



High female desert tortoise mortality in the western Sonoran Desert during California's epic 2012–2016 drought

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ABSTRACT: We conducted population surveys for desert tortoises *Gopherus agassizii* at 2 nearby sites in the western Sonoran Desert of California, USA, from 2015–2018, during the driest ongoing 22 yr period (2000–2021) in the southwestern USA in over 1200 yr. We hypothesized that drought-induced mortality would be female-biased due to water and energy losses attributable to egg production during protracted periods of resource limitation. At the higher-elevation, cooler, wetter Cottonwood site from 2015–2016, the sex ratio of live adult tortoises was biased toward males and the sex ratio of tortoises estimated to have died during the intensified drought conditions from 2012–2016 was essentially even. At the lower-elevation, warmer, drier Orocopia site from 2017–2018, the sex ratio of live adult tortoises was biased toward males and the sex ratio of tortoises with estimated times of death from 2012–2016 was biased toward females. High female mortality at the Orocopia site may have resulted from the interaction of drought effects and the bet-hedging reproductive strategy of tortoises wherein they continue to produce clutches of eggs in drought years. Annual reproductive output results in an estimated loss of up to 13.5% of female tortoise body mass including over 0.20 l of water. Combined with dehydration during severe droughts, these losses may compromise their ability to survive droughts lasting more than 2 yr. The low tortoise density and high mortality of females observed may reflect reduced survival of tortoises near the southern edge of their range due to climate change, including protracted and intensified droughts.

KEY WORDS: Climate · Drought · *Gopherus agassizii* · Mortality · Sex ratio · Bet-hedging

1. INTRODUCTION

The desert southwest region of North America continues to experience significant and protracted drought. Analysis of soil moisture deficits from tree ring data suggest that the interval from 2000–2021 was the driest 22 yr period in ≈1200 yr (Williams et al. 2022). The ongoing multi-decadal drought is thought to be driven by both natural variability in soil moisture and anthropogenic warming (Diffenbaugh et al.

2015, Williams et al. 2020, 2022). Aridity in the region intensified in California, USA, from 2012–2016, with record-setting low measures of precipitation, high annual temperatures, and the most extreme drought indicators on record (Griffin & Anchukaitis 2014, Diffenbaugh et al. 2015). The years 2012–2016 were essentially a more severe drought within an ongoing multi-decadal megadrought.

Even without the current drought conditions, the Mojave and Sonoran Deserts are the most arid eco-

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systems in North America. Organisms living there have varying degrees and types of behavioral and physiological adaptations (Schmidt-Nielsen 1964, Ezcurra et al. 2014) to the spatially and temporally unpredictable seasonal and interannual water availability characterizing deserts (Noy-Meir 1973). Survival under such extreme environmental conditions is difficult without the additional challenges created by protracted severe droughts that the region is currently experiencing.

The effects of drought on the survival of desert plants and animals vary among species due to differences in their adaptations to resource scarcity and competition (Prugh et al. 2018, Riddell et al. 2021). For example, severe mortality was observed in drought-deciduous shrubs, especially those in the genus *Ambrosia*, in portions of both deserts in 2003, early in the ongoing drought cycle (McAuliffe & Hamerlynck 2010) but following a year with extreme precipitation deficits. Drought has also been implicated in the collapse of the bird community in the Mojave Desert since the early 20th century, with sites losing an average of 43% of their species (Iknayan & Beissinger 2018). In contrast, small mammal communities remained relatively stable during the same time period, perhaps due to burrowing behavior and nocturnal activity (Walsberg 2000) that buffers them against environmental extremes (Riddell et al. 2021). Regionally, Landsat data show large decreases in vegetation cover in the Sonoran Desert of California from 1984–2017 attributable to decreased precipitation and warming summer temperatures (Hantson et al. 2021). Additional environmental impacts of severe drought include increased wildfire risk (Littell et al. 2016) as well as reduced carbon uptake by plants (Schwalm et al. 2012).

Agassiz's desert tortoise *Gopherus agassizii* is a conservation-reliant (Averill-Murray et al. 2012), flagship species that lives in portions of both the Mojave and Sonoran Deserts (Berry & Murphy 2019). Although populations north and west of the Colorado River are protected under the US Endangered Species Act of 1990, the species exhibited significant declines throughout its range from 2004–2014 (Allison & McLuckie 2018), attributable to drought and other factors. Other long-term threats to the continued survival of desert tortoises include habitat destruction and fragmentation, invasive plant species, predation from subsidized predators, fire, and road mortality (Ernst & Lovich 2009, Berry & Murphy 2019). A more recent threat is habitat destruction associated with a buildup of utility-scale wind (Lovich & Ennen 2013) and solar (Lovich & Ennen 2011, Agha et al. 2020) en-

ergy development in the desert southwest. The additive and interactive effects of these threats (e.g. drought and fire) can have particularly negative consequences for wildlife populations in the arid southwest region of North America (Lovich et al. 2017).

We studied the demography and reproductive ecology of desert tortoises (hereafter used interchangeably with 'tortoises') in Shavers Valley, California, from 2015–2018 as part of surveys supporting the research and monitoring requirements of the Coachella Valley Multiple Species Habitat Conservation Plan (www.cvmshcp.org/). We were particularly interested in documenting trends in mortality and how they affected population structure, including adult (≥ 180 mm carapace length, Berry & Murphy 2019) sex ratios.

Several field studies support the importance of drought as a mortality factor in *G. agassizii* populations throughout their range in California and Nevada, including the eastern, central, and western Mojave Desert (Peterson 1994, Berry et al. 2002, Longshore et al. 2003), and the western Sonoran Desert (Lovich et al. 2014a). Protracted drought kills desert tortoises directly through the effects of extreme dehydration (Berry et al. 2002), or indirectly through the phenomenon of 'prey switching'. The latter occurs when desert carnivore prey populations, typically rabbits and rodents, decline during droughts, and predators like coyotes *Canis latrans* shift their diets to include desert tortoises that are not typically preferred (see review by Lovich et al. 2014a). In addition, modeling predicts that suitable desert tortoise habitat will be reduced by as much as 88% in the western Sonoran Desert portion of Joshua Tree National Park (JTNP) under a warming, drying climate scenario (Barrows 2011), further emphasizing the negative effects of drought on survival of the species.

Previous studies have not fully examined the possible differential effects of drought on mortality of male and female desert tortoises, although Esque et al. (2010) observed that females were more likely than males to be killed by coyotes during drought. Similarly, other studies involving translocation of desert tortoises found that females were more likely to die than males, but the cause of sex-biased mortality was unknown (Field et al. 2007, Germano et al. 2017). Increasing global temperatures can disrupt population sex ratios in species that have environmental sex determination (Hulin et al. 2009), like the desert tortoise (Lewis-Winokur and Winokur 1995). Biased hatchling sex ratios can lead to mate shortages, reduced population growth, and increased extinction risk, especially when ratios are male-biased (Lovich 1996, Edmands 2021).

