



Science Newsletter

Updates on respiratory disease affecting desert bighorn sheep in and near Mojave National Preserve

Clinton W. Epps¹, Daniella Dekelaita¹, and Brian Dugovich²

Desert bighorn sheep (*Ovis canadensis nelsoni*) are an iconic mammal of the desert southwest and are found in small mountain ranges scattered across Mojave National Preserve (Preserve) and nearby desert habitats in southeastern California. In many areas, they are the only large native herbivore that can persist, inhabiting places that are too hot, dry, and sparsely vegetated for deer. California is thought to be home to ~3000-5000 desert bighorn in total (1); desert bighorn sheep are uniquely adapted for the harsh environment of the southwest deserts and populations appear to be resilient in spite of threats from poaching, climate change, drought, and habitat fragmentation (2, 3). In the Mojave Desert, bighorn sheep populations are strongly fragmented by expanses of flat desert between mountain ranges, and in some cases, by behavioral and physical barriers such as interstate highways (4). Yet, southeastern California, including the Preserve, represents the largest intact “metapopulation” of naturally

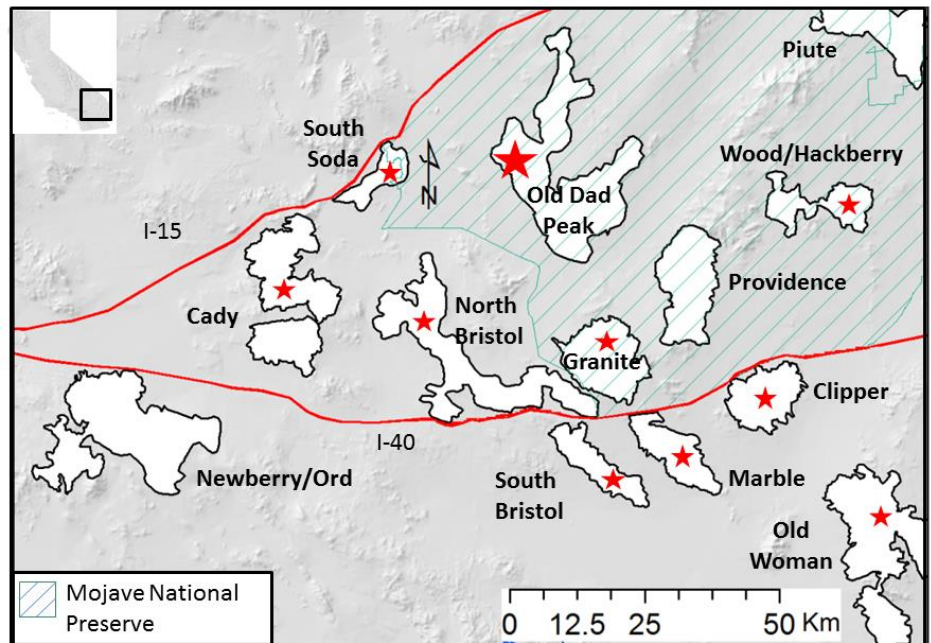


Figure 1. Map of Mojave National Preserve and nearby areas in southeastern California, showing mountain ranges (white polygons) where respiratory disease of bighorn sheep is being studied using GPS collars, remote cameras, disease screening of captured animals, fecal DNA, immunological and genetic measures, and other methods. The respiratory pathogen *Mycoplasma ovipneumoniae* was first reported at Old Dad Peak in spring of 2013 (large red star); current infection or past exposure has been confirmed at other red-starred ranges. Providence and Piute Mountain Ranges have not yet been tested; only four animals from the Newberry/Ord population were tested in 2014, but no definitive evidence of disease in those animals was found.

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¹ Department of Fisheries and Wildlife
Oregon State University, Corvallis.

² Department of Integrative Biology
Oregon State University, Corvallis.

persisting desert bighorn sheep – a system of small populations linked by intermountain movements and experiencing local extinctions (loss of entire populations) and recolonizations (populations reestablished in empty habitat by natural dispersal from other occupied populations) (2, 3, 5, 6). Although numerous population extinctions occurred in the 20th century, in recent decades desert bighorn sheep populations in the region appear to have expanded (1, 7), bolstered in part by human-made water developments and translocations (8), but also by natural recolonization (6).

A previously underestimated threat to desert bighorn sheep in the Preserve has recently emerged. Potentially fatal respiratory disease,

originally contracted by direct contact with domestic sheep or goats but then presumably spread by natural movements of bighorn sheep across wide areas (9-11), appeared in the Mojave Desert in 2013. Across western North America, domestic ovine (sheep) and caprine (goat) respiratory pathogens have been identified as one of the major threats to persistence of bighorn sheep (9, 12). Until recently, outbreaks were more commonly reported in the Rocky Mountain subspecies (*O. c. canadensis*) (13, 14), with major outbreaks occurring in nearly every state where that subspecies is found. However, in recent years, scientists in the Southwest have observed respiratory disease outbreaks in many desert bighorn sheep populations, including Arizona, Nevada, Utah, and California (15). One

such outbreak was reported in the Preserve in spring of 2013, when sick and dying bighorn sheep were reported in the Old Dad Peak population (16) (Figure 1). Because of the relative isolation of this population (4, 17), biologists responding to the initial outbreak were hopeful that it might be contained to that mountain range. Two months later, however, sick bighorn were reported over 30 km away in the Marble Mountains south of Interstate 40 (Figure 1), and it was clear that a widespread epidemic was underway.

The National Park Service (NPS) and California Department of Fish and Wildlife (CDFW), in collaboration with researchers at Oregon State University and volunteers from the Society for the Conservation of Bighorn Sheep and the California Chapter for the Foundation for Wild Sheep, initiated monitoring and research immediately after the detection of the disease to determine: 1) the extent of the current disease outbreak, 2) likely patterns of spread among bighorn sheep populations in different mountain ranges, and 3) consequences for the bighorn sheep population at Old Dad Peak and other affected areas, in terms of survival of adults and lambs. Here, we describe what we have learned after the first two years of work to diagnose the disease, establish its extent and understand the potential for spread, and track its impacts on this unique species.

Detecting the disease—Establishing the extent of the disease was the first challenge. Infectious pneumonia in bighorn sheep is a respiratory disease complex with multiple pathogens, often acting concurrently, but disagreement persists as to the exact role played by different pathogens and parasites (11). A variety of pathogens have been associated with pneumonia in bighorn sheep, including *Mannheimia haemolytica* and *Biberstera trehelosi* (11), species from the Pasteurellaceae family of bacteria. In recent years, another bacterium, *Mycoplasma ovipneumoniae* (*Movi*), has been recognized as an important pathogen capable of causing bighorn pneumonia or possibly acting in concert with other bacteria to greatly worsen their effects (11, 14, 18, 19). Indeed, *Movi* has been implicated in most recent outbreaks of bighorn pneumonia throughout the West (11, 12). When a

bighorn sheep has severe pneumonia – marked loss of functional lung tissue due to bacterial infection, inflammation, and fluid accumulation – death can occur very quickly. However, before that point, a sick animal may show few obvious symptoms. Coughing and nasal discharge are the first telltale signs, but are not entirely specific to pneumonia, and even with pneumonia may only be present when the animal exerts itself. Therefore, identifying potentially diseased animals in the field requires close observation of bighorn sheep for long periods of time; reliable detection of the disease and identification of the pathogens involved requires prompt necropsy of dead animals (i.e., by opening the carcass and examining the lungs) before rapid deterioration in the desert environment, or collection of blood and other samples from captured animals, followed in both cases by laboratory testing for pathogens.

Two basic laboratory tests are used to detect *Movi*, and those tests give different information: the first, ELISA (enzyme-linked immunosorbent assay), screens for antibodies to respiratory pathogens in the animal's blood. This serological test, if positive, indicates that the animal was infected by that pathogen some time in the past, creating a response in its immune system specific to that pathogen. The ELISA test is advantageous because it can be conducted on fresh or archived samples, such as blood serum samples collected in previous decades and stored in freezers. However, from a single sample, this test cannot distinguish animals that are currently infected and shedding pathogens from animals exposed to the pathogen in the past and now less likely to be contagious. The second test, PCR (polymerase chain reaction) is a newer diagnostic tool with significant advantages over older, slower culture-based methods (methods that require growing bacteria), which are less sensitive for many bacteria that do not grow readily in the laboratory. PCR identifies pathogen DNA currently present in the host, which indicates that the animal is actively or recently infected. During capture operations, or on recently-dead carcasses, biologists swab a bighorn sheep's nose, throat, or ear canal, where the pathogens are likely to be present in an infected animal. The swab is tested for DNA specific to the pathogens of interest by amplifying bits of DNA and matching sequences to a

pathogen library. That DNA sequence can be compared to other known strains, which helps determine whether outbreaks in different places come from the same initial source. Although *Movi* testing is increasingly used, additional tests are often used to screen for some of the other bacteria associated with bighorn pneumonia, such as the Pasteurella-type bacteria mentioned previously.

What is the extent of the disease?—In the Preserve outbreak, pneumonia was first confirmed at Old Dad Peak by examining bighorn sheep found dying or dead; subsequent laboratory tests found that *Movi* was present. Later that summer, when animals were reported coughing in the large Marble Mountains population to the south (Figure 1), sick animals were collected and tested, once again confirming *Movi*. Subsequently, this strain was found to be identical both to the one detected in the Old Dad Peak population as well as to a strain of *Movi* detected in a 2013 outbreak in western Nevada. At this point, the pathogen appeared to have widespread distribution in the region.

Efficient testing for disease detection requires capturing multiple bighorn sheep in each population, at which point swabs and blood samples can be taken for PCR and ELISA diagnostics. Therefore, we captured bighorn sheep in most of the populations across the Preserve in November of 2013 (70 females, 2 males, Figure 1), expanded to other more distant areas in November 2014 (33 females, 11 males, Figure 1), and captured an additional 60 animals in the study area in November of 2015 (43 females, 17 males). Although the captures serve other research purposes (survival, movement, and immunogenetic studies; Figure 2) they have also provided us with a relatively comprehensive picture of the current extent of *Movi* in the Preserve and other parts of California's Mojave and Sonoran Deserts.

We detected bighorn sheep with active *Movi* infection (PCR) or evidence of past *Movi* infection (ELISA) in all 9 populations tested in 2013 (Figure 1); all infections were the same *Movi* strain as first detected at Old Dad Peak (20). Despite varying levels of population isolation in the various mountain ranges, *Movi* seemed to be

infectious enough to invade the entire study region. In 2014, captures over a wider area returned mixed results. Two bighorn sheep captured in southern Death Valley National Park showed no evidence of current or past *Movi* infection, nor did 4 bighorn sheep captured in the Newberry Mountains south of I-40 but well to the west of the initial outbreak (Figure 1); however, these sample sizes were too small to confidently determine that these populations were not affected (9). Nevertheless, *Movi* was verified in several different populations including the Old Woman, Cady, and Orocopia Mountains (Figure 1), although the *Movi* in the Orocopia Mountains appears to be a different strain than the 2013 outbreak. In summer 2015, sick bighorn sheep were reported in Joshua Tree National Park, and recent lab tests on a dead bighorn recovered for testing have confirmed that yet another strain of *Movi* is present. Recent tests have confirmed that the *Movi* strain found in the Preserve is now present in a bighorn sheep population in Arizona, suggesting transmission via bighorn sheep that reportedly occasionally cross the Colorado River along the California-Arizona border (21). As information on distribution of *Movi* strains improves, biologists in the affected states will be able to ask questions about whether different *Movi* strains affect populations in different ways.

