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Western pond turtles in the Mojave Desert? A review of their past, present, and possible future

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Abstract

The western pond turtle (WPT) was formerly considered a single species (*Actinemys* or *Emys marmorata*) that ranged from southern British Columbia, Canada to Baja California, México. More recently it was divided into a northern and a southern species. WPTs are found primarily in streams that drain into the Pacific Ocean, although scattered populations exist in endorheic drainages of the Great Basin and Mojave deserts. Populations in the Mojave Desert were long thought to be restricted to the Mojave River, but recently another population was documented in Piute Ponds, a terminal wetland complex associated with Amargosa Creek on Edwards Air Force Base. WPT fossils in the Mojave Desert are known from the Miocene to the Pleistocene. Recently, Pleistocene fossils have been found as far into the desert as Salt Springs, just south of Death Valley. The oldest fossil records suggest that WPTs were present in wetlands and drainages of the geological feature known as the Mojave block prior to the uplift of the Sierra Nevada Range about 8 Ma and prior to the ~ 3 Ma uplift of the Transverse Ranges. Archaeological records document use of turtles by Native Americans for food and cultural purposes 1,000 or more years ago at the Cronese Lakes on the lower Mojave River and Oro Grande on the upper river. The first modern publication documenting their presence in the Mojave River was 1861. Museum specimens were collected as early as 1937. These fossil and early literature records support the indigenous status of WPTs to the Mojave River. However, mtDNA-based genetic evidence shows that Mojave River turtles share an identical haplotype with turtles on the California coast. Limited nuclear data show some minor differences. Overdraft of water from the Mojave River for municipal and agricultural uses, urban development, and saltcedar expansion are threats to the continued survival of WPTs in the Mojave River.

Keywords

Actinemys, *Emys*, fossil, *marmorata*, Pacific pond turtle, *pallida*, relict population

Introduction

North America has a diverse turtle fauna represented by 9 of the 14 living families worldwide. With 62 species (89 total taxa) currently recognized, the USA has more turtle species and subspecies than any other country followed by México with 49 species, some of which overlap between the two countries (Turtle Taxonomy Working Group 2017). However, turtle diversity is unequally distributed across North America based on variation in climate, primary productivity, water availability, topography, and latitude (Ennen et al. 2016). Most diversity is concentrated in the southeastern USA (Buhlmann et al. 2009) making it a globally important biodiversity hotspot for turtles (Mittermeier et al. 2015). In contrast, the arid western part of North America has a comparatively depauperate turtle fauna. The western pond turtle (WPT) genus (*Actinemys* Agassiz, 1857 or *Emys* Duméril, 1805: *fide* Turtle Taxonomy Working Group 2017) includes two of only three native freshwater turtle species (the third being the painted turtle, *Chrysemys picta* Schneider, 1783) with ranges that occur along portions of the Pacific coast of North America (Lovich and Beaman 2008).

The taxonomic placement of WPTs has been in flux at both the genus and species levels. They have been variously placed in the genera *Actinemys*, *Clemmys* (Ritgen, 1828), and *Emys* by multiple authors for over 160 years. Since generic assignment is extraneous to the context of this paper, the reader is referred to summaries in Ernst and Lovich (2009), Fritz et al. (2011), and Spinks et al. (2014) for additional details and other references on the taxonomic debate regarding WPTs and their relationships. For simplicity, we refer to the genus as *Actinemys* without taking a position in this paper on its relationship to Blanding's turtles, *Emydoidea blandingii* (Holbrook, 1838), or European pond turtles, *Emys orbicularis* (Linnaeus, 1758), and *E. trinacris* (Fritz, Fattizzo, Guicking, Tripepi, Pennisi, Lenk, Joger, and Wink, 2005), as debated by others (Holman and Fritz 2001; Feldman and Parham 2002; Fritz et al. 2011).

Seeliger (1945) recognized two subspecies of what was formerly a single species (then placed in the genus *Clemmys*): *A. m. marmorata* north of about San Francisco Bay, and *A. m. pallida* to the south. One of the traits used to separate the two forms was the presence of conspicuous inguinal scutes in *A. m. marmorata* that were poorly developed or missing in *A. m. pallida*. More recent genetic analyses confirmed Seeliger's suggestion that there were two taxa involved, but Spinks et al. (2014) elevated them to full species and better defined their geographic distribution, particularly in central California (CA). In conformance with the Turtle Taxonomy Working Group (2017), we hereafter refer to the two species by their scientific names or more generally as western pond turtles (WPTs). Their combined modern ranges are confined mostly to drainages along the Pacific slope of North America from the state of Washington, USA southward into Baja California, México (Bury 2012). The current distribution contrasts with a wider distribution in the western USA in the past as shown by the fossil record (Brattstrom and Sturn 1959; Gustafson 1978). Their individual ranges are shown in detail in Spinks et al. (2014) and Thomson et al. (2016).

In addition to their coastal distribution, relict populations of WPTs are found in several endorheic drainages of the Great Basin (Bury 2017), Mojave Desert (Lovich and Meyer 2002), and other desert locations including isolated oases in Baja California, México (Grismer and McGuire 1993; Valdez-Villavicencio et al. 2016). Great Basin records have been reported from the Susan, Truckee and Carson Rivers (LaRivers 1942; Thomson et al. 2016; Bury 2017). At least some of these populations have been considered to be introduced (Thomson et al. 2016) from stock native to Pacific drainages. For example, Thomson et al. (2016) reported that, *One hundred and eighty individuals of this species were introduced in the state of Nevada in 1887, and these may have been the source of the population in the Truckee and/or Carson Rivers* (*Cary 1889*). In discussing Cary's 1889 report, La Rivers (1962) noted that, *Either these were the Pacific Terrapin* (Clemmys marmorata)*, which were undoubtedly introduced to the State at one time or another* (*La Rivers 1942*) *or something else which did not survive – Cary fails to say where he got them.*

However, the possibility that La Rivers' reference to "something else" (e.g., another turtle species) that was introduced cannot be ruled out. For example, diamond–backed terrapins (*Malaclemys terrapin*), native to the east and Gulf coasts of the USA were highly sought after as an expensive food item at that time. They were introduced (unsuccessfully) into areas far from their native range including San Francisco Bay (Taft 1944; Hildebrand and Prytherch 1947), Iowa (Coker 1920), and even Italy (Carr 1952). WPTs were eaten in the 1880s in San Francisco (Buskirk 2002; Bettelheim 2005), but they were considered "much inferior to the diamond-back in food value" (Smith 1895). It is certainly possible that the turtles mentioned by Cary (1889) were WPTs, but it could have been another species that failed to survive. As other authors have noted, determining the indigenous status of turtles in the western USA, including WPTs, is not always straightforward (e.g., Miller 1946; Velo-Antón et al. 2011; Lovich et al. 2014a, 2019; Bury 2017; Bettelheim 2020). Genetic analyses are underway to resolve the provenance of WPTs in Nevada (Jason Jones, Nevada Department of Wildlife, personal communication).

Occupancy of WPTs (presumed to be *A. pallida* based on Spinks et al. (2014) and apparent lack of inguinal scutes) in or near the endorheic Mojave River of CA is well-documented based on fossil records extending from the late Miocene through the Pleistocene, and historical observations of living specimens into the present times. Nevertheless, records for the Mojave River are relatively scarce, and there is no summary of the disparate fossils, archaeological occurrences, museum specimens, literature records, photographs, or sightings of this California Department of Fish and Wildlife Species of Special Concern in the Mojave Desert. The objectives of this paper are to compile known paleontological, archaeological, and modern records of relict populations of WPTs (Lovich and Meyer 2002) in the Mojave Desert, provide a preliminary assessment of their genetic relationships, and briefly discuss current and future conservation challenges faced by WPTs (Manzo et al. *unpublished*) in the Mojave Desert.