We have conducted field studies on desert tortoises at various locations in the western Sonoran Desert of California for 25 yr (e.g. Cummings et al. 2020, Lovich et al. 1999, 2014a, 2015, 2018, 2020). More recently, we noticed differential mortality of adult male and female desert tortoises that we hypothesized was attributed to drought effects described as ‘extraordinary’ (Swain et al. 2014) or ‘epic’ (Berg & Hall 2017) that occurred from 2012–2016, during the ongoing multi-decadal megadrought (Williams et al. 2022). Because some previous studies suggested that female mortality was higher, we hypothesized that in our samples the sex ratio of living adult tortoises would be statistically biased toward males and that the sex ratio of adults estimated to have died during the epic drought of 2012–2016 would be statistically biased toward females. We further hypothesized that drought-induced mortality of females could be caused by water and energy losses attributable to egg production during protracted periods of extreme resource limitation.

2. MATERIALS AND METHODS

2.1. Study sites

Research was conducted at 2 study sites in Shavers Valley, between the Cottonwood and Orocopia Mountains, about 70 km east–southeast of Palm Springs, Riverside County, California. Both sites are part of the hydrographic Salton Trough, a large, low-elevation, tectonic basin (Lovich et al. 2020). Vegetation in the region is typical of the Sonoran Desert ecosystem in southeastern California, as described in more detail elsewhere (Lovich et al. 2018, 2020, Cummings et al. 2020), but general site summaries are provided below. The study sites are approximately 4–5 km apart and separated by Interstate 10, thus isolating the tortoise populations from the possibility of intermingling during our study. Despite their proximity, local differences in topography and their concomitant effects on precipitation, even during the drought, resulted in variation in limited germination of winter annual food plants necessary for desert tortoise survival (Jennings & Berry 2015).

The Cottonwood study site (CoSS) is located in the southernmost portion of JTNP, in an area drained by Shavers Wash, north of Interstate 10 (Fig. 1). The site is characterized by the steep, boulder-strewn, southern versant of the Cottonwood Mountains that meets sloping bajadas (tilted outwash plains at the base of mountain slopes) and arroyos (ephemeral stream

channels) running southward toward Interstate 10. The area surveyed encompassed approximately 5.75 km². Tortoises occupied elevations from 530 to 780 m. Details of the perennial vegetation are described in the citations in the previous paragraph but included scattered ironwood *Olneya tesota* and blue palo verde *Parkinsonia florida* trees as well as ocotillos *Fouquieria splendens*.

The lower-elevation Orocopia study site (OrSS) is located on the northern versant of the Orocopia Mountains, south of Interstate 10 and JTNP, and to the west of Chiriaco Summit, California. The area is bounded by the Orocopia Mountains to the south, with a total area surveyed for tortoises of about 21 km² (Fig. 1). Most of this land is managed by the Bureau of Land Management. The area was heavily impacted by WWII military training activities during the early 1940s associated with the former existence of Camp Young (Lathrop 1983, Prose 1985, Prose & Metzger 1985, Henley 2000). Tank and jeep tracks are still visible throughout the study site, resulting in long-lasting negative changes to soil conditions and plant communities that are still detectable almost 80 yr later (Lovich & Bainbridge 1999). The effects of these enduring habitat impacts on modern tortoise populations are unknown.

The site is dominated by gently sloping bajadas and arroyos running northward to Interstate 10 and Maniobra Wash. These bajadas rise to meet the Orocopia Mountains to the south. Elevations of known tortoise locations at OrSS ranged from approximately 480 to 620 m. Ironwood, blue palo verde, and ocotillo plants were less abundant than at CoSS. See Cummings et al. (2020) for a more detailed site description.

2.2. Field techniques

Surveys similar to those described by Lovich et al. (2014a) were conducted to locate live tortoises and additional tortoise sign such as burrows, carcasses, and scat. Transects were conducted throughout the areas of interest with 10–25 m spacing between 2 or more observers. During each year, surveys were conducted over 2 or 3 d periods 2–3 times every month from February through July. Additional surveys were conducted once per month while radio-tracking tortoises (see below) from August through January. Live tortoises were notched with a unique combination of marginal scutes using a triangular file for future identification (Cagle 1939). Body sizes of live tortoises and carcasses were measured using straight-line carapace