What are the consequences of the disease?— Although ovine pneumonia has been observed and studied for decades in Rocky Mountain bighorn sheep (e.g., 13, 22, 23), we still know little about how the disease affects desert bighorn sheep, or whether the disease is likely to persist once a metapopulation is exposed. The initial investigation at Old Dad Peak showed that this outbreak was capable of killing adult bighorn sheep, as dozens of dead rams and several sick and dying ewes were found in spring and summer of 2013, including all four radio-collared ewes present before the outbreak. Therefore, the second important goal for the 2013 collaring was to get real-time information on survival of adult bighorn sheep around the Preserve. Unlike earlier studies in the region, we now have the opportunity to deploy modern GPS collars designed for large animals that are capable of providing 1-12 precise locations per day, uploaded by satellite link and then observable by computer. Each collar also contains a “mortality



Figure 2. Bighorn sheep are captured by skilled teams using a helicopter, and in some cases are transported to a base camp for examination by veterinarians (Photo by B. Dugovich).

alert”, which sends a special message when the collar does not move for a predetermined length of time. Thus, we can now monitor movement, understand habitat use, and track survival for more than 150 bighorn sheep in or near the Preserve.

In 2014, we initiated a graduate research project to determine how environmental factors such as rainfall and nutrition interact with the disease to influence bighorn populations in the Preserve. Besides tracking adult survival and movement, we are also working to characterize another likely consequence of the disease: poor lamb recruitment. After the first contact of a population with respiratory pathogens, an all-ages die-off may occur. However, unless new strains of pathogens are introduced, adult bighorn appear to gain some resistance to *Movi*, and less often die from pneumonia after that initial period of high mortality. Unfortunately, low lamb survival may persist for many years (22). This ongoing lamb mortality may be caused by persistent chronic infection in at least some of the ewes that “shed” the pathogen to their lambs (24). Lamb survival can vary widely depending on rainfall and forage quality (25), therefore another key piece of information for this study will be separating effects of disease and environmental variation, especially the effects of rainfall on forage and the subsequent impact on lamb recruitment (i.e.,

surviving to the yearling stage) (26). This is being attempted both spatially, by studying 9 bighorn populations, and temporally, by taking advantage of many years of remote camera data collected by Dr. John Wehausen of White Mountain Research Center in several key populations predating the disease outbreak. Lamb survival can be difficult to monitor on large landscapes: while radio-collaring individual lambs would give the best information, finding and capturing new lambs is extremely difficult among the cliffs and remote mountainsides favored by desert bighorn ewes in early spring. Therefore, we are using remote cameras to capture images of bighorn sheep at water sources during the summer (Figure 3), allowing us to estimate lamb to ewe ratios (a typical index of how many lambs survive over the course of the year). In some cases, we supplement those estimates with direct lamb and ewe counts collected by ground observers in several key populations. We are also collecting fecal samples for diet quality analysis (25), linking current conditions to more than 30 years of diet quality data collected in several mountain ranges, as well as remotely-sensed measures of vegetation growth (27). Combining those data will help us determine whether lamb to ewe ratios diverge from those expected given pre-outbreak relationships with precipitation and diet quality, how they vary across the study area with environmental conditions after the start of the

outbreak, and whether the seasonal timing of lamb mortality has changed because of the disease.

Although formal analysis is just beginning, the GPS collar and camera data have demonstrated two important conclusions about the current course of the disease: Firstly, we have not observed large numbers of adult bighorn dying from the disease since the first collars were placed in November 2013, either in Old Dad Peak or in other affected ranges. Secondly, we are seeing few lambs accompanying ewes by the end of the summer in many ranges. In combination with field observations of ewe groups and reports of coughing lambs from field personnel, this suggests that the disease is curtailing lamb recruitment and therefore could have significant effects on population dynamics. However, precise conclusions will require collecting several years' more data and completing formal analysis.

How does the disease spread?—Pneumonia-causing pathogens such as *Mov* are spread by contact, probably including indirect contact via airborne particles over short distances (28). Because bighorn sheep associate loosely in small groups throughout the year (29), and because rams actively pursue ewes in different groups for several months during the rut, individual contacts among bighorn appear to be sufficient to spread the disease rapidly both within and among populations. However, the pattern of such contacts among bighorn sheep probably varies widely across different ecosystems. For instance, in this region, large numbers of animals congregate at the few available water sources (natural and man-made) from late spring through fall, unlike many more northern bighorn habitats where water is less restricted. Thus, contact among desert bighorn at water sources may play an important role in disease transmission. For instance, the 2013 Old Dad Peak die-off appeared to begin early in the season of water use, and many bighorn sheep died near water sources.

With the unprecedented volume and quality of data now available from GPS collars, we hope to learn much more about how bighorn sheep move within populations - as well as, occasionally,



Figure 3. Remote cameras can provide detailed information on survival, reproduction, and physical condition of bighorn sheep during summer months when they use surface water frequently (Photo by D. Dekelaita).

between them. Our current understanding of how bighorn sheep move between mountain ranges in the Preserve is largely derived from genetic data collected and analyzed in the early 2000s (4, 30), as well as occasional movements observed using radio telemetry (reviewed in 17). That work suggested that the rates of movement among ranges varied widely depending on distance and topography (17); in some instances, little or no movement was suspected, such as across Interstate 40. Gene flow and infectious disease spread can both result from movements between the disparate populations. However, gene flow is a different process than a disease outbreak: for gene flow, animals must move, then stay and reproduce in the new area. Infectious disease, on the other hand, could be transmitted by even a very brief visit by a single animal. Therefore, the combination of genetic data and GPS collar data may provide the best picture of short and long-term movement patterns across the region. The GPS collar data collected to date have revealed some surprising movements by individual bighorn sheep, including very short-term forays into different populations, movements by females of >65 km, and in several cases, movement by males and one female across Interstate 40. GPS collar data will also help us to determine how

environmental conditions and availability of water sources influence seasonal movements and distribution of bighorn sheep.

When the outbreak at Old Dad Peak was first detected, we were initially hopeful that the disease might not spread to other ranges - assuming it originated at Old Dad Peak in the first place - because gene flow maps created in the early 2000s suggested this population was relatively isolated. However, in the dynamic Mojave metapopulation, even 12 years (two bighorn generations) can see substantial change. In that time, some populations appear to have grown (1), habitat in the North Bristol Mountains that had previously apparently only received occasional ram use became home to a reproducing population, and bighorn sheep appear to have discovered new ways to move around the landscape. During 2013-2015, we have resampled populations across the Preserve and the surrounding region to reanalyze genetic structure and learn whether new gene flow maps correspond with the spread of disease. Our preliminary results suggest that they do. For instance, we can now see that Old Dad Peak is clearly linked to the North Bristol Mountains by gene flow; bighorn in the North Bristol Mountains,

in turn, are clearly linked to populations in the Cady Mountains and the Granite Mountains (Figure 4) (31). In most cases, these links are being verified by movements we detect from GPS-collared ewes or rams. Thus, the rapid spread of *Movi* to both Old Dad Peak and the Marble Mountains population in a short time period conforms to our new understanding of bighorn sheep movements across the study area.

Why are some individuals or populations of bighorn sheep more susceptible to disease?—Respiratory disease mortality differs among individual bighorn sheep. Habitat fragmentation and fluctuating levels of connectivity have led to desert bighorn sheep populations with varying levels of genetic diversity from altered gene flow and inbreeding (30, 32). Therefore, even within the Preserve, detectable genetic differences exist between populations (Figure 4, 4), raising the likelihood that individuals and populations may have different variants of immune system genes related to genetic diversity. Thus, population responses to pneumonia may differ, and some of those differences may have a genetic basis influenced by habitat fragmentation and connectivity.

Researchers at Oregon State University (OSU) have taken advantage of the bighorn sheep captures in the Preserve to investigate “ecoimmunology” of desert bighorn sheep, a growing field of inquiry in which researchers attempt to relate immune system function to the ecology of the study animal and the disease (33). Goals for this part of the study include evaluating whether bighorn sheep immune system function varies among populations, and to explore the possible role of major histocompatibility complex (MHC) genes in determining how bighorn sheep experience respiratory disease. MHC genes are a key component of mammalian immune systems and influence how they fight pathogens such as harmful bacteria. MHC diversity is commonly studied in wildlife populations, because high diversity of MHC genes is thought to decrease disease susceptibility (34). In addition, “immunophenotype” - a characterization of how strongly an individual’s immune system reacts to pathogens - is being measured for bighorn sheep across the study area by counting immune system cells in blood samples from captured

