



# Conservation of Mojave Desert springs and associated biota: status, threats, and policy opportunities

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## Abstract

In arid landscapes where fresh water is a limiting resource, the expression of groundwater in springs sustains important landscape functions, globally-recognized biodiversity hotspots, and both aquatic endemic and wide-ranging terrestrial species. Desert springs and associated groundwater dependent ecosystems are threatened by unsustainable groundwater pumping, and the Mojave Desert has seen extinctions of species due to the human use and modification of springs. To support changes in policy and management that would address the vulnerabilities of springs to unsustainable groundwater extraction and other threats, a better understanding of current spring condition is needed. Here we present the results of a comprehensive survey of Mojave Desert springs including hydrological and ecological observations, and an eDNA pilot study. Together, these investigations provide information about the present status of Mojave Desert springs, conservation challenges that they face, and needs that must be met to protect them. We also provide an overview of the current state of federal and state policy that could be used to better manage these critical freshwater resources.

**Keywords** Freshwater · Biodiversity · Groundwater dependent ecosystems · Aquifer · Basin

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## Introduction

Fresh water is rare, covering just 0.8% of the Earth's surface. It is also ecologically important, as freshwater habitats support about 9.5% of all known animal species, and 65% of described species (Dudgeon et al. 2006; Balian et al. 2008). In arid landscapes, where fresh water is a limiting resource, the expression of groundwater in springs is often the only source of perennially-available surface water (Bogan 2014). Springs and the groundwater dependent ecosystems (GDEs) (Brown 2011) they support can be examples of small natural features—places that provide disproportionate ecological importance in comparison with their size (Hunter 2017). In deserts, these systems play an important role in supporting both aquatic biota and migratory and wide-ranging terrestrial animals (Davis et al. 2017). Springs and their associated GDEs also sustain a number of important landscape functions (Cohen et al. 2016), and are globally-recognized biodiversity hotspots (Suhling et al. 2006; Stevens and Meretsky 2008; Fensham et al. 2011; Cantonati et al. 2012; Murphy et al. 2015) that support locally endemic species. For example, the areas of highest local endemism in North America are found at desert springs (Stevens and Meretsky 2008).

Desert springs are threatened by human activity; they have been characterized as “endangered” (Shepard 1993) and are recognized as one of the most threatened ecosystems in the world (Kodric-Brown and Brown 2007). Human uses of groundwater can have a variety of impacts on springs (Zektser et al. 2005; Dudgeon et al. 2006). Groundwater pumping that causes aquifer levels to drop can result in a spring drying out, even if the amount of groundwater stored in the aquifer is still very large. In places where unsustainable groundwater extraction has depleted aquifers and caused springs to dry up, spring-dwelling and groundwater-dependent species have gone extinct (Ponder 1986; Danielopol et al. 2003; Strayer 2006). An example of these impacts can be seen in some areas of the Mojave Desert of California and Nevada (Fig. 1). For example, in Ash Meadows, Nevada, dropping groundwater levels and decreasing flow in springs has been caused by local agricultural extraction and use of groundwater (Pister 1991; Unmack and Minckley 2008). Impacts to GDEs caused by overdrafts in the Owens River Valley are due to water diversions and groundwater pumping by the Los Angeles Department of Water and Power (Zektser et al. 2005). Within the Great Basin region of North America, a portion of which is overlaid by the Mojave Desert Ecoregion (Madsen et al. 2002), at least 16 aquatic endemic species, subspecies, or distinctive populations have gone extinct since the late 1880s, including 12 fishes, three mollusks, and one aquatic insect (Sada and Vinyard 2002). While the reasons for these extinctions are varied, groundwater pumping and surface water flow diversions have both been identified as causes.

To support changes in policy and management that would address the vulnerabilities of desert springs and the biota they support to unsustainable groundwater extraction, a better understanding of the current condition of these springs is needed. Baseline conditions must be well-understood, a time horizon for management needs to be set (Sophocleus 2002), analysis and predictive modeling (Mirchi et al. 2019) should be used, and a well-designed monitoring system with trigger conditions must be put into place to allow for adaptive management (Gleeson et al. 2012) to avert harm. Identification of water resource impacts becomes problematic if initial baseline conditions are unknown or poorly understood.

Data regarding springs in the Mojave Desert is sparse, including biological inventories. The region's smaller springs frequently get overlooked in hydrological investigations because their discharges are inconsequential to the overall water budget of the area being

studied. In addition, some seeps and springs are not well mapped, so they are frequently overlooked in biological investigations. Such oversight is problematic when evaluating the sensitivity of critically important resources for plant diversity and wildlife. In addition, rapid human population growth and use for water resources in the Mojave Desert is an issue resulting in the need for a balancing of competing uses and priorities. These include providing water for human needs, preserving water-dependent ecological resources, and expanding commercial development including renewable energy generation facilities. The goal of our study is to investigate and provide a hydrological and ecological assessment of the Mojave Desert's springs, provide an analysis of the threats these ecosystems currently face, and discuss opportunities for policy and management into the future.