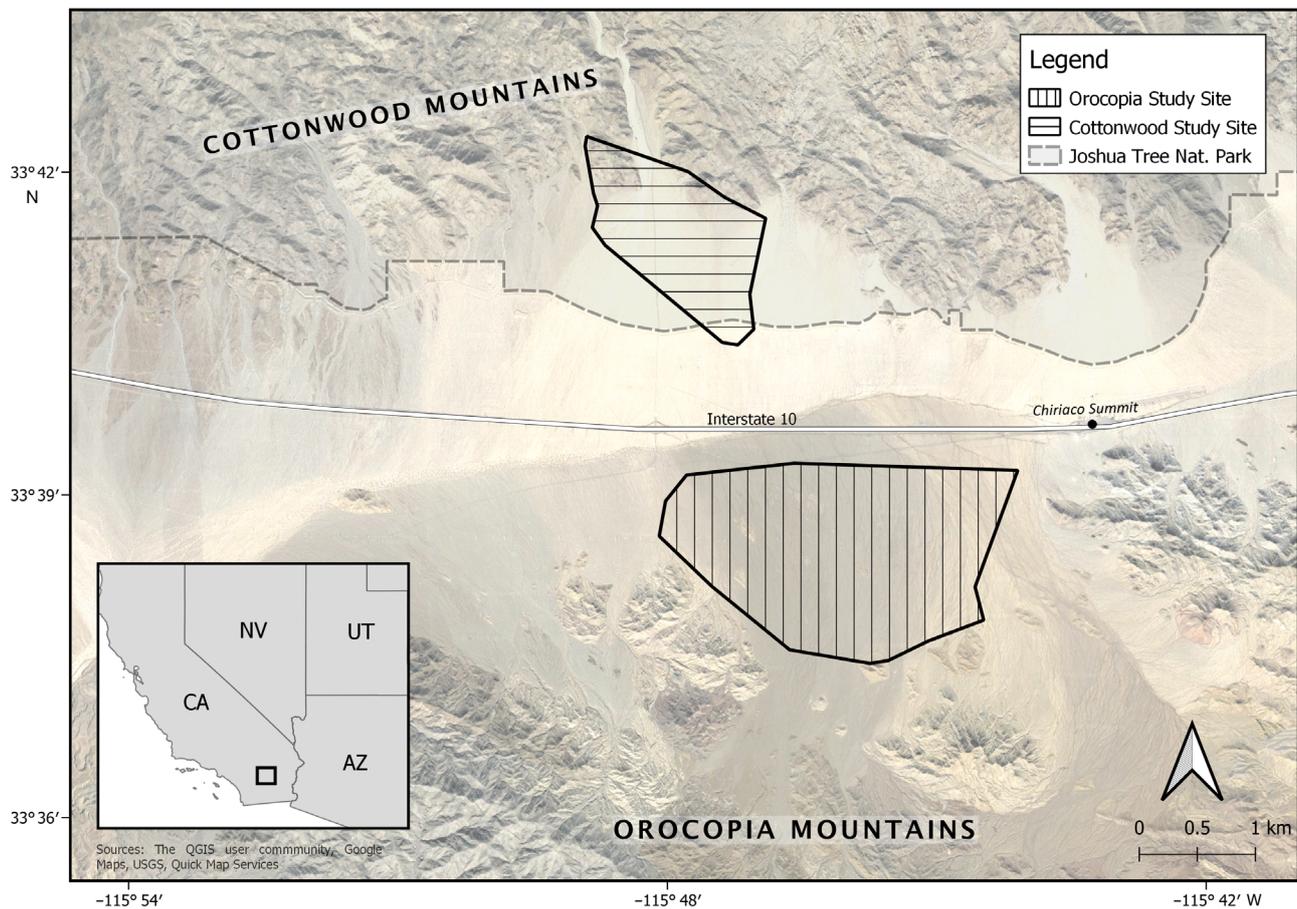


Fig. 1. Locations of the 2 study sites in California (USA) in relation to Joshua Tree National Park. Polygons circumscribe the general areas surveyed for desert tortoises and carcasses at each site. CA: California, NV: Nevada, UT: Utah, AZ: Arizona

length with tree calipers (± 1 mm) when possible. Sex was determined using characteristics described by Ernst & Lovich (2009). Some carcasses were highly weathered and disarticulated, making it difficult or impossible to determine their sex. When possible, we rearticulated those carcasses to determine sex and measure carapace length. GPS locations were recorded using a Garmin Oregon 550T. When whole shells or shell fragments of dead tortoises were located, detailed notes were recorded on the state of the remains and photographs were usually taken to estimate their time of death (see Section 2.3).

A subsample of tortoises was outfitted with radio transmitters at both sites (Advanced Telemetry Systems models R1850, R1860; or Wildlife Materials reptile transmitters with replaceable batteries). At CoSS, 12 tortoises (4 males and 8 females) were fitted with transmitters but 2 malfunctioned early in the study (1 male and 1 female) leaving 10 to monitor. Ten tortoises (6 males and 4 females) were radioed at OrSS. Not all radioed tortoises were monitored in both

years at our 2 study sites due to radio malfunctions in Year 1 and finding and affixing transmitters to new tortoises in Year 2. During the tortoise activity season from March to July, all radio-transmitted tortoises were located approximately every 10–14 d, and once per month for the remainder of the year. Radio transmitters were initially deployed on tortoises at CoSS in March 2015 and at OrSS in February 2017. As the conclusion of the studies neared, radio transmitters were removed from tortoises, with the final transmitter removed in July 2016 at CoSS and August 2018 at OrSS.

X-radiography was used to quantify reproductive output. Females with radio transmitters (CoSS $n = 8$; OrSS $n = 4$) were X-radiographed from April to July. The period from April to July overlaps known earliest and latest dates of the production of shelled eggs in JTNP (Lovich et al. 1999, 2018). X-radiographs were obtained in the field using a digital X-ray generator (model TR80; Min-X-ray) connected to a custom Canon X-radiography system. Exposures were taken

using the settings described by Lovich et al. (2015) at doses that are considered safe for tortoises (Hinton et al. 1997).

2.3. Estimating time of death from carcasses

We estimated time of death for tortoise carcasses and remains found during our surveys as detailed below. Our analyses focused on remains estimated to have died during the time period from 2012–2016, for 2 reasons. First, even though the megadrought has so far persisted from 2000–2021 (and continues), drought conditions intensified in California from 2012–2016, compounding the effects of the preceding drought. Second, it is difficult to accurately estimate time of death based on carcass condition after about 4 yr. However, the time of death in tortoises can be estimated in the first few years post mortem based on stages of carcass deterioration. Several factors have to be considered relative to deterioration rates, including the size of the tortoise and the condition of the scutes and bones at the time of death, especially the amount of predation or scavenging that may have been inflicted on the carcass. Predation or scavenging can remove scutes and separate bones, allowing increased exposure to areas that may not be exposed initially. Shell surfaces that are exposed to sunlight or precipitation may disarticulate at different rates than those that are not (e.g. those that are shaded by shrubs). Smaller-sized tortoises (e.g. juveniles) degrade at a faster rate due to the light, thin nature of their small scutes and incomplete ossification of their skeletons (Berry 1984).

According to Dodd (1995), the shells of 6 different turtle species in Florida disintegrate in a relatively predictable pattern. Generally, the keratinized scutes covering the bony shell begin to exhibit dullness and curling, followed by peeling from the larger vertebral scutes down to the marginal scutes around the periphery of the shell. The marginal scutes are usually the last to be exfoliated. Underlying shell bones (post-scute deterioration) also go through stages as they age post mortem. Skeletal shell bones begin either white to dirty brown in color (if the scutes have recently exfoliated) and have a solid, fresh appearance without cracks, pits, or peeling. As the bones are exposed to the elements, they progress to a cracking, peeling, pitted, or disarticulated state as scavenging and environmental factors cause further deterioration (Dodd 1995). The rate of decomposition is slower in arid environments (Berry 1984) but follows a similar general progression of stages.

All carcasses located at both study sites were assessed and placed into 1 of 7 categories of decomposition according to specific criteria (Table 1, Fig. 2), which included analyzing the overall intactness of the carcass, scute condition, and bone condition. The categories are derived from a classification system based on a compilation of previous schemes used by Dodd (1995) and Berry (1984: Appendices 6 & 7, cited by Berry 1986 and used by Lovich et al. 2014a). Carcasses were examined for recency of death by first looking for the presence of soft tissue within the shell. Scutes, when present, were then assessed for any fading, peeling, shrinkage, and attachment to the underlying bone. Next, shell bones were examined (where exposed) for color, strength, cracking, chalkiness, or separations. Carcasses were assessed for structural rigidity by determining whether the bones were intact (with or without suture separation or minor predation/scavenging damage) or completely or partially disarticulated. Signs of predation or scavenging, particularly tooth marks or breakage that did not correspond to sutures, were also noted, since this can influence deterioration rates (Fig. 3). In recognition of the differences in ossification between juvenile and adult shells that may cause variation in decomposition rate, we report data on juvenile carcasses (<180 mm) scored using our decomposition classification system but did not include those data in our statistical analyses.

Estimated time since death was assigned from categories summarized in Table 1. The first category (A) is for a fresh carcass dead for only a couple of weeks. The shell appears fully intact with no disarticulations (unless damaged with breaks away from sutures caused by a predator or scavenger). Scutes are fully intact and appear shiny and fresh, and abundant tissue is still present inside the shell.

The second category (B) (Table 1, Fig. 2) includes carcasses that died over a period of up to 2 yr prior to discovery, which would include deaths at both study sites during the 2012–2016 drought conditions described above. This category could also include carcasses that died immediately post-drought at OrSS, depending on the year of discovery. In this stage, the external surface still has the same fresh appearance of a live tortoise, but internal tissues are dried up and/or have been consumed by predators or scavengers. The scutes have a smooth surface and are not yet peeling or fading. The bone (if exposed) is a solid, non-chalky white or brown color without pits or cracks.