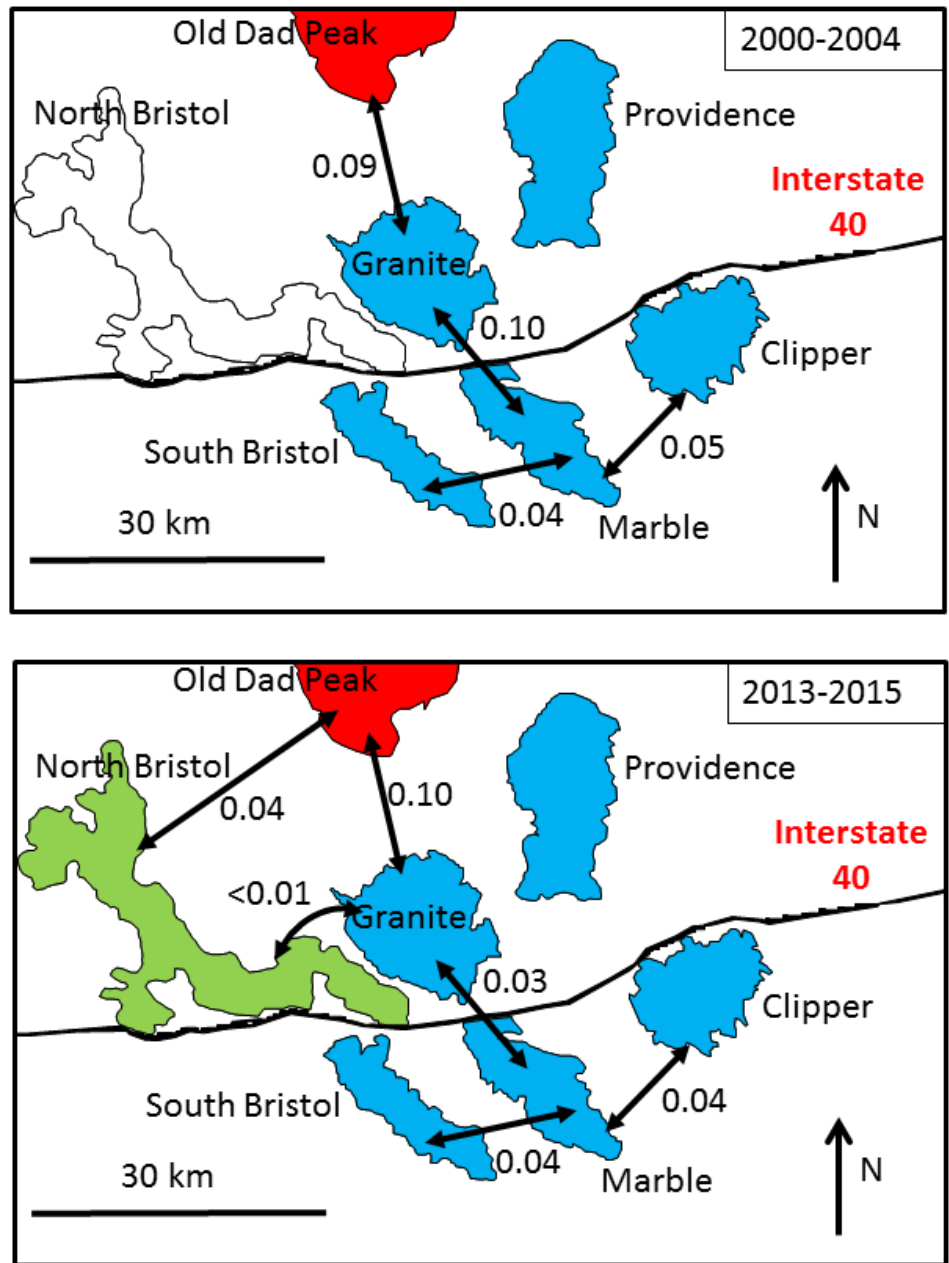


Figure 4. Preliminary analysis of recent nuclear DNA (16 microsatellites) recovered from fecal pellets of bighorn sheep and captured animals 2013-2015 suggests that movement of bighorn sheep among populations (colored polygons) has changed significantly since the first systematic characterization of gene flow conducted in 2000-2004 (39). Here, we show preliminary estimates of genetic structure (F_{ST} , numbers next to arrows) between selected ranges. F_{ST} is a measure of genetic distance, in this case, among pairs of populations; F_{ST} values range from 0 (complete mixing of individuals among populations) to a theoretical maximum of 1 (no shared genetic variation). In this system, F_{ST} values ≤ 0.05 are associated with frequent interpopulation movements (6), and maximum values do not exceed 0.40 (4). In 2000-2004, genetic structure suggested that bighorn did not move across Interstate 40, e.g. between the Marble and Granite Mountains, the North Bristol Mountains apparently lacked a resident population, and Old Dad Peak (red polygon) was relatively isolated. Both the new genetic data and observations of collared animals from 2013-2015 show that bighorn sheep now move across Interstate 40 between the Marble and Granite Mountains, and that strong gene flow and movements of collared animals link the Granite Mountains with the recently established North Bristol Mountains (green polygon) and the North Bristol Mountains with Old Dad Peak. Thus, the rapid spread of respiratory disease to both Old Dad Peak and Marble Mountains conforms to our new understanding of movements of bighorn sheep in the study area. Not all comparisons among populations are shown.

animals, as well as other tests such as the bacterial killing assay (BKA) (33). The BKA examines how well blood plasma and its associated anti-microbial components can kill test bacteria, in this case, *E. coli*, under laboratory conditions (Figure 6). In 2013, the OSU research team set up a temporary laboratory at the University of California's Sweeney Granite Mountains Desert Research Center to process blood samples and initiated laboratory analyses. Subsequent captures have also relied on a temporary mobile laboratory set up in a truck-towed trailer (Figure 5) or large tent.

Preliminary analysis of combining these ecoimmunology results with the disease testing results and previous genetic work (32, 35, 36) has revealed some intriguing patterns. During the initial 2013 *Movi* outbreak, we observed more actively-infected individual bighorn sheep in populations with lower genetic diversity at genetic markers linked to immune-system genes (37), although the different timing of disease spread to different populations may offer a counter explanation. Expression (essentially, whether the gene is "turned on" or not) of MHC genes also differs markedly among populations in the study area, as does the ability of blood plasma of bighorn sheep in those populations to kill bacteria (BKA, Figure 6) (38). These early analyses suggest that different populations could experience different impacts from the disease based on their genetic makeup, and reinforce the possibility that the natural and human-caused fragmentation of desert bighorn sheep populations in the Mojave may contribute to varied responses of bighorn sheep to respiratory pathogens in different mountain ranges.

Where next?—In fall of 2015, 60 additional bighorn sheep were collared to augment sample sizes in the movement and demography study in the Preserve, as well as to further contribute to the study of immunogenetic variation and immune system function. Field work to assess lamb survival, adult survival, and disease impacts will continue. Ultimately, we hope that these interlocking research efforts in the Preserve will contribute to new fundamental knowledge about the impact of habitat fragmentation, disease, and evolutionary processes on desert bighorn sheep. Our aim is to strengthen the ability of the NPS,



Figure 5. Initial laboratory analysis of blood and fecal samples collected during bighorn sheep captures takes place in temporary laboratory facilities set up in the field (Photo by B. Dugovich).

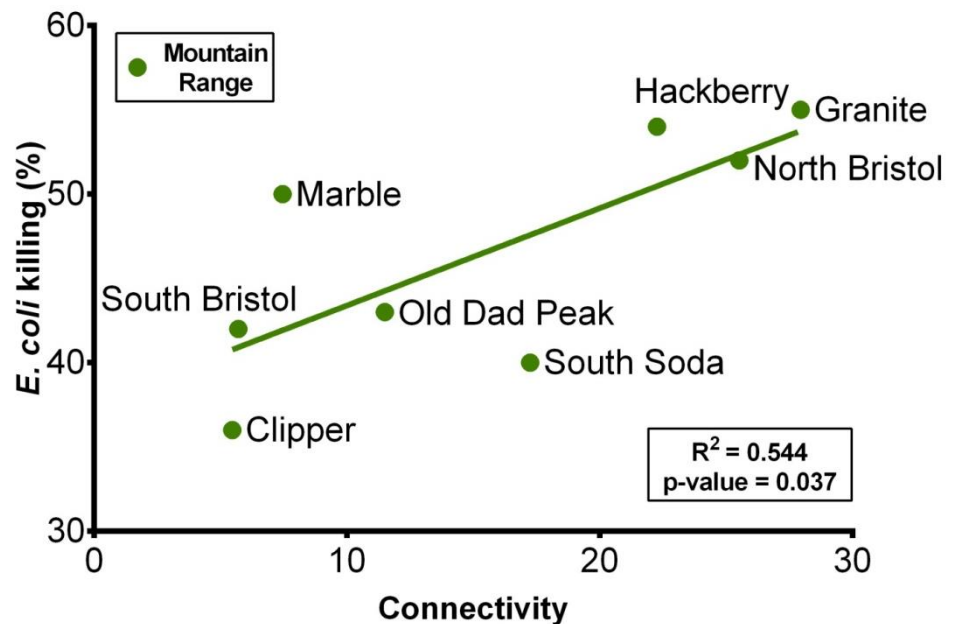


Figure 6. The percentage of test bacteria (*E. coli*) killed by plasma from bighorn sheep blood samples (bacteria killing assay [BKA]) from 8 populations in the Mojave study area increases significantly in populations with higher connectivity (Demographic Weighted Closeness, (35)). Connectivity of each population is determined from the number and proximity of nearby bighorn sheep populations, based on a dispersal model derived from genetic data (35). The BKA test provides a measure of immune system function. Genetic diversity of desert bighorn sheep populations also increases strongly with population connectivity (30, 32); thus, one hypothesis to explain this relationship between immune system function and connectivity is that populations with higher genetic diversity have immune systems better equipped to kill certain pathogens (40).

CDFW, and others to manage this iconic species in the face of new threats and contribute to a better appreciation of the unique ecosystems found in the Mojave Desert.

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Ovis canadensis drawing by Pat Hansen.

Habitat selection and head-starting of desert tortoises in Mojave National Preserve

A. Justin Nowakowski¹ and Brian D. Todd¹

The Mojave desert tortoise (*Gopherus agassizii*) was listed as federally threatened under the Endangered Species Act in 1990 due to widespread population declines attributed to an array of threats, including but not limited to: illegal collecting and hunting, disease, increased fire frequency and severity, the spread of non-native plants, changing climate, and continued habitat loss from urbanization, renewable energy projects, and road construction (1). Nearly 2.5 million hectares of critical habitat have been identified for the recovery of Mojave desert tortoise, primarily on federal lands. Critical habitat is an officially designated area that contains essential features (e.g., food and shelter) that allow for population growth, normal behavior, and therefore species recovery. The recovery and persistence of desert tortoise populations depends on ameliorating threats by protecting existing populations and habitat, as well as developing strategies to aid in their recovery.

Of growing concern is the conflict between maintaining healthy desert tortoise populations on public lands and recent policies that are increasing the footprint of renewable energy in the desert Southwest, possibly degrading or fragmenting areas of critical habitat (2). As of 2010, applications were approved for seven solar energy projects on public lands and three on private lands, totaling 14,500 ha across the range of the desert tortoise (1). This rapid expansion of renewable energy infrastructure demonstrates an urgent need for research-based strategies to reconcile state and federal renewable energy goals with the Desert Tortoise Recovery Plan (1). These strategies should aim to minimize the potential negative effects of renewable energy projects on local (e.g., individual mortality) and landscape-scale (e.g., connectivity and gene flow) population processes and identify viable mitigation methods. In this context, mitigation

¹ Department of Wildlife, Fish, and Conservation Biology
University of California, Davis.

methods refer to actions that aim to limit or offset the negative effects of development projects on tortoise populations, occasionally through promoting recovery or better protection of populations elsewhere, but may also include actions such as translocation and captive breeding programs. Our goals were two-fold: 1) to assess survivorship and growth rates in juvenile tortoises when raised in captivity versus the wild, and 2) to learn more about the ecology of juvenile tortoises, in particular habitat selection at very early stages in life (additional details of the project are provided in 3).

Our project first aims to evaluate the effectiveness and feasibility of a head-starting program as a means to increase juvenile survival and growth rates and therefore support greater recruitment when these animals are released in natural populations. Head-starting desert tortoises consists of captive rearing of animals through the early stages of life, followed by their release into the wild once they have reached a size class (>105 mm in length) that is less vulnerable to predation or desiccation (4). Our study estimates survival of animals released early in life (much less than 105 mm) for comparison with later releases of animals larger than 105 mm. Although head-starting is not a panacea that will save desert tortoises, limited application of this method may be useful as a short-term recovery or mitigation tool, augmenting populations and thereby offsetting the loss of individuals in specific areas while scientists continue to work on longer-term strategies to promote species recovery and protection. Secondly, in order to learn more about the habitat selection process, we attached radio transmitters to juvenile desert tortoises and tracked them in their natural habitat for three years. This study was specifically interested in identifying fine-scale habitat characteristics that may influence a juvenile tortoise in selecting a home range. These data will help fill a critical information gap about the survival and growth of juveniles into adults, an important determinant of

population growth rates in turtle populations (5). A better understanding of juvenile desert tortoise habitat selection may help inform placement or construction of energy infrastructure in a way that spares areas of high quality habitat. Information on juvenile habitat use can also improve targeted field surveys for individual tortoises that may need to be relocated away from construction sites.

The efficacy of head-starting desert tortoises as a recovery tool requires additional study, however, the potential benefits of such a program are clear. Tortoises are long-lived (50-80 years) and can take up to 20 years to reach sexual maturity. Because juvenile tortoises typically have lower survival rates than adults, head-starting programs that increase juvenile survival can increase population growth in the long-term as long as adult survival remains high (4,6). Population models suggest that even small increases in juvenile survival can promote population persistence under some circumstances (7). In areas where humans are encroaching on pristine desert habitat, there is a concomitant increase in raven and coyote populations; these predators thrive near human developments and have been linked to a reduction in desert tortoise survival (8, 9). Increasing juvenile survivorship and growth rates in captivity, followed by successful establishment of these captive-reared individuals in areas of high quality habitat, may help managers reverse the ongoing declines of desert tortoise populations.