## Methods: spring assessment

An assessment of springs and seeps in the Mojave Desert (Andy Zdon and Associates 2016) identified 436 springs (Fig. 1) across the California portion of the Mojave Desert Ecoregion on public lands managed by the Bureau of Land Management (BLM) and on lands owned by the Transition Habitat Conservancy, Mojave Desert Land Trust, Amargosa Conservancy, The Nature Conservancy, and Shoshone Village. We conducted an extensive data and literature review to obtain hydrogeologic, natural history, and cultural history information associated with these springs. Based on this information and ease of access, 312 of the 436 springs were field inspected between September 2015 and February 2016. Aerial imagery and information from various other sources was used to provide a remote overview of the 124 unvisited springs. Subsequent studies of many of these remaining springs have been conducted since the 2015–2016 spring survey and are discussed in Zdon et al. (2018) and Love and Zdon (2018).

Our field visits of springs included confirmation of geographic coordinates, estimation of surface discharge, and measurement of water quality parameters (pH, temperature, conductivity and dissolved oxygen). We quantified spring discharge using a variety of methods, including visual estimation, measuring the time required to fill a container of known volume, use of a solid-state flow meter placed in a flowing channel of water, or measuring outfall characteristics from a pipe of known size. At all springs where surface water was present, water samples were analyzed for stable isotopes of oxygen ( $^{18}\text{O}/^{16}\text{O}$ ) and hydrogen ( $^2\text{H}/^1\text{H}$ ). At selected springs in the southeastern Mojave Desert (i.e., the Clipper Mountains) and in the west Mojave Desert (i.e., McDonald Well) radiocarbon ( $^{14}\text{C}$ ), tritium ( $^3\text{H}$ ) or other analytes were analyzed. All isotopes were analyzed using mass spectrometry.

We made flora and fauna observations for native and non-native species at each spring surveyed. The observations included making records of non-native plant species that could negatively impact local hydrology and ecology such as giant reed (*Arundo donax*) and saltcedar (*Tamarix ramosissima*). Special note was made when livestock, burro, or wild horses were present at springs, as non-native ungulates are known to have negative impacts on vegetation.

We sampled water from a single desert spring (Ahn Spring; Fig. 1) as part of a pilot study to test the use of Environmental DNA (eDNA) methods (Taberlet et al. 2012; Thomsen and Willerslev 2015) for surveying spring biota. The method of eDNA metabarcoding allows for DNA sequencing and assignment of multiple species to potentially detect for the presence of organisms at any given location based on an environmental sample (Deiner et al. 2015; Ruppert et al. 2019). Located in the Transition Habitat

**Fig. 1** Map of 436 springs on public lands managed by the Bureau of Land Management, and on private lands owned and managed by Transition Habitat Conservancy, Mojave Desert Land Trust, Amargosa Conservancy, and The Nature Conservancy across the Mojave Desert of California and southwestern Nevada. Springs that were visited during the 2015–2016 spring assessment are shown as black circles. Those shown as white diamonds were not visited. Particular springs of note are shown with slightly enlarged black circles and labelled with black numerals. These include Ahn Spring (1), Bonanza Spring (2), Chappo Spring (3), Chris Wicht Camp Spring (4), Dove Spring (5), Jack Spring (6), McDonald Well (7), Mesquite Spring (8), Poison Spring (9), Shoshone Spring (10), Tecopa Hot Spring (11), Tan Tan Well (12), and Willow Creek Camp Spring (13)