The third category (C) (Table 1, Fig. 2) includes carcasses that died during the period 2–4 yr prior to

Table 1. Classification system we used for estimating time since death of *Gopherus agassizii* carcasses, including summary of decomposition descriptions. Table adapted from criteria described by Berry (1984) and Dodd (1995). Estimating time since death after 4 yr is difficult or impossible under variable conditions. Although categories D–G have the same estimated time since death, we assumed that they represent sequentially older remains because of their progressing stages of decomposition

Shell decomposition rating	Decomposition description	Estimated time since death
A	Fresh carcass, viscera still attached. All scutes attached with no fading, curling, or seam detachment as would be on live tortoise (unless removed or damaged by predator). Bone shiny, not visibly porous, as would be on live tortoise.	Days to 2 wk
B	Shell intact. Fresh viscera no longer attached but may still have dried skin attached. Scutes are shiny, not faded or curling, minimal separation at seams or from shell, appear as on a live tortoise. No weathering of carapace. Bone appears as on a live tortoise, solid and smooth with a shine and no visible roughness or porosity. May have a brown hue if just separated from scutes.	<1–2 yr
C	Shell intact. More than 50% scutes still on shell (unless disturbed by predator). Scutes fading, lack shine, growth lamina starting to peel away from bone. Bone is dull in color and rough, starting to peel, crack, or chip off.	2–4 yr
D	Shell intact but may be developing suture cracks. Less than 50% scutes still on shell. Attached scutes may be curling/peeling, loose, or brittle. Bone is pitted and porous.	>4 yr
E	Shell intact with suture cracks widening. Few or no scutes remaining on shell, although scutes still present on ground. Bone is chalky white.	>4 yr
F	Shell disarticulating but still partially intact. Few or no scutes present on ground. Bone is chalky white, possibly pinkish color. Bone becoming brittle and sometimes crushed between fingers.	>4 yr
G	Shell completely disarticulated, in pieces on ground. Few or no scutes present on ground. Bones bleached.	>4 yr

discovery and can include tortoises that died during the 2012–2016 drought, depending on the year the carcass was discovered. As decomposition progresses, scutes begin to fade, causing a dullness on the scute surface, and they may start to peel away from the bone. However, there is still greater than 50% area of the shell with scutes attached. The bone begins to show signs of wear (surface cracking or dullness) where it is exposed. This category represents a liberal estimate for tortoise mortality at CoSS that occurred during the severe drought period 2012–2016. If a carcass at CoSS was placed into this category, it is possible that the tortoise died either during the drought (up to 3 yr prior to discovery), including during the first year of the drought in 2012 before the drought effects intensified, or just before (4 yr prior). This is a liberal estimate because we included any tortoises at CoSS that fell into this category in our count of tortoise deaths during the drought since we cannot determine with certainty the exact year of death. Carcasses in this category located at OrSS died during the 2012–2016 drought.

Category D (Table 1, Fig. 2) represents the first category encompassing an estimated time since death of >4 yr. Carcasses in this category have <50% of scutes covering the shell, and the remaining scutes

are peeling, shrinking, curling, loose, or brittle. The bone shows signs of aging at this point, including pitting, porous texture, and possible development of suture cracks along the margins. Carcasses in this category located at CoSS died prior to the beginning of the 2012–2016 drought. This is a liberal estimate of tortoises that died at OrSS during the epic drought because it would include tortoises that died during the first year of the drought in 2012 before the drought effects intensified.

Category E (Table 1, Fig. 2) also includes carcasses that died more than 4 yr prior to discovery, but in this stage, there are few to no scutes remaining on the shell although scutes may still be present on the ground surrounding the carcass. The bone is white and chalky with suture cracks widening, but the carcass is still intact. Carcasses at both study sites placed into this category, or either of the categories listed below, died prior to the beginning of the epic drought.

Category F (Table 1, Fig. 2) is the next stage of decomposition also encompassing an estimated time since death of >4 yr. Sutures are separated, and the carcass is mostly disarticulated, with a few large pieces still connected at suture margins. Scutes may or may not be visible on the ground. The bone is brittle and white or pink colored.

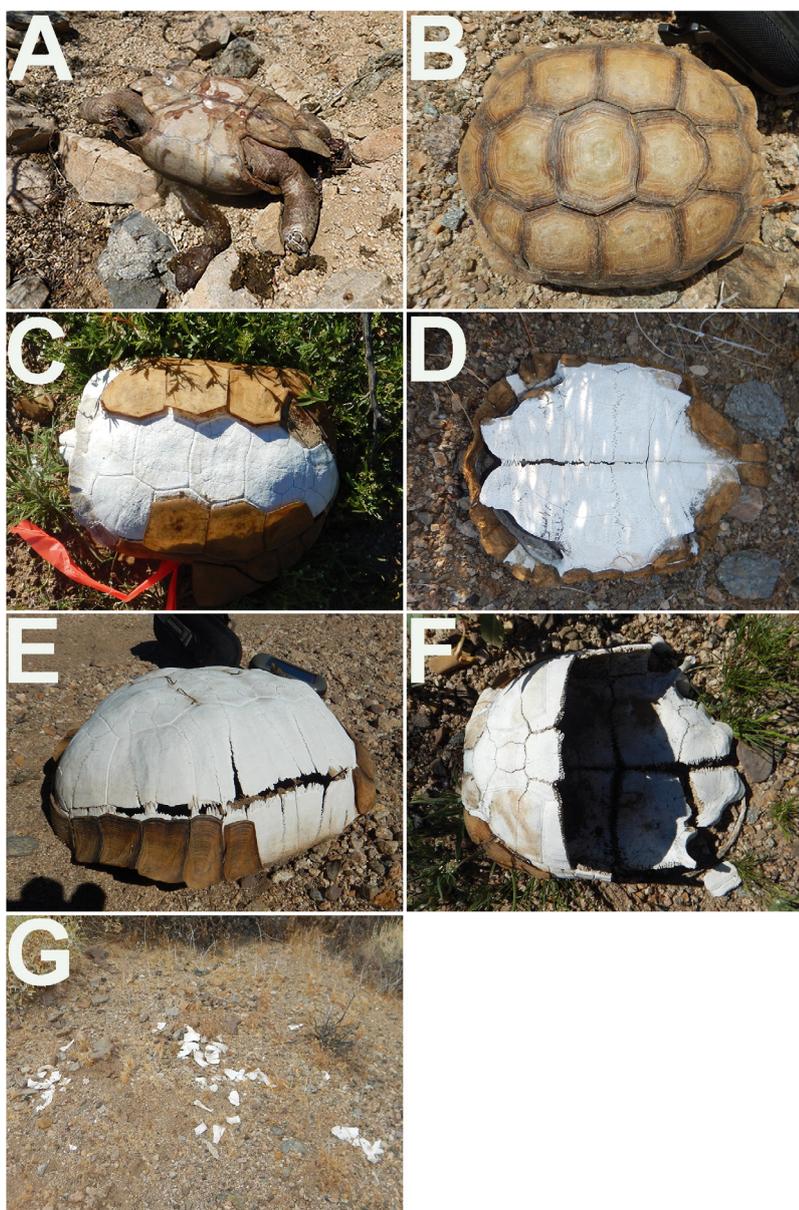


Fig. 2. Carcasses exemplifying assigned categories of decomposition and disintegration based on combined criteria for aging tortoise remains as given by Dodd (1995) and Berry (1984) (see Table 1 for decomposition category descriptions). Photos are assigned to categories as follows: category A: dead for only a couple of weeks, fresh carcass with viscera and scutes still attached as they would be on a live tortoise; category B: dead <1–2 yr, shell intact, scutes attached; category C: dead 2–4 yr, shell intact, more than 50% scutes still attached; category D: dead >4 yr, bone developing suture separation; category E: dead >4 yr, suture separations widening; category F: dead >4 yr, shell is disarticulating, partially intact; category G: dead >4 yr, shell is completely disarticulated and bone is weathered

