowhole shorelines, TP-EH foragers undertook many scraping (the thick scrapers and retouched flakes with steep edge angles) and cutting (the utilized flakes and retouched flakes with acute edge angles) activities, and discarded or replaced portions of the hunting weaponry.

This research summarized and compared the lithic technological and settlement patterns TP-EH foragers employed at two areas around Soda Lake. Foragers in the Soda Mountains directly quarried felsite to create large bifaces and flake blanks, leaving behind many thousands, perhaps even millions, of felsite artifacts at numerous quarries and workshops in this mountain range. Survey and analysis of more than 2,000 lithic artifacts in the Johnny Fan area of the Soda Mountains indicate that knappers tested the quality of stones and reduced bulk weight by removing unwanted cortex, and produced large flake blanks and early stage bifaces for transport and completion outside the study area. Where knappers brought these products remains uncertain, though some were discarded on the east shoreline of Lake Mojave (e.g., Little Cowhole Mountain survey area) with others possibly transported northwest to Ft. Irwin (5). Conversely, TP-EH foragers in the Little Cowhole area camped along the ancient shorelines of Lake Mojave and gradually shifted their encampments to lower shorelines as Lake Mojave receded. Here these foragers discarded tools made from local and nonlocal stones, produced and maintained late stage bifacial tools, and used bifacial and unifacial tools for cutting and scraping activities. From these encampments foragers likely undertook short distance forays to nearby mountains and piedmonts to hunt terrestrial animals (e.g., rabbits, bighorn sheep), and procured floral and faunal resources from marshes that once likely dotted Lake Mojave's shoreline.

The Soda Mountains and Little Cowhole comparison is but one facet of an ongoing, long-term project to better understand human lifeways around Lake Mojave. The MDAP has surveyed and analyzed lithic artifacts from other areas with shorelines around Soda Lake (Hanks Mountain and an area between Hanks and Little Cowhole

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

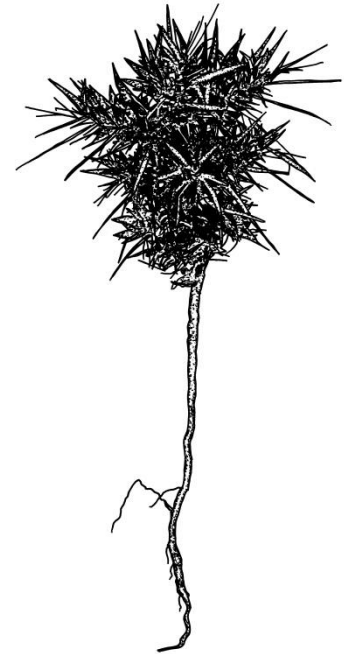


Figure 1. *Chorizanthe rigida* from the Mojave Desert.

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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?

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



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).

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 involucre is attached to the plant by a pedicel that when wet, softens, allowing raindrops to detach them. The remaining attached involucre is 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 involucre. 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

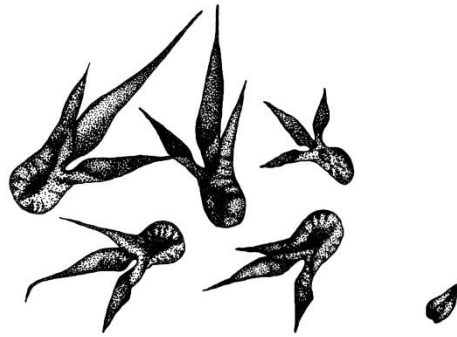


Figure 3. *Chorizanthe rigida* propagules formed by the involucre (left) containing an achene (right).

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

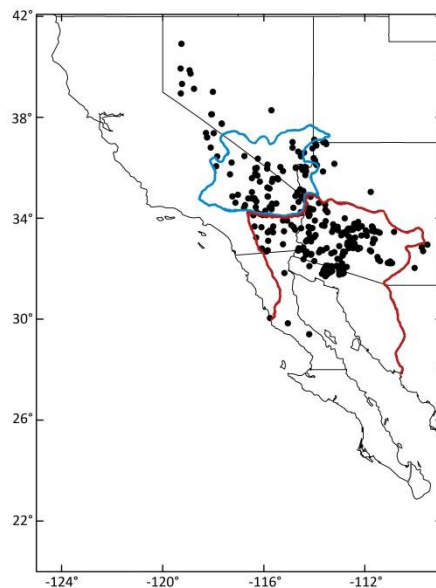


Figure 4. *Chorizanthe rigida* is distributed from the Mojave (blue) to the Sonoran (red) deserts.



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 unpredictability, 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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offer unique opportunities for comparative study.

Sand wasp females dig nests in the ground, both in isolation and in subsocial aggregations. In many species, males gather near females in mass swarms termed “sun dances”(7). Males often form highly mobile, aggressive groups (3, 8), and competition among males can sometimes be dangerous to females in these aggregations (2, 8). In most bembicine species, females are larger (by up to 2.5 times) than males (3, 4), but there are a few exceptions in which sexual size dimorphism is either absent or reversed (3). *Steniolia nigripes* is one of the very few species of sand wasps with fully reversed sexual size dimorphism, such that males are substantially larger than females (3, 8). This species occurs in the Eastern Mojave Desert in California, as well as the Owens Valley and the Sonoran Desert zones of Southern California (9). Despite its unique patterns of size dimorphism, *S. nigripes* has been studied very little and is almost nonexistent in the scientific literature. Here, I describe my general findings and observations about an eastern Mojave Desert population in order to expand our understanding of sand wasp natural history. Investigating unusual species such as *S. nigripes* provides context for future studies, and an important contrast for comparative research.

I examined the sand wasp *Steniolia nigripes* at the Granite Mountains Desert Research Center (GMDRC) from 2008 to 2013. The GMDRC is a University of California reserve located within Mojave National Preserve, 128 km east of Barstow, CA. The Granite Mountains range from 1,128 – 2,071 m above sea level and include a variety of habitats characteristic of the Sonoran, Great Basin, and Mojave Desert ecosystems. The average precipitation is only 23 cm per year, with high interannual variability. The slopes of the Granite Mountains consist primarily of fractured granitic boulders, which produce a highly complex habitat structure. Compared to the surrounding areas, this type of rock retains more snowmelt and rain runoff (12). Due to their unique transitional location, wide elevation range, and precipitation retention, the Granite Mountains are impressively diverse in both flora and fauna (12). *Steniolia nigripes* was found primarily on the southeastern side of the Granite Mountains,

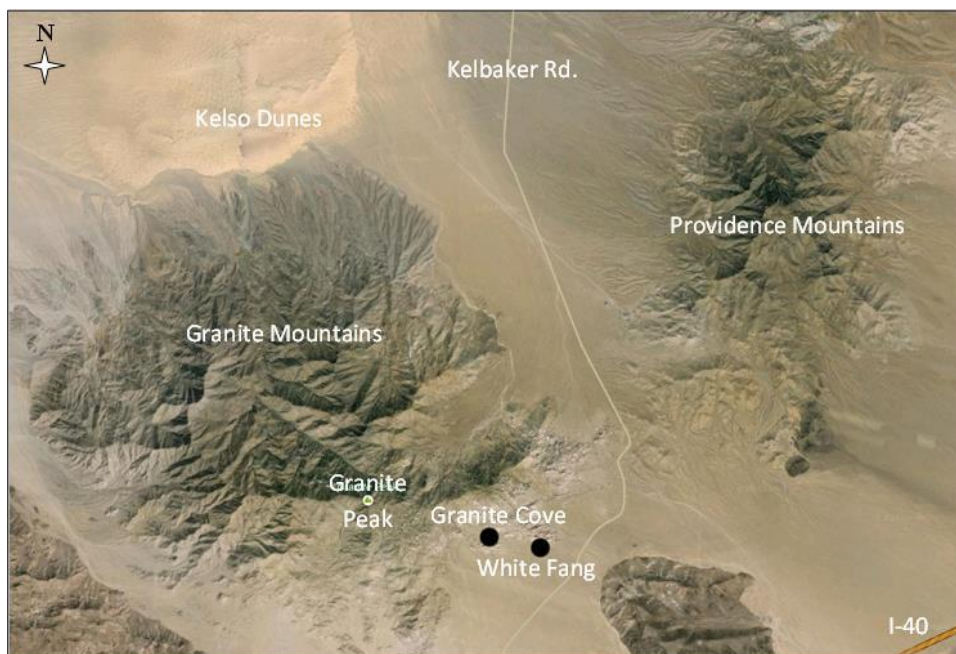


Figure 1. Map of the Granite Mountains and surrounding areas. Black dots represent the major locations of *S. nigripes*. Image © Google 2014.