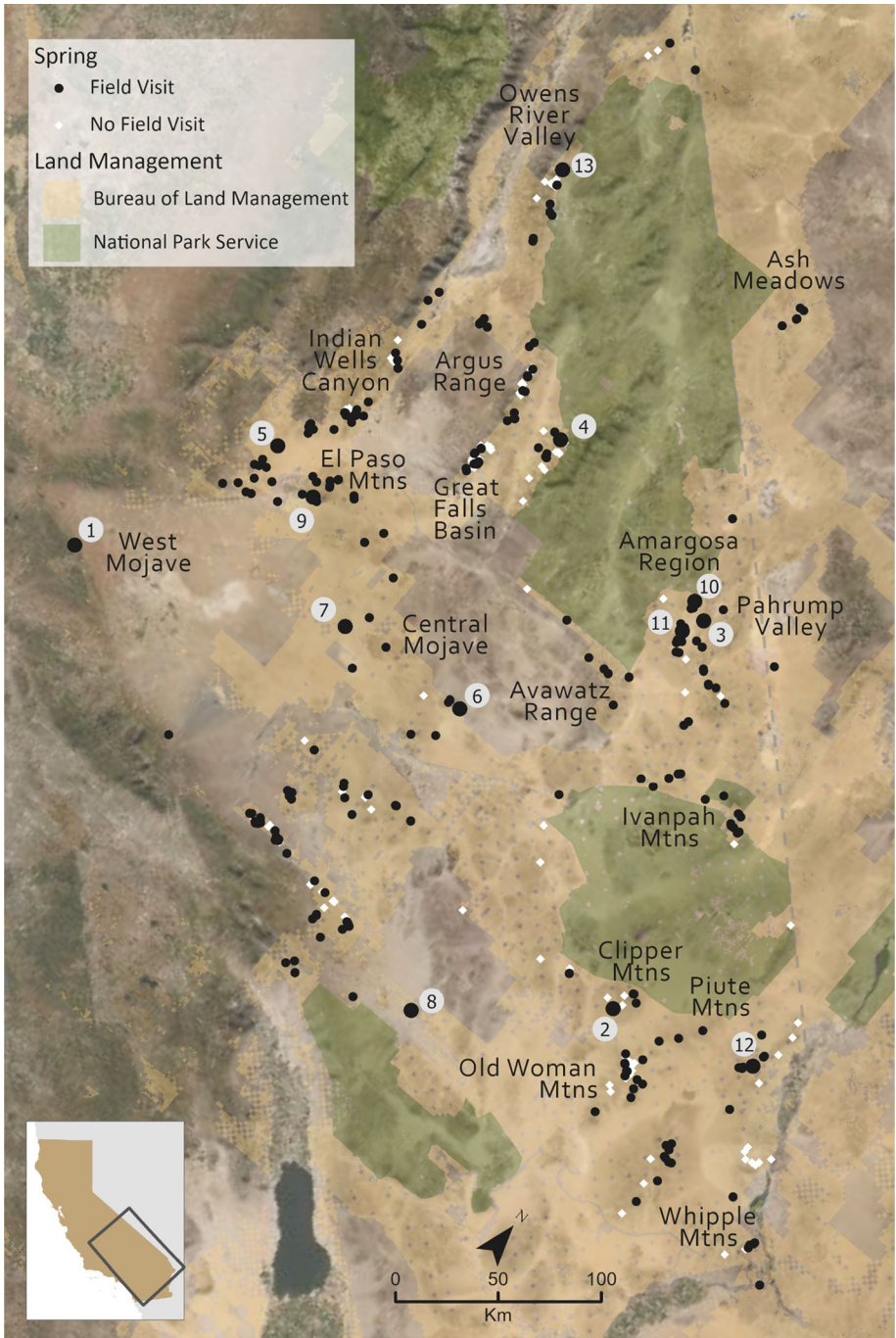
Conservancy’s Portal Ridge Preserve, 18 miles west of Lancaster, California, Ahn Spring has been monitored with camera traps for 6 years, which allows us to test the accuracy and sensitivity of eDNA methods in detecting animals known to visit the spring.

For eDNA sampling, we took 3, 1 l water samples on May 6, 2019, and filtered these immediately through 0.22 µm Sterivex millipore filters (Millipore, MA, USA) using a Masterflex® L/S portable Peristaltic pump (Cole-Parmer, Vernon Hills, IL, USA). Samples were transported on ice and stored in a -20° C freezer. We extracted DNA within 1 week of field sampling following the protocol developed by Spens et al. (2017), and removed inhibitors using the Zymo One Step Inhibitor removal Kit (Zymo Research, Irvine, California, USA). Library preparation methods followed Li et al. (2018); we amplified for two barcodes, a modified Vertebrate 16S (Ve16S; Evans et al. 2016), which targets vertebrates, and Plant Internal Transcribed Spacer 2 (PITS; Gu et al. 2013), which targets plants. Two rounds of PCR were utilized to amplify targeted fragments from eDNA extracts and prep libraries for Illumina sequencing (Olds et al. 2016). Samples also included a positive control mix of marine species, as they are not expected to be found in the Mojave Desert, and a PCR blank. The libraries were pooled to equal molar concentrations and the Illumina MiSeq sequencing run consisted of a 2 × 300 base pairs. The sequencing data was checked for quality and assigned taxonomy using the default parameters in the Anacapa Toolkit software (Curd et al. 2018). Sequence classification for the vertebrate (Ve16S) and plant (PITS) primers were cross verified using the Web BLAST NCBI nucleotide database and the BOLD database (Ratnasigham and Hebert 2003).

## Results: current status of mojave desert springs

Springs in the Mojave Desert constitute a diverse range of aquatic habitats and GDEs (Tables 1 and 2, Fig. 2). Field-assessed springs varied in their landscape context. While all were located on Bureau of Land Management or land trust lands, some were more distant from other springs. The springs of the Amargosa region (e.g., Shoshone Spring) and the Great Falls Basin in the Argus Range (Inyo County) regions can be thought of as “spring complexes.” In contrast, other springs, such as McDonald Well, provide the only reliable, free-flowing surface water for more than 500 square miles. A total of 27 springs (approximately 8%) showed signs of livestock use, including erosion and/or compaction of soils, grazed and trampled vegetation, and deposition of manure.