The final category including carcasses that died over 4 yr since discovery is category G, which is also the last stage of decomposition (Table 1, Fig. 2). This category includes carcasses that are completely disarticulated into pieces scattered on the ground. Sex is usually in-

discernible, scutes are rarely present, and bones are bleached white.

All of these categories apply to general time periods, since many variables affect rates of decomposition as discussed above, and this makes exact aging impossible. The decomposition study by Berry (1984) was performed in a similar environment to that of our study—both were within California deserts with comparable climates—which makes the study by Berry (1984) the best candidate for approximations of time since death. However, age studies were not included in that study for tortoises thought to have died more than 4 yr prior to discovery. We assumed that categories E–G represent sequentially older remains than category D because of their increased stages of decomposition. We considered carcasses both with and without signs of potential predation that were estimated to have died between 2012 and 2016 to be victims of the epic drought. This is due to recognition that one of the effects of drought in the California deserts is prey switching, described in Section 1. As noted by Lovich et al. (2014a, p. 221): ‘... we cannot determine with certainty if all tortoise remains with carnivore tooth marks, missing limbs and broken shells were predated or scavenged after dying from some other cause (drought, disease, etc.). However, our experience radio tracking live tortoises at [Joshua Tree National Park] from 1997–1999 (Lovich et al. 1999) confirmed that some tortoises were alive and well one week and then killed and partially or almost completely consumed by coyotes (that left their hair on the tortoise carcass) the next week.’ In addition, suspected badger *Taxidea taxus* predation on a large male desert tortoise was reported at CoSS in 2015 (Smith et al. 2016).

2.4. Statistical techniques

We assumed that the probability of finding male or female tortoises (carcasses or alive) did not differ. While live male tortoises may have higher detection



Fig. 3. Example of a carcass that was assigned to the 'death during drought' category that had evidence of biting and chewing from predation and/or scavenging. Even if death occurred as a result of predation during the drought, it was still scored as a drought-induced mortality due to the effect of 'prey switching' that occurs during droughts (Lovich et al. 2014a). This carcass was found at the Orocopia study site on 10 May 2017 and was scored category C (see Fig. 2)

probabilities than female tortoises within short survey periods (Mitchell et al. 2021), this difference dissipates when within-year capture data are pooled (Freilich et al. 2000). Thus, our data pooled over 2 yr are less likely to be affected by any differences in detectability between male and female tortoises.

We used a 2×2 Fisher's exact test calculator (<https://www.omnicalculator.com/statistics/fishers-exact-test>) to compare the number of adult male and female carcasses to the number of living adult male and female tortoises at each site. Since previous studies suggested that females are more likely than males to die for various reasons, our tests were 1-tailed. We set alpha at 0.05 to test for the significance of association between status (living or dead) and sex ratios (male or female). Adult sex ratio indices were calculated using the method of Lovich & Gibbons (1992) and Lovich et al. (2014b).

2.5. Weather data

We estimated mean air temperatures and precipitation data for the time periods during our tortoise surveys with the WestMap Climate Analysis Tool (www.cefa.dri.edu/Westmap/Westmap_home.php)

using a pixel point near the center of each study site (Table 2). Following Ennen et al. (2017), data were collected according to wet season (1 October–30 March) and dry season (1 April–30 September) estimated amounts. Mean temperatures (overall means, mean high and low temperatures) were also estimated for each study site over the period of the study. Wet season (winter) precipitation influences annual tortoise food plant productivity in the spring (Beatley 1974, Bowers 2005). Dry season precipitation can trigger summer annual plant germination. When dry season precipitation fell at our study sites, the result was dense fields of chinchweed *Pectis papposa*, but this species is rare in the diet of desert tortoises (Esque 1994). Long-term data on climate at each study site were also estimated using WestMap by looking at means for precipitation and temperatures over the 25 yr period from 1993–2018, an amount of time equivalent to the approximate generation time of desert tortoises (USFWS 2011, Edwards et al. 2004), according to winter wet season and summer dry season. Event timing, including survey dates and overall drought conditions, are summarized in Fig. 4.

3. RESULTS

3.1. Adult sex ratios and body sizes

At CoSS, we located an almost equal number of carcasses (4 males and 3 females) with a known (see Smith et al. 2016) or estimated time of death during the severe drought period 2012–2016. We found only 1 freshly dead tortoise at CoSS and none at OrSS (Table 1, Fig. 2; see Smith et al. 2016 for details). The sex ratio of living tortoises at CoSS was 22 males and 9 females (Table 3). Despite the strongly biased live tortoise sex ratio, a 1-tailed 2×2 Fisher's exact test comparing the number of adult male and female carcasses to the number of living adult male and female tortoises yielded a probability of 0.385. This suggests that sex was independent of status (dead vs. living) at CoSS. However, a chi-squared test comparing just the number of living males and females was significantly biased toward males ($\chi^2 = 5.45$, $df = 1$, $p = 0.020$).

Table 2. Estimated climate data for 2 study sites at the eastern end of the Coachella Valley Multiple Species Habitat Conservation Plan area: Cottonwood (CoSS) and Orocopia (OrSS). Data for each study site were obtained using the pixel function of WestMap, with the point location chosen near the center of each site. Location of pixel at the Cottonwood study site was 33.697°N, 115.803°W. Location of pixel at the Orocopia study site was 33.645°N, 115.763°W. Data were calculated according to patterns of the estimated total winter wet season (1 October–30 March) and summer dry season (1 April–30 September) precipitation

Study site	Year	Season	Est. mean min temp (°C)	Est. mean max temp (°C)	Est. mean temp (°C)	Est. precipitation (cm)
Cottonwood	2014–2015	Dry	16.4	32.8	24.6	4.2
		Wet	7.3	21.6	14.4	5.1
Cottonwood	2015–2016	Dry	16.1	32.4	24.2	2.8
		Wet ^a	5.8	20.3	13.1	4.9
Cottonwood	2016	Dry	16.4	32.8	24.6	5.0
Cottonwood	1993–2018 ^b	Dry	15.4	32.6	24.0	3.6
		Wet	5.3	19.4	12.4	8.1
Orocopia	2016–2017	Dry	18.6	34.8	26.7	3.7
		Wet	8.1	22.2	15.2	11.6
Orocopia	2017–2018	Dry	18.8	35.1	26.9	1.9
		Wet	7.8	23.1	15.4	1.3
Orocopia	2018	Dry	19.5	35.6	27.6	0.3
Orocopia	1993 – 2018 ^b	Dry	17.9	34.5	26.2	3.1
		Wet	6.8	21.3	14.0	7.5