Methods

Study areas

When first considered, the Mojave Desert appears to be completely unsuitable for freshwater turtles since water availability is an important determinant of turtle habitat suitability (Ennen et al. 2016). Although it is the most arid ecosystem in North America, there are scattered wetlands that support various aquatic species, including WPTs. The largest river within the Mojave Desert, the Mojave River, flows northward from its headwaters in the San Bernardino Mountains, then eastward after passing Helendale, CA, to its usual terminus in Soda Dry Lake about 200 river km from its source. In extremely wet years the river can spill over into Silver, East Cronese, and West Cronese (also known as Cronise) dry lakes. With no outlet to the ocean, the river lies within the hydrographic boundary of the Great Basin (Grayson 1993) even though from a biogeographic/floristic standpoint the river is entirely within the Mojave Desert ecosystem (Vasek and Barbour 1977) after leaving the San Bernardino Mountains. Vegetation along much of the desert course of the river, long dominated by native riparian species like cottonwood (*Populus fremontii*), willows (*Salix* spp.) and mesquite (*Prosopis* spp.), has changed considerably since the 1800s due to overdraft of the river's water for municipal and agricultural uses (Lines 1999; Webb et al. 2001). Large areas of the riparian zone have been replaced with the exotic pest plant saltcedar (*Tamarix ramosissima*) (Lines and Bilhorn 1996) to the detriment of some wildlife species (Lovich and de Gouvenain 1998), including WPTs (Lovich and Meyer 2002). Perennial water occurs naturally (or through groundwater pumping) in several areas along the river, including Mojave Narrows Regional Park, locations downstream of Victorville, Camp Cady Wildlife Area (or simply Camp Cady; Cummings et al. 2018), Afton Canyon Area of Critical Environmental Concern (or simply Afton Canyon; Lovich and Meyer 2002) and several other sites.

Farther west in the Mojave Desert, Piute Ponds constitute a large wetland complex as the terminal basin for drainage from Amargosa Creek, another endorheic stream system known to have a population of WPTs in 1997 (RNF, personal observation; David Muth, *in litt.*). Amargosa Creek flows between the Angeles National Forest and the Sierra Pelona Mountains that border the extreme western Mojave Desert. The head of Amargosa Creek is adjacent to the head of Castaic Creek where a larger population (150–200) of WPTs existed at nearby Elizabeth Lake until it was extirpated by drought and fire (Lovich et al. 2017). Piute Ponds receive treated wastewater and they are managed for recreation, including waterfowl hunting.

Data collection

An effort was made to compile paleontological, archaeological, and modern records of WPTs in the Mojave Desert including literature and database searches, and examination of resource management agency files. Staff of those agencies were contacted for additional records and photographs. Museum zoological records were located using the search engine provided on VertNet (http://vertnet.org)

We conducted turtle trapping at various locations along the Mojave River from 1998–1999 (Lovich and Meyer 2002) and 2016–2020 to find out where WPTs persisted and estimated the size and composition of their populations (Lovich unpublished). Even though WPTs are protected by the state of CA, details of our study sites are not given in some cases to protect tenuous declining populations from illegal collection (e.g., Grandmaison and Frary 2012; Sung et al. 2013). Following techniques outlined by Gibbons (1988, 1990), we used hoop traps measuring 0.76 m in diameter by 1.83 m in length, with 3.8 cm mesh, baited with sardines or canned cat food. Similar techniques were used from 2019–2020 at Piute Ponds on Edwards Air Force Base.

Genetic analyses

We conducted a preliminary assessment of genetic relationships of turtles in the Mojave River relative to populations in coastal southern CA using a single mitochondrial gene marker (mtDNA). We collected tail-tip tissue from 16 WPTs (Spinks et al. 2014) from three locations along the Mojave River (Afton Canyon, California Desert Discovery Center, and an undisclosed site on the Mojave River) for mtDNA sequencing (Table 1). DNA was extracted from tissue samples using a salt extraction protocol (Sambrook and Russell 2001) and 742 base pairs of the ND4 + flanking tRNAHis gene (hereafter ND4) were amplified following the protocol of Spinks and Shaffer (2005). ND4 was sequenced (GENEWIZ, Los Angeles, CA, USA) and edited and aligned using SEQUENCHER 5.4 (Gene Codes Corp., Inc., Ann Arbor, MI, USA). All ND4 sequences of *A. pallida* from Spinks and Shaffer (2005) and Spinks et al. (2014) from more coastal areas in San Diego, San Bernardino, and Los Angeles counties were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/genbank) and aligned to these newly generated sequences in MESQUITE 3.10 (Maddison and Maddison 2015) using OPAL (Wheeler and Kececioglu 2007). The sequence alignment was trimmed to 725 base pairs as

Table 1. Records associated with tail-tip tissue collection from individual *Actinemys pallida* captured at multiple locations along the Mojave River, San Bernardino County, California, USA. Location: AC = Afton Canyon Area of Critical Environmental Concern, CDDC = California Desert Discovery Center. Sex: M = male, F = female. CL indicates a straight-line midline carapace length.

Location	Date	ID	Sex	CL (cm)
AC	05/03/2017	AJW	F	14.6
CDDC	09/27/2016	AJV	M	12.5
CDDC	09/27/2016	ALV	M	11.4
CDDC	09/27/2016	AHW	F	12.2
CDDC	09/27/2016	AIW	M	12.5
CDDC	07/26/2017	AKW	M	13.2
Undisclosed site	07/27/2017	ALW	F	16.5
Undisclosed site	07/27/2017	AHX	F	18.2
Undisclosed site	08/23/2017	AIX	M	18.1
Undisclosed site	08/23/2017	AJX	M	15.5
Undisclosed site	08/23/2017	AKX	F	16.3
Undisclosed site	09/12/2017	ALX	F	17.4
Undisclosed site	09/12/2017	AMV	M	16.5
Undisclosed site	09/12/2017	ANV	F	15.7
Undisclosed site	09/12/2017	AOV	M	15.7
Undisclosed site	09/12/2017	APV	M	15.6

that was the length of most ND4 fragments from Spinks et al. (2014) and reduced to two identical haplotypes per sampling location (see Supplementary File 1: Table S1). A ND4 haplotype network was made in R 3.4.4 (R Development Core Team 2014) using the PEGAS (Paradis 2010) and APE (Paradis and Schliep 2018) packages. Genetic samples were also collected from WPTs at Piute Ponds but the results are not yet available.

Paleontological records

A literature search of paleontological data sources was performed, and pertinent museum collections examined including the data repository at the University of California Museum of Paleontology. Latest Miocene, Pliocene, and Pleistocene fossil vertebrate assemblage data sets (see below) were searched to compile a list of reported occurrences of WPTs within the far western US and northwestern México. These data were queried using the following criteria: 1) all assemblages (sites, localities and/or local faunas) that contain the various taxonomic names that have been used for the WPT genus including *Actinemys, Clemmys* or *Emys*; 2) Blancan, Irvingtonian and Rancholabrean North American Land Mammal Ages (NALMA), and 3) assemblages that fall within the greater Mojave Desert region of Arizona, southern CA desert regions (Imperial, Inyo, Los Angeles, Riverside, San Bernardino, and San Diego Counties), southern Nevada, Baja California and northwestern Sonora, México. We also include assemblage data (Table 2) retrieved from the following Stout Research Center library archival sources (electronic file names are shown in brackets):

Catalogue of Blancan and early Quaternary vertebrate fossils from Arizona, [Arizona early Quaternary 18 May 2012.doc], in preparation, data tables on file Colorado Desert District Stout Research Center Library archive. (revised 18 May 2012).

