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Desert salt flats as refugia for terrestrial arthropods

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At first glance, salt flats may not appear to be hospitable to animal life (Figure 1). Often located in hot, arid places, they can readily flood, and their salinity presents special challenges to water regulation. However, there is evidence that these seemingly inhospitable habitats may act as refugia (a location of an isolated population of a once more widespread species) for terrestrial arthropods (1). Soda Lake in Mojave National Preserve is one such salt flat that is a remnant of a much wetter period in the history of southwestern North America. The Desert Southwest, which includes some of the driest deserts on Earth, was largely composed of riparian woodland and scrub habitats before the Quaternary began (1.64 million years ago). During the Pleistocene (2.5 million to 11,700 years ago) there were several advances and retreats of glaciers, and during times of



Figure 1. Panamint Lake, Panamint Valley, California. A typical and seemingly inhospitable salt flat.



Figure 2. Ancient (2.5 million to 126,000 years BP) waterways in the Mojave and Colorado Deserts of southern California. Dashed lines indicate connections disputed by geologic evidence. This is not comprehensive or to scale, but meant to provide a general idea of what the Southwest was like prior to desertification.

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advancement when the overall climate was cooler and wetter, many large lakes occupied the Southwest. Some of these lakes were even connected to one another via river corridors (Figure 2); a much different past climatic regime is evidenced by the presence of arroyos and dry lake beds. Occasionally these features flood, revealing ancient corridors that aquatic organisms, such as springsnails and pupfish, once used to disperse (2, 3, 4, 5, 6), and today some of the dry lake beds are covered with a salt crust. These crusts form due to chemicals that leach out of the surrounding mountains or are left over from rapid evaporation of water during desertification, often occurring in an enclosed basin that precludes the salts from being washed away. These crusts differ among the lakes in both salinity and chemical composition (7).

Despite the harshness, a community of arthropods lives secret lives in the salt flats, making their homes in the layer between the salt crust and the soil and/or in cracks and holes in the salt or the substrate. Thus far, our research has primarily focused on the salt flat spider

Saltonia incerta (Banks, 1898) (Figure 3). When we began our study, only a handful of specimens (3) had been collected since its discovery, the species was presumed extinct (8), and its relationship to other spiders was elusive. *Saltonia incerta* was first collected in 1897 in Salton, California. This type locality (location from where a species is first recorded) had since been submerged when the Colorado River flooded the Salton Basin in 1905, creating the Salton Sea. A second specimen was collected in 1941 on the west side of the Salton Sea at Fish Springs; however, that locality was also lost, being transformed by human development. *Saltonia incerta* was also collected at an alleged third locality, but the exact location is unclear (9), making re-collection impossible. In the 1990s, much to everyone's surprise, the species was collected in pitfall traps from two localities some distance away from the Salton Basin – China Lake and Soda Lake (D. Ubick & W. Savary, unpubl. data). This result led the first author to explore other salt flats throughout the Desert Southwest in search of the spider. *Saltonia incerta* has now been found at 15 salt flats,

including sites as far east as New Mexico (1) (Figure 4).

Because *Saltonia incerta* is found under the salt crust of salt flats and not in the intervening desert, we aimed to determine the factors responsible for this striking distribution. We focused on three scenarios – one of complete isolation, one of dispersal during intermittent flooding, and a scenario involving aerial dispersal. The first scenario assumes that suitable habitats were more extensive in the wetter periods of the past and, as desertification occurred, the spiders retreated to areas where moisture persisted. The second scenario is governed by the premise that spiders would, assuming water is a limiting factor, rarely disperse except in times of flooding when there is sufficient moisture in the intervening areas for the spiders to survive the journey. Finally, a scenario of aerial dispersal relies on the ability of spiders to balloon (a form of dispersal in which immature spiders drift on air currents using silk threads) to suitable habitat. Each scenario produces distinct patterns in the genetic connectivity of populations. These patterns can be predicted both among individual salt flats, as well as among groups of salt flats located within ancient drainage basins. Analyzing the DNA of the spiders allowed us to determine which scenario was most likely based on these patterns.

We analyzed both a mitochondrial DNA gene (Cox1) and a nuclear DNA gene (H3) for 81 spiders from 13 salt flats in 6 drainage systems



Figure 3. The spider (*Saltonia incerta*) on its web made within the thin layer between salt crust and soil substrate on the surface of the dry lake bed.