To evaluate the efficacy of a desert tortoise head-starting program, we recorded the survivorship and growth rates of hatchling and juvenile (hereafter juvenile) desert tortoises that were released directly into the desert (within 18 months of hatching) and compared them to their siblings that were kept in protected outdoor enclosures over the same period. The directly released tortoises were radio-tracked in Mojave National Preserve (MNP) upon release and will

continue to be tracked for as long as funding will allow. The head-started tortoises are being raised in outdoor enclosures that exclude predators and receive supplemental rainfall from an aquifer-fed sprinkler system. This research is being conducted at the Ivanpah Desert Tortoise Research Facility (IDTRF) in MNP (Figure 1). The IDTRF was built in 2010 to facilitate recovery of the desert tortoise through research in MNP, and more specifically to study protocols for augmenting natural populations with individuals raised in captivity. In order to produce juvenile tortoises at the facility, researchers monitored nearly 30 wild adult female tortoises in Ivanpah Valley between 2011–2013, thus providing three annual cohorts of hatchlings (2011, 2012, 2013) for this study. When females were examined (radiographed) and found to have eggs (Figure 2), they were brought to the IDTRF and allowed to nest inside the predator-proof enclosures. Once they laid their eggs (mid-April through early July), females were then returned to their burrows in MNP and released, usually within just 15–20 days. Eggs were left to incubate in the protected enclosures for approximately 80 days after they were laid. When the eggs hatched in late summer and early fall, the hatchling tortoises were each given a unique mark by notching the marginal scutes (bony scales) of the shell and all were measured to determine body size and weight.

Over three years (2011–2013 inclusive), a total of 197 hatchling desert tortoises were produced and assigned to one of three treatments; siblings from the same clutch were evenly distributed among treatments. The three treatment groups included: 1) those released into MNP after hatching (age at release was 0, 6, 12, or 18 months; the “direct release” group), 2) those head-started in enclosures supplemented with “low rainfall” (4.5 cm per year; the “LR” group) and 3) those head-started in enclosures supplemented with “high rainfall” (8-9 cm per year; the “HR” group). Each enclosure measured 30 x 30 m and was subdivided into smaller 10 x 10 m enclosures. It would be negligent to study animals in captivity without providing some type of protection from predators or supplemental dietary/nutritional needs, therefore it was a requirement of the study to ensure proper health and safety measures were taken for the tortoises. We



Figure 1. The Ivanpah Desert Tortoise Research Facility was built to support the research and recovery of desert tortoises.

excluded terrestrial predators using corrugated metal sheets partially buried along the perimeter of the enclosures, and we excluded aerial predators by covering enclosures with mesh netting (Figure 3). In order to mimic natural conditions, the timing of added rainfall followed typical precipitation patterns for the eastern Mojave Desert of California, which is primarily winter rainfall with additional summer monsoonal rains. Enclosures were carefully constructed within natural habitat with an effort to maintain the original vegetation on site. The artificial conditions of captivity are unavoidable and will obviously influence survivorship and growth rates of tortoises reared in captivity; however, the goal of this project was to provide additional data for developing viable strategies for augmentation programs using head-started animals.

For the direct release treatment, a total of 46 juveniles representing different year cohorts and age classes were released into MNP in Fall 2012, Spring 2013, and Fall 2013. Prior to release, we recorded weight and length of each tortoise and then affixed a small radio-transmitter to the shell (Figure 4). To estimate survival of the direct release group, we radio-tracked each tortoise 2–4 times per month during the winter (when tortoises spend most of their time below ground) and 1–2 times per week during the rest of the year when tortoises are active. When an individual was located, we recorded its position with a handheld GPS unit and measured its



Figure 2. A radiograph of a gravid female Mojave desert tortoise showing five highly calcified eggs that are ready to be laid. Also visible are a radio-transmitter (top right) and small temperature recorder (top left), both attached externally to the carapace of the animal.

weight and length. As of November 2014, only 16 of the initial 46 direct release tortoises were still known to be alive. Twelve individuals had fates that could not be definitively determined, and while their disappearance may have been due to transmitter failure or predation, we treated these disappearances as mortalities when estimating survival of the direct release animals. We calculated monthly survival as the proportion of released individuals known to be alive in a given month, which represents a conservative, lower-end estimate of survival. To estimate survival of the head-started tortoises (both the LR and HR groups), we searched the pens extensively every six months, measuring and weighing each

tortoise, and also recorded any surface-active animals observed on a monthly basis. These captive animals will continue to be monitored under their current treatments until they attain a minimum of 105 mm in length, after which they will be tracked and monitored for a second phase of this project.

By the end of 2014, the annual survival rate of head-started tortoises (combining LR and HR treatments) ranged from 84.3 – 100%, whereas the annual survival rates for direct release tortoises was much lower and ranged from 33.3% – 55.6%. Although there was no discernable difference in survival between the two head-started groups that received differing levels of supplemental rainfall, growth rates were slightly higher in the high-rainfall group (13.9 ± 0.99 mm/yr; $n=19$) than in the low-rainfall group (11.0 ± 0.78 mm/yr; $n=20$) based on the first cohort of animals, suggesting that rain supplementation could be used to increase annual growth rates in captive animals. Additionally, growth rates were higher (12.5 ± 1.03 mm/yr; $n=39$) for those head-started animals than the wild direct release animals (9.71 ± 1.30 mm/yr; $n=10$). Mortality of direct release and head-started individuals typically occurred over the winter when animals were inside burrows. Although canids or avian predators were the likely cause of death for four of the direct release individuals, the majority of dead tortoises found outside of burrows appear to have died from exposure to heat or dehydration. In addition, tortoises that were released into the wild directly after hatching were consistently smaller than their siblings that spent time (6, 12, or 18 months) in the enclosures. The greater annual survival and growth rates of captive, head-started tortoises compared to the direct release tortoises demonstrates the potential for head-start programs to increase the number of larger juveniles and possibly aid recruitment into adult populations after eventual release, offering some hope that the method could be used to augment populations for short-term recovery or mitigation. However, based on the results of this portion of the study, releasing animals that were captive for 6 to 18 months does not confer a higher survivorship in the wild.

The second major objective of our project was to determine the habitat needs of juvenile desert

tortoises. Juveniles are rarely seen in the wild, creating a knowledge gap in the basic ecology of desert tortoises, which can hinder recovery efforts for the species. We compared habitat characteristics between known tortoise locations and random points to identify habitat features that may be important predictors of tortoise locations, and therefore, likely represent key components of juvenile desert tortoise habitat. To do this, each time we located one of the 46 direct released tortoises, we collected data about the surrounding habitat where it was found, as well as at a paired random point 200 m from the animal's location, a distance the animals were capable of moving based on data of their movements from this study (Figure 5). We recorded information about the availability of cover (any aboveground structure, typically shrubs, that provides shade and/or concealment from predators), the type of substrate, the composition of the plant community, the distance to the nearest burrow and wash, and the number of small mammal burrows within one square meter.

We found that, in general, tortoises located at burrows were typically under shrub cover, and the immediate area had greater densities of creosote (*Larrea tridentata*), had more washes and fewer white bursage (*Ambrosia dumosa*) than at random points. Also, there was a positive association between the location of a tortoise and the number of small mammal burrows within one square meter, likely because juvenile desert tortoises are not as proficient as adult tortoises at digging their own extensive burrows for shelter. Instead, juvenile tortoises find existing mammal burrows and repurpose them for their own use (10). When tortoises were found away from their burrows, they tended to be closer to washes and perennial plants than were random points. These results build on previous broad-scale studies of habitat suitability for desert tortoises (11, 12) by filling a major information gap on fine-scale habitat selection in juvenile desert tortoises. Habitat selection is a fundamental behavioral process that ultimately contributes to population growth by allowing individuals to choose appropriate habitat in which to grow and survive. These new insights into juvenile desert tortoise habitat use may be valuable for future recovery efforts.



Figure 3. Mojave desert tortoises in the outdoor enclosures were protected from predators by durable corrugated metal walls and fencing and an overhead net that excluded birds. Aquifer-fed sprinklers, shown here in operation, were also used to provide supplemental rainfall to simulate natural precipitation patterns.



Figure 4. Juvenile desert tortoises in the direct release treatment were outfitted with small radio-transmitters and released shortly after hatching. Their growth and survival in the wild was compared to that of tortoises kept in outdoor enclosures and provided with additional supplemental rain and safety from predators.

Our study provides new information on two methods to reduce the negative effects of proposed development projects on desert tortoise populations. First, head-starting programs may be an effective short-term mitigation tool that allows land management agencies to increase juvenile survival and growth in local populations while focusing on broader recovery objectives and management issues. Juvenile desert tortoises are more vulnerable to dehydration and predation than adult tortoises. The addition of supplemental rainfall and exclusion of predators resulted in greater survival of head-started individuals compared to direct release tortoises. Survival of direct release tortoises in this study was similar to that of tortoises released after being reared for 2–15 years in enclosures without supplemental rainfall in a previous study (13). It remains to be seen whether the benefits of head-

starting in concert with supplemental rainfall will improve post-release survival in the wild, something that we will continue to study in later phases of our research. Our results also suggest that as little as 4.5 cm of additional rainfall may be sufficient to increase the growth rates of juvenile tortoises, decreasing the time it takes for them to reach a size at which predation risk decreases in the wild (approx. 105 mm in length). Although our findings show that head-starting can increase survival in the juvenile age class, additional study is needed to fully evaluate the effectiveness of head-starting programs as a mitigation tool. For example, it may be necessary to minimize the time animals spend in captivity to reduce the chance of animals habituating to captivity and subsequently failing to establish and thrive in the wild when released after extended time in captivity.

A second way in which our results may be useful is that we identified important habitat features for juvenile desert tortoises, including small mammal burrows, washes, and perennial shrubs such as creosote bushes. The presence of creosote likely benefits juvenile tortoises in multiple ways: creosote provides cover from extreme temperatures and predation; it also attracts small mammals that, in turn, create burrows that are used by juvenile tortoises; and creosote facilitates establishment of annual forbs that provide forage for tortoises (14). Washes may attract juvenile tortoises, in part, because forage plants may grow in higher densities along wash margins. Information about key habitat features, such as small mammal burrows and perennial shrubs, can help guide planning locations of development, such as renewable energy infrastructure, in a way that preserves key habitat features for juvenile desert tortoises. In addition, the effectiveness of translocation efforts, site selection for release of head-started individuals, and habitat restoration activities can be improved by incorporating information on juvenile habitat use. For example, the results of our work suggest that habitat restoration for desert tortoises will need to include the propagation and planting of creosote shrubs and the recovery of small mammal communities. Additional study will be needed to evaluate methods for applying habitat-selection data to recovery efforts and to determine the long-term efficacy of head-starting



Figure 5. Researchers collected data on the plant communities and other landscape features at each tortoise location and at a paired random point to determine the types of habitat preferred and used most often used by the direct release juvenile tortoises.

programs. Ultimately, however, the conclusions drawn from this study should help land management agencies formulate strategies for balancing renewable energy goals with the recovery of the Mojave desert tortoise.