Surface water was present at 145 of the 312 spring locations (Table 1). All spring locations where surface water was not observed had phreatophytic vegetation of widely varying amounts, indicating that the belowground water source was discharging through plant transpiration. These springs were noted as “dry–evapotranspiration only” to acknowledge that the simple notation of a spring being “dry” ignores that the spring is still discharging water and can lead to poor assumptions about the ecological importance of springs. Of the 145 springs with measurable flow, flows ranged from less than one gallon



**Table 1** Ten of the 312 Mojave Desert springs visited during the 2015–2016 spring assessment, demonstrating the diverse range in spring flow, chemistry, and organisms observed

Spring Name	Nearest Groundwater Basin	Coordinates (lat/lon)	Elevation (m)	Flow (LPM)	Temp. (°C)	pH	Salinity (ppm)	$\delta^2\text{H}$	$\delta^{18}\text{O}$	Notable species observed at spring (* = non-native):
Ahn Spring	Antelope Valley	34.71829, – 118.49961	1153	< 4	16.6	7.02	204	– 67.5	– 9.89	Mountain lion ( <i>Puma concolor</i> )
Bonanza Spring	Fenner Valley	34.68513, – 115.40538	642	< 4*	14.2*	7.85*	620*	– 82.1	– 10.25	Western Bluebird ( <i>Sialia mexicana</i> )
Chris Wicht Camp Spring	Darwin Valley	36.11229, – 117.17275	847	757	9.2	8.37	213	– 96.6	– 13.22	American Dipper ( <i>Cinclus mexicanus</i> )
Dove Spring	Indian Wells Valley	35.45305, – 118.10049	1300	11.4	19.5	7.09	226	– 92.7	– 11.99	LeConte's Thrasher ( <i>Toxostoma lecontei</i> )
Jack Spring	Coyote Lake Valley	35.15482, – 116.75648	726	< 4	19.8	7.28	620	– 78.8	– 9.20	Marsh Wren ( <i>Cistothorus palustris</i> )
McDonald Well	Harper Valley	35.11528, – 117.37045	780	< 4	21.1	7.34	629	– 95.6	– 11.36	Goldfish ( <i>Carassius auratus</i> )*
Poison Spring	Fremont Valley	35.39413, – 117.83908	700	5.7	23.7	7.19	1643	– 96.5	– 12.06	Yerba Mansa ( <i>Anemopsis californica</i> )
Tecopa Hot Spring	Middle Amargosa Valley	35.87191, – 116.232145	431	114	40.2	7.93	1570	– 98.1	– 12.93	Three-square Bulrush ( <i>Schoenoplectus americanus</i> ), Amargosa vole ( <i>Microtus californicus</i> subsp. <i>scirpensis</i> ), Amargosa niterwort ( <i>Nitrophila molhavesis</i> ), Tecopa bird's beak ( <i>Chloropyron tecopense</i> ) [nearby]
Tan Tan Well	Needles Valley	34.84826, – 114.77914	478	< 4	21.7	7.03	240	– 75.0	– 9.98	Phainopepla ( <i>Phainopepla nitens</i> )
Willow Creek Camp Spring	Saline Valley	36.84212, – 117.92284	747	95	15.7	7.13	660	– 106.5	– 13.68	Willow ( <i>Salix</i> sp.)

\*Measured downstream from source

**Table 2** Vertebrate and plant species detected from water samples at Ahn Springs using eDNA techniques, compared with camera trap or field observations

Scientific Name	Common Name	% identity	Reads	Camera trap or observed
<i>Microtus levis</i>	Vole sp.	94.542	11,847	Vole tunnel tracks observed in the area
<i>Neotoma macrotis</i>	Big eared woodrat	94.032	5920	
<i>Dipodomys agilis</i>	Agile kangaroo rat	98.211	3439	Kangaroo rats observed in the area
<i>Sciurus spadiceus</i>	Squirrel sp.	96.016	1960	
<i>Odocoileus hemionus</i>	Mule deer	99.657	1817	
<i>Sceloporus occidentalis</i>	Western fenced lizard	98.529	596	Observed in the area
<i>Aphelocoma californica</i>	California Scrub Jay	98.540	84	
<i>Tamias umbrinus</i>	Chipmunk sp.	96.906	24	Observed in the area
<i>Lepus californicus</i>	Black tailed jackrabbit	100	1046	Observed in the area
<i>Anaxyrus punctatus</i>	Red spotted toad	100	154	Not observed
<i>Peromyscus</i> sp.	Rodent	89.7	59	Observed in the area
<i>Phacelia umbrosal</i>	Colorado Desert phacelia	97.97	141	Related species based on geographic distribution
<i>Quercus chrysolepis</i>	Canyon live oak	98.84	504	Observed
<i>Nerium oleander</i>	Oleander	100	7268	Not observed
<i>Chaenactis douglasii</i>	Douglas' dustymaiden	92.98	55	Related species based on geographic distribution

Table 2 continued

Scientific Name	Common Name	% identity	Reads	Camera trap or observed
<i>Hordeum murinum</i>	Wall barley	100	14	Potential unidentified grass species
<i>Forestiera neomexicana</i>	Desert Olive	98.95	147	Not observed

Images courtesy of Roy Dunn, Transition Habitat Conservancy



**Fig. 2** Photographs of Mojave Desert springs. Borax Spring (a) and Bonanza Spring (b), are located in the California portion of the Mojave Desert, whereas Point of Rocks Spring (c), is part of a large spring complex in Ash Meadows National Wildlife Refuge in Nevada. The flow from Stone Canyon Spring (d) has been directed into a guzzler used by wildlife. Photo credits: William T. Christian (photos a, b, and c) and Andy Zdon (d)

per minute at 59 springs, up to 265 gallons per minute at Shoshone Spring in the Amargosa region. Pipes or other infrastructure were installed into a spring or seep face to enhance flow at 91 of 312 of the springs.