(for detailed methodology, see (1)). Spiders were assigned to the following drainage basins – 1) Owens River Drainage, 2) Amargosa River Drainage, 3) Mojave River Drainage, 4) Bristol Basin Drainage, 5) Colorado River Drainage, and 6) Lake Otero (Figures 2, 4). We found a total of 41 haplotypes (unique DNA sequences). There is deep genetic divergence between the populations of New Mexico (Lake Otero) spiders and the populations of California spiders (Figure 5), and although no morphological differences were detected, they have likely been separated from each other for a long time/many generations. Within California, there were several salt flats with genetically unique populations that

corresponded to two ancient lake beds. These include specimens from ancient Lake Tecopa, and Badwater and Cottonball Basin specimens from ancient Lake Manly in Death Valley. Only the New Mexico specimens exhibit strong genetic isolation in relation to their drainage basin. This latter result is perhaps not surprising given that Lake Otero is a closed basin, without possible connections to other basins. An AMOVA (Analysis of Molecular Variance) indicated significant genetic variation at three levels: 1) among basins, 2) among individual salt flats within basins, and 3) among individuals within salt flats. Because of apparent admixture of genes between the Bristol and Colorado River Drainage Basins, we examined these groups for evidence of migration. The results of this analysis indicate that migration rates in either direction are very low, but slightly higher for migration from the Colorado River Drainage Basin to the Bristol Basin (south to north). Modeling migration rates also allowed us to determine that populations may have diverged 1.59 million to 89,300 years ago which is credible considering geological and climatological data. Finally, no pattern of isolation by distance was detected, indicating that the distance between salt flats or drainages is not important for predicting genetic divergence.



Figure 4. All known localities of *Saltonia incerta*, including three new ones that have yet to be included in analyses: Panamint Lake, California and Holloman Wildlife Refuge and Lazy Lagoon at Bottomless Lakes State Park, New Mexico.

Of the three proposed scenarios responsible for the distribution of *Saltonia incerta*, the data most strongly support complete isolation, the scenario

where suitable habitats were more extensive in the wetter periods of the past and, as desertification occurred, the spiders retreated to areas where moisture persisted. The data are not consistent with the dispersal via intermittent waterways scenario because we would expect less genetic change if this was the case. Additionally, many of the patterns present in the data are inconsistent with geological data. We also consider a scenario of aerial ballooning unlikely given the amount of genetic variation found in the data. Ballooning is also a very risky behavior for animals that live in a specialized habitat because there is no guarantee that they will land in a suitable area. Furthermore, there have been no observations of ballooning in *Saltonia incerta*. We also examined wind patterns and wind regime data to determine whether the directionality of migration mirrored wind direction. Prevailing winds in the Mojave Desert are usually from the west and the south (10), indicating migration could occur from the Colorado Drainage to the Bristol Basin. Our results indicate a very low probability of migration in this direction. Also, when examining more local wind patterns determined by topographical features, there is an overall trend of wind moving from west to east (11). This is opposite to the pattern indicated by the data, and is thus inconsistent with the species dispersing via ballooning. The scenario that populations are isolated with little to no gene flow is supported in all analyses and is consistent with geological data. There is high genetic structure between basins and between salt flats within basins, but low genetic structure within salt flats. Overall, the evidence thus far indicates that *S. incerta* was once more widespread than it is currently, and as drying has occurred, this species has retreated to salt flat habitats (1).

Although living in a salt flat may seem like a bizarre life history strategy, it does have its advantages. First, there is almost always some moisture between the underlying substrate and the salt crust. Second, the temperature beneath the salt is much cooler than the ambient air temperature. Finally, there are very few predators. Therefore, if animals can tolerate the osmotic challenges, this habitat may act as a type of oasis in an otherwise harsh environment. In addition to these advantages, once we

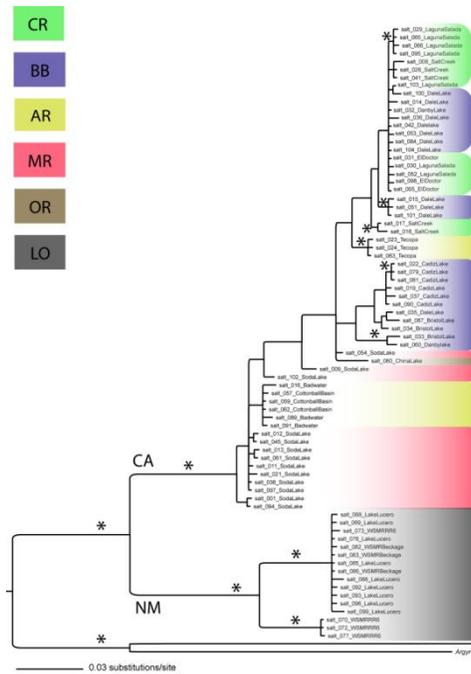


Figure 5. 50% majority rule consensus phylogram from 120,000 trees. Asterisks denote nodes supported by >95% Bayesian posterior probabilities. Colors represent drainages. CR = Colorado River, BB = Bristol Basin, AR = Amargosa River, MR = Mojave River, OR = Owens River, LO = Lake Otero, CA = California, NM = New Mexico.

consider where *Saltonia incerta* resides within the spider tree of life, salt flats may not seem like such a peculiar place to make a living.