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Insolation-related mechanical weathering of desert pavement rocks in the Mojave Desert

Martha-Cary Eppes¹

Physical weathering is a primary part of sediment production, chemical weathering, and overall landscape evolution (e.g. 1), yet very little is known about the rates, processes, and environmental factors that are characteristic of the mechanical breakdown of rock at Earth's surface in different settings. In particular, the role of the sun in producing cracks in desert rocks has been disputed and more or less discounted for over a century (e.g. 2).

Recent evidence suggests, however, that thermal stresses produced in rocks during the sun's east to west transition across the sky may play a key role in generating and propagating cracks (e.g. 3, 4, 5). This solar transit is hypothesized to subject rocks to a repeating thermal field geometry (Figure 1) resulting in a thermal-stress geometry that ultimately produces cracks with certain orientations. This hypothesis is supported by the fact that preferred north-east (NE) orientations are common to most cracks in desert rocks observed at mid-latitudes around the globe (3, 4, 6).

If these NE-oriented cracks in surface rocks are attributable to insolation-related processes, then key questions remain: How do specific rock properties (rock type, rock shape, or surface exposure age) affect cracking? Over what time scale does cracking operate to break down rocks to form the uniform desert pavement surfaces common in the Mojave Desert?

In answering these questions, we may gain further insights into the exact mechanisms by which cracking operates. For example, solar-induced thermal stresses may be higher for heterogeneous rocks because they contain adjacent minerals with higher differences in their coefficients of thermal expansion (7, 8). To test this hypothesis, it is predicted that crack densities will be higher in plutonic rocks than in basalts or

¹ Geography & Earth Sciences
University of North Carolina, Charlotte.

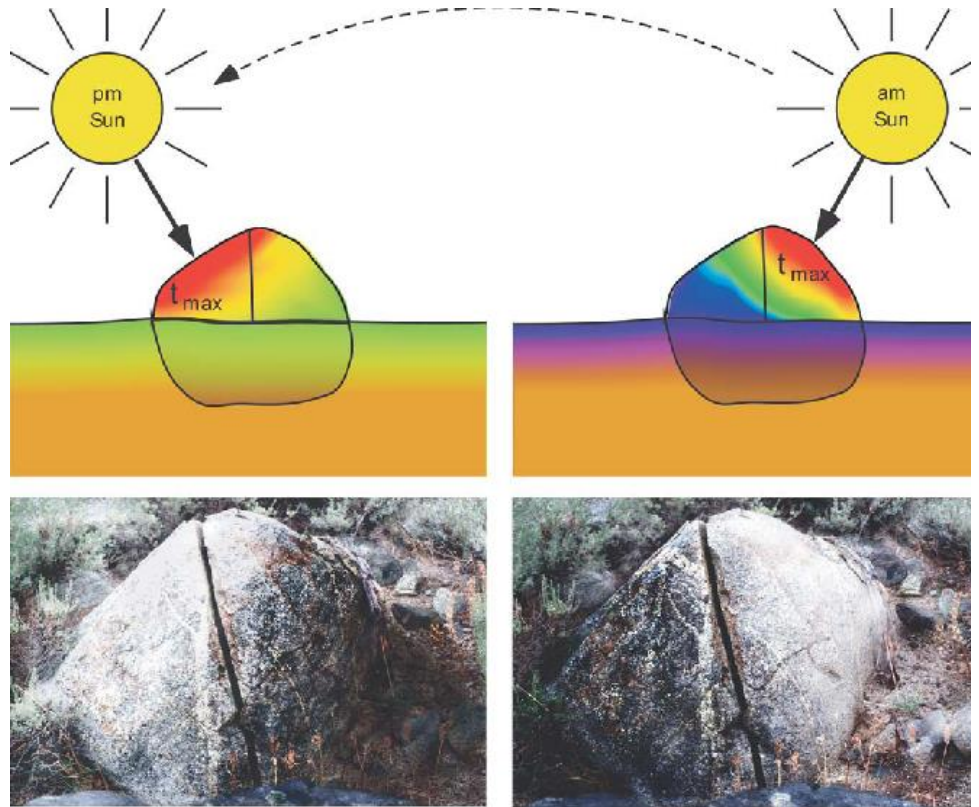


Figure 1. Conceptual model of directional solar-induced temperature fields arising from daily heating and cooling of a rock surface. It is inferred that solar-induced stresses resulting from these temperature fields would share a related geometry, and thus would serve to propagate cracks in directions related to the stress. Modified from (5).

carbonates, which are more homogeneous.

Despite the fact that such relatively simple field-derived metrics might provide key insights into mechanical weathering processes, few, if any, studies have collected comprehensive data regarding rock cracking characteristics. It was therefore the goal of this research to examine, to our knowledge for the first time, the detailed cracking characteristics of rocks found in desert pavements.

The Mojave Desert is an ideal location for studying the evolution of cracking in rocks of different size, shape, and surface exposure time. In particular, alluvial fan surfaces of the Providence Mountains (Figure 2) have been mapped in great detail and range in age from nearly 1000 years up to almost 200,000 years. In

addition, the fans are characterized by desert pavement surfaces with a variety of rock types (Figure 3) ranging from granite to meta-volcanic rocks to limestone (7). In this study, we specifically examined cracks in rocks on five different aged alluvial fan surfaces (Figure 2), Qf7 – ~1ka, Qf6 – 4ka, Qf5 8 – 12ka, Qf4 20 – 40ka, and Qf3 60 – 80ka (7, 8), as well as the 140 ka Basalt Flow I (9) in the Cima volcanic field.

On each of the five alluvial fans and the basalt flow we collected two different data sets. In the first, we collected measurements for all rocks greater than 5 cm in maximum length, referred to as "all rock transects." In the second, in order to examine a statistically significant population of larger rocks, which were not as common on any given surface, we collected measurements for all rocks greater than 15 cm in maximum length

(referred to as “large rock transects”). For both datasets, rocks were chosen at set increments along transects established within mapped fan units (Figure 3A); any boulder with a long axis greater than 2 m was not counted.

We collected data for approximately 150 rocks on each of the five different aged alluvial fans and the basalt flow, for a total of 1027 rocks in the entire study. Each rock was observed for cracks, which are defined here as a linear void >2 cm in length, then data were collected regarding crack size, orientation, and relationship to other features on the rock surface (Table 1). These data were collected for a total of 3131 cracks. Geometric and weathering details for each rock were also measured or noted (Table 1). We assigned rocks to one of three broad categories: plutonic - coarse grained igneous intrusive rocks; carbonate - any limestone or marble; and volcanic - fine-grained igneous extrusive rocks and meta-intrusive rocks.

Here we present results for two primary crack characteristics, density and orientation, as a function of surface age and rock type (Figures 4-11). Orientations are presented as strikes and dips (Figure 12). Crack strike refers to the orientation of the crack plane relative to true north if you were to draw a horizontal line on the crack plane surface, whereas the dip refers to the angle (from zero to 90) of the slope of the crack face below a horizontal plane. Orientation data were always collected using the right-hand-rule; because strike “goes” in two directions, for consistency, the right-hand-rule chooses the strike direction where dip is down to the right.

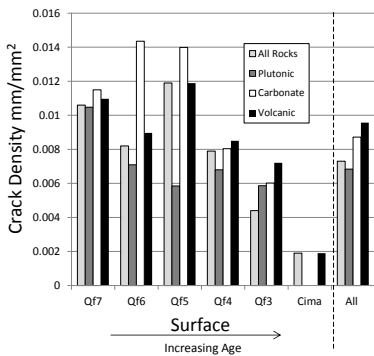


Figure 4. Comparisons of crack density for different aged surfaces (indicated by Qf designations, as given in the text) and for different rock types. See text for ages of surfaces and for calculation methods. In general, density decreases with surface age.

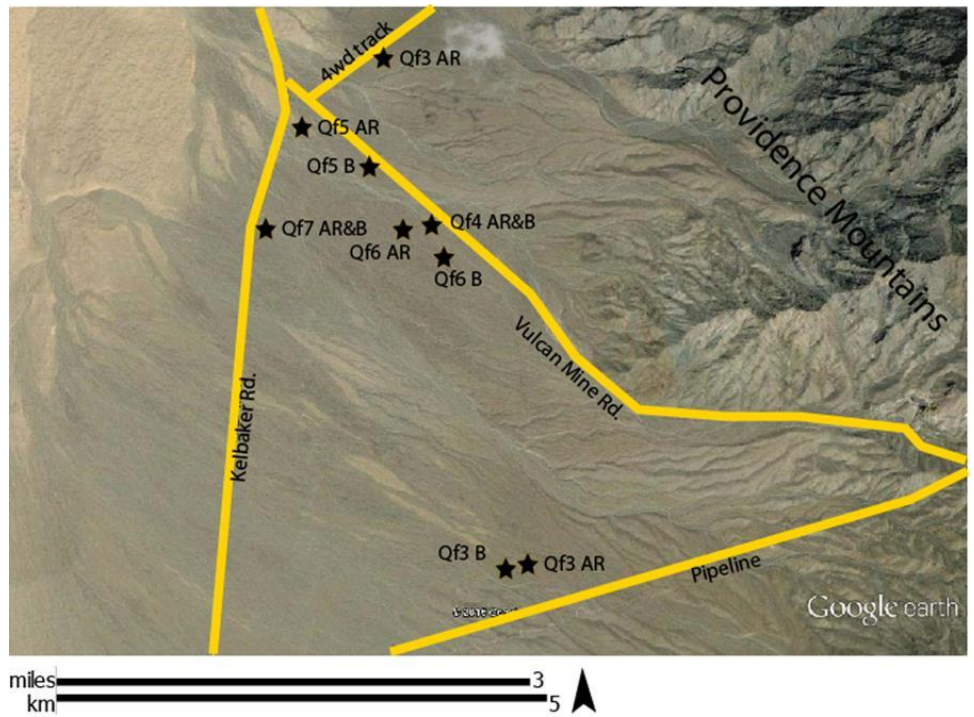


Figure 2. Google Earth image of the field area with the specific sites for data collection for each alluvial fan surface marked with a star. Unique, representative down-fan transects were selected for all data collection. Fans of different ages are distinguishable in the photograph by color, where older fans are generally darker in color due to increasing degrees of desert varnish. AR refers to “all rock transects” and B refers to “large rock transects”.



Figure 3. Photographs taken during data collection. A. A typical transect on a fan surface. B. A close-up of a typical pavement surface showing rocks with visible cracks for which measurements were made. C. A basalt rock with a high density of vesicles. Such clasts exhibited fewer cracks than those with fewer vesicles.

For crack orientation data, the presented Rao and Rayleigh statistics are circular statistical tests for uniformity, or randomness, of the measurements. The Rayleigh test assumes uni-modal data and the Rao test assumes multi-

modes. P-values less than 0.05 for both tests indicate statistically non-uniform, or preferred, orientations (i.e. orientation is not random). Crack density is presented in units of mm/mm² (crack length/rock surface area). We estimated rock

surface area by using measured rock dimensions to calculate their surface area as a ½ ellipsoid. It should be noted, however, that crack width was not accounted for in the calculations of crack density; thus the total volume of damage to the rock may differ from reported values.

We found that crack density varies as a function of surface age (Table 2) as well as rock type (Figure 4). Overall crack densities range from 0.014 – 0.002 mm/mm², and typically decrease with increasing surface age regardless of rock type. The basalt rocks of the Cima volcanic field exhibit significantly lower crack density than other rock types, and those rocks also more commonly have zero cracks (i.e. ~60% of basalt rocks exhibited 0 cracks, compared to 30-35% for all other rock types on the next oldest surface, Qf3). Interestingly, we found that as the density of basalt vesicles (resulting from air pockets in the cooling lava) increased, the average number of cracks decreased per rock (Figure 3C). Plutonic rocks consistently exhibited less cracking than the volcanic and carbonate rocks of the Providence Mountains.