where average annual precipitation is estimated to be 2-4 cm greater than in other parts of the range. In 2008-2010 I extensively surveyed the Granite Mountains and other nearby ranges in order to determine the distribution of *S. nigripes*. The population at the Granite Mountains appeared to be quite isolated, as I did not find *S. nigripes* more than approximately 5 km from the GMDRC. I searched in possible habitat within 25 km of the Granite Mountains, including the Providence Mountains and the Kelso Dunes, as well as on other aspects of the Granites. *Steniolia nigripes* was not detected in these surrounding regions, although they do live near multiple springs within the Granite Mountains. The vast majority of the population was located in the areas of Granite Cove and nearby White Fang (Figure 1), both of which contain several large washes fed by Cove Spring. Smaller numbers of wasps were found along Kelbaker Road within 2 km of the GMDRC entrance. I located *S. nigripes* mainly in washes and near roads, where more water is available and plants flower more often. Although many species of sand wasps form large, easily found aggregations, *S. nigripes* was most readily found in the field by observing flowering plants. *Steniolia nigripes* visited a number of plant species for nectar feeding and hunting, and was abundant enough in washes to be present on most flowering plants. The only widespread wash plant that was not used by *S.*

nigripes is creosote bush (*Larrea tridentata*); other characteristic wash plants, such as catclaw acacia (*Acacia greggii*) and sandpaper plant (*Petalonyx thurberi*), were frequented. There was no apparent explanation for why *S. nigripes* avoids creosote bush. Wasps were most commonly seen flying or foraging in washes, often following boundaries such as wash banks or a road edge. They also used mixed creosote shrub and woody succulent habitat near washes for foraging and nesting. Nesting seemed to occur mainly on wash banks, but I rarely found nest holes despite extensive searching. It thus seems likely that nest holes were closed when the wasp was away.

In 2009 only, I found another subpopulation of wasps along the trail leading up from Granite Cove to Granite Peak, where the trail intersected with a shady part of the spring bed containing standing water. This area was highly populated by many different species of insects, since water is a scarce resource. *Steniolia nigripes* females were clearly hunting insects that had come to collect water. Males flew over the water in groups of 3-5, chasing each other and females, but I was unable to discern any territoriality (i.e., behaviors that males used to aggressively exclude others from specific locations). Due to the difficult terrain, it was not obvious where the wasps were feeding and nesting, but I found no evidence that

wasps individually marked in this location mixed with those at lower elevations. Interestingly, the wasps at the spring were significantly larger than those in Granite Cove and White Fang (Table 1, Figure 2). In particular, females at higher elevations closer to the spring were approximately 30% larger than females in low washes. Furthermore, females at the spring chased larger potential prey items (such as robber flies, Asilidae) than those in other locations. Thus, it is possible that large size in this population may be an adaptation to the size of available prey items, although this was not directly tested. In 2010, *S. nigripes* was not present at the spring, though another sand wasp species (likely *Stictiella* sp.) occupied the same area. This second species did not emerge every year in the Granite Mountains, and I did not observe them in 2008 or 2009. From 2011 to 2013, the area did not have any standing water, perhaps explaining why no wasps were present. The possible relationship between *S. nigripes* body size and proximity to water sources in wet years requires further investigation, since it may have important consequences for male and female behavioral tactics.

Steniolia nigripes appeared to be a bivoltine species in the Granite Mountains, with two non-overlapping reproductive periods every year. There were two peaks in *S. nigripes* populations per year, the first occurring in June and the second in September, following the monsoonal rains which make up a substantial proportion of yearly precipitation. Based on tracking of marked individuals, individual wasps lived for up to 2-3 weeks. The two population peaks represented separate generations. In the spring of 2013, I observed a strongly female-biased sex ratio in the population, perhaps as a result of extreme drought conditions – female wasps are smaller than males, and thus require less food during development. Without very many males present, female wasps may have been forced to create sons rather than daughters, if they could not acquire sperm with which to fertilize their eggs. In the fall of 2013, the population was strongly male-biased, suggesting that these individuals were the offspring produced by the many unmated females in the spring. These males were also slightly smaller than males of previous years (11), further implying an effect of resource

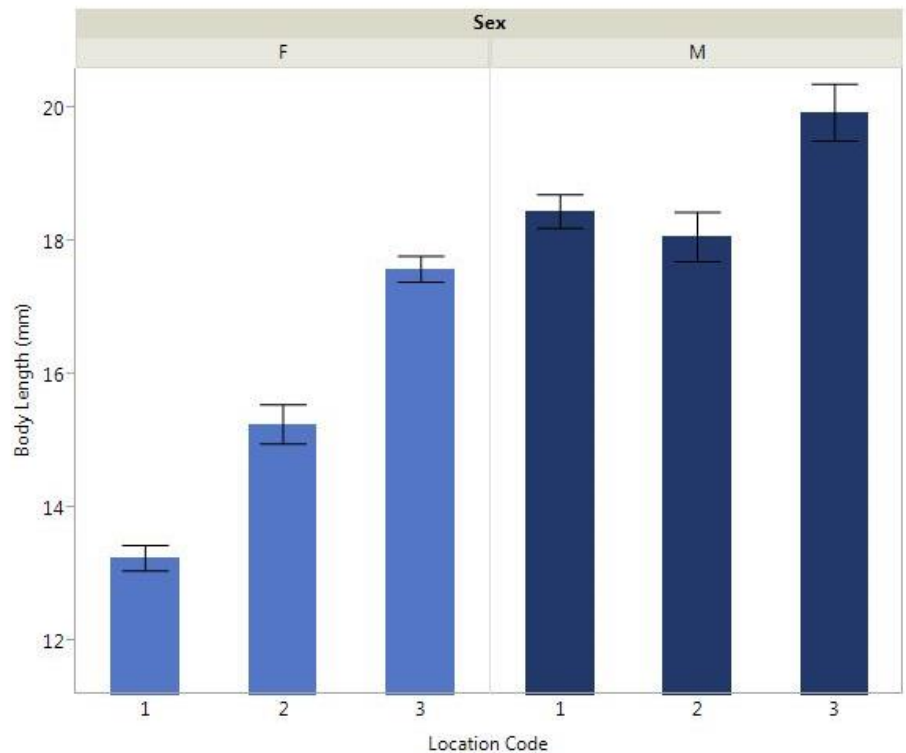


Figure 2. Body size vs. elevation. Body size of both male and female *S. nigripes* increases at higher elevations closer to a water source. Location 1: low elevation sandy wash; Location 2: mid elevation sandy wash; Location 3: higher elevation wash with standing water. Data are from 2009 only.