Of the 145 springs with surface water, 118 (81.4%) contained fresh water with total dissolved solids (TDS) concentrations below 1000 mg/l. The remaining 27 springs contained brackish water with TDS concentrations between 1000 and 10,000 mg/l. None of the springs had saline water (TDS over 10,000 mg/l). Spring water temperatures varied from  $\sim 0$  °C at French Madam Spring in the Argus Range (measured in December 2015 when the spring outfall was covered in an ice sheet) to 41.3 °C at Paradise Hot Spring in



the Central Mojave region. Measurements of pH generally ranged from 6.21 at Lower Centennial Spring (South) to 9.71 at Borax Spring in the Amargosa region, with most of springs containing waters with a pH between 7.0 and 8.5.

The  $\delta^{18}\text{O}$  and  $\delta\text{D}$  abundances in spring waters reflect differences in the origin of precipitation across the Mojave Desert. In general, lower observed  $\delta^{18}\text{O}$  and  $\delta\text{D}$  isotope values in precipitation occur at higher elevations and with further distance from the California coast. However, across the Mojave Desert, total precipitation includes two different storm sources: winter maritime storms with lower (more negative) isotope values and summertime monsoonal storms with higher (less negative) isotope values. These variable sources yield a systematic difference in  $\delta\text{D}$  and  $\delta^{18}\text{O}$  abundance in accumulated precipitation across the Mojave Desert (Friedman et al., 1992). The spring water found in the southern Mojave Desert has higher (less negative)  $\delta\text{D}$  and  $\delta^{18}\text{O}$  values than that found in springs in the northern Mojave Desert. For  $\delta\text{D}$ , the average isotope values for the northwest and northeast Mojave Desert are  $-91.6$  and  $-86.4$ , respectively. In contrast, the average values for the southwest and southeast Mojave Desert are  $-77.7$  and  $-71.6$ , respectively (Zdon et al. 2018). Where tested, age-dating of spring discharge using radiocarbon and tritium techniques has yielded ages from very recent seasonal (e.g., at Bird Spring) to apparent ages of more than 10,000 years at Bonanza Spring (Love and Zdon 2018).

Plant species present at springs included emergent aquatics such as watercress (*Nasturtium officinale*), and obligate phreatophytes that require groundwater and are common in GDEs such as chairmaker's bullrush (*Schoenoplectus americanus*), common reed (*Phragmites australis*), Fremont's cottonwood (*Populus fremontii*), southern cattail (*Typha domingensis*), western honey mesquite (*Prosopis glandulosa* subsp. *torreyana*), several willow species (*Salix exigua*, *S. lasiolepis*, *S. laevigata*, and *S. goodingii*), and willow baccharis (*Baccharis salicina*). Other native plant species that are known to occur both in areas of high groundwater and in uplands unassociated with GDEs and are considered facultative phreatophytes were recorded, including desert brickellbush (*Brickellia desertorum*), iodine bush (*Suaeda nigra*), saltbush (*Atriplex* sp.), and saltgrass (*Distichlis spicata*). Non-native plant species included those that are persisting from cultivation such as black locust (*Robinia pseudoacacia*) and black mulberry (*Morus nigra*), and plant species naturalizing from cultivated sources such as date palm (*Phoenix dactylifera*) and fan palms (*Washingtonia* sp.). Invasive species that are considered to have severe ecological impacts, such as saltcedar and giant reed, were also present (Cal-IPC 2019). Saltcedar was particularly abundant in the Whipple Wash area of the Whipple Mountains, in washes in the Old Woman Mountains, and areas along the Amargosa River where there is perennial water flow. Giant reed was noted at Ricky Spring in the Ivanpah Mountains, and in areas where eradication efforts have occurred in the past, such as Sacramento Spring and Bonanza Spring.

At springs where surface water was present, aquatic animals observed included macroinvertebrate species such as water striders (Family Gerridae), and freshwater snails (including both *Physa* sp. and *Pyrgulopsis* sp.). Amphibians were commonly observed, including red-spotted toad (*Anaxyrus punctatus*). During September and October, neotropical migratory birds were observed at nearly every spring where surface water was present. Mammals observed during the survey included desert bighorn sheep (*Ovis canadensis nelsoni*), American badger (*Taxidea taxus*) and a bobcat (*Lynx rufus*). Mountain lion (*Felix concolor*) sign was observed in various locations, with bobcat and coyote (*Canis latrans*) scat and tracks plentiful. Desert kit fox (*Vulpes macrotis*) tracks were observed in the Avawatz Range, and American black bear (*Ursus americanus*) tracks and scat were observed at Siebert Spring in the eastern Sierra Nevada in Indian Wells Canyon.