We found that crack width increases as a function of surface age (Figure 11), although the correlation is poor. When cracks of all sizes and a variety of rock types are considered, as in this study, crack widening is less predictable and considerably slower than published rates of crack widening for the exposed granitic rocks of the Owens Valley (Figure 11)(10). Crack orientations also vary somewhat by rock type, age, and size (Figures 5-8). When all cracks are considered together (Figure 5A), they exhibit preferred NE strikes and SE dip directions. Smaller rocks generally exhibit more variance than larger ones (Figures 5B and 5C), however dip angles are very similar.

Crack orientations between rock types appear to vary only slightly when all data are considered (Figure 6); however there are distinct differences between rock type orientations when compared on a single surface (Figure 7). For example, the western striking, north-dipping mode common to most rock types is notably less prominent in plutonic rocks (Figures 6 and 7).

Crack orientations do not vary significantly between surfaces of different ages when all rocks

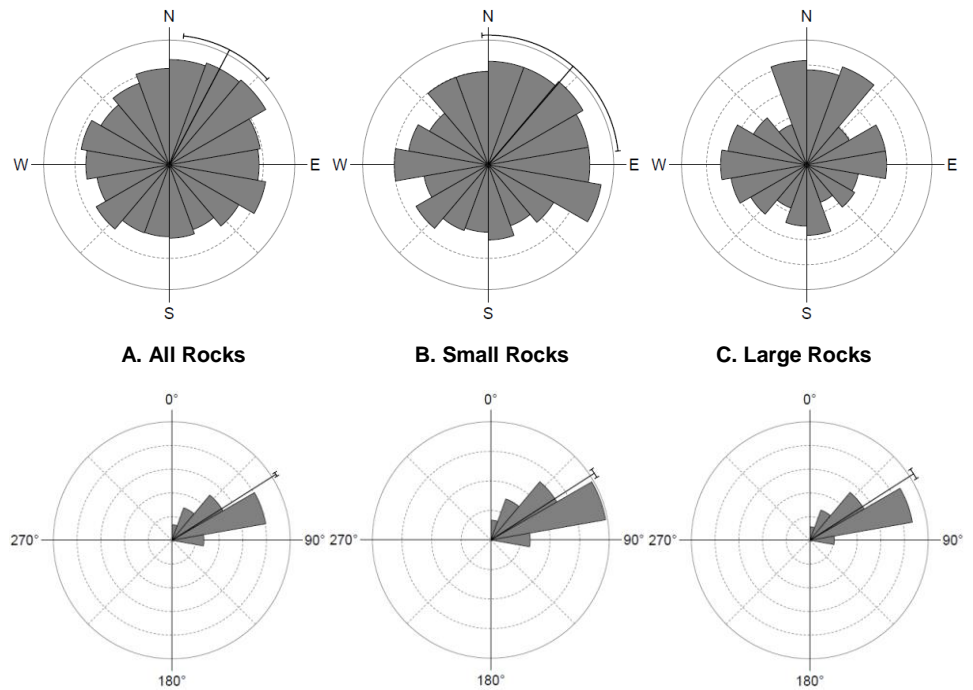


Figure 5. Circular histograms of crack strike orientations (upper row) and dip angles (lower row). Lines and brackets indicate vector mean and 95% confidence interval. All rocks are characterized by cracks with statistically preferred strike and dip orientations (see stats below). Large rocks exhibit stronger crack orientation preferences than do small rocks, a result that is predicted by numerical modeling (11) that shows larger rocks are subject to greater solar-induced thermal stresses.

A. All cracks (n = 3124) found in all rocks examined in the study. Rayleigh and Rao P <0.01. Average Dip Angle: 57.6°. B. All cracks (n = 602) found in all rocks with surface areas <10,000 mm². Rayleigh and Rao P <0.01. Average Dip Angle: 57.1°. C. All cracks (n = 407) found in all rocks with surface areas >100,000 mm². Rayleigh and Rao P <0.05. Average Dip Angle: 57.3°.

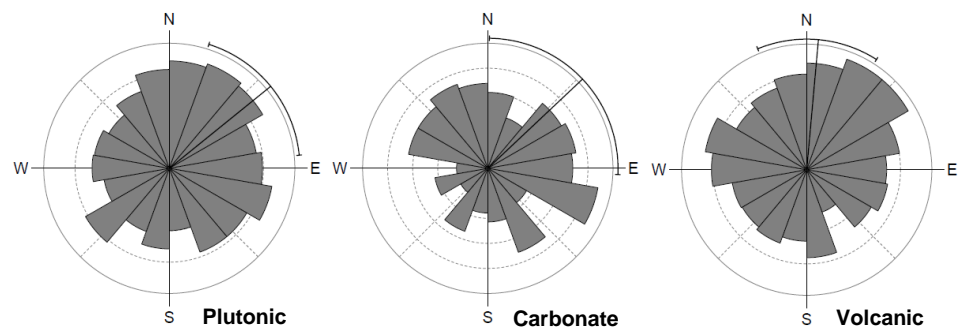


Figure 6. Circular histograms of crack orientations for all rocks divided into general rock-type bins. Carbonate rocks exhibit a stronger E-W mode of cracking than the other two rock types. Lines and brackets indicate vector mean and 95% confidence interval.

are considered (Figure 8) with the exceptions of Qf5 and the Cima basalt flow, which exhibit prominent SW modes that are not as evident on the other surfaces. Given the differences in crack orientations between rock types on a single surface, however, the overall variance between different surfaces could be attributable to the differences in rock type proportions or to different rock sizes on any given surface (Table 2). Finally, cracks observed in this study exhibited orientations that appear to be related to rock

shape, as has been observed in other studies (4, 5). Namely, surface-parallel cracks and cracks parallel to the long-axis of the rock were both observed during this study. However, here we attempted to quantify that correlation by examining the orientations of any flat faces on the rock surface (Figure 9) and of the long-axis of measured rocks. We found that overall crack orientation is different from those of the rock long-axes and rock faces.

Results from this study provide interesting insights into rock cracking characteristics. In general, crack orientations presented herein are consistent with those measured in other deserts of the United States and elsewhere (3). It is unknown how the consistent dip angles that we observe in all rocks and surfaces in this study (Figure 5) compare with other sites, as dip angles had not yet been measured for other locations.

The fact that different rock types exhibit different orientations (Figures 6 and 7) is consistent with a solar-induced origin for their formation: the different mineral compositions of different rock types will be expected to produce differences in insolation-related stresses. In other words, the magnitude and timing of insolation-induced stresses may produce different outcomes depending on rock type. For example, calcite is one of the few minerals that contracts somewhat upon heating rather than expanding. Therefore stresses that arise in carbonate rocks might preferentially occur during the cooling period of sunset, resulting in different crack orientation as

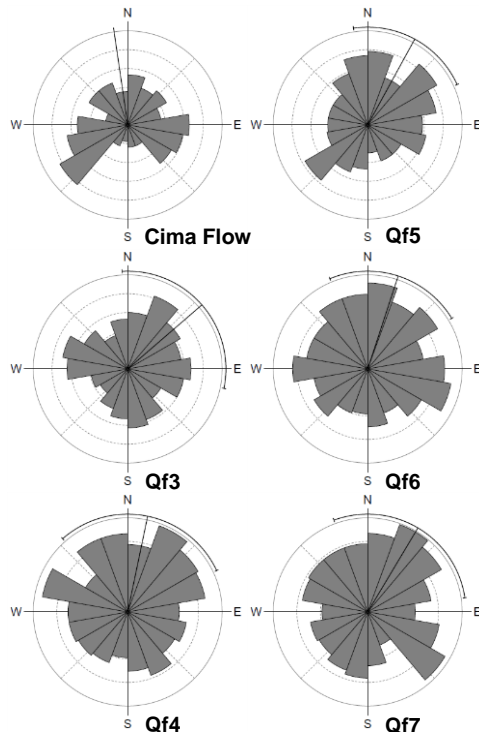


Figure 8. Circular histograms of crack orientations for all rocks found on each surface indicated. Overall, crack orientations are similar for surfaces of different ages. Lines and brackets indicate vector mean and 95% confidence interval. Confidence intervals are not presented for the Cima Flow due to the fact that they are >180 degrees because of the strongly multi-modal nature of the data.

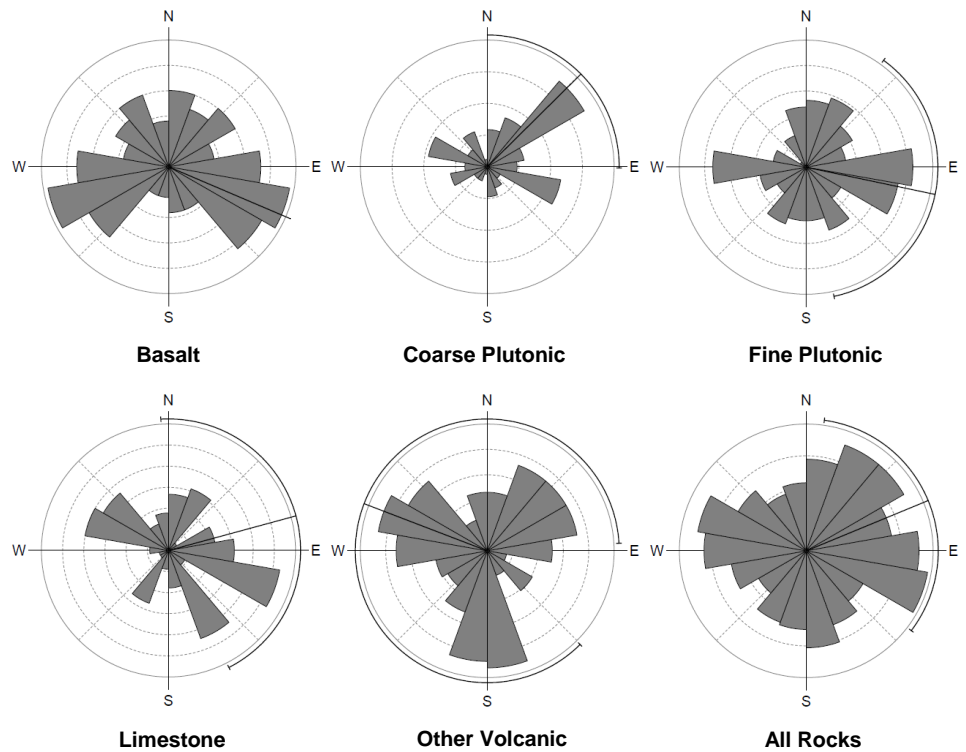


Figure 7. Circular histograms of crack orientations for all rocks examined on Cima Basalt surface and for the Qf3 surface divided into rock-type bins. Different rock types exhibit markedly different crack orientations as might be expected given their differences in mineralogy and thus their susceptibility to thermal stresses. Lines and brackets indicate vector mean and 95% confidence interval. Confidence intervals are not presented for Basalt due to the fact that they are >180 degrees because of the strongly multi-modal nature of the data.