Location Code	Location Description	Females		Males	
		Average Body Length (mm)	N	Average Body Length (mm)	N
1	Low elevation sandy wash	13.254 ± 1.213	23	18.456 ± 1.290	22
2	Mid elevation sandy wash	15.263 ± 1.215	25	18.077 ± 1.290	15
3	Higher elevation wash with standing water	17.591 ± 1.217	37	19.942 ± 1.290	9

Table 1. Mean (± SD) body size of females and males at each location.

limitation in 2013. Thus, spring populations yielded offspring in the fall, and vice versa, rather than in two separate yearly cycles. *Steniolia nigripes* were highly sensitive to shifts in weather, on all temporal scales. Population emergence depended on warming spring temperatures. In 2012, when the spring was colder and windier than usual, wasps emerged several weeks late. Most striking, however, was their strong response to daily and hourly weather changes. Typically, wasps did not appear unless the temperature reached at least 28°C, and they were most active when temperatures were

around 32°C. If the weather was particularly cloudy or windy, wasps were not active, regardless of temperature. In fact, even momentary shading caused by a cloud passing in front of the sun resulted in the sudden disappearance of wasps. Once direct sunlight returned, wasps immediately reappeared. It was not entirely clear where they went in these short cloudy intervals, but they were likely resting on the ground under or near plants. Similarly, high winds (common in the Mojave) caused wasps to retreat due to the difficulty of controlled flight in windy conditions. Given the highly variable

climate of the Mojave, the flexibility of *S. nigripes* in response to shifting conditions may be an important adaptation.

Aside from mating, the daily behavior of male *S. nigripes* may be classified into two broad categories: foraging and aggression. All males foraged, but there was significant variation in the amount and type of aggressive behavior. The diet of adult males appeared to consist entirely of nectar collected from flowering bushes. When foraging, males landed on a flower and visibly extended the labium (lower lip or tongue), which is exceptionally long in all *Steniolia*. Wasps quickly inserted and removed the labium from each flower in a small area of 3 centimeters at most, with no clear pattern. They usually did not try every flower. When finished with one area, wasps flew in a short hopping motion to another area, and repeated the feeding movements. However, males often alternated between foraging and other behaviors. This was especially true of highly aggressive males, which needed to forage, but rarely spent more than a few seconds at a time foraging. Rather, highly aggressive males only fed when no potential competitors (or mates) were nearby. Males foraged at a variety of plant species, and transitioned from species to species as they bloomed. Male aggressive behavior took several forms. The most commonly observed aggressive behavior was patrolling flowers. A patrolling male circled over the top of a plant, usually around 10 cm above the plant. Patrolling males flew in a stereotyped, repeated path from plant to plant, although they stopped to forage, change direction, or interact with other insects along the path. A small number of males patrolled the same plants consistently, and prevented other males from patrolling there via aggressive interactions (11). These males patrolled and defended certain areas for days at a time. When a male encountered another insect while patrolling, several outcomes could result. Some males chased any insect they saw, whether it was another male, a female, or an entirely different insect species. Alternatively, some males patrolled and chased, but did not actively pursue other individuals as often. When two or more males met, they chased and circled each other in flight for up to 10 seconds. Chases usually took males away from the plant territory, and ended when one male flew away and the

other (victorious) male returned to the plant. Aggressive interactions could involve multiple individuals, with 5 or more males chasing each other or a female and covering large areas. If no especially aggressive males were present, several wasps would investigate and forage on a single plant, but patrolling males typically prevented other males from nearing the plant they were defending.

When a patrolling male detected a female, he attempted to interact with her immediately. More aggressive males dove rapidly onto a female, grabbed her, and attempted to mate with repeated probing motions of the abdomen. However, females typically resisted these attempts, and often escaped from the male's hold. Once a female was out from underneath the male, she would either fly away entirely, or the male would continue to chase her up into the air. Due to the swift, elevated nature of these interactions, it was nearly impossible to observe mating taking place in the field. Most commonly, a male was observed pursuing a female, but not actually contacting her. In some cases, this may have been a combination of territorial behavior and mating behavior.

Male *S. nigripes* exhibited variation in abdominal color that appeared related to body size. In general, male wasps had bright yellow and black patterning. However, in larger males the yellow was tinted green or blue, and especially large males could appear more blue than yellow (Figure 3). Females did not show any blue coloration, regardless of body size. In other species of solitary wasps, color variation can have a strong effect on thermoregulation because darker colors absorb more solar radiation than light colors (4, 12, 13). Large body

size also affects thermoregulation, as larger wasps warm more quickly and maintain higher body temperatures while active (12, 14, 15), in addition to experiencing larger energetic costs during flight (16). Thus, large dark insects may be more active at cooler temperatures, while small bright insects may be more active at higher temperatures (13). The size-linked color variation in male *S. nigripes* is potentially an adaptation for the differing physiological requirements of aggressive behavior and foraging. Due to the high energetic demands of flight, large aggressive males may be subject to higher heat stress. For example, in the sand wasp *Bembecinus quinquespinosus*, larger males engage in more intensive scramble competition, experience hotter microenvironments, and show higher proportions of yellow instead of black coloration (2, 17). However, *S. nigripes* males differ in color tint, rather than proportion of light to dark colors, so it is not entirely clear what drives the size-linked color variation in this species.

Female *S. nigripes* spent the majority of their time on food acquisition, either for themselves or for their offspring. However, females were also highly vigilant, and responsive to the presence or movement of any other insects. The foraging of adult females appeared very similar to that of males – they took nectar from flowers using their long tongues and moved frequently between flower clusters. Before foraging on flowers, females almost always observed the plant from a short distance, either in flight or resting on the ground. Females often circled plants or clusters of plants, flying very near the ground and landing occasionally. These behaviors were termed active vigilance and resting vigilance due to the female's high awareness of and responsiveness to any nearby insects. Females typically avoided

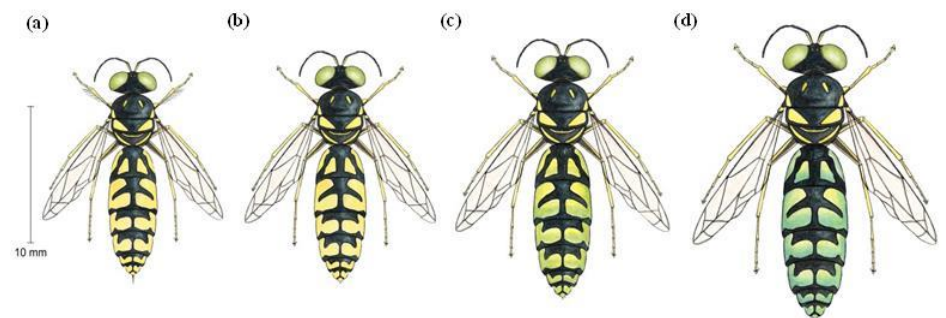


Figure 3. Size and color variation in *S. nigripes*. a. female, b-d. male. Illustration by Julie Himes.

proximity to other insects, unless they were hunting. If a female did not encounter other insects during this time, she proceeded to the flowers to forage. Unlike males, who remained near the tops of plants, female wasps often foraged on low flowers.

Female wasps of different body sizes demonstrated variable space use on plants. I observed females in the field and recorded their body size and relative location on the plant (bottom third, middle third, or top third). Body size was either directly measured from captured females, or visually estimated as small (11-12 mm), medium (13-14 mm), or large (15 mm or more). The accuracy of these estimates was frequently checked by subsequently catching the female and measuring the precise body length. Female body size was strongly related to the relative height of the female on the plant, for both measurement techniques (Figures 4 & 5). Typically, the higher portions of the plant were where most of the flowers were located, and hence where most insects were found. Smaller females may have been attempting to avoid interactions with other insects by remaining low on plants. Larger females went farther up on plants, where they were more likely to encounter harassment from males or other insects. Higher areas also likely had lower ambient temperatures, which may have been an advantage to wasps of larger body size (15, 16). Females did not appear to defend portions of plants in any way.

