



Climatic variation and tortoise survival: Has a desert species met its match? ☆



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ABSTRACT

While demographic changes in short-lived species may be observed relatively quickly in response to climate changes, measuring population responses of long-lived species requires long-term studies that are not always available. We analyzed data from a population of threatened Agassiz's desert tortoises (*Gopherus agassizii*) at a 2.59 km² study plot in the Sonoran Desert ecosystem of Joshua Tree National Park, California, USA from 1978 to 2012 to examine variation in apparent survival and demography in this long-lived species. Transect-based, mark-recapture surveys were conducted in 10 of those years to locate living and dead tortoises. Previous modeling suggested that this area would become unsuitable as tortoise habitat under a warming and drying climate scenario. Estimated adult population size declined greatly from 1996 to 2012. The population appeared to have high apparent survival from 1978 to 1996 but apparent survival decreased from 1997 to 2002, concurrent with persistent drought. The best model relating apparent survivorship of tortoises ≥ 18 cm over time was based on a three year moving average of estimated winter precipitation. The postures and positions of a majority of dead tortoises found in 2012 were consistent with death by dehydration and starvation. Some live and many dead tortoises found in 2012 showed signs of predation or scavenging by mammalian carnivores. Coyote (*Canis latrans*) scats and other evidence from the site confirmed their role as tortoise predators and scavengers. Predation rates may be exacerbated by drought if carnivores switch from preferred mammalian prey to tortoises during dry years. Climate modeling suggests that the region will be subjected to even longer duration droughts in the future and that the plot may become unsuitable for continued tortoise survival. Our results showing wide fluctuations in apparent survival and decreasing tortoise density over time may be early signals of that possible outcome.

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1. Introduction

Evidence of the biological impacts of global climate change have been documented throughout the biosphere (Parmesan and Yohe, 2003; Root et al., 2003), across diverse taxa and ecosystems (Walther, 2010; Walther et al., 2002), with new supporting evi-

dence accumulating on a regular basis (Thompson et al., 2013). Confirmation of climate change and a global warming trend is manifested through well-documented changes in the survival (Griffiths et al., 2010), physiology, distribution, and phenology (Lovich et al., 2012) of both animals and plants (Willis et al., 2008) that are consistent with theoretical expectations (Hughes, 2000). Indeed, global warming now poses a serious challenge to conservation of biodiversity (Bellard et al., 2012; Heller and Zavaleta, 2009) through projected (Thomas et al., 2004) and empirically validated (Sinervo et al., 2010) increases in extinction risk. Although there has been considerable debate about the drivers causing an increase in global average temperatures (Stott et al., 2000), the broad congruence of so many individual case-studies now provides essentially undeniable support for the phenomenon. What is less certain is how warming will affect the distribution and survival of many species of plants and animals and if the effects

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will be positive (Vieites et al., 2007) or negative. Given this uncertainty, there is an urgent need for research on how conservation-reliant species like Agassiz's desert tortoise (*Gopherus agassizii*) will respond to warming.

While range shifts or demographic changes in short-lived species may be observed relatively quickly in response to climate changes, measuring population responses of long-lived species require data from long-term studies that are not always available (Tinkle, 1979). Although short-term studies of long-lived species can sometimes reveal drastic changes in demographic parameters, it is also true that estimates of those parameters over shorter time periods can mask the importance of extreme climatic events if those events are missed. Despite the value of long-term studies, they are rarely conducted due to limitations imposed by amounts and cycles of funding, labor and logistics required to support field research over many years (Congdon et al., 1993; van Loben Sels et al., 1997), and by the duration of a human research career or lifetime (Hobbie et al., 2003). The alternative, short-term research projects, are rarely adequate for understanding processes that occur over long periods of time (Callahan, 1984), leading to potential misjudgments in attempts to understand and predict biological change (Magnuson, 1990). The general lack of long-term studies for most species complicates efforts to understand the effects of climate change, especially on long-lived organisms.

The life history traits of many turtle species, including Agassiz's desert tortoise (*G. agassizii*), are characterized by delayed maturity and impressive longevity (Congdon et al., 1994; Ernst and Lovich, 2009) requiring long-term studies to quantify vital rates that affect stability and persistence of populations. Agassiz's desert tortoise is protected under the U.S. Endangered Species Act as threatened in Arizona, California, Nevada and Utah where populations appear to be declining rangewide (Esque et al., 2010) with few possible exceptions (Lovich et al., 2011). Known and suspected threats to tortoise survival include climate change due to increased temperatures and decreased rainfall (Barrows, 2011; Ihlow et al., 2012; McCoy et al., 2011). Habitat loss and degradation (Lovich and Bainbridge, 1999); disease (Berry et al., 2006); and increased pressure from subsidized predators (Esque et al., 2010) such as ravens (*Corvus corax*) and coyotes (*Canis latrans*), are contributing and synergistic factors. Only two published long-term studies of desert tortoises are available with details about survivorship (Medica et al., 2012; Zylstra et al., 2012), but neither focus on the role of climate change on free-living *G. agassizii* populations.