Basalt (n = 81), Rayleigh P = 0.923, Rao P = 0.90 > p > 0.50. Coarse Plutonic (n = 89), Rayleigh P = 0.01, Rao P = 0.50 > p > 0.10. Fine Plutonic (n = 152), Rayleigh P = 0.083, Rao P = 0.50 > p > 0.10. Limestone (n = 90), Rayleigh P = 0.17, Rao P = 0.50 > p > 0.10. Other Volcanic (n = 195), Rayleigh P = 0.449, Rao P < 0.01. All Rocks (n = 609), Rayleigh P = 0.059, Rao P < 0.01.

compared to rocks that are susceptible to midday stresses that arise during peak heating (timing of insolation-induced stresses discussed in 11).

The fact that most cracks observed in this study were not parallel to the orientation of rock faces or longitudinal axes suggests that cracks do not solely propagate along pre-existing heterogeneities. It is likely, however, that such heterogeneities are influential in the overall direction of crack propagation. If external stresses are favorably oriented with respect to these heterogeneities, then cracks would be particularly susceptible to propagation in those directions. In the case of the Providence Mountain alluvial fans, longitudinal axes are preferentially oriented to the northeast, a direction that is normal to overall fan slope. Such orientations of longitudinal axes are typical of stream-flow and hyper-concentrated flow deposits of fans (e.g. 12). If such long axes are

related to heterogeneities of individual clasts, then it might be expected that crack orientations would be oriented parallel to long axes. Crack densities also provide insights into the

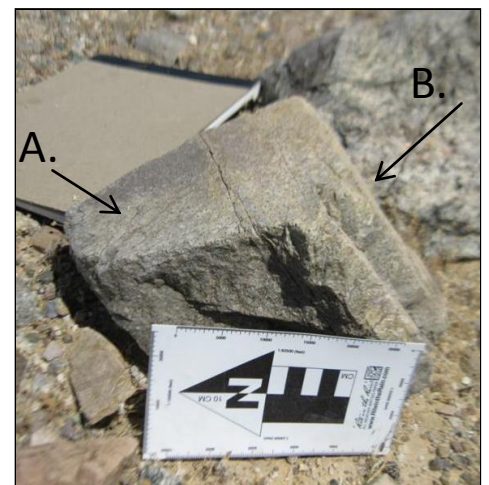


Figure 9. Photograph of a rock with prominent flat faces (A and B). The B arrow also points to a crack that is parallel to that surface.

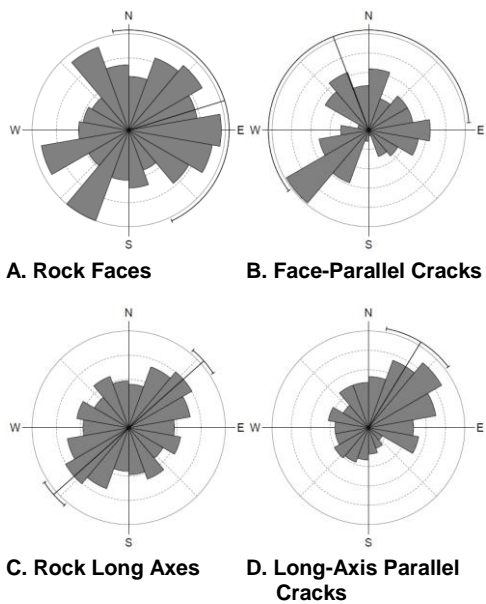


Figure 10. Comparison of the orientations of rock features with the orientations of cracks found on the same rocks. Although some similarities exist, there are differences that cannot be accounted for by these heterogeneities. Circular histograms of **A. Strikes of all flat faces found on all rocks of the Qf5 surface; Mean Vector= 73°, Rayleigh P = 0.198, Rao P = <0.01.** **B. Strikes of all cracks that were noted to be parallel to flat faces (surface-parallel) on all rocks of the Qf5 surface; Mean Vector= 339°, Rayleigh P = 0.383, Rao P = 0.05 <p <0.1.** For both graphs, lines and brackets indicate vector mean and 95% confidence interval. **C. Biaxial strikes of the long-axes of all rocks measured in the “all rock transects” on all six surfaces; Mean Vector = 48°, Raleigh P = <0.01, Rao P = <0.01.** **D. Strikes of all long-axis parallel cracks measured in the “all rock transects” on all six surfaces; Mean Vector = 32°, Rayleigh and Rao P = <0.01.**

mechanisms of crack formation. For example, the fact that crack densities decrease as a function of increased surface age is not attributable to a concomitant decrease in grain size (Table 1) on older surfaces, which would necessarily limit the maximum crack density. An alternative explanation for lower crack density with increasing surface age, however, is that early on in a rock’s exposure history, pre-existing fractures are exploited and propagated and ultimately result in the splitting of the rock. As these pre-existing heterogeneities are thus depleted, so too is the propensity for new fractures to develop and propagate. Also, calculated solar-induced stresses decrease with decreasing rock size, thus as rocks break down to desert-pavement size pieces, the amount of stresses they experience, and thus the associated cracking, should diminish, as our data

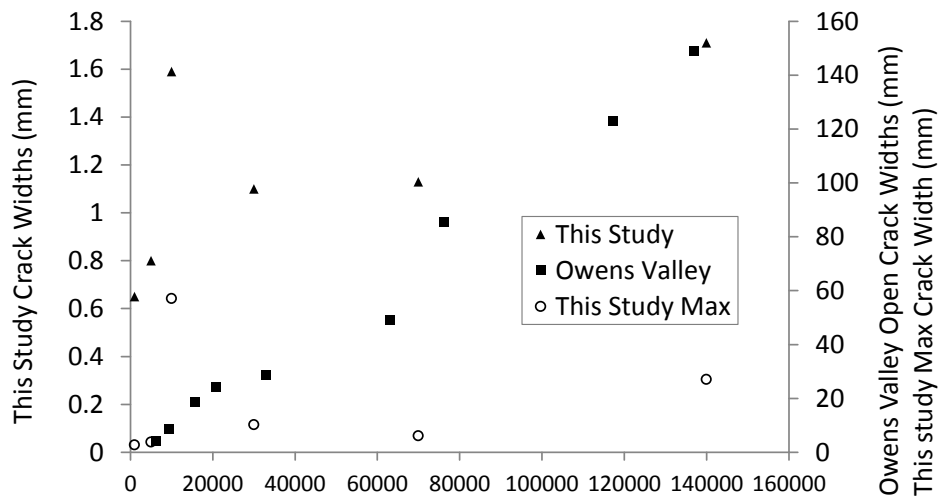


Figure 11. Graphs of Surface Age vs. Crack Width for cracks measured in this study and for those presented in (10). Note the two different scales on the y-axes for width data. For this study, both average and maximum measured crack widths are presented. Crack widening measured herein is considerably slower than that measured on larger, fully split cracks measured in rocks of alluvial fans in Owens Valley (10).

support. We see some evidence in our data that erosion of rock surfaces following cracking also contributes to lower crack densities. For example, plutonic rocks exhibit the lowest overall crack densities. These coarse-grained rocks often exhibited evidence of granular disintegration (individual loose crystals); such intergranular cracks would not have met our 2 cm crack criteria. Thus rather than growing indefinitely, cracks propagating in these rocks terminate

along grain boundaries and result in the disaggregation of individual crystals, resulting in a lower overall visible crack density. The fact that basalts exhibit the lowest fracture density may be attributable to the old age of the basalt surface; however, the observed low fracture density may also be caused by the vesicular nature of these rocks. If fractures are generally propagated by insolation-related stresses, it would be expected that such stresses

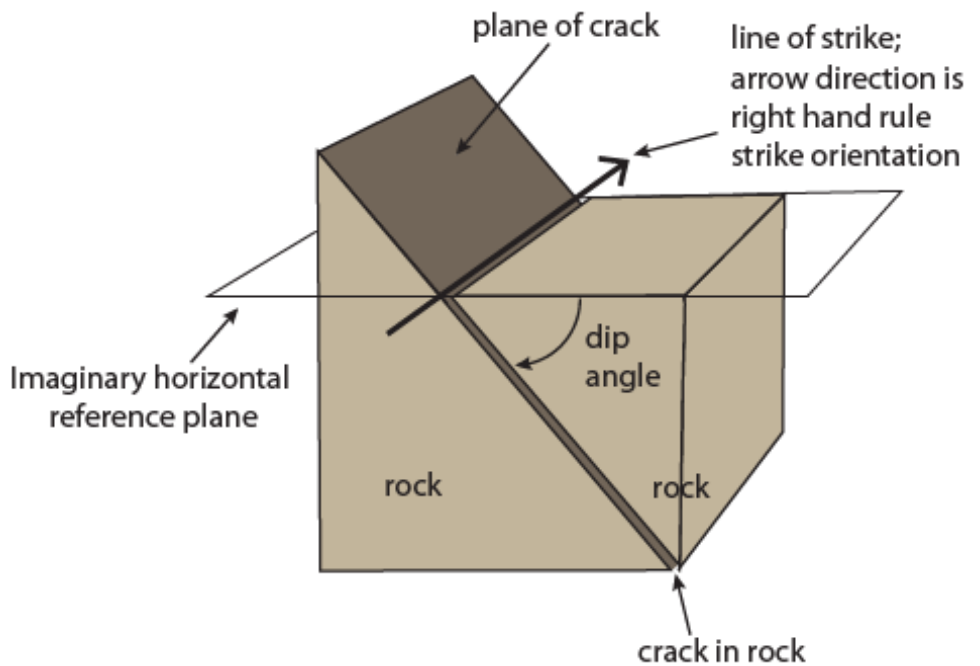


Figure 12. Conceptual diagram of the geometric meaning of “strike” and “dip”. By convention, strikes are reported in degrees from 0-360, where 0 is north, 90 is east, etc. Dips are reported in degrees from 0-90.

might be low in porous rocks where heat can be readily dissipated and/or distributed throughout the rock surface. The result would be lower overall thermal related stress and thus lower fracture density, just as we observed for highly vesicular rocks.

Overall, the results of this study indicate that the characteristics of cracks in desert pavement rocks in the Mojave Desert vary as a function of both surface age and rock type. Cracks in different rock types exhibit distinct preferred orientations and crack densities, as might be expected given their differences in mineralogy and grain size, which likely influence their mechanical properties. Differences in crack orientation among different aged surfaces are less clear; however, there is an overall decreasing trend in crack density with increasing surface age that can also be attributed to rock fracturing processes. This study demonstrates how detailed field examination of rock cracking in a setting such as the Mojave Desert can provide insights regarding the key factors that contribute to mechanical breakdown of rock on the surface of Earth and other planets.

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Table 1. List of data collected for all rocks and cracks measured for this study. Cracks were defined as any linear void >2 cm in length.

Rocks	Cracks
Length	Length
Width	Maximum Width
Height (above the ground surface)	Strike (right hand rule)
Rock type (volcanic, plutonic, carbonate)	Dip
Evidence of fabric-like bedding (y or n)	Is crack parallel to flat surfaces on the rock, long axis of the rock, fabric in the rock (y or n)
Evidence of granular disintegration (y or n)	

Table 2. Data for rock size (length and volume), crack density and width for each of the six surfaces. Rock sizes are only reported for “all rock transects” to give an accurate view of rock size distribution across all surfaces.