Female hunting behavior was quite distinct from nectar foraging. When hunting, females often hovered nearly motionless, observing potential prey from a short distance. This hunting vigilance was accompanied by a high-pitched noise produced by the rapid, contained wing movement necessary for hovering. Hunting females would slowly move within the inner branches of a plant, while continuing to hover. This behavior was easily differentiated from nectar feeding because the female rarely landed. When tracking a potential prey, females began hovering in a single spot, increased their wing speed (as evidenced by increased volume and pitch of wing noise), and then quickly dove towards the prey. Females grabbed the prey insect with their legs and mandibles, and immediately attempted to

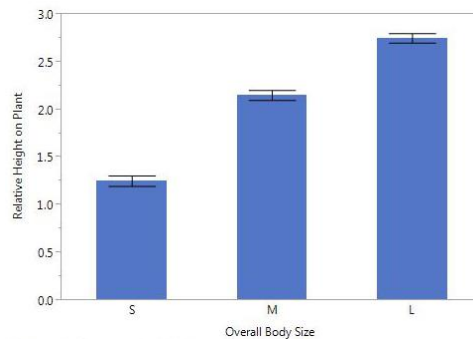


Figure 4. Relative female body size and space usage on plants. Small females remain at low heights, while larger females will fly to higher parts of the plant (N = 240, $\chi^2 = 142.5$, df = 2, $p < 0.0001$).

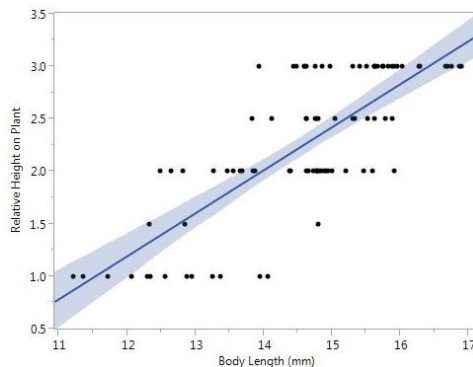


Figure 5. Female body size vs. height on plants. Female body size is strongly correlated with how high they will travel on plants (N = 87, Spearman's $\rho = 0.714$, $p < 0.0001$).

sting it. It was not uncommon for a hunting dive to fail. Insects could fly away before the female could catch them, struggle to such an extent that she lost her grip, or escape before she was able to sting sufficiently. In some cases the female stung the insect once to slow it down, landed while still holding on to it, and stung a second time. Once a female had successfully immobilized the prey, she carried it in flight to a nest hole using her legs.

Although females occasionally pursued honey bees or robber flies, *S. nigripes* were never observed successfully capturing anything other than Diptera, and the most common prey type was small Diptera. These dipterans belonged to any of a number of apparently widespread species, but were usually Bombyliidae approximately 3-8 mm in length. This is consistent with observations of other *Steniolia* species (3). Most Bembicini are progressive provisioners (3), meaning that females provide hatched larvae with a continuous supply of new prey items. This was assumed to be the case in

S. nigripes, but as the nests were difficult to find, it was not possible to directly examine nest contents. Given the extensive sexual size dimorphism in *S. nigripes*, offspring provisioning must be sex-biased so that daughters receive substantially fewer or smaller prey items than sons.

Female *S. nigripes* have an extensive fringe of setae, called rake spines, on the front legs, which are used for nest digging (4, 9). Like other sand wasps, they usually dig in variably sandy substrate, either along the banks of washes or in open areas such as parking lots or clearings (1, 3). The nests may be either clumped or solitary, as was more common in the Granite Mountains. When clumped, nest aggregations were small, ranging up to approximately 10 nest holes which were as close as several centimeters to each other. Nests were difficult to find, and it was more common to find either a single individual nest or trial holes only. Many sand wasps create huge, obvious aggregations of hundreds or even thousands of nests (1, 3), so the nests of *S. nigripes* were less well suited to study than those of other species. Marking of individual females indicated that females dig more than one nest, often right next to each other. It was not clear whether these holes represent false nests or in fact contain multiple larvae, and both strategies have been found in other species of sand wasps (1, 3, 4).

These observations represent the first comprehensive study of *Steniolia nigripes*. This species is a fairly derived sand wasp (9) with a number of intriguing characteristics, including male territoriality, color variation, reversed sexual size dimorphism, intersexual aggression, and variable use of resources (11). However, there is still much that is unknown about this species. For example, sand wasps either sleep in shallow burrows or in clusters on branches (1, 3), but it is not clear where *S. nigripes* spends the night. Further study is needed on many aspects of their life history, especially the timing of reproduction and dispersal. In addition, future research should investigate the fecundity of wasps of various sizes, and the extent to which size is heritable. This species potentially presents a rich study system applicable to a variety of research questions.

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Morphological and genetic diversity in reptiles at Mojave National Preserve

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Science is the study of variation. Why some things are different from others is what all scientists are trying to explain, whether the “things” are atomic particles or individuals or ecosystems. Evolutionary biologists are interested in genetic variation among individuals and populations, and how that may lead to adaptation and to new species. In order to understand evolution we look for study systems that exhibit variation appropriate for the hypotheses we are testing and are likely to reflect natural evolutionary processes rather than more recent anthropogenic (human-caused) events. For the study of evolution in reptiles, Mojave National Preserve near Baker, California could be renamed the Mojave National Laboratory. It has a rich diversity of snakes and lizards that vary greatly in morphology, abundance, and demography. The Preserve is relatively undisturbed by human development, and is likely very similar to the way it was before humans settled the region. We have been studying genetic variation in the Preserve’s reptiles, trying to understand the forces that determine the amount of variation in species. Understanding these forces not only helps us understand evolution but can also inform management decisions regarding population size and habitat preservation.

hydrothermal balance and foraging patterns of a sphecid wasp *Cerceris arenaria*. *Ecol. Entomol.* **10**:469–479.

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We started by trying to understand morphological (color pattern) variation in the side-blotched lizard, *Uta stansburiana* (1). Side-blotched lizards are small, insectivorous lizards that don't look like much. But they are actually one of the most successful species of reptiles. Side-blotched lizards are extremely abundant, usually the most common lizard wherever they are found (including the Preserve, according to 2007 surveys done by Persons and Nowak (2)). This is probably because they can live in a wide variety of habitats, from sand dunes to rock outcrops and even cliff faces (3). Of particular interest to us are the side-blotched lizards that live on and near the Cinder Cones National Natural Landmark (Figure 1). These lava outcrops are the remnants of volcanoes that erupted on and off over the last 7.6 million years, the last eruption occurring about 10,000 years ago (4). The lava rock is extremely dark compared to the rocks and sandy areas that surround it, and side-blotched lizards reflect that color variation. Lizards living on the lava are dark, while lizards living in the areas surrounding the lava are much lighter (Figure 1), presumably because matching the rock they are sitting on helps them avoid predators. Although this color variation is potentially caused by individual lizards adjusting their color patterns to match the background, it is also possible that natural selection has favored genetically based color patterns that match the background of the lizards. So we sought to answer three questions: 1) Do individual side-blotched lizards change color depending on their substrate? 2) If not, is the gene *melanocortin receptor 1 (MC1R)* responsible for the color differences, as has been shown in other lizard species? (5) 3) Does natural selection for different colors interfere with gene exchange between the lizards that live on the lava

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and those that live on lighter substrates?

To test the first question we brought some light and dark lizards into the laboratory and raised them on light colored surfaces, to see if the dark lizards would turn a lighter color. After a year on the light colored surfaces, all lizards were essentially the same color as when they started. This suggests that the reason that some lizards were light and some were dark was innate, and not a physiological response to their background. (We have not yet tested newly hatched lizards, so individual color changes might occur early in life and become permanent later. But this has never been reported for lizards.)

To test the second and third questions we sequenced the *MC1R* gene (found on the chromosomes in the cell's nucleus) and two other genes - *cytochrome b (cytb)* and *NADH dehydrogenase 4(ND4)*, both found on the DNA located in organelles called mitochondria - from over 100 side-blotched lizards. We collected lizard tissue samples (tail tips) from the lava (dark lizards), the areas surrounding the lava (light lizards) and some additional light lizards collected near the Desert Studies Center, which is located 23 km west of the lava flows and is separated from them by a dry soda lake that is not suitable habitat for the lizards. If the *MC1R* gene is itself causing the color difference between light and dark lizards as we hypothesized in question 2), we would expect that the individual mutations that cause the difference would be segregated in the two forms. That is, there should be certain alleles (different forms of the same gene are called "alleles") that are found much more often in either the dark lizards or the light lizards. The mitochondrial genes were chosen to see if there were genetic differences between the light and dark form for genetic markers that were unlikely to be involved in color determination and are not linked to (found on the same chromosome as) *MC1R*.