Other special status species were observed during the course of the field work (Table 1), including live desert tortoise in three locations: on the alluvial fan below the Great Falls Basin spring area, on the alluvial fan south of Hummingbird Spring in the Clipper Mountains, and south of Blackwater Well and north of McDonald Well in the West Mojave. A desert tortoise shell at Pothole Seep in the Argus Range was also found. Numerous Least Bell's Vireo (*Vireo bellii pusillus*) were observed singing along Willow Creek; this species was also present at Vole Spring and Shoshone Spring. One Inyo California Towhee (*Pipilo crissalis eremophilus*) was observed in Great Falls Basin near Twin Springs.

Many of the species we detected during field observations or with camera traps were also detected by eDNA techniques (Table 2). However, the suite of species detected using each method varied, and the percent identity of eDNA detection of species varied. Two plant species—the native desert olive (*Forestiera pubescens*) and the non-native oleander (*Nerium oleander*) were observed using eDNA techniques, but were not observed in the field at Ahn Spring. A wide-ranging mammal and apex predator at this spring, the Mountain Lion, has been observed in camera trap photos many times, but was not detected using eDNA techniques.

## Discussion

### Conservation challenges

In recent decades, researchers have repeatedly and increasingly named groundwater extraction (and associated aquifer drawdown) by humans as a major, and frequently the most important, threat to desert springs (e.g., Shepard 1993; Sada and Vinyard 2002; Deacon et al. 2007; Unmack and Minckley 2008; Fensham et al. 2011; Davis et al. 2013, 2017; Bogan et al. 2014). In the Mojave Desert, our study sets a baseline for understanding spring flow for many springs where this has not been recorded in the past. But for springs where historical records or more recent observations exist, it is evident that many springs appear to be impacted by regional groundwater use by human communities. Spring depletions due to regional groundwater use can occur slowly, over very long periods of time, making depletions particularly difficult to observe and manage. The depletion of several springs in the Amargosa region provides one example. To the east and north of the Amargosa River Basin, pumping of groundwater in the Pahrump and Amargosa Valleys of Nevada and nearby landscapes may be impacting the Amargosa groundwater system. Records from Pahrump Valley indicate that groundwater pumping there increased more than an order of magnitude over less than a decade, growing from 1,428,656 m<sup>3</sup> year<sup>-1</sup> in 1959 to 59,106,184 m<sup>3</sup> year<sup>-1</sup> in 1968. Since that time, groundwater pumping has gradually decreased in Pahrump Valley, and in 2011, total groundwater pumping was 16,458,514 m<sup>3</sup> year<sup>-1</sup>, the lowest pumpage recorded since 1959. While groundwater levels in the Pahrump Valley have steadily declined since 1959, impacts to springs in the Middle Amargosa Basin have largely gone unmeasured. Thompson (1929) estimated flow at Yeoman Spring (now known as Chappo Spring), and noted that settlers had stated, “a warm or hot spring at the ranch of Alec Yeoman, about 5 miles southeast of Shoshone, is said to flow 10 miner’s inches (approximately 110 gallons per minute). It has been used for irrigation.” Early reports indicate that nearby Resting Springs had flows of up to 250 gallons per minute. Today, both springs flow at rates substantially lower than those historically reported. There is presently no obvious flow at the source of Chappo

Spring, only standing water in a small pool (Andy Zdon and Associates 2016). Additionally, groundwater levels in a monitoring well installed north of Shoshone Spring are very slowly decreasing over time. This may indicate that there is a slow, currently unmeasurable, decrease in spring flow at Shoshone Spring that would be only be identifiable after several decades and with well-engineered monitoring infrastructure. While the changes at some springs may be the result of spring modification and additional vegetation uptake, it is likely that spring flow in the Middle Amargosa Basin has been affected by past pumping in Pahrump Valley.

Impacts from groundwater pumping in the Middle Amargosa Basin are significant because of the presence of exceptional biodiversity associated with spring flows and GDEs (Parker et al. 2018). There are 26 taxa known to be endemic to Ash Meadows Wildlife Refuge (Sada 1990), but several other rare plant and animal species occur in the Middle Amargosa Basin outside of the Refuge. Rare plant species associated with GDEs outside of the refuge include alkali mariposa lily (*Calochortus striatus*), Amargosa niterwort (*Nitrophila mohavensis*), Ash Meadows gumplant (*Grindelia fraxinipratensis*), spring loving centaury (*Zeltnera namophila*), and Tecopa bird's beak (*Chloropyron tecopense*). Endemic animals such the Amargosa vole (*Microtus californicus* subsp. *scirpensis*) and Shoshone pupfish (*Cyprinodon nevadensis* subsp. *shoshone*) are restricted to spring-fed habitats.

Springs in other areas of the Mojave Desert have seen similar declines in water flow when compared with historic conditions. We found that Mesquite Springs had no standing water, and the only plant species present was western honey mesquite (Andy Zdon and Associates 2016). However, there may have been a broader suite of plants growing at the site in the past. Historical records indicate that “water from the flowing wells was piped directly into the house [in 1934]” (Keeling 1976), and “wild roses, as well as wild grapes, grew profusely at Mesquite Springs, a matter that has been remembered throughout the years by several of the first women to pioneer this section” (Wynn 1963).