^aEl Niño conditions were observed; ^b25 yr period in which averages across the entire time span were calculated

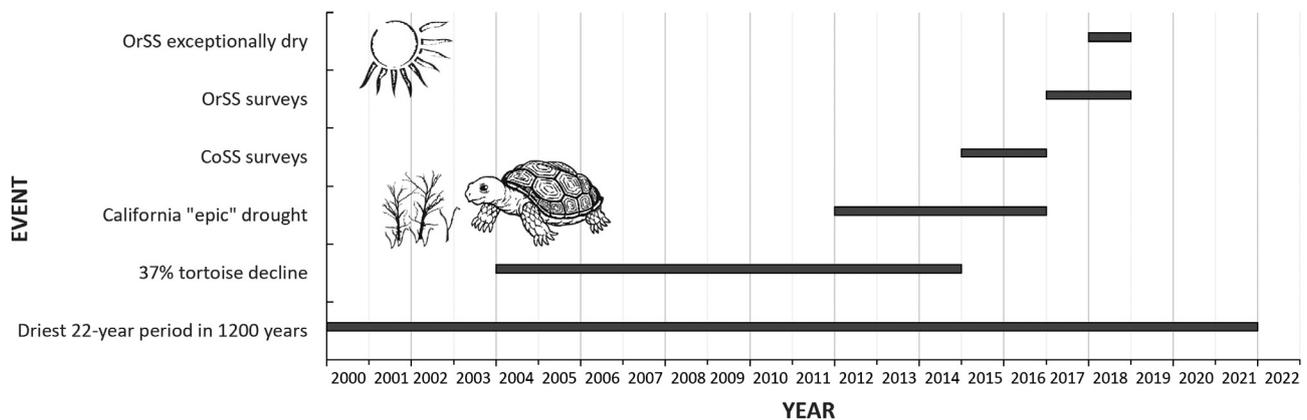


Fig. 4. Timing of surveys and drought conditions discussed in the text. CoSS: Cottonwood study site; OrSS: Orocopia study site

In contrast, at OrSS, the sex ratio of carcasses was decidedly female biased with 4 males and 15 females estimated to have died during the intensified drought period. Similar to, but more biased than, CoSS, living males outnumbered living females 16 to 5 at OrSS (Table 3). The one-tailed 2 × 2 Fisher's exact test probability of 0.0006 suggests that sex was not independent of status (dead vs. living) at OrSS. The upright posture and location of many of the carcasses outside of burrows is consistent with the behavior of tortoises dying from dehydration and starvation (Berry et al. 2002).

Other than the non-transmitted male that appeared to have been killed by a badger (Smith et al. 2016), we are unaware of any mortalities of our marked or transmitted tortoises during the period of study. In addition, the cause of a radio malfunction involving another small male at CoSS could not be determined since he was never relocated despite multiple attempts to do so. It is conceivable that a large predator such as a coyote carried him away, but it is also possible that the radio stopped sending a signal.

At CoSS, mean carapace length of living females ≥ 180 mm (221 mm, n = 9) was smaller than that of liv-

Table 3. Summary of all desert tortoise carcasses and live tortoises located during 2015–2016 at the Cottonwood study site (CoSS) and 2017–2018 at the Orocopia study site (OrSS). Numerals in parentheses represent tortoises or carcasses per km². Carcasses were assessed for approximate time of death according to their state of decomposition and deterioration (see Table 1 and Section 2.3 for descriptions of decomposition categories). Carcasses were broken down into 2 categories: death pre-drought (died prior to the beginning of the 2012–2016 epic drought) and death during drought (died sometime during the 2012–2016 epic drought)

Sex	Cottonwood				Orocopia			
	Death pre-drought	Death during drought	Total carcasses	Live tortoises	Death pre-drought	Death during drought	Total carcasses	Live tortoises
Male	1 (0.17)	4 (0.70)	5 ^a (0.87)	22 ^a (3.83)	13 (0.62)	4 (0.19)	17 (0.81)	16 (0.76)
Female	2 (0.35)	3 (0.52)	5 (0.87)	9 (1.57)	10 (0.48)	15 (0.71)	25 (1.19)	5 (0.24)
Juvenile ^b	2 (0.35)	1 (0.17)	3 (0.52)	3 (0.52)	1 (0.05)	–	2 (0.10)	1 (0.05)
Unknown	2 (0.35)	1 (0.17)	3 (0.52)	–	15 (0.71)	2 (0.10)	16 (0.76)	–
Total	7 (1.22)	9 (1.57)	16 ^a (2.78)	34 ^a (5.91)	39 (1.86)	21 (1.00)	60 (2.86)	22 (1.05)

^aThese numbers include 1 adult male tortoise that was initially located alive and healthy on 1 April 2015 but was subsequently found freshly predated on 13 April 2015 (see Smith et al. 2016 for additional information). This tortoise is also included in the carcass count

^bNumbers for juveniles were scored using the same classification system as adults and are reported here; however, we recognize that differences in ossification between adult and juvenile shells may cause differences in decomposition rates

ing males in the same size range (268 mm, $n = 22$), and the differences were statistically significant (2-sample t -test, $t = -5.30$, $df = 29$, $p < 0.001$). In contrast, at OrSS, mean size of living females (234 mm, $n = 5$) was not statistically different from the mean size of living males (263 mm, $n = 16$) (2-sample t -test, $t = -1.77$, $df = 19$, $p = 0.09$).

3.2. Reproductive output

Females reproduced during the 2012–2016 drought and afterwards in the exceptionally dry year of 2018. At CoSS, 7 of 8 monitored females produced at least 1 clutch of eggs during 2015–2016. Not every female was monitored during both years due to radio failure and location of new individuals during the second year of study. A single female did not produce eggs in either 2015 or 2016. One female monitored only during 2016 produced a single clutch of one egg. Four females monitored during both years produced 2 clutches each year, and 3 females that were monitored for a single year (1 in 2015, 2 in 2016) each produced 2 clutches during the year they were monitored (Lovich et al. 2018).

At OrSS, at least 1 small female did not reproduce in the exceptionally dry conditions of 2018, although we only had a single year of data for her, so we cannot definitively say that she was capable of reproducing. Two females produced 2 clutches each in 2017, and then each produced only a single clutch in 2018. A fourth female produced at least 1 clutch in 2017 while none was observed in 2018. However, we were

unable to handle and X-radiograph this tortoise on sequential captures during the reproductive season, so it is possible that the appearance and disappearance of other clutches were missed in both years.