Sequencing of *MC1R* showed us that this gene is not directly affecting color pattern in our side-blotched lizard populations. We know this because no alleles (or sets of related alleles) were restricted to a particular color of lizard. But even more importantly, most of the DNA sequence variation that we discovered does not

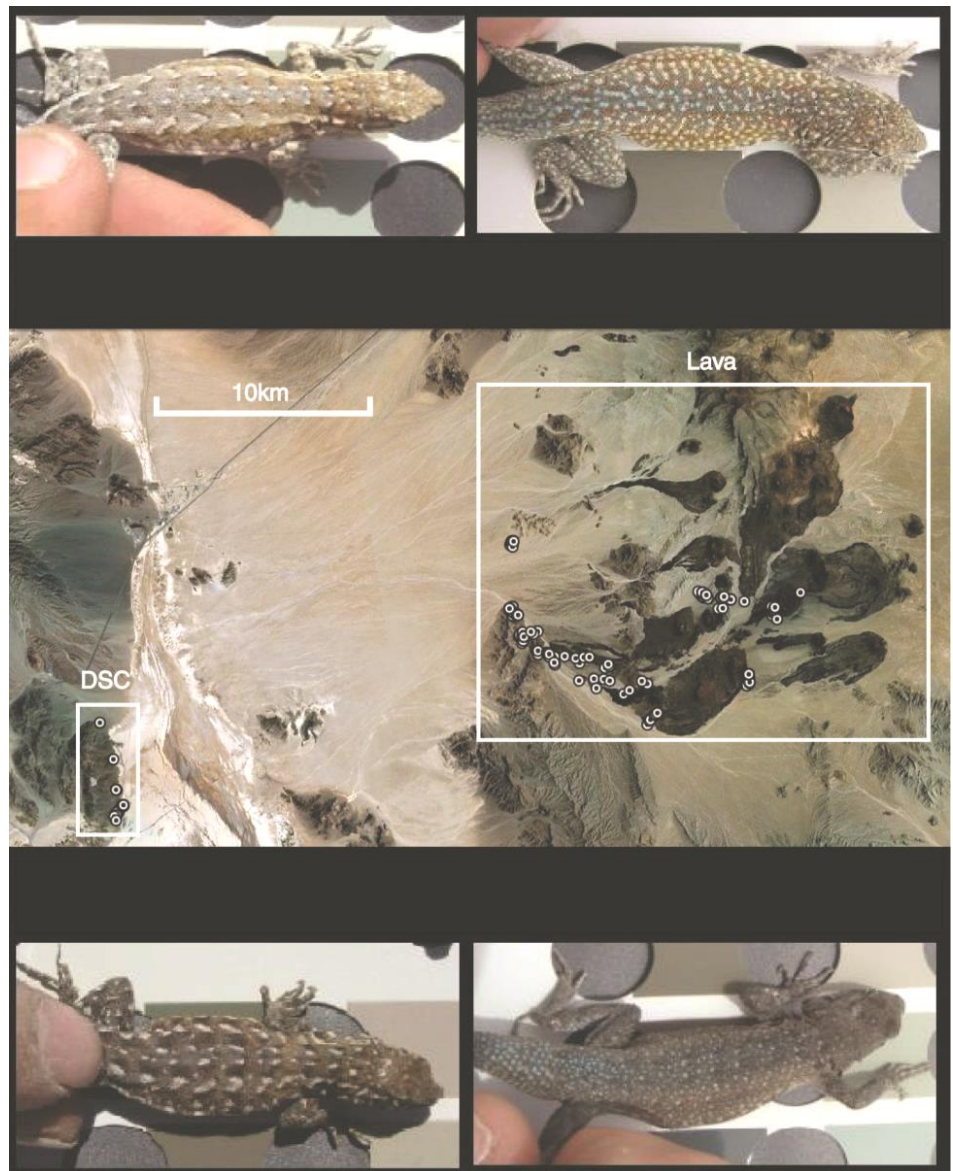


Figure 1. Collecting localities for side-blotched lizards flanked by photographs of dark lizards collected from the lava (bottom) and light lizards collected from surrounding areas (top). Because side blotched lizards are sexually dimorphic, both females (left) and males (right) are shown. The box labeled "Lava" surrounds the Cinder Cones National Natural Landmark. The box labeled "DSC" surrounds the collecting localities at the Desert Studies Center.

cause any differences in the *MC1R* protein. We can translate the genetic code of any gene sequence into the amino acids that are the building blocks of the protein that the gene codes for. Because the genetic code contains redundancy, there are multiple sequences that code for the same amino acid. For example, there are two different 3-base DNA sequences, TTC and TTT, that code for the amino acid phenylalanine. If two otherwise identical alleles each have one of these sequences, they are different at the DNA level but produce identical proteins, which should also function identically.

We found only five DNA changes that actually caused a difference in the amino acid sequence of the *MC1R* protein, and they were found in only five lizards. Therefore these DNA mutations couldn't explain all the differences among the 66 dark and 44 light lizards that we sampled from the area on and around the lava. (It is still possible that this gene is affecting color differences, but only if other genes are regulating protein production by the *MC1R* gene. However our molecular methods could not address this issue.)

Even if the *MC1R* gene is not responsible for the color variation in side-blotched lizards, selection against light lizards on the dark lava and against dark lizards in the lighter surrounding areas could reduce gene exchange between the two color forms, leading to differences between the color morphs in marker genes like our mitochondrial markers and *MC1R* (now that we know that *MC1R* is not affecting color variation, it is effectively just a marker gene). Because the mitochondrial genes are completely linked, we analyzed them together as a single genetic unit. We can measure genetic differentiation among groups as the variance among those groups in the frequencies of their alleles, weighted by the mutational differences among them. This statistic, called Φ_{st} , takes on its highest value (1) when populations are completely different and assumes values close to zero when populations are identical. When we grouped lizards into light and dark populations, Φ_{st} values for both mitochondrial DNA and *MC1R* were low and could not be distinguished from zero with statistical tests. When we compared lizards from lava to the Desert Studies Center (DSC) population, (separated by the long distance around the soda lake) Φ_{st} was higher and statistically significantly greater than 0. This suggests that distance reduces gene exchange among populations, as we might expect, but that selection for color has not resulted in genetic differences between light and dark lizards.

Although we did not discover the genetic basis of the color variation in side-blotched lizards, our genetic surveys serendipitously uncovered something that has led us to refocus our research to a more general problem - the maintenance of genetic diversity. The allelic diversity for both mtDNA and *MC1R* was extraordinarily high. Gene diversity, the probability of randomly sampling two copies of a gene from a population that are different alleles, was well over 90% for both mitochondrial and nuclear genetic markers, even for samples taken only from the small area on and around the lava. Marine biologists analyzing fish samples taken from all over the world as if they are from a single population find gene diversities this high, but most single population samples from terrestrial species have much lower values. Why populations vary in genetic diversity is a question that evolutionary