In addition to pumping of groundwater for human uses, development of springs through the addition of pipes, troughs, and other infrastructure can also negatively impact spring flow. These flow enhancements are commonly made for livestock, wildlife, or mining use. This approach is similar to approaches used in geotechnical remedial activities to drain off groundwater and enhance ground stability landslide areas. In both cases, the installation of hardware in springs can lead to dewatering the saturated systems. With springs, the hardware can yield flow that cannot be sustained naturally. We saw an example of this during our study at Mesquite Springs along the south slope of the El Paso Mountains.

Spring waters and GDEs supported by spring flow are degraded by a variety of human activities, including livestock grazing, wild horse and burro presence, and adverse human use (e.g., off-highway vehicle and other recreational use). Waters are polluted and contaminated directly by these activities, and indirectly when spring-adjacent lands endure erosion and increased rates of sedimentation and nutrient and pollutant loading (Unmack and Minckley 2008). We found that some springs on livestock allotments on BLM lands in the California Mojave (i.e., Mound and Vaughn Springs) were in relatively good condition, indicating active management on the part of ranchers of public lands used as grazing allotments, while others were trampled and highly grazed (i.e., Barrel Spring in the Piute Mountains). While fencing can be used to help mitigate the negative impacts of livestock grazing, grazing exclusions must be managed with care. Fencing to exclude grazers has been found to lead to the development of dense vegetation growth, shading of waters (Shepard 1993), and may exclude wide-ranging mammals from using springs as water source. Researchers working in Ash Meadows, the largest spring complex in the Mojave

Desert, have found that in order to maintain native biodiversity and endemic biota, management of some small desert springs needs to include disturbance to mimic the actions of large Pleistocene megaherbivores and aboriginal human communities that are no longer present (Kodric-Brown and Brown 2007).

The invasion of non-native species and the extirpation or extinction of native species also impact the conservation value of desert springs. Our study found evidence of a broad variety of non-native species at the springs we surveyed in the California Mojave Desert, but a different suite of species was detected using each method (i.e., field observations, camera trapping, or eDNA). This result demonstrates the potential to enhance our ability to identify and study the true community of organisms at Mojave Desert springs by combining a number of different techniques. Use of multiple techniques may also decrease the pitfalls associated with each method. For example, camera traps have restrictions on photographic range and detectable size of species (Ishige et al. 2017), whereas eDNA methods can give false positives (Ficetola et al. 2016). Our study underscores the need for a better genetic reference database for the community of organisms associated with Mojave Desert springs, which, like many understudied ecosystems, had low percent identities at the species level (Wangensteen et al. 2018; Sinniger et al. 2016), particularly for mammals and plants.

As noted by Davis et al. 2017, the threats facing desert springs are additive and interacting, posing a major challenge for managers. In addition to the proximal threats of water extractions and diversions, habitat degradation, invasive species, and global changes threaten to exacerbate current impacts to desert springs. As the climate warms and the human population grows, desert areas will be under increasing pressure to extract groundwater and develop surface diversions in order to support human uses (Vicuna 2007). This is likely to adversely impact the conservation value of desert springs by increasing the drought stress for native species within GDEs. This may cause a contraction in the size of spring-fed GDEs and the number, or abundance, of obligate phreatophyte plant species contained within them. Rising water temperatures and the growing competitive advantage of more drought-tolerant non-native species may negatively impact Mojave Desert fishes and other native aquatic organisms in desert springs (Archer and Predick 2008), as some of these native species are living near their physiological limits and are vulnerable to shifts in community composition.

Climate change will also affect springs in the Mojave Desert as temperature increases evaporative processes and likely decreases groundwater recharge that ultimately surfaces as spring discharge (Meixner et al. 2016). Tagestad et al. (2016) identified 30 to 40-year long wet/dry cycles in the Mojave Desert, including an early-century wet period (1905–1946), a mid-century drought (1947–1975), and a later-century wet period (1975–2010). Annual precipitation has generally been below the 1975–2010 average since 2010. As we enter what may be a multi-decade drier than normal period (based on these trends), the imprint of climate change on these drier than normal periods with anticipated increasing competition for water resources will add to the vulnerability of springs and GDEs.

## Policy implications

Given the severe consequences of unsustainable groundwater extraction, and in recognition of the importance of groundwater to the health and survival of human and natural communities, the State of California put into place the Sustainable Groundwater Management

Act (SGMA) in 2014. This law limits the amount of pumping that can occur from aquifers to prevent undesirable impacts to beneficial uses of groundwater, including impacts to GDEs (Rohde et al. 2017). The enactment of the SGMA is significant; after more than a century of essentially no regulation of groundwater extraction, California state law now recognizes the needs of plants and wildlife for water, alongside providing for human uses such as domestic, irrigation and industrial consumption of water.

Unfortunately, very few Mojave Desert basins in California are covered under SGMA. This leaves over 1 million acres (nearly half) of the GDEs in California (Howard and Merrifield 2010)—those found in the Mojave and Sonoran deserts—vulnerable to continued unsustainable extraction. For the great majority of desert basins, and especially remote desert basins where aquifers support many critical springs, there is no effective limitation on groundwater withdrawals apart from county ordinances that have usually proved inadequate to limit unsustainable pumping. As one example, the Cadiz Valley Water Conservation, Recovery and Storage Project proposes to grossly overdraft a Mojave desert basin, pumping and exporting groundwater from an aquifer that supports vital springs. Despite the proposed overdraft and ecological impacts, SGMA does not apply to the basin. A county groundwater management ordinance that would have precluded overdrafting was waived after the project agreed to supply water to the county.