Catalogue of late Quaternary and Holocene Vertebrates from Arizona, [Arizona late Pleistocene catalogue.doc], data tables on file Colorado Desert District Stout Research Center Library archive. (revised 25 May 2012).

Catalogue of late Quaternary Vertebrates from California; [California data and references.doc], amended data for Jefferson (1991), data tables on file Colorado Desert District Stout Research Center Library archive. (revised 25 April 2018).

Northwestern México; [México northwest.wpd], data tables on file Colorado Desert District Stout Research Center Library archive. (revised 20 July 2016).

Catalogue of late Quaternary vertebrates from Nevada, amended data for Jefferson et al. (2004), [Nevada Paleontology-Occ. Paper working.wpd], data tables on file Colorado Desert District Stout Research Center Library archive. (revised 08 September 2017).

Repositories, Institutional acronyms or Institutional abbreviations

Acronyms for institutional repositories of fossil and modern specimens examined are as follows: **LACM** = Los Angeles County Museum; **MVZ** = Museum of Vertebrate Zoology, University of California; **SBCM** = San Bernardino County Museum; **SDNHM** = San Diego Museum of Natural History; **UCMP V** = University of California Museum of Paleontology. We collected fossil samples from Salt Springs (San Bernardino County, CA) with the permission of the Bureau of Land Management

Table 2. Fossil and recent records of *Actinemys* from the desert regions of Arizona (AZ) and California (CA), USA. Other abbreviations are as follows: Fm = formation, USGS = U.S. Geological Survey. Museum acronyms are listed in the text. Captive specimens at the California Desert Discovery Center in Barstow are discussed in the text. Although we prefer the spelling "Mojave" to "Mohave" (Jones 2016), some earlier records listed below use the latter form.

Location and County	Geologic Age and NALMA	Geologic Formation	Date Collected or Observed	Specimen Number	Data Source or Reference	Comments
Red Rock Canyon State Park, Kern County, CA	Miocene, Clarendonian NALMA, 12.4–9 Ma	Dove Spring Fm.	—	—	Whistler et al. (2009)	fossils
Horned Toad Hills, Kern County, CA	Pliocene, Blancan NALMA, < 4.8 Ma	Horned Toad Fm.	—	—	May and Repenning (1982)	fossils
Santa Fe Railroad, Golden Shores, Mojave County, AZ	Pliocene, Blancan NALMA, > 3.3 Ma	Bullhead Alluvium	—	USGS HO6WS-17	Reynolds et al. (2016)	fossils
Cushenbury, San Bernardino County, CA	Plio-Pliocene, Blancan NALMA, 2–3 Ma	Old Woman Sandstone	—	UCMP V 149157	May and Repenning (1982)	fossils
Anza Borrego Desert State Park, San Diego County, CA	Pleistocene, Irvingtonian NALMA, 1–0.6 Ma	Bautista Fm, Ocotillo Fm.	—	—	Jolly (2000); Gensler et al. (2006)	fossils
Flowing-Wells Number 3, Imperial County, CA	Late Pleistocene, Irvingtonian NALMA	–	—	—	Reynolds (1989)	fossils
Lake Manix, San Bernardino County, CA	Late Pleistocene, Irvingtonian and Rancholabren NALMA	Manix Fm.	—	—	Jefferson (1987, 1989, 2003)	fossils
Salt Springs, San Bernardino County, CA	Late Pleistocene	—	—	—	Jefferson (1990); Reynolds (2018)	fossils
Stevens Lake, San Bernardino County, CA	Late Pleistocene, Rancholabrean NALMA	Manix Fm.	—	SBCM 830	Jefferson (1989)	fossils
Lake Manix, San Bernardino County, CA	Late Pleistocene, Irvingtonian to Rancholabrean NALMA	Manix Fm.	—	UCMP V 310516, 310517, 310540, 310550, 310575, 310598, 315668	Jefferson (2003)	fossils
Mojave River, San Bernardino County, CA	Recent	—	—	LACM 164103, 164105, 165111	See supp. file 2: Figs S8-S11	165111 not examined
Andreas Canyon, Riverside County, CA	Recent	—	—	—	Jennings and Hayes (1994)	observational record
Mojave River, San Bernardino County (near Cajon Pass), CA	Recent	—	1860–1861	—	Cooper (1869)	"A water turtle (*Actinemys marmorata*) also lives in the river."
Mojave River, San Bernardino County, CA	Recent	—	1902	—	Meek (1905)	"This species is not rare in ponds along the Mojave River." Paper states that no specimens were secured
Yermo, San Bernardino County, CA	Recent	—	02 May 1937	LACM 7997	See supp. file 2: Figs S2–S3	hatchling
Mohave River (5 mi E of Yermo), San Bernardino County, CA	Recent	—	13 July 1937	SDNHM 17135	See supp. file 2: Figs S4–S5	Adult male
Mohave River (5 mi E of Yermo), San Bernardino County, CA	Recent	—	13 July 1937	SDNHM 17136	See supp. file 2: Figs S6–S7	Adult male
Mohave R., (just below bridge north of Victorville), San Bernardino County, CA	Recent	—	08 April 1939	MVZ 28328	C. Spencer (pers. comm.)	Specimen presumed lost since 1991. Last sent on loan to Louisiana State University
Deep Creek (tributary to Mojave River), San Bernardino County, CA	Recent	—	Late 1980s	—	Brattstrom and Messer (1988)	Turtle tracks seen in mud

Location and County	Geologic Age and NALMA	Geologic Formation	Date Collected or Observed	Specimen Number	Data Source or Reference	Comments
Deep Creek (tributary to Mojave River), San Bernardino County, CA	Recent	—	2004	—	Madden-Smith and Fisher (2005)	No turtles observed
Afton Canyon, Mojave River, San Bernardino County, CA	Recent	—	28 May 1987	MVZ 227728	See supp. file 2: Figs S12–S13	Female
Camp Cady, Mojave River, San Bernardino County, CA	Recent	—	28 September 1992	—	J. Lovich 1992 field notes	Three or more individual turtles captured by BLM for translocation to Zzyzx and California Desert Information Center
Mojave River Narrows, San Bernardino County, CA	Recent	—	18 April 1994	—	K. Beaman (pers. comm.)	Two individuals seen basking on a log by R. Goodrich
Camp Cady, Mojave River, San Bernardino County, CA	Recent	—	1998–1999	—	Lovich and Meyer (2002), see Fig. 1A	21 individual turtles captured, marked and monitored
Afton Canyon, Mojave River, San Bernardino County, CA	Recent	—	1998–1999	—	Lovich and Meyer (2002)	14 individual turtles captured, marked and monitored
Camp Cady, Mojave River, San Bernardino County, CA	Recent	—	April 2004	—	Dead specimen	Shell found after cleaning out Pond three
Afton Canyon, Mojave River, San Bernardino County, CA	Recent	—	spring 2005	—	Photographic documentation (see Fig. 1B)	Photographed by B. Espinoza
Camp Cady, Mojave River, San Bernardino County, CA	Recent	—	April or May 2014	—	Photographic documentation (see Fig. 1D)	Two WPTs observed basking in “Bud’s pond”
Big Morongo Canyon, San Bernardino County, CA	Recent	—	03 August 2014	—	Photographic documentation (see Fig. 1H)	Juvenile seen and photographed by P. Siminski
Afton Canyon, Mojave River, San Bernardino County, CA	Recent	—	16 April 2016	—	Photographic documentation (see Fig. 1E)	Hatchling-sized specimen, caught by J. Warner
Afton Canyon, Mojave River, San Bernardino County, CA	Recent	—	03 May 2017	—	Adult female (see Fig. 1F)	—
Piute Ponds, Edwards Air Force Base, Kern County, CA	Recent	—	2014, 2019, 2020	—	Petersen et al. (2018), this paper (see Fig. 1G)	12 live animals captured and released

in an attempt to obtain a precise radiocarbon age using the carbon extraction and graphitization system at the U.S. Geological Survey Radiocarbon Laboratory.