3.3. Weather data

Despite severe drought conditions, some germination of winter annual food plants for tortoises was observed at CoSS in 2015. The winter of 2015–2016 was characterized by a strong El Niño event in terms of the amount of warming that occurred, and although that did not result in higher-than-average precipitation in California, the precipitation at CoSS was adequate to again support limited germination of tortoise food plants (see Table 2). In contrast, the OrSS had limited germination in 2017 following higher precipitation totals during the winter of 2016–2017, but a complete lack of winter annual plant germination for the duration of our study in 2018. A single rainfall event during the winter of 2017–2018 was inadequate to prevent severe drought conditions at OrSS the following spring. The lower-elevation OrSS has a climate that is warmer and drier than that of the neighboring CoSS. During the 25 yr period 1993–2018, both the winter wet season (October–March) and summer dry season (April–September) had higher average precipitation and lower averages for maximum, minimum, and mean temperatures at CoSS than at OrSS (based on estimated temperatures and precipitation calculated using WestMap; Table 2).

4. DISCUSSION

Our data suggest that adult tortoise mortality in the western Sonoran Desert during the epic drought conditions of 2012–2016 appears to be statistically biased toward females at the lower elevation OrSS. Conversely, the sex ratio of living adult tortoises at OrSS was biased toward males, consistent with the hypothesis that female mortality may have been higher than that of males. This is particularly interesting since studies elsewhere suggest that annual survival of females is generally greater than survival of males (Berry et al. 2020). The number of tortoises that were estimated to have died during the epic drought at OrSS ($n = 21$) is almost equal to the number of live tortoises located at the site ($n = 22$), suggesting a significant mortality event for such a long-lived species (Germano 1992). Although the biases above were not statistically significant for the 1-tailed 2×2 Fisher's exact test at the higher-elevation, wetter CoSS (Table 2), the number of live males ($n = 22$) greatly exceeded the number of live females ($n = 9$), a finding that is generally consistent with our hypothesis of greater adult female mortality. However, we found 4 male and 3 female carcasses estimated to have died during the epic drought at CoSS, but these figures should be interpreted with caution due to the small sample size.

Independent support for our hypothesis was provided in 2017 when the US Fish and Wildlife Service conducted tortoise surveys within the much larger Chuckwalla Tortoise Conservation Area (that includes OrSS and areas to the southeast) with a different survey technique: line distance sampling (Allison & McLuckie 2018). Their numbers also suggested a male-biased sex ratio of live tortoises as well as a greater number of female carcasses. They located 39 live adult females and 50 males, as well as the carcasses of 16 adult females and 12 adult males (L. Allison pers. comm.). Estimates of the time of death were not recorded during their surveys.

The high mortality rate we observed at OrSS was mirrored by earlier data collected in the footprint of a large, proposed development located less than 10 km to the west of OrSS. Tortoise surveys there in 2000, reported in an unpublished environmental compliance document, noted a small number of live tortoises ($n = 10$) compared to a very large number of tortoise carcasses ($n = 123$) in various stages of deterioration in April and May 2003 over an area of approximately 27 km^2 (Psomas 2003). Sex was determined for only a small fraction of the carcasses located but was not significantly different from 1:1 (16 males, 14 females).

The surveyors used a system to assign categories of shell deterioration but did not estimate times of death (Psomas 2003). Most carcasses were disarticulated, suggesting death 4 or more years prior (according to our classification system).

Similarly, high rates of mortality were reported based on 2014 surveys just over 20 km to the north of CoSS and OrSS in the Pinto Basin of JTNP. A large number of carcasses ($n = 64$) were found, compared to a small number of live tortoises ($n = 14$) during surveys in 2012 that only noted sex ratios of live tortoises (Lovich et al. 2014a). Live tortoise sex ratios in 13 surveys between 1978 and 2012 ranged from 1:1, to male-biased, to female-biased with no trend in any one direction. The die-off in the Pinto Basin was attributed to the effects of drought and prey switching by predators, with estimated survival rates being coincident with 3 yr moving average precipitation trends. The strong adult female-biased mortality we observed at OrSS is of interest, since many females appear to have died during the recent epic drought in California (2012–2016). However, the effects of the ongoing megadrought on long-lived species like tortoises imposed stresses to survival that extended both before and after the intensified 2012–2016 drought. For example, tortoise population declines in the larger Sonoran Desert region of California (often referred to as the Colorado Desert) suggest a loss of 37 578 ($\pm 11\,006$ SE) adults from 2004–2014 (Allison & McLuckie 2018).

Sex ratios in turtle populations vary due to the effects of 5 factors (Lovich & Gibbons 1990, Lovich 1996). First, sampling bias can result in the perception of skewed adult sex ratios. Given the fact that line distance sampling transects conducted by the US Fish and Wildlife Service in the Chuckwalla Tortoise Conservation Area (including our OrSS) observed an adult female carcass bias (see above) as we did, we believe that it is unlikely that our results were affected by sampling bias.

Second, desert tortoises, like many turtles, have environmental sex determination with high incubation temperatures producing more female hatchlings and low incubation temperatures producing more males (Ewert et al. 1994, Spotila et al. 1994). Given concerns about global warming, some authors have suggested that turtle and tortoise populations may face extinction due to a strong sex ratio bias (Janzen 1994, Hulin et al. 2009). However, in the case of desert tortoises, warming would potentially lead to a sex ratio bias opposite to that which we observed (i.e. the number of live tortoises in a population would be female-biased).

The third possible explanation is differential age of maturity of the sexes, or bimaturism (Lovich et al. 2014b). Simply stated, the sex that matures earlier predominates in adult sex ratios assuming all other factors have little influence. Age of maturity largely determines adult size, with little evidence for additional growth (Congdon et al. 2018), although adult tortoises appear to exhibit some growth after maturity (Nafus 2015). Adult male tortoises tend to be slightly larger than females, but sexual size dimorphism of populations, when present, is not pronounced as it is in other species of turtles (e.g. Lovich & Gibbons 1990). Male and female tortoises mature at approximately the same age, so it is unlikely that bimaturism would be a significant factor. Indeed, the mean sex ratio of desert tortoises in 22 populations (Berry & Murphy 2019) was almost exactly 1:1, with a sex ratio index of 0.003 (Lovich & Gibbons 1992, Lovich et al. 2014b).

The fourth reason adult sex ratios can be biased is the possible effect of differential immigration or emigration of one sex or the other. Since desert tortoises are not migratory animals and typically have relatively small home ranges (Ernst & Lovich 2009), it is unlikely that this affected our results.