Saltonia incerta was originally placed in Agelenidae (12), but was moved to Dictynidae by Lehtinen (13). In a study by Spagna et al. (14), *S. incerta* formed a clade (evolutionarily related group) with 2 other genera – *Paratheuma* and *Argyroneta* – neither of which were placed in Desidae based on morphological characters. Many desids are intertidal spiders that have enlarged tracheal trunks. *Paratheuma* is also an intertidal spider with enlarged tracheal trunks; however, this shared morphological character may represent an adaptation to a semi-aquatic lifestyle rather than a shared evolutionary history. First described by Banks (15) from Bermuda, Roth and Brown (16) later described a species from the shores of the Sea of Cortez, with many other species described from Pacific Islands, eastern and western Asia, including Iran (17, 18, 19, 20). In the latter paper, Zamani et al. (20) transferred *Paratheuma* to Dictynidae from Desidae based on genitalic characteristics, often

used for grouping and separating spider family, genera, and species.

The latter species that formed a clade with *Saltonia incerta*, *Argyroneta*, has been placed in several families, including its own – Argyronetidae – over the years owing to its unique morphology and lifestyle. According to the World Spider Catalog (21), this genus is currently placed in Cybaeidae. This spider is the only known representative of Araneae to live fully submerged in freshwater. Therefore, given this group of related “aquatic” spiders (14), *Saltonia*’s affinity for remnant aquatic habitats makes sense because this species may have been pre-adapted to living in such habitats. An ongoing study by the authors and colleagues is reconsidering the current placement of *Argyroneta* and other semi-aquatic spiders.

Saltonia incerta is not the only arthropod to exploit salt flat habitats. The salt flats are home to entire communities of arthropods, many of which are endemic. These include brine flies (*Ephedra*), salt flat ant-like flower beetles (*Tanarthrus*) (Figure 6), as well as other spiders of the families Lycosidae and Salticidae. Currently we are focusing on these groups to produce community-level data. The salt flats are excellent natural laboratories of nearly repeated ecosystems. Future work will be to obtain more molecular data that includes additional markers for *S. incerta* as well as additional samples of the spider to produce more detailed population history results. There are also areas where the spider may be that we have yet to find it, so we are still looking for additional distribution records. For instance, in early 2016, we found the species at three new localities: Panamint Lake in Panamint Valley, California and Bottomless Lakes State Park and Holloman AFB Wildlife Refuge in New Mexico. Notably, on any given salt flat at any given time, two distinct sizes of adults can be collected – small adults and large adults. We aren’t yet sure why this occurs, although one idea is that smaller adults reproduce sooner and therefore require fewer resources: i.e. a reproductive strategy ensuring a next generation is produced even when resources are scarce.

Next, we want to expand our studies to include a broad range of arthropod groups from which to

obtain genetic data. This will include arthropods that are sedentary (spiders) and those that fly (beetles, flies) to compare evolutionary histories and produce robust evolutionary hypotheses for salt flat organisms of the Desert Southwest. We also plan to focus more intensely on a small number of salt flats, including Soda Lake, to examine community level processes, such as food webs, using systematic collecting and new genetic methods like DNA 'barcoding'. Finally, we will examine the physiological mechanisms of heat and salt tolerance in some of the arthropod groups. It has been suggested that differences in the chemical make-up of the salt flats may have been responsible for speciation in some fly species (7).

The Mojave Desert is truly a special place that harbors many endemic organisms, often associated with unique microhabitats with very limited geographical range. Numerous habitats in the Desert Southwest, such as dune systems and salt flats, support their own suite of organisms, adding to the biological diversity found in these ecosystems. Unfortunately, this biodiversity is rarely accounted for; instead the desert is often considered a wasteland without much biodiversity, and it is constantly under threat from development and other human impacts. Currently, much of the desert, including land in the immediate vicinity of Soda Lake in Mojave National Preserve, is being considered for use as large solar farms (23, 24). This is occurring despite potentially negative environmental impacts caused by solar farms and despite the availability of alternative methods for meeting our energy demands like solar panels on rooftops in urban areas (25, 26). Although there are studies demonstrating the detrimental effects of habitat alteration to the arthropods that depend on these sensitive habitats (22), these organisms have rarely, if ever, been considered when assessing the environmental impacts for proposed solar projects. Long term assessment of salt flat arthropod communities can provide insight into the disturbance of these unique habitats; however, the pace of alternative energy development in the Desert Southwest may limit our ability to learn enough about these ecosystems before they are irrevocably altered.

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Figure 6. Salt flat ant-like flower beetles of the genus *Tanarthrus*.

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