Results

Paleontological records

Fossil remains of WPTs are well-documented throughout much of the current range of the taxon (Ernst and Lovich 2009) although they had a wider distribution in the distant past (e.g., Brattstrom and Sturn 1959; Jefferson 1991; Jolly 2000; Gensler et al. 2006), including Blancan NALMA remains in western Arizona (Reynolds et al. 2016). WPT remains have been found in Pliocene (Blancan) deposits of CA and Oregon outside the Mojave Desert, as summarized by Ernst and Lovich (2009). WPTs have also been recovered outside the Mojave Desert from Pleistocene (Irvingtonian and Rancholabrean NALMA) deposits in CA and Washington (Brattstrom 1953a, 1953b, 1955; Brattstrom and Sturn 1959; Miller 1971; Hudson and Brattstrom 1977; Gustafson 1978; Jefferson 1991; Dundas et al. 1996).

The oldest recorded fossil WPT remains from the Mojave Desert are from the Miocene Dove Spring Formation (Reynolds and Miller 2011), located in Red Rock Canyon north of the town of Mojave in the northwestern Mojave Desert. WPTs have been recovered stratigraphically throughout the Dove Spring Formation, with occurrences ranging from 12.4 to ~ 9 Ma (Whistler et al. 2009).

Remains of WPTs have been recovered from lacustrine Member 3 of the Horned Toad Formation in the northwestern Mojave Desert. The fossil material was recovered stratigraphically above the late Miocene Lawlor Tuff, which has been dated at 4.8 Ma. (May 1981; May et al. 2011).

Other material has been recovered from the Pliocene Blancan NALMA Old Woman Sandstone at Cushenbury in San Bernardino County, CA (VertNet, Table 2). The Old Woman Sandstone ranges from 3.5 to 2.5 Ma (May and Repenning 1982). The locality is about 40 km from the present course of the Mojave River, but only 8 km from Baldwin Lake where there were stickleback fish of the genus *Gasterosteus* in the Pleistocene (Reynolds 2005) and now (Swift et al. 1993).

WPTs are well-represented in Pleistocene Irvingtonian and Rancholabrean NALMA deposits in Lake Manix. This locality along the Mojave River is 12 km upstream from an extant population in Afton Canyon (Jefferson 1987, 2003; Lovich and Meyer 2002; Lovich et al. 2018; Table 2).

The fossil record suggests that WPTs were present in wetlands and drainages of what geologists refer to as the Mojave block (Glazner et al. 2002) prior to the uplift of the Sierra Nevada Range about 8 Ma (Frankel et al. 2008), and prior to the ~ 3 Ma uplift of the Transverse Ranges (Meisling and Weldon 1989), when WPTs were more widely distributed in the Pliocene. When the climate became dryer about 10,000 ybp, their range contracted and shifted toward the Pacific coast (Brattstrom and Sturn 1959), presumably leaving remnant populations in the Great Basin and Mojave deserts. The late post-Pleistocene history of the WPT in the Mojave Desert is a lesson in survival (Lovich and Meyer 2002).

Interestingly, the Plio–Pleistocene (Blancan, Irvingtonian and Rancholabrean NALMA) fossil record of WPTs within North American deserts (Arizona, CA, Nevada, Baja California del Norte and Sonora, México) is restricted to the present Mojave River drainage system and the Salton Trough (see Lovich et al. 2020 for a description of the Salton Trough) in the Sonoran Desert of CA. Although fossiliferous deposits of this age are known throughout the southwestern deserts, most fossil assemblages lack WPT remains (see Stout Research Center library archival sources vertebrate assemblage data sets in Data Search Methods above, Table 2).

Recently, additional fossils of WPTs (see Supplementary File 2: Fig. S1) have been found farther into the Mojave Desert at Salt Springs, well beyond the current range or modern dispersal ability of the species (Jefferson 1990; Reynolds 2018), near southern Death Valley. The marshland sediments at this site are Rancholabrean NALMA in age (Jefferson 1990). Unfortunately, we were unable to obtain a radiocarbon age estimate from these fossils because the samples were too degraded and contaminated with secondary carbon (as shown by the low %C and %N, as well as the high C:N ratio) to yield a reliable age.

Archaeological records

Archaeological sites have yielded remains of WPTs from several locations along or near the Mojave River that suggest their use as food or for other cultural purposes (Schneider and Everson 1989). Schneider and Everson (1989) reported WPTs in the Cronese Lakes based on the work of Drover (1979). These lakes are near one Holocene terminus of the Mojave River and only fill today during periods of heavy precipitation and flooding. Ironically, archaeologic WPT remains were not found at Afton Canyon (see below), a site where WPTs appear to persist, although in smaller numbers than in the late 1990s (Lovich and Meyer 2002; Lovich et al. unpublished). It is unlikely that Mojave River scour contributed to the removal of archaeological remains of WPTs at Afton Canyon since Schneider and Everson (1989) reported remains of Agassiz's desert tortoises (*Gopherus agassizii*) there.

Schneider and Everson (1989) also reviewed records provided by Rector et al. (1983) from Oro Grande, just downstream from Victorville. The latter authors found rattles made from WPT shells that bore evidence of drill holes and stains from asphaltum used as an adhesive seal. Native Americans throughout the southwestern USA (Lovich et al. 2014b) used turtle shells of various species, including WPTs, as rattles (Bettelheim 2020). The span of occupation of the Oro Grande site ranges from a maximum of 840–1300 A.D. (Rector et al. 1983).

Museum zoological records

All credible extant/modern desert records (Table 2), except for those in Baja California, México, are in the hydrographic Great Basin defined by Grayson (1993). We found only six museum specimens of WPTs collected from the Mojave River and all are presumed to represent *A. pallida* based on the results of Spinks et al. (2014) and the absence of well-defined inguinal scutes (Seeliger 1945). The first was collected on 2 May 1937 at Yermo. It is a hatchling with no visible growth rings (see Supplementary File 2: Fig. S2) and a yolk scar on the plastron (see Supplementary File 2: Fig. S3), deposited in the Los Angeles County Museum (LACM 7997). The carapace length is 28.2 mm, within the range of values for hatchlings reported in the literature (Ernst and Lovich 2009).

Later in 1937 (13 July), two adult male specimens were collected by the San Diego Natural History Museum five miles east of Yermo. One male (SDNHM 17135) has a carapace length of 134.8 mm (see Supplementary File 2: Figs S4–S5) and the other (SDNHM 17136) has a carapace length of 120.2 mm (see Supplementary File 2: Figs S6–S7). Although devoid of water in more recent times (other than artificial ponds associated with housing developments) the Mojave River ponded above ground near Yermo in the 1800s and early 1900s at a place called Hawley's Station. There may be an aquitard in the area associated with the Calico Fault (Oskin et al. 2007) that caused water to pond there in wetter times such as occurred in the Mojave Desert region from 1905–ca.1941 (Hereford et al. 2006). The last specimen collected in the 1930s was MVZ 28328 north of Victorville on 8 April 1939. Additional details on that specimen are unavailable as it is presumed lost (Table 2).