The fifth, and we believe most likely, reason for the female-biased carcass sex ratio we observed at OrSS is due to differential mortality. For some reason, it appears that females were more likely to die during the drought of 2012–2016 than males, whether by dehydration and starvation or by predation via prey switching as detailed by Lovich et al. (2014a). If so, the question remains, why? As stated above, adult female tortoises tend to be somewhat smaller, on average, than males, so it is possible that they are more vulnerable to predation than males as suggested by Esque et al. (2010). However, mean carapace length of live males was not significantly greater than that of live females at OrSS, where the sex ratio of dead tortoises was most biased toward females. It is worth reiterating that we could not determine if carcasses that bore marks from teeth of carnivores were a result of predation, scavenging, or both. It is also possible that females are more susceptible to death by drought and starvation due to their smaller size in some populations, therefore reducing their ability to store water and nutrients. The upright orientation and location of many of the carcasses we found outside of burrows is consistent with the behavior of tortoises dying from dehydration and starvation (Berry et al. 2002, Lovich et al. 2014a), although alternative explanations are possible (e.g. sex-biased mortality from disease: see Wendland et

al. 2010). However, we found no evidence of shell disease, previously reported nearby (Jacobson et al. 1994), or obvious symptoms of upper respiratory tract disease (URTD) (Jacobson et al. 2014) such as mucus exudate from the nares.

URTD was previously reported from tortoises in JTNP (Homer et al. 1998), so it may have played a role at our study sites since it may also be exacerbated by drought (Lederle et al. 1997). It is also worth noting that clinical signs of URTD are not always present in tortoises that are seropositive for exposure to the pathogen (Schumacher et al. 1997). If URTD was a factor in the mortality of tortoises at our study sites, that still does not explain why females were disproportionately affected. The likelihood of testing positive for antibodies after exposure to the URTD pathogen does not appear to differ between the sexes (Lederle et al. 1997).

A possible mechanism for the sex-biased mortality we observed as a result of drought relates to female reproductive strategy. We hypothesized that drought-induced mortality would be female-biased due to water and energy losses attributable to egg production during protracted periods of resource limitation. Female desert tortoises have a ‘bet-hedging’ reproductive strategy whereby they make a small reproductive ‘wager’ every year (Ennen et al. 2017). Bet-hedging theory predicts that, if juvenile survival is low and unpredictable, organisms should consistently reduce short-term reproductive output to minimize the risk of reproductive failure in the long term (Lovich et al. 2015). By producing relatively small single or multiple clutches that are spatially and temporally isolated (Lovich et al. 2014c), female tortoises reduce the risk of reproductive failure in any one year. Since female tortoises cannot predict the environmental conditions that hatchlings will encounter when they hatch 74–100 d after oviposition (Ennen et al. 2012), females further hedge their bets by rarely skipping even bad years to reproduce, including drought years (Henen 1997, Averill-Murray et al. 2014, Lovich et al. 2015).

Reproducing in bad years has consequences on reserves of energy necessary for growth, storage, and maintenance (Congdon 1989), as well as on osmotic condition. Desert tortoise eggs range in mass from about 31 to 42 g (Turner et al. 1984), with an estimated median of 36.5 g. Mean clutch size of first and second clutches in the region is about 4.3 eggs, and females produce 1.78 clutches per annum (Lovich et al. 2018). In addition, females lose about 10 g of uterine fluid with each clutch during oviposition (Turner et al. 1984). Assuming a grand mean

female mass of about 2469 g at our study sites (J. Lovich et al. unpubl. data) yields the following estimate of the percentage of mass lost to a typical female annually by ovipositing 2 clutches of eggs in a year:

$$(4.3 \text{ eggs} \times 36.5 \text{ g} \times 2 \text{ clutches}) + (2 \text{ clutches} \times 10 \text{ g uterine fluid}) / 2469 \text{ g body mass} \times 100 = 13.5\% \text{ of body mass lost}$$

If desert tortoise eggs have a mean water content of 65.26%, like the congeneric *Gopherus polyphemus* (Congdon & Gibbons 1985), then females at our study sites that produce 2 average-sized clutches lose an estimated 218 g of water annually to reproduction, or over 0.20 l, before accounting for additional losses due to the effects of drought. Females that produce only a single clutch lose an estimated 7.7% of body mass, including 109 g of water, or over 0.10 l, still a substantial loss during drought.

Desert tortoises have remarkable adaptations or exaptations (Bradshaw 1988) to survive short-term droughts. They do so by relaxing control of energy and water homeostasis to withstand wide physiological fluctuations via anhomeostasis. For example, during times of drought, tortoise body mass may decrease 40%, and their total body water content may decline to 60% or less of their body mass (Peterson 1996). In addition, females have the ability to reduce their field metabolic rates 70–90% during a drought, and these adaptations partially contribute to their ability to produce a few eggs under adverse conditions (Henen 1997, 2002). Henen (2004, p. 65) noted that even with these capabilities, tortoises have their limits: ‘Although relaxing homeostasis facilitates survival and reproduction, desert tortoises are vulnerable in particularly dry periods.’ Droughts lasting more than 2 yr reduce the survivorship of tortoise populations (Lovich et al. 2014a), and the 2012–2016 epic drought lasted 5 yr with no sign of letting up as of 2022 as part of the ongoing megadrought that started in 2000. It is possible that bet-hedging female tortoises exhausted stored resources necessary for their own survival during the epic drought by producing clutches of eggs almost every year. At OrSS, some females produced eggs in both 2017 and 2018 despite the return to extreme drought conditions in 2018.

This scenario of higher adult female mortality due to reproductive output is not unprecedented in turtles. In a study of over 1100 marked individuals of the freshwater turtle *Mauremys reevesii* on an island in Japan, the estimated sex ratio of younger age class turtles was essentially equal, but slightly skewed toward males in intermediate age classes, and signif-

icantly male biased in older age classes. Carcass surveys found a significantly female-biased sex ratio of dead, mostly adult, turtles (Takenaka & Hasegawa 2001), similar to our results. Since there were no native mammalian predators on the island capable of killing turtles, the authors concluded that some females were unable to recover nutritionally from energetically costly reproductive output before becoming inactive for the winter. This in turn, led to increased mortality of females but not males at their overwintering sites.

Modeling shows that population growth of desert tortoises is sensitive to the survival of large adult females (Doak et al. 1994, Berry et al. 2020). Given the high mortality (especially adult females) and low density of living tortoises that we and others (e.g. Psomas 2003, Lovich et al. 2014a, L. Allison pers. comm.) observed at or near our study sites, the viability of these southernmost populations is not necessarily assured. The location of a single live juvenile (approximately 4 yr old) and 1 live subadult male indicate that some recruitment has occurred at OrSS during the last several years, but further monitoring would be required to determine if there is enough recruitment occurring to offset mortality in the population.

5. CONCLUSION

A preponderance of evidence from our research (e.g. male-biased living adult sex ratios at both study sites, female-biased mortality at OrSS) points to the conclusion that drought is causing female-biased mortality of tortoises at these study sites, especially at OrSS. We suggest that declines of tortoise populations, especially females, in the Sonoran Desert of California are exacerbated by increasing climatic extremes in low, hot, and dry areas like OrSS that are near the southern edge of the range for desert tortoises (Berry & Murphy 2019), as predicted by Barrows (2011) and supported by the previous findings of Lovich et al. (2014a). With climatic extremes becoming more prevalent (Cayan 2010), extended periods of protracted drought are expected to continue to affect tortoise sex ratios, survival, reproduction, and recruitment in the region. Sex ratio bias can be an overlooked threat to population persistence, especially in populations of long-lived organisms (Grayson et al. 2014), like Agassiz’s desert tortoise.

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