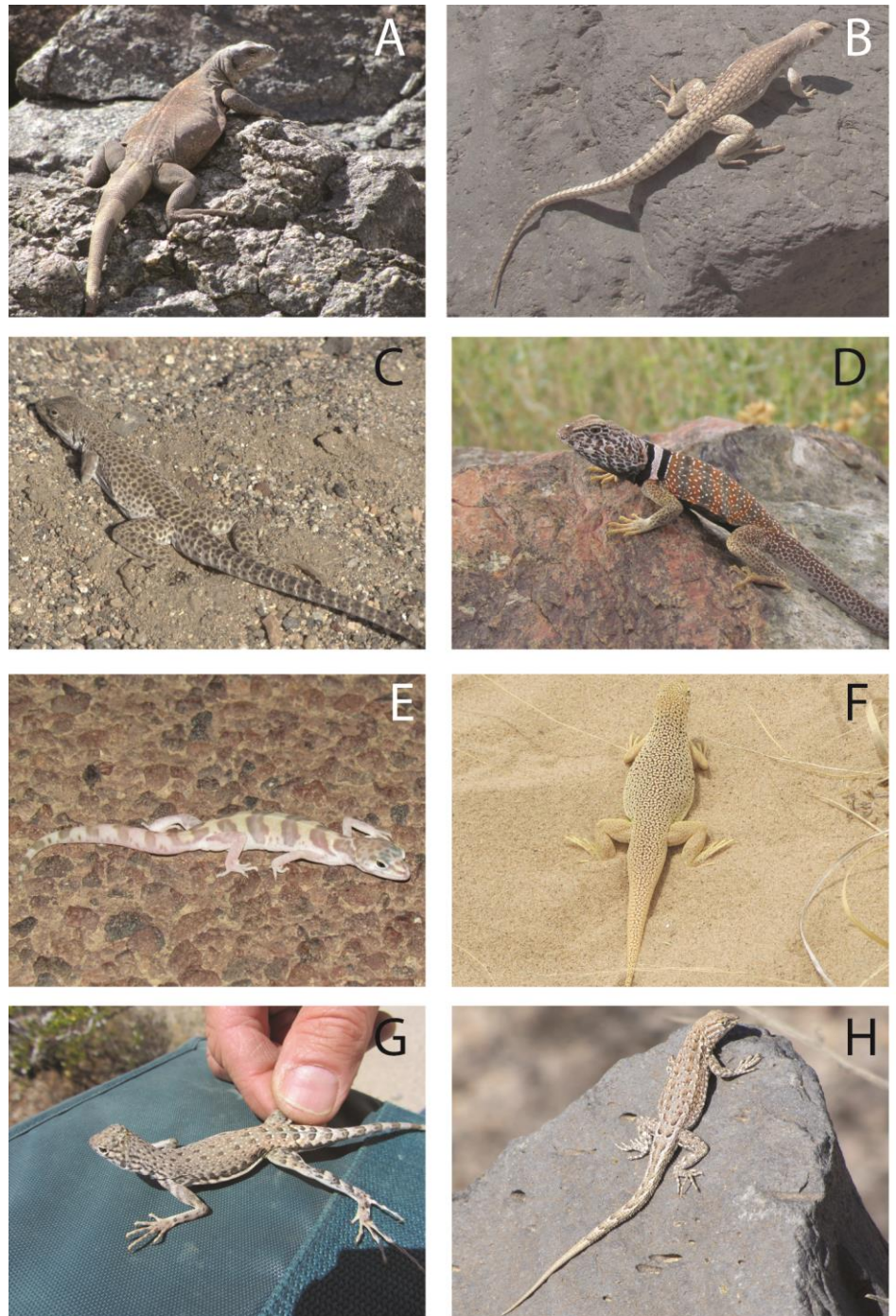


Figure 2. Lizard species surveyed for genetic variation. A) Common Chuckwalla. B) Desert Iguana. C) Long-nosed Leopard lizard. D) Great Basin Collared Lizard. E) Western Banded Gecko. F) Mojave Fringe-toed Lizard. G) Zebra-tailed Lizard. H) Side-blotched Lizard.

theorists have been studying for many years. Because of the large number of reptile species living sympatrically in the Preserve, it is possible to test some of these theories. The two main theories explaining DNA sequence variation are the neutral theory and genetic drift. The neutral theory (6, 7) postulates that most DNA variants are neutral with respect to function and the fitness of the individuals that have them.

Their dynamics are entirely a function of the mutation rates of the genes and the population size: the larger the population, the higher the gene diversity. Genetic drift (8) is a complex theory that proposes that selection directly acting on individual genes found throughout the genome occurs frequently enough that even neutral marker genes will be affected. The math of this theory predicts that genetic diversity will be

independent of population size. We are testing the two diametrically opposed predictions by comparing genetic diversities for 3 genes (*cytb*, *MC1R*, and an additional nuclear gene, *recombination activation gene 1, RAG1*) for many species of snakes and lizards in this region of the Preserve.

We are still in the process of collecting specimens and amplifying and sequencing the genes. However, we have preliminary data for several species that differ in population size on the Preserve. We sequenced the genes for three additional small bodied, high density species: the Zebra-tailed lizard, *Callisaurus draconoides*, the Western Banded Gecko, *Coleonyx variegatus*, and the Mojave Fringe-toed Lizard, *Uma scoparia* (Figure 2). These species are extremely common where they are found. We have also sequenced all three genes for two large bodied lizards with lower population densities: the Common Chuckwalla, *Sauromalus ater*, and the Desert Iguana, *Dipsosaurus dorsalis*. Finally we have finished sequencing *cytb* for two additional large bodied, lower density lizards, the Great Basin Collared Lizard, *Crotaphytus bicinctores*, and the Long-nosed Leopard Lizard, *Gambelia wislizenii*. Figure 3 shows the gene diversities for *cytb* (the other genes show similar results for those species that have been surveyed so far). Note that, with two exceptions, the smaller species with higher population densities have higher gene diversities than the larger lizards with lower densities.

The exceptions to this pattern are the leopard lizard and the fringe-toed lizard. The leopard lizard is much less common than the gecko, the zebra-tailed lizard, and the side-blotched lizard. When we walk through suitable habitat, we often see dozens of the common species for every individual leopard lizard. Yet, although it has a lower genetic diversity estimate, statistical tests cannot differentiate the leopard lizard's gene diversity from those of the common three species. We have yet to survey the other 2 genes for leopard lizards, so this result may be an anomaly. The fringe-toed lizard is an interesting case that in fact may not really be an exception to the pattern. This lizard is strongly adapted to life on extremely sandy areas (like the Kelso Dunes, where our specimens were collected), and is not

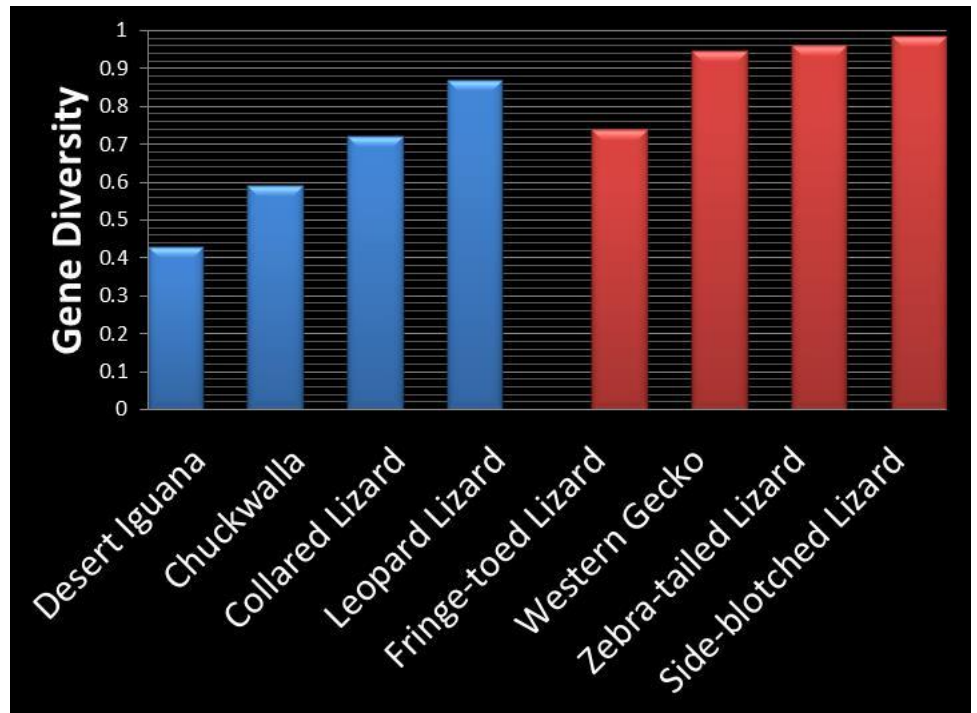


Figure 3. Gene diversities for the 8 species of lizards shown in Figure 2. Species with high population densities are in red, species with low population densities are in blue.

found in most of the habitats in the Preserve. Because the Kelso Dunes are restricted to a small area of the Preserve, and are not connected to other populations of fringe-toed lizards on other sand dune systems, the high density of lizards at Kelso Dunes does not translate to a high overall population size. Thus, the lower genetic diversity is consistent with the idea that smaller populations have lower gene diversities.