Two additional specimens reside in the Los Angeles County Museum collections from the "Mojave River" without any additional locality data or date of collection. One is an adult male (LACM 164103) with a carapace length of 123.2 mm (see Supplementary File 2: Figs S8–S9). This specimen has only four vertebral scutes instead of the normal five. At least eleven growth rings are visible on the plastron. The other is an adult female (LACM 164105) with a carapace length of 134.1 mm (see Supplementary File 2: Figs S10–S11) with no clear growth rings. The posterior margin of the carapace appears to have been chewed on by a mammalian predator. The last specimen known to be collected from the Mojave River is a 3–4-year-old female found at Afton Canyon on 28 May, 1987 (see Supplementary File 2: Figs S12–S13) and placed in the University of California, Museum of Vertebrate Zoology (MVZ 227728). The young age of this specimen is evident because the hatchling scutes are still visible.

Photographic and trapping records at Camp Cady and Afton Canyon

Both of these sites are on the lower Mojave River. The first photographs of WPTs from the Mojave River available to us (e.g., Fig. 1A) were taken by one of the authors (JEL) at both Camp Cady and Afton Canyon in 1998 when ecological research (Lovich and Meyer 2002) on the species was first initiated. In 2005, Bobby Espinoza, a Professor at California State University, Northridge, photographed a specimen in Afton Canyon during the spring of that year (Fig. 1B). Then in either 2007 or 2008, Art Basulto, a Bureau of Land Management employee, photographed another WPT at Afton Canyon (Fig. 1C). WPTs are presumed to have existed at Camp Cady continuously from at least 1998 to 2014 when the last two were photographed in what is known as "Bud's Pond" (Pond 2 of Lovich and Meyer 2002) by Bruce Kenyon in either April or May 2014 (Fig. 1D). Trapping and visual searches at Camp Cady from 2016–2017 (360 trap hours) failed to find any more WPTs. The next WPT documented at Afton Canyon via photography was a near hatchling–sized individual found on a class field trip from California State University, Northridge by Jason Warner on 16 April 2016 (Fig. 1E). Despite efforts to trap or observe more turtles at Afton Canyon from 2016–2019 (916 trap hours), only one more was found, an adult female captured 3 May 2017 and released (Fig. 1F).

Piute Ponds records

WPTs were only recently documented in the Piute Ponds at Edwards Air Force Base (Petersen et al. 2018). In 2019 and 2020, 12 WPTs were captured at Piute Ponds (Fig. 1G), including three juveniles suggesting that the population is reproducing. The genetic relationships of this population to others in southern CA are not yet known. Our preliminary hypothesis is that the population is native and derived from the source population that resides farther up Amargosa Creek. It is interesting to note that Piute Ponds WPTs appear to have conspicuous inguinal scutes typical of *A. marmorata*. Spinks et al. (2014) determined that *A. marmorata* occurred near Tehachapi, CA, a location close to the Garlock Fault that defines the northwestern boundary of the Mojave Desert. The Piute Ponds complex is only about 37 km from the nearest point along the Garlock Fault. If turtles at Piute Ponds are indeed assignable to this taxon, there are two species of freshwater turtles in the Mojave Desert.

California Desert Discovery Center

This facility (formerly called the California Desert Information Center) in Barstow, CA is dedicated to providing information to the public about the natural, cultural, and historic resources associated with the Mojave Desert. Their interpretive displays include a large, concrete patio pond containing endangered Mojave tui chubs, *Siphateles bicolor* (Girard, 1856), and at least five WPTs, including one female. The initial stock of turtles came from Camp Cady in 1992 where artificially constructed ponds are maintained next to the formerly ponded (as late as the 1990s) riverbed for endangered fish. The origin of turtles at Camp Cady is debated. Some say that they were translocated from coastal southern CA but correspondence between JEL and a retired employee of the California Department of Fish and Wildlife suggests that the turtles found the ponds after they were constructed. Sporadic reproduction occurred at the Discovery Center since 1992 as evidenced by periodic observation of juveniles. Other than the two WPTs reported from Afton Canyon (above), these are the only known remaining lower Mojave River WPTs. Recently observed juveniles eventually disappeared, possible victims of ravens (*Corvus corax*) that drink from the pond and are known to eat juvenile turtles in the Mojave Desert (Boarman 2003). The future status of this captive population is tenuous given that only one female survives[1].

Extralimital records

Outside the Mojave Desert there are other records of WPTs in the Sonoran Desert of CA, which most likely represent releases. A juvenile WPT (Fig. 1H) was photographed by Peter Siminski on 3 August 2014 at Big Morongo Canyon in San Bernardino County. This site is at the interface of the Mojave and Sonoran deserts near Palm Springs, CA. Jennings and Hayes (1994) reported a record for Andreas Canyon in the Sonoran Desert of Riverside County, also near Palm Springs. Fossil records reported by Jolly (2000) in Anza Borrego Desert State Park establish the former presence of the species in the Sonoran Desert ecoregion but no modern populations have been identified there. Various other sightings and records are summarized in Table 2.

Literature records

The first mention of WPTs found in the literature for the Mojave River is Cooper (1869) who noted, *A water turtle* (Actinemys marmorata) *also lives in the river*. He trav-

1 As of May 2021 only two males survive.

Figure 1. Recent photographs of western pond turtles (*Actinemys* spp.) from the Mojave Desert region in California, USA. Adult *Actinemys* in this region rarely exceed 18.0 cm in straight-line carapace length. **A** *Actinemys pallida* collected at the Camp Cady Wildlife Area, San Bernardino County, California, 5 September 1998. This specimen was exceptionally patterned relative to other turtles collected at the site. Photo by Jeffrey E. Lovich **B** *Actinemys pallida* seen at Afton Canyon Area of Critical Environmental Concern in the spring of 2005 by Bobby Espinoza **C** *Actinemys pallida* photographed at Afton Canyon Area of Critical Environmental Concern by Art Basulto of the Bureau of Land Management in either 2007 or 2008 **D** *Actinemys pallida* at Camp Cady Wildlife Area photographed by Bruce Kenyon in April or May 2014. No other western pond turtles were observed there after this photograph despite intensive trapping from 2016–2017. The population is considered to be extirpated **E** Hatchling *Actinemys pallida* at Afton Canyon Area of Critical Environmental Concern photographed by Jason Warner 16 April 2016 **F** Adult female *Actinemys pallida* captured at Afton Canyon Area of Critical Environmental Concern 3 May 2017. Photo by Jeffrey E. Lovich **G** Photograph of a female *Actinemys marmorata* from Piute Ponds, Edwards Air Force Base, Kern County, California. Photo by Doug Gomez **H** Juvenile *Actinemys* sp. photographed by Peter Siminski at Big Morongo Canyon, San Bernardino County on 3 August 2014. It is undoubtedly a released specimen of either *A. marmorata* or *A. pallida*.