While SGMA may not cover Mojave Desert basins in California, other protections exist at the state level. The California Department of Fish and Wildlife (DFW) and State Lands Commission (SLC) have specific statutory duties to protect resources. DFW must protect the fish, wildlife and natural resources of the state. This duty extends beyond protection for listed species to all biological resources of the state. The SLC is obligated to maximize the economic value of state-owned lands across California's Mojave and Sonoran Deserts. If groundwater resources under these desert lands are depleted, the value of state-owned lands is likely to be greatly reduced for most potential uses. California's water laws require property owners sharing access to a groundwater aquifer to equitably share the water, giving the SLC the legal right to seek limitations on excessive pumping, even on private or public lands where it would reduce the value of state-owned lands.

Federal limitations on groundwater pumping to protect GDEs have not been commonly asserted in agency land use decisions. Some exceptions exist, primarily where federally threatened or endangered species are dependent on flows from a groundwater aquifer. At Ash Meadows National Wildlife Refuge and Devils Hole, a disjunct unit of Death Valley National Park, federal agencies have asserted rights to control groundwater extraction, but usually only where the federal rights precede the grant of conflicting state water rights, and where it is quite clear that the listed species is at risk from groundwater pumping. An example of the successful assertion of the primacy of federal water rights over state rights is described in the landmark 1976 case of *Cappaert v. United States*, where the US Supreme Court ruled that state water rights were subservient to the federal reserved water rights needed to protect the endangered Devils Hole pupfish (*Cyprinodon diabolis*).

Beyond these limited exceptions, federal policy has traditionally deferred virtually complete control over groundwater resources to states (Leshy 2004, 2008). However, this may be changing. BLM's most recent desert resource management plan amendments recognize more clearly the agency's duties under the Federal Land Policy and Management Act of 1976 to protect GDEs, especially in the Mojave and Sonoran Desert. The Desert Renewable Energy Conservation Plan (DRECP), an amendment to the California Desert Conservation Area Plan instituted by the agency primarily to provide for the siting and regulation of desert renewable energy facilities, incorporates limitations on groundwater use, invoking protection of springs, seeps and wetlands and their associated species,

irrespective of whether those species are listed as threatened or endangered. These provisions require extensive hydrogeologic knowledge, impose predictive modeling and monitoring of the effects of pumping, and protect GDEs. The groundwater provisions of the DRECP have yet to be widely employed, but they promise to make significant, positive changes in BLM's handling of actions affecting groundwater and desert springs.

Lastly, application of the Public Trust Doctrine under both federal and state law may be expanded to encompass protection of desert springs and GDEs. For example, in the 1983 case *National Audubon Society v. Superior Court*, the Supreme Court of California ruled that California's public trust doctrine required reduction of water extraction from tributaries of Mono Lake to maintain the lake's functional ecosystems. In a 2018 case, *Environmental Law Foundation v. State Water Resources Control Board*, California's Supreme Court ruled that groundwater pumping adjacent to the Scott River was subject to limitation based on the public trust doctrine. It appears that the public trust doctrine could therefore be expanded further to include desert groundwater aquifer systems, springs, and the GDEs they support.

Existing state and federal agency legislative and regulatory provisions can and should be expanded to better ensure the long-term sustainability of wildlife and natural communities. In the Mojave Desert, maintaining springs and seeps through careful regulation of pumping from source aquifers is of cardinal importance to life. Obtaining adequate knowledge about springs and their sources is the first step in delivering on that important project.

## Conclusion

Effective spring monitoring is needed to ensure the long-term viability of desert springs and to protect the biodiversity they support. Recording both biotic and abiotic conditions for springs is critical because springs and their associated flora and fauna can be particularly susceptible to small changes in groundwater elevation, and in the Mojave Desert, these changes can occur very slowly (Andy Zdon and Associates 2014). Our study demonstrates that the need for monitoring in the Mojave Desert is particularly acute, given that we established a hydrological and ecological baseline for many springs even as human uses of groundwater continue to take place. Our study, while valuable for future comparisons, is a "snapshot in time" of conditions that continue to change. Unfortunately, the identification of hydrological or biological change at a spring can occur too late to affect meaningful change in water management to preserve a spring. This is because the slow movement of groundwater can result in groundwater levels continuing to drop even after pumping has ceased. Continued spring monitoring is therefore critical, and an expanded network of monitoring, including at monitoring wells away from spring areas, will be needed to protect the springs of the Mojave Desert. Additionally, while many spring areas on public lands are protected by conservation designations such as Wilderness or National Monument status, impacts to these springs may occur from stresses to aquifer systems many miles away, and those impacts may occur over decades. Therefore, a periodic monitoring program for the entire region will be required to understand these spring systems and identify future attributable impacts in a defensible manner.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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