Ultimately, the results for these three genes, even when the data from all of our sample species are collected, are insufficient to fully test whether the neutral theory or genetic drift is a better explanation for the level of genetic diversity found in nature. For our study, we need to survey many more genes to get a conclusive answer. Fortunately, thanks to developments in next-generation DNA sequencing, it is now possible to sequence many genes from an individual. Unfortunately, the cost of this sequencing is still quite high, and we are applying for a National Science Foundation grant to fund the research. In addition to our research at Mojave National Preserve, many more similar studies on a variety of animal and plant groups will be required in order to really be able to say whether periodic selection is frequent enough to be the major

factor governing the dynamics of genetic diversity. All of these studies will need to have places like Mojave National Preserve, where many species coexist undisturbed in natural habitats.

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Endolithic cyanobacteria in the Mojave Desert: a cold habitat in a hot desert?

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The presence of photosynthetic microorganisms in desert rocks has come to be expected.

Research conducted by Dr. E. I. Friedmann and others over the past 50 years has shown that at sites from around the world, including the

Antarctic Dry Valleys, the Negev Desert in Israel and the Atacama Desert in Chile, wherever high aridity precludes the establishment of so-called epilithic organisms on the surfaces of stones and rock outcrops, hardy photosynthetic microorganisms, especially single-celled cyanobacteria of the genus *Chroococcidiopsis*, thrive in cryptic, protected habitats (1–3). These include the underside of translucent stones (the hypolithic habitat), pore spaces below the surface of sandstones and gypsum (the cryptoendolithic habitat), and near-surface fissures and crevices in weathered granite (the chasmolithic habitat). The rocks provide a measure of protection from harmful ions and molecules created by excessive solar radiation under the dry conditions and yet still permit sufficient access to sunlight for photosynthesis to occur. Given this background, our discovery of *Chroococcidiopsis* in the granite

outcrops near the southern end of Mojave National Preserve, at the Sweeney Granite Mountains Desert Research Center (Figures 1, 2), did not excite us initially.

When we looked at it more closely, however, the system became much more interesting. While the cyanobacteria in the rock appear uniform under the microscope, DNA sequence analysis revealed that the population is, in fact, a mixture of different strains or even species. (The taxonomy of the genus *Chroococcidiopsis* is still unresolved.) Some of the strains appear to be closely related to strains from the Tibetan Plateau (Figure 3). This is not entirely unexpected since we know that the Jet Stream brings Asian dust to the southwestern United States yearly. We also know that desert cyanobacteria, being desiccation- and radiation-tolerant (4, 5), could readily survive such a journey. Although their climate conditions are not the same, it is not entirely out of the realm of possibility that Tibetan microorganisms could survive and establish themselves in the Mojave. But this is not all. The DNA analysis also revealed that the dominant strain, accounting for 71% of the cyanobacterial population, has its closest relatives in Antarctic Dry Valleys and islands in the high Arctic (Figure 3). To appreciate this result, one needs to consider the fact that the annual average temperature in the Mojave Desert is 17°C, while the annual average temperature in the Dry Valleys is -21°C. At first glance, the result seemed utterly implausible.

So often in science, results that initially seem counterintuitive turn out to be our greatest discoveries. When the complete environment is considered, this result, in fact, makes perfect ecological sense. Regardless of their location on the planet, desert microorganisms are metabolically active for only a portion of the time, i.e. when liquid water is available. More specifically whether in a hot or a polar desert,



Figure 1. Granite Peak, Sweeney Granite Mountains Desert Research Center.

endolithic microbial activity occurs only when the rock is wet. In Antarctica, temperatures high enough to melt snow, the only form of precipitation there, only occur from late November through mid February (6). During this window, the ambient air temperature rarely reaches 0°C. Rocks, however, are warmed by solar insolation. In the sandstones where the organisms reside, temperatures intermittently rise above zero, sometimes reaching as high as 15°C. Thus, in Antarctica, biologically-relevant temperatures range from 0°C to 15°C. Indeed, the growth temperature optima of isolated organisms are consistent with this result. All endolithic isolates studied so far grow best between 18°C and 20°C (2). In microbiological parlance, these are not cold-loving (psychrophilic) organisms. They are, rather, cold-tolerant mesophiles.

To determine the range of biologically relevant temperatures in the Mojave, we monitored the relative humidity of the ambient air, the temperature in the granite, and rock conductivity (as an indicator of the presence of liquid water) continuously for over a year. Some of the data are shown in Figure 4. The humidity and wetness

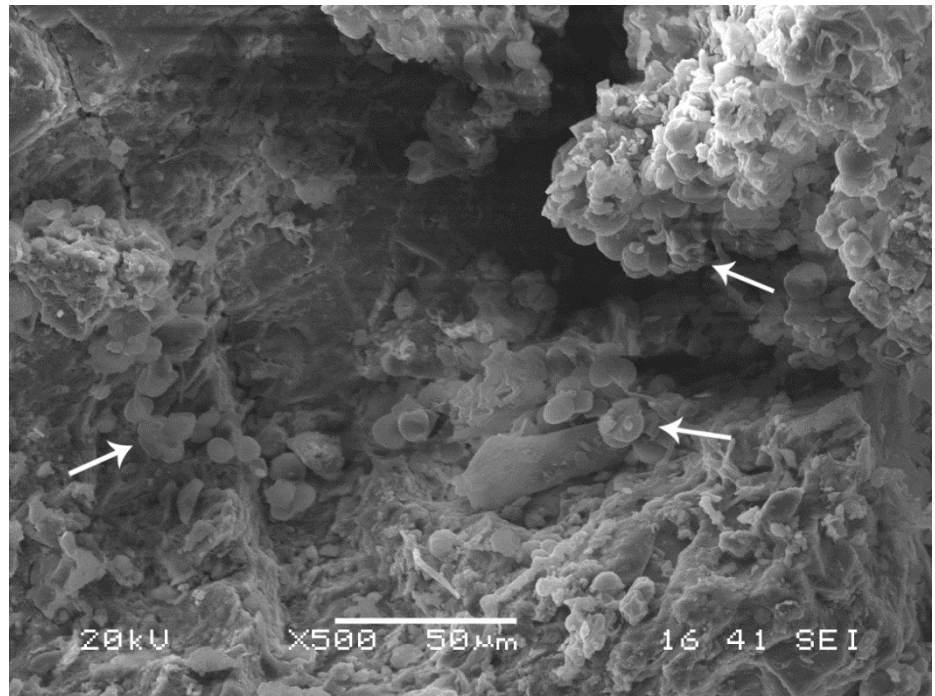


Figure 2. Fractured granite under the scanning electron microscope, showing *Chroococcidiopsis* cyanobacteria. Arrows indicate clusters of microorganisms.

data are consistent with what we know about the climate in the Mojave Desert. Although the summer monsoon does penetrate the Mojave July through September, it delivers very few rain events. Also, these rains come at a time when

the air is both hot and dry; thus their effects are short-lived. Consequently, like in the Antarctic desert, the rock does not stay wet over most of the year in this hot desert. Conversely, in winter and spring (from November to May), the Pacific Jet Stream brings rain to the Mojave at a much higher frequency. This fact, coupled with high relative humidities and cool temperatures, results in a virtually continuous wet condition within the rock seasonally. In fact, rock temperatures during much of this time period range from 0°C to 20°C, similar to the biologically relevant temperature range in Antarctica. In other words, from a microbiological perspective, they are effectively the same habitat! The variation in conditions may also explain why, in the Mojave, different cyanobacteria strains can coexist in the same rock. The rock temperatures are very different in the summer and winter. The endolithic habitat is likely temporally differentiated into hot and cold niches, and possibly everything in between.