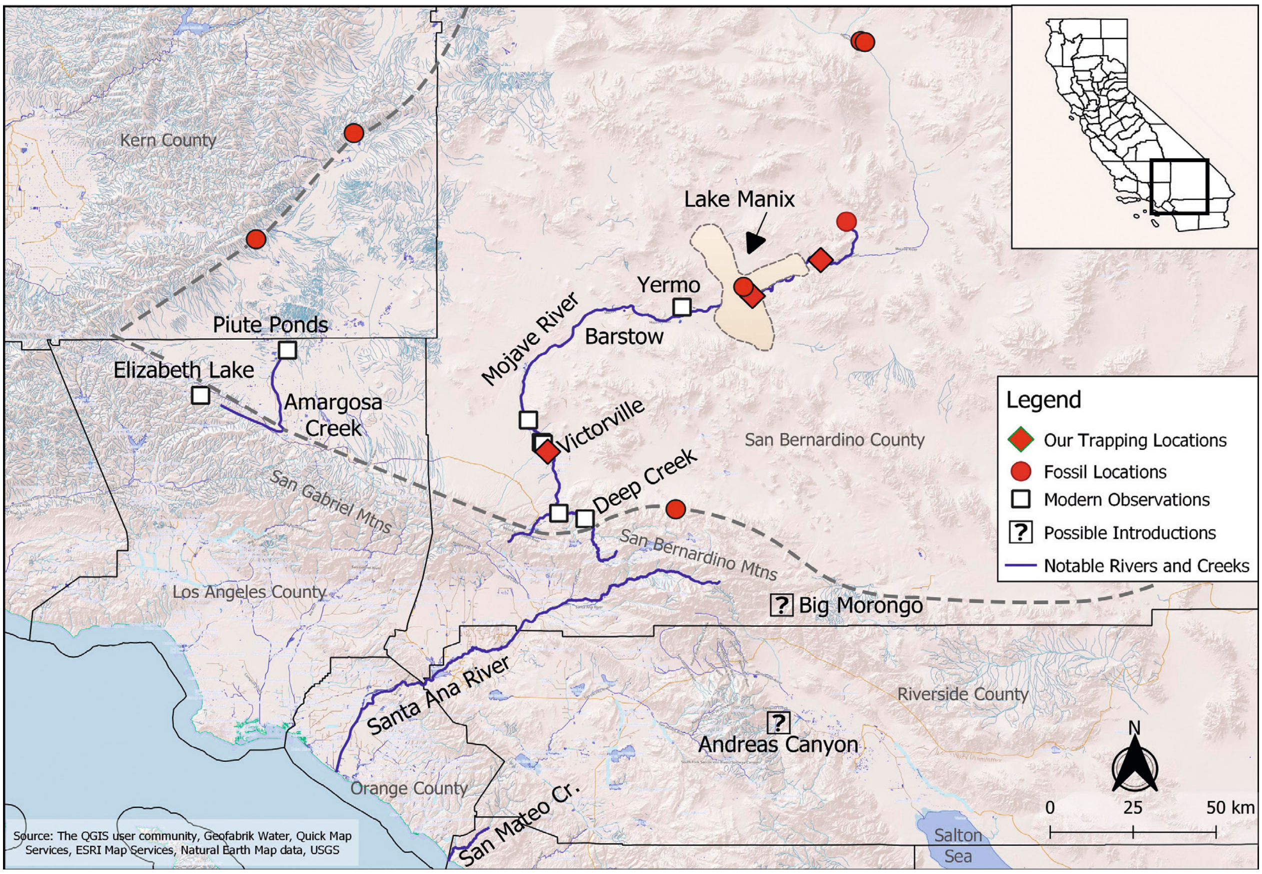

Figure 2. Location of selected *Actinemys* records discussed in the text and in Table 2. The approximate boundary of the Mojave Desert is outlined with gray dashed lines. Not all fossil records are shown (e.g., Anza Borrego Desert State Park, California and Golden Shores, Arizona). Modern records include early historical accounts discussed in the text as well as more recent records. Not all recent records or trapping locations are shown to protect sensitive populations of *Actinemys*. Some locations are approximations based on lack of information available. The captive population at the California Desert Discovery Center in Barstow, California is not labeled.

elled along the Mojave River on his way from Los Angeles to Fort Mojave on the Colorado River in December 1860, returning in June 1861. His record was followed next by Meek (1905) who stated, without providing additional details, *This species is not rare in ponds along the Mojave River*. His description of the river is compatible with the pre-European colonization portrayed in the journal entries of Jedidiah Smith. Smith was one of the first explorers to cross the Mojave Desert in 1826, partly by following the Mojave River. He called the Mojave the "Inconstant River" (Reynolds 2018) presumably because it was normally discontinuous with long sandy stretches interspersed with isolated pools and rivulets of surface water. Izbicki (2007) discusses the conditions that contribute to the sporadic nature of the perennial reaches of the river in greater detail. Specimens listed in Table 2 from Victorville and Yermo were examined by Seeliger (1945) in her study of geographic variation in the species. A map summarizing the preceding records is shown in Fig. 2.

Western pond turtle genetics

Based on analysis of mitochondrial DNA only, all new Mojave River samples of *A. pallida* we collected were found to be identical to the previously sequenced Camp Cady Mojave River samples and one of the three haplotypes found within San Mateo Creek (Fig. 3) in San Diego County, CA (Spinks and Shaffer 2005; Spinks et al. 2014). This haplotype is two mutations away from the most abundant ND4 haplotype that occurs in both San Mateo Creek and the rest of San Diego County (see Supplementary File 1: Table S1). Two much more extensive genetic analyses using RADseq and whole genome resequencing data are in progress.

Modern observations and ecological research

The California Natural Diversity Database (https://wildlife.ca.gov/Data/CNDDB) contains a short list of recent (since 1989) observations of WPTs in the Victorville area including near the regional water treatment plant. Despite interest in recording observations of WPTs in the Mojave River, only a single study has been published on their ecology. Lovich and Meyer (2002) conducted a mark-recapture study at Camp Cady and Afton Canyon 23 km downstream. At Camp Cady, 21 individual turtles were marked, while at Afton Canyon only 14 turtles were marked despite significant trapping efforts, a reflection of the tenuous survival status of those populations

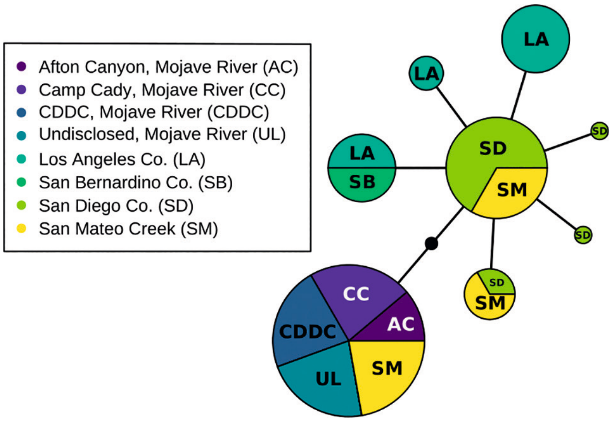

Figure 3. A haplotype network of the mtDNA ND4 gene for *Actinemys pallida* from the Mojave River and available sequenced populations from San Diego, Los Angeles, and San Bernardino Counties, California. Each filled circle represents a sampled haplotype, with lines showing the most parsimonious relationship of haplotype relationships. Dots on lines represent unsampled haplotypes. For visual clarity, populations with more than two identical haplotypes were reduced to display only n=2 haplotypes from that population. The haplotype network clearly shows that the four Mojave River populations sampled (blue colors), have haplotypes that are identical to one of the three haplotypes sampled in San Mateo Creek, San Diego Co. California (yellow color).

at the time. Reproductive females at both sites combined ranged in straight-line carapace length from 13.3–16.0 cm. Clutch size determined by X-radiography ranged from 3–6 eggs ($\bar{x}$ = 4.46 eggs). Females nested from 6 June–8 July, and most migrated away from artificially maintained ponds at Camp Cady to nest in the sand of the adjacent dry riverbed. No live juveniles were observed at either site during that research although ants apparently killed one hatchling at Camp Cady.