Surface	Average Max Rock Length (cm)	Max Rock Length (cm)	Median Rock Length (cm)	Average exposed rock volume (cm ³)	Crack Density (mm/mm ²) All rock transects	Crack Density (mm/mm ²) both transects	Average Crack Width (mm)
Qf7	9.9	21.8	8.4	239	.0139	.0106	0.65
Qf6	10.8	31	8.6	272	.0108	.0082	0.80
Qf5	10.6	52	7.5	169	.0069	.0119	1.59
Qf4	12.5	46	10.1	408	.0083	.0079	1.10
Qf3	13.7	58	10.1	485	.0069	.0044	1.13
Cima	11.4	41	9.2	327	.0023	.0019	1.71

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Old dog, new tricks: advancing facilitation theory in the Mojave Desert

Alessandro Filazzola¹, Amanda Rae Liczner¹, and Ally Ruttan¹

Facilitation is a central component of community ecology and is described as a positive interaction that occurs between two individuals (1, 2). These positive interactions have been frequently observed among plant species in environments characterized by high abiotic stress and resource limitation, such as deserts (3, 4). In these systems, dominant benefactor plants are typically perennials, larger than the beneficiary species, and provide some functional role to positively affect the species within their vicinity. For instance, shrubs in deserts primarily facilitate species composition by ameliorating abiotic stress through reductions in temperature extremes and increasing relative humidity (5, 6), but may also increase water or nutrient availability (7, 8). In addition, some studies have focused on how shrubs may buffer understory plant species from consumer pressure in desert environments (9, 10). Thus, there are a series of mechanistic pathways that shrubs can significantly influence community composition in desert systems.

Positive interactions have often been examined in the Mojave Desert, including some of the seminal studies addressing facilitation (e.g. 11, 12). In one such study (13) several shrubs were shown to facilitate the recruitment of the iconic Joshua tree (*Yucca brevifolia*). This was one of the few studies showing facilitation effects on another perennial and was later expanded upon in the Mediterranean by using shrubs to facilitate tree recruitment (14). Facilitation studies commonly examine the benefit of shrubs on annual plants, however, the first study examining the converse (i.e. annuals on shrubs) was conducted within the Mojave Desert and showed that annuals negatively affect the shrubs (15). This area of research has since been expanded globally to demonstrate how benefactors can be negatively impacted by the plants they are benefiting (16, 17). Research from the Mojave

¹ Department of Biology

York University, Toronto, Ontario.

Desert has also reported on a mechanism of facilitation that occurs between shrubs and soil characteristics. Walker and others (7) found that under *Ambrosia dumosa* canopies, water content, organic matter, and soil nutrients were all significantly higher than open microsites. More recently, facilitation studies conducted in the Mojave Desert have focused on the dynamics of invasion and how non-native species interact with native shrubs (18). Despite the large number of studies conducted on the topic, there is still great opportunity for facilitation theories to be tested in the landscape of the Mojave Desert (6). Here, we aim to provide an overview of some of these understudied topics including: i) seed trapping, ii) plant-pollinator interactions, and iii) influences of facilitation on evolutionary trajectories (Figure 1). Further research can only help elucidate known mechanisms and perhaps expose new mechanisms or aspects of facilitation that are shaping both species and community composition in the Mojave Desert.

Shrubs can directly increase seed arrival by physically obstructing seeds, or indirectly by mediating animal dispersal and/or increasing seed production (8, Figure 2). In many desert systems, such as the Mojave, shrubs are the dominant perennial cover and a defining physiognomic feature of the landscape. Consequently, shrubs can directly mediate seed movement by physically obstructing seeds that are dispersed by wind or water (19, 20). Some annual plant seeds have evolved traits that increase their ability to become trapped within the shrub canopy, which may be a more favorable environment for germination (21). Shrubs can also increase seed arrival through indirect pathways by mediating animal dispersal of seeds, for example by functioning as a bird or bat perch (22, 23). One study, conducted in the Mojave Desert, found that seed-caching rodents preferentially deposited seeds of the Joshua Tree (*Yucca brevifolia*) within shrub canopies (24). There are also indirect pathways of facilitated

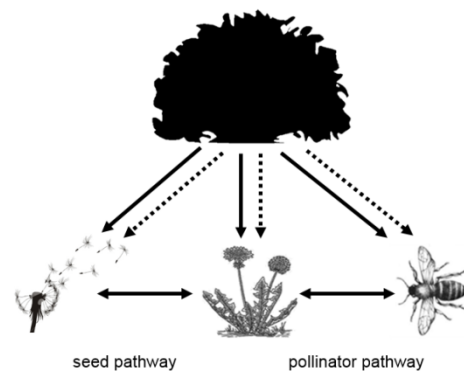


Figure 1. The direct and indirect facilitation pathways of a shrub on the annual community through seed trapping and increased pollinator visitation. Indirectly, shrubs facilitate the understory plant species by increasing seed arrival or by increasing pollinator visitation. Shrubs can also directly increase understory seed and flower production, thereby indirectly increasing seed arrival or pollinator visitation. Thus, there are positive feedback loops initiated by shrub facilitation.

seed arrival, such as higher seed rain under the shrub as a consequence of the shrub facilitating understory plant individuals to produce more seeds (25). Though the shrub may increase seed arrival, there may not be a net-positive effect on the species because the benefit is offset by a cost at a different life stage (26). For instance, higher seed densities within shrubs may result in greater competition for germination and establishment among individual plants (27). Thus, the spatial correlation between shrubs and annual seeds may be a consequence of both increased seed arrival and other positive mechanisms that may reduce seed dormancy (28) or granivory (29). While these pathways of seed trapping and facilitation have been proposed, further research is required to decouple the role of shrubs in altering plant dispersal.

Research on positive interactions has generally been focused within one trophic level, most commonly involving interactions among plants. However, positive interactions can occur across multiple taxa and these interactions have been generally neglected in facilitation research (30).

For example, the indirect facilitation by shrubs for the pollination of understory annual plants is a relatively new and highly understudied avenue of research (6, 31). Currently, the majority of studies on pollinator facilitation have been conducted in alpine environments with cushion plants used as the benefactor species (32, 33, 34, 35). Cushion plants have been found to benefit insects by providing them with a physical refuge (36), as well as access to the beneficiary species growing on them (34, 35). Additionally, shrubs may extend the flowering period of understory annuals through stress amelioration, thereby extending the potential pollination window (37). Benefactor species have also been found to act as magnets for the pollination of nearby beneficiaries. This idea, termed the magnet hypothesis, proposes that an attractive species can indirectly facilitate less-appealing neighbors by drawing in a pollinator community to plants that would otherwise have little access to pollinators (38, 39, 40). This idea can also be applied inversely, with the beneficiary plant species acting as magnets for the pollination of the benefactor plant (a double magnet), forming a reciprocal facilitation pathway and positive feedback. While these ideas have rarely been tested in arid environments (but see 40), locations such as the Mojave Desert provide ample opportunity for research of this type. Mojave National Preserve is abundant in flowering plants, including annuals and many perennial species such as shrubs that may act as benefactors. One of the most dominant plants within the preserve, *Larrea tridentata*, has been recognized for its ability to facilitate the annual plant community through various mechanisms (e.g. 41, 42). *Larrea tridentata* also supports over 120 species of bees (43, 44, 45), suggesting its potential importance in attracting the pollinator community for neighboring plants (Figure 3). The broad range of annual plants that frequently bloom at the same time as *L. tridentata* and other benefactor species provide an ideal system to study the single and double magnet hypotheses and the facilitation of pollinators in general.

The facilitative mechanisms of shrubs may influence evolutionary processes of understory plant species. The altered environmental conditions within the understory of the shrub may exert different selection pressures on understory

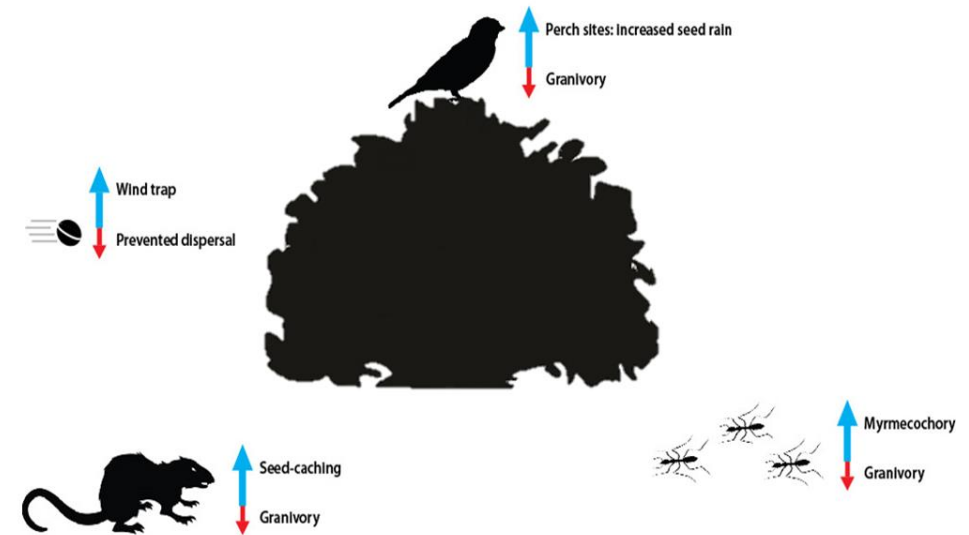


Figure 2. Direct and indirect mechanisms in which a shrub may increase or inhibit seed abundance within the canopy. Shrubs may directly increase seed arrival by physically obstructing seeds that are transported by wind or water. Shrubs may also indirectly increase seed arrival through secondary dispersal, such as birds using the shrub as a perching site, rodents as burrowing caches or insects for habitat.

plant species than currently existing in the surrounding environment (46). This may cause differential trait expression among individuals found within the shrub understory and those within the surrounding open environment. Plants from the shrub-understory may express traits that are more competitive, while open plants may express traits better suited to stress tolerance (47). This may lead to ecotypic differentiation as plant individuals from the same species may display different trait expression when present under shrubs or in open microsites (48). Over evolutionary time, plants may have evolved to be associated with the facilitation effect of the shrub microsites as an alternative to evolving stress tolerance (49). At the local or regional scale, positive interactions may be responsible for increasing biodiversity by increasing the heterogeneity of desert systems (50). In more recent work, positive interactions from shrubs have been observed to favour distantly related plant species, thereby increasing phylogenetic diversity of plant communities (51, 52). Although it is often a conclusion of facilitation studies that shrubs can alter evolution trajectories of annual plants species, more research is required to empirically test this pathway.

Since the inclusion of facilitation into ecological theory, there have been new advances and research into the various pathways of positive interactions. The Mojave Desert has remained a

relevant and commonly tested system when examining these pathways. Herein, we have emphasized the opportunity and highlighted the necessity to study new pathways of facilitation in desert systems (Figure 1). Increased pollinator visitation, seed trapping and shrub-mediated evolution all represent potential areas of future research that may strongly determine community structure in deserts. Positive interactions have been repeatedly shown as central in maintaining biodiversity in resource limited systems. Thus, it is necessary to better understand plant interactions, particularly the role of the shrub, to make more informed decisions about how to effectively manage and protect arid landscapes. This is especially relevant given the projected climate change for the Mojave Desert and the sensitivity to invasion that threatens biodiversity.

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Figure 3. A strong facilitation effect of the shrub *Larrea tridentata* on the yellow wildflower *Malacothrix glabrata* (left) and pollination of *M. glabrata* occurring within the shrub canopy (right).

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Editors:

Debra Hughson
Mojave National Preserve

Tasha La Doux and James André
Sweeney Granite Mountains Desert Research Center

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