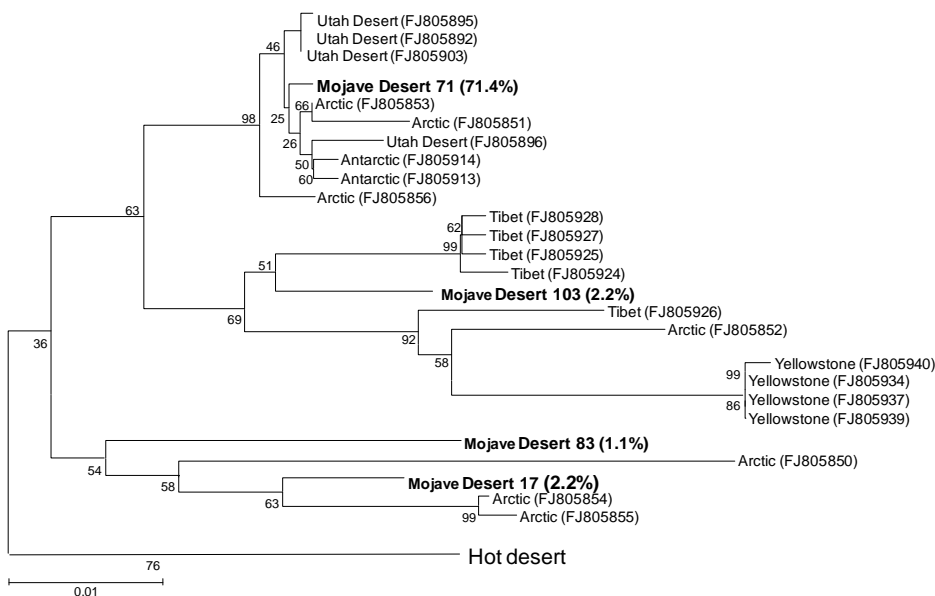


Figure 3. Genetic relationship between Mojave *Chroococcidiopsis* and close relatives. The numbers at the branches (nodes) give an indication of the degree of confidence we have that the relationship is real and not the result of a statistical fluke; higher values indicate higher confidence. The percentages associated with the Mojave *Chroococcidiopsis* indicate the proportion of DNA sequences recovered from the site that are represented by the indicated sequence. The length of the horizontal lines in the dendrogram is an indicator of the amount of evolutionary change a lineage has undergone since it separated from its closest relative. The scale bar used for measuring the horizontal lines represents the number of changes per 100 nucleotide sites.

evolution in macroscopic plants and animals do not exist for microorganisms (8). As succinctly and famously summarized by him, the biogeographic patterns of microorganisms are governed instead by the general principle "alles is overal: maar het milieu selecteert" ("everything is everywhere, but the environment selects"). Nowhere does this paradigm appear to be truer than in the case of desert cyanobacteria like *Chroococciopsis*. Specifically, we hypothesize that, through aeolian mixing, all deserts contribute to a global pool of potential colonists that circulate constantly around the globe. A new desert receives the entire pool, but only those microorganisms that are pre-adapted to be competitive in the new environment take hold. These organisms will continue to change and evolve in the newfound habitat. But, unlike in the case of most large animals and plants, the entire evolutionary history of the species is not spatially confined to a specific geographic region. Whether this phenomenon is unique to desert microorganisms, which possess a suite of adaptations allowing them to survive the harsh conditions accompanying long-term aeolian transport, or is more generally true for all microorganisms is worthy of further investigation.

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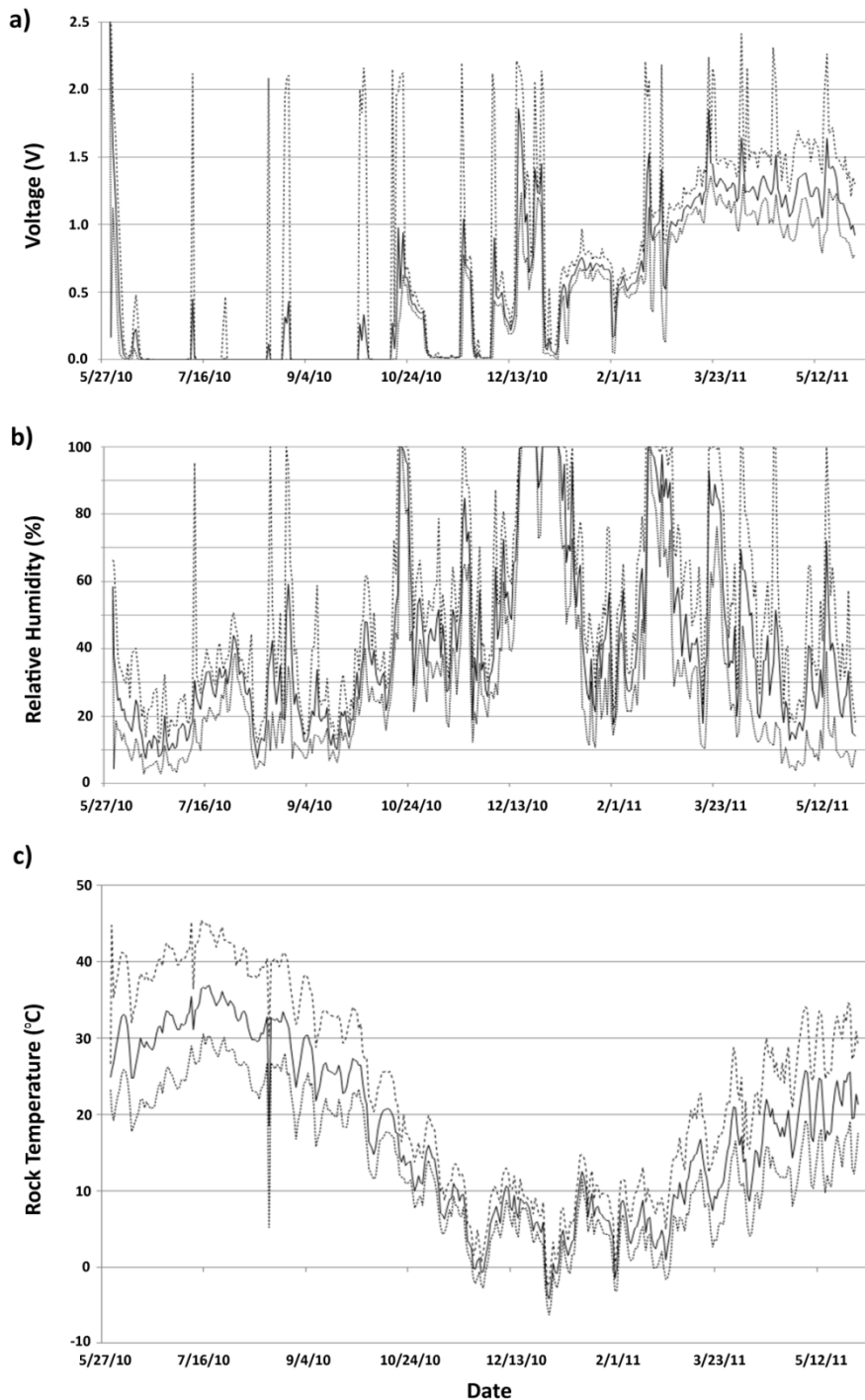


Figure 4. Environmental parameters associated with a granite outcrop colonized by cryptoendolithic cyanobacteria, Sweeney Granite Mountains Desert Research Center. a) Rock moisture as monitored by the voltage drop across two electrodes embedded in the rock surface; for the system used, higher voltages indicate the presence of liquid water connecting the two electrodes. b) Air relative humidity measured near the surface of the rock. c) Temperature of the rock as indicated by a temperature sensor embedded just below the surface of the rock. In all three graphs, _____ indicates the daily average, indicates the daily minimum and - - - - - indicates the daily maximum.

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