Additional surveys of WPTs by JEL and various collaborators continued from 2016–2020 along the Mojave River from near the headwaters, downstream to Afton Canyon, as well as at Piute Ponds in the western Mojave Desert (Lovich *unpublished*). Repeated efforts to trap or observe turtles at Camp Cady were unsuccessful during that time, and the small population that lived there in the late 1990s (Lovich and Meyer 2002) is extirpated (Cummings et al. 2018). According to the caretaker of Camp Cady, the last specimens observed there were two turtles photographed in April or May 2014 (Fig. 1D). Substantial survey efforts at Mojave Narrows Regional Park and Palisades Ranch on the upper river failed to detect WPTs at those locations as of 2020. As previously mentioned, on 16 April 2016, a hatchling sized WPT was observed and released at Afton Canyon (Fig. 1E). A single adult female (14.6 cm carapace length) was captured at Afton Canyon on 3 May 2017 (Table 2), marked and released (Fig. 1F). Substantial effort was expended to capture the two turtles at Afton Canyon, and that contrasts with the relative ease with which turtles were captured in 1998–1999 (Lovich and Meyer 2002). This suggests that the extant population is very small.

From 2017–2020 JEL and collaborators initiated a mark-recapture study of a remnant population at an undisclosed location on the Mojave River (Table 1) and at Piute Ponds (2019–2020). Details of that research will be presented elsewhere. Additional records of recent observations along the Mojave River are shown in Table 2.

Discussion

The fossil record for WPTs from Tertiary and early Quaternary deposits in the Mojave Desert, starting well before human occupation of North America, provides irrefutable evidence that the genus is indigenous to the region. It is of interest to note that all fossil and modern credible records of WPTs in the Mojave Desert are in the internally-draining portion of that desert and not in the portion that drains into the Colorado River (see Grayson 1993). Also, despite the fossil record of the genus from the adjacent Sonoran Desert in western Arizona (Reynolds et al. 2016) and the Salton Trough in Anza Borrego Desert State Park (Table 2), there are no records of native modern populations in the Sonoran Desert ecosystem.

We assume that the fossils from the Mojave River represent *A. pallida*, based on the modern population assignment analysis of Spinks et al. (2014). It is possible that some fossils represent extinct species, but abundant Pleistocene and Pliocene fossils referable to *A. marmorata* (*sensu lato*) suggest otherwise (Brattstrom and Sturn 1959; and references reviewed in Ernst and Lovich 2009). Subsequent archaeological and early historical records provide additional support for the inference of continuous occupation of WPTs in the Mojave Desert, but it may have been compounded by the possibility of human transport from coastal areas during pre-historic and historic times (see below).

The location of fossil WPTs at Salt Springs, near Death Valley, implies that during pluvial periods in the Pleistocene (Reheis et al. 2014; Wells et al. 2003), WPTs extended farther into the Mojave Desert than they do today. During wet periods, Lake Mojave (a combination of today's Soda and Silver dry lakes) may have spilled over into Salt Springs and eventually into the Amargosa River (not to be confused with Amargosa Creek), on its way to Lake Manly in the Death Valley sink (Reynolds 2018). Four wet intervals (intermittent between about 29 and 23 ka, and again at about 18 ka) are preserved in "Lake Dumont" (core DU-2) (Bright and Anderson 2007). The Salt Springs ground water discharge sediments and the wet drainages into them likely formed at this time (Miller et al. 2017, page 11).

Bright and Anderson (2007) stated: *The lack of evidence for a Mojave River-supported lake in the Salt Springs basin is unexpected. All presently available information suggests that the basin was not inundated by a late Pleistocene lake (Lake Dumont). The majority of the sediment previously interpreted as "lacustrine" in Salt Spring basin and the ostracode-bearing sediment in* *core DU-2 are here reinterpreted as representing local groundwater-supported, high Ca/alk wetlands. The presence of the Mojave River in the basin is not contested, as it logically must have flowed through the basin when the sill at Silver Lake* (*Lake Mojave*) *was breached*. It is important to note that the presence of WPT fossils in the area does not require evidence of a prehistoric lake as a perennial marsh would provide adequate habitat.

Even if a continuous chain of interconnected lakes and streams did not occur at the same time (Reheis et al. 2008), turtles were able to disperse far out into the Mojave Desert, most likely facilitated by fill-and-spill drainage basin integration toward the northeast beginning in the Pliocene (Reheis et al. 2014). Reynolds (2018) concluded, *The presence of an articulated skeleton of* Actinemys pallida *at Salt Springs suggests that occasional overflow from Silver Lake provided a moist or riparian route for turtles to reach Salt Springs*. WPTs are semi-aquatic (Ernst and Lovich 2009), and capable of spending up to half the year in terrestrial habitats in non-desert environments to avoid environmental extremes (Bury 2012; Lovich et al. 2017). However, they must have access to water to survive for longer periods. It should be noted that a previous study of WPTs in the Mojave River found no evidence of terrestrial habitat use other than by nesting females (Lovich and Meyer 2002). The distribution of fish in the Mojave Desert also has been linked to the process of lake integration via spillover events (Soltz and Naiman 1978).

Various researchers have used WPTs from the Mojave River in genetic analyses to determine their relationship to other populations. DNA fingerprinting, a technique that estimates genetic similarity based on migration patterns of anonymous DNA fragments, showed high intrapopulation genetic variability and low among-population divergence for three southern CA sites (Gray 1995), including one that appears to be from the Mojave River based on a map in that publication. Previous range-wide analyses of mtDNA for WPTs showed high levels of divergence among populations in southern CA, but unexpectedly, samples from the only available location along the Mojave River (Camp Cady) were identical, or very closely related to, samples collected in San Mateo Creek, San Diego County, CA. (Spinks and Shaffer 2005). Nuclear DNA also demonstrated high inter-population variation in southern CA (Spinks et al. 2010). Using 89 nuclear single nucleotide polymorphisms (SNPs), Spinks et al. (2014) split the species into two using the genus *Emys*: *E. marmorata* and *E. pallida*, the latter of which appears to inhabit southern and coastal CA south of the San Francisco Bay area, including the Mojave River.

In a recent extensive genetic study, Fisher et al. (2013) stated the following based on analyses that included a single specimen from Camp Cady on the lower Mojave River: *The only Mojave River sample in our study is the Camp Cady Wildlife Area* (*DFW*) *sample previously collected by Dan Holland* (*Holland 1991*)*. These still link with haplotypes* (*2 different ones*) *from San Mateo Creek, San Diego County, and a few other turtles from Camp Pendleton sites. They lacked unique haplotypes as might be expected from their remote location. It appears these turtles are introduced from northern San Diego to the artificial ponds along the Mojave River. Unfortunately, we still lack any "natural" Mojave River pond turtle samples.* Our new data, including from Afton Canyon, show the same relationships (Fig. 3), and suggest that the deep divergence that might be expected for a long-isolated population is not present, at least in mtDNA sequences.

However, the results of the earlier genetic analysis suggesting that WPTs in the Mojave River are a result of translocation of San Mateo Creek turtles by humans (Fisher et al. 2013) is at odds with the paleontological records confirming the presence of *Actinemys* in the Mojave Desert since at least the Miocene, well before human-aided translocation was possible. In addition, if they were introduced into ponds at Camp Cady from coastal southern CA locations, that does not explain the similarity of haplotypes we now have along the length of the river which spans a distance of about 200 km. Given the discontinuous nature of the river and inhospitable habitat in between known turtle populations, it is virtually impossible that introduced stock would make it upstream from Camp Cady following a contemporary introduction.

Also, populations of WPTs occurred in coastal drainages much closer to the Mojave River in the past including the Santa Ana River in Riverside County (Ingles 1929) and the West Fork of the San Gabriel River in Los Angeles County (Goodman 1997). It is likely that if turtles were transplanted by humans to augment those that previously existed in the Mojave River based on the fossil record, they would have come from these more proximate locations, not more distant San Mateo Creek. However, given the importance of turtles to Native Americans, long range translocations by indigenous people (Adler 1970) cannot be completely ruled out during human occupation of the Mojave Desert (Schneider and Everson 1989).

There are several possible explanations for the provenance/kinship of Mojave River turtles to geographically distant populations in San Diego and Orange County, CA. All start with recognition that WPTs were most likely native to the Mojave drainage in the deep past as supported by the fossil record. Possibilities include:

1) Current stock of WPTs is native to the Mojave River having continuously occupied the region from the earliest fossil records to the present.
2) Native in the past, then extirpated at some point and reintroduced from coastal populations by Native Americans (who used them for food and rattles as documented for the Oro Grande site by Rector et al. [1983]).
3) Native in the past then extirpated and reintroduced from coastal populations by European colonists.
4) Native in the past but declined to the point where the remnant population was augmented by Native Americans and coastal population genes dominated in the survivors.
5) Native in the past but declined and the remnant population was augmented by Anglo Americans and coastal genes dominated in the survivors.

6) Coastal and desert populations were part of a larger meta-population that was sundered by the uplift of the Transverse Ranges as recently as only 3 Ma (Meisling and Weldon 1989), a comparatively short period of time given the hypothesized rate of evolution of mtDNA in turtles (Avise et al. 1992). It is also possible that they were washed out of drainages in the Transverse Ranges during heavy pluvial periods in the Pleistocene as has been suggested for stickleback fish (*Gasterosteus*) by Reynolds (2005). However, given the relatively fine-scale differentiation of mtDNA haplotypes in southern CA populations of WPTs, one would expect populations in the Mojave River to have divergent haplotypes if separated from a larger metapopulation by uplift of a mountain range.

The possibility that Mojave River WPTs are naturally occurring could still be possible if: 1) selection is acting on both coastal and Mojave population ND4 mtDNA genes causing the observed similarity in haplotypes in both populations; or, 2) a historic introduction of a few WPTs from southern CA occurred, followed by a mtDNA sweep of a coastal haplotype throughout the Mojave River. If the latter possibility is true, genomic-scale analyses should be able to detect that most of the genome of Mojave River WPTs differs from coastal populations even though they share mtDNA haplotypes.

Genetic evidence on the origin of Mojave River samples is currently both limited and mixed, and we can only speculate pending additional data. Mitochondrial DNA of all four Mojave river populations (California Desert Discovery Center, Afton Canyon, Camp Cady, and an undisclosed location) revealed a single haplotype identical to one of those found in San Mateo Creek (Fig. 3), suggesting that the entire drainage may represent a recent introduction from that coastal watershed. However, limited nuclear data based on SNPs, currently restricted to Camp Cady on the Mojave drainage (n=7) and San Mateo Creek (n=25), returned evidence of SNP alleles found in some Camp Cady individuals that were not represented in San Mateo Creek. Six of the 89 SNPs analyzed by Spinks et al (2014) showed this pattern, suggesting that the Camp Cady individuals may not be uniquely derived from San Mateo Creek (no nuclear data are currently available for the other Mojave River sites). We emphasize that these inferences are based on very limited data, and that ongoing work using both RADseq and whole genome resequencing should clarify the likely history of the Mojave River turtles.

Future prospects for western pond turtles in the Mojave Desert

Although ample fossil evidence suggests that turtles of the genus *Actinemys* have existed continuously in the Mojave Desert since at least the Miocene, their continued survival faces increasing challenges from human population growth (Hunter et al. 2003) in the region and its attendant impacts on wildlife habitat (Lovich and Bainbridge 1999). This is especially true in the western Mojave Desert where most extant WPT populations remain, because of its proximity to burgeoning coastal southern CA population centers. Along with human population growth comes increased demand for water in a region that is already arid and facing overdraft of the Mojave River water table (Lines and Bilhorn 1996; Lines 1999). Overdraft is occurring because usage is greater than natural recharge rates that may take longer than 20,000 years in parts of the Mojave River aquifer (Izbicki et al. 1995; Izbicki 2007). Overuse of water beyond the ability of natural recharge rates to replenish the aquifer has led to decreased availability of perennial surface water in the Mojave River. Additional development is projected in the western Mojave Desert (Hunter et al. 2003) further reducing water available for WPTs and other wildlife. If the southwestern USA continues to transition to a warmer, dryer climate (Weiss and Overpeck 2005; Seager et al. 2007) the results on wildlife will be exacerbated (Barrows 2011; Lovich et al. 2014a).

WPT populations have already experienced significant declines in the Mojave Desert during the last 25 years as mentioned above. For example, in 1998, there were at least 14 WPTs at Afton Canyon (Lovich and Meyer 2002). Since 2015, only two WPTs were detected there despite similar efforts to trap them. At Camp Cady, there were at least 21 WPTs in 1998 (Lovich and Meyer 2002). The last WPT was observed there in 2014 and they are now extirpated (Cummings et al. 2018).

In response to overuse of water in the Mojave Desert, WPTs face many other threats (Manzo et al. *unpublished*) and both *A. marmorata* and *A. pallida* are currently under review by the U.S. Fish and Wildlife Service for possible listing under the Endangered Species Act. This is the second time such a review has occurred. A determination that they did not warrant protection was made in 1993, after the first such review, but their current status is being reevaluated after nearly 30 years and the accumulation of much more data. They remain a Species of Special Concern by the state of CA. Given the tenuous status of WPTs on the lower Mojave River, active management through habitat improvement, captive breeding, establishment of assurance colonies, and population augmentation may be required to secure the future of WPTs in the Mojave River, especially the remnant population at Afton Canyon. Regardless of their provenance, remaining populations of WPTs should be considered native elements of the Mojave Desert fauna until compelling evidence proves otherwise.

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Supplementary Material

File 1

Authors: Lovich JE, Jefferson G, Reynolds R, Scott PA, Shaffer HB, Puffer S, Greely S, Cummings K, Fisher RN, Meyer-Wilkins K, Gomez D, Ford M, Otahal CD (2021)

Data type: .pdf

Explanation note: Supplemental Table S1. Sampling localities for pond turtles in California (USA) used in genetic analyses. Listed for each record, if available, are GenBank accession numbers for ND4 sequences, catalog numbers, and location descriptions, site coordinates, and haplotype identifiers for novel samples and those included from Spinks et al. (2014). Abbreviations are as follows: CDDC = California Desert Discovery Center, NWS (USN) = Naval Weapons Station (United States Navy), SB = San Bernardino, LA = Los Angeles, SD = San Diego, and USMC = United States Marine Corps.

Link: https://doi.org/10.3897/vz.71.e63987.suppl1

File 2

Authors: Lovich JE, Jefferson G, Reynolds R, Scott PA, Shaffer HB, Puffer S, Greely S, Cummings K, Fisher RN, Meyer-Wilkins K, Gomez D, Ford M, Otahal CD (2021)

Data type: .pdf

Explanation note: Supplemental Figures S1–S13. *Actinemys pallida* from the Mojave Desert. All photos by Morgan Ford.

Link: https://doi.org/10.3897/vz.71.e63987.suppl2