In the southwestern United States, the Mojave and Sonoran Deserts occupied by *G. agassizii* are model ecosystems for examining the effects of climate change. Precipitation is the “master input” in these water-limited ecosystems (Noy-Meir, 1973) making them particularly sensitive to changes in water availability. Concomitantly, water availability has profound effects on the physiology (Henen et al., 1998; Peterson, 1996) and survivorship (Peterson, 1994a) of Agassiz's desert tortoise. Research indicates that this already arid region is in the process of transitioning to an even dryer and warmer climate (Seager et al., 2007) with changes in the onset of spring (Cayan et al., 2001) as well as increased drought frequency and duration (Cayan et al., 2010). The drying trend is validated by decreasing ratios of precipitation received as snowfall in high elevation areas of the western United States, that appear to be at least partially attributable to truly long-term climatic shifts beyond the Pacific decadal oscillation (Knowles et al., 2006), as well as increased large wildfire frequency, duration and longer wildfire seasons in western forests (Westerling et al., 2006). These and other factors are already affecting plant community structure and phenology in the Desert Southwest United States (Bowers, 2007; Brown et al., 1997; Turner, 1990), with empirically unverified consequences for Agassiz's desert tortoise. However, modeling suggests that avail-

able habitat for *G. agassizii* in the western Sonoran Desert will shrink dramatically under a future climate scenario with warmer and dryer conditions (Barrows, 2011).

One way organisms like tortoises endure stochastic environmental conditions is through longevity. Simply stated, if environmental variation results in concomitantly variable reproductive success, selection will favor reduced reproductive output in iteroparous species, greater longevity, and a longer reproductive lifespan (Murphy, 1968; Schaffer, 1974). Recent analyses support the contention that population vital rates (survival, reproduction, growth) of long-lived species are better buffered against environmental variability than those of short-lived species (Morris et al., 2008). The desert tortoise is characterized by delayed maturity at an age of 14–15 years (Germano, 1994), an estimated generation time of about 25 years (Edwards et al., 2004; Service, 1990), and potential longevity exceeding 50 years (Germano, 1992). As a result, published studies of survivorship and demographic parameters based on long-term data sets for *G. agassizii* are rare (Bury and Corn, 1995; Corn, 1994; Germano and Bury, 1994). Population fluctuations in such long-lived species are especially difficult to quantify in time scales relevant to either generation times or climate change.

A population of *G. agassizii* has been sampled in the western Sonoran Desert of eastern Joshua Tree National Park, Riverside County, California, USA at various times from 1978 (Barrow, 1979; Freilich et al., 2000) to 2012, or about 1.4 tortoise generations, providing rare insight into demographic variation in this long-lived species over more than three decades characterized by extreme inter-annual variation in weather. Because of the longevity of desert tortoises, it is possible that some of the adults first examined by Barrow were born early in the 20th century. Data collected in 2012 allowed us to quantify fluctuations in apparent survivorship of the population since 1990 and show its strong relationship to climate, as reflected in multi-decadal precipitation patterns, especially persistent drought. Although the presence of tortoises in Joshua Tree National Park over the centuries attests to their ability to withstand desert conditions, our study site is located in an area predicted to become unsuitable for tortoises under a warming and drying climate change scenario (Barrows, 2011). In addition to examining demographic changes in the declining population since 1978, we estimated annual adult population size over about a decade of the study when capture probabilities were highest. Finally, we used evidence of coyote predation based on analysis of tortoise carcasses and coyote scats to identify possible mechanisms for the observed decline and their linkage to climate change.

2. Materials and methods

2.1. Study site description and field techniques

The study site, known as the “Barrow Plot” (hereafter the Plot) was established in 1978 (Barrow, 1979) to determine the size and demographic structure of a *G. agassizii* population within the boundaries of a 1 mi² area (2.59 km²). Although Barrow did not have GPS technology available, Plot corners on file at JTNP were 616171, 3745819; 617558, 3746656; 618396, 3745269; 617008, 3744431, all in Universal Transverse Mercator, Zone 11, North American Datum 1983. The Plot is located in the Sonoran Desert ecosystem portion of JTNP (Barrows, 2011) as part of the Pinto Basin and has a relatively uniform topography with elevations ranging from 654 to 718 meters and a mean slope of <2% (range 1.2–10.4%). Vegetation is dominated by creosote bush (*Larrea tridentata*), white bur-sage (*Ambrosia dumosa*), white rhatany (*Krameria grayi*), and pencil cholla (*Opuntia ramosissima*) (Freilich et al., 2000). A narrow dirt road, Black Eagle Mine Road, bisects

the Plot into north and south sections with the former slightly larger in area than the latter. The road receives regular traffic from visiting tourists and recreational gold miners. Traffic was monitored from 10 February, 2012 to 18 December, 2012 and ranged from 0 to 35 cars/day or 8 to 103 cars/week. A large proportion of traffic volume (45%) occurred during the months of March–June when adult tortoises were most active above ground at the site.

Desert tortoise surveys conducted throughout the park in 1987–1988 recorded the highest estimated densities in the vicinity of the Plot, reaching 77 tortoises per km² (Karl, 1988). Although the area in the Plot did not have the highest density of tortoises in the Pinto Basin, the Plot was typical of those areas where tortoises could be found with relative ease. Our conclusion was supported by numerous small plot surveys and distance-sampling transects conducted in those years (Freilich et al., 2000) showing that tortoise distributions were contagious with a small number of “hot spots” interspersed in a matrix of lower density areas containing 0–7 animals per km².

The Plot has been surveyed by different researchers using variations of the same set of transect-based survey techniques (Table 1). The first surveyor (Barrow, 1979) initially walked transects across the entire Plot at 45 m intervals during 25 days in the spring and fall of 1978 looking for live and dead tortoises. Using a metal file, he and subsequent researchers created unique identification marks by cutting notches into the scutes around the margin of the upper shell or carapace (Cagle, 1939) of living tortoises. The next surveys were conducted yearly from 1991 to 1996 (Freilich et al., 2000). From 1991 to 1992 transects involved only the north side of Black Eagle Mine Road and from 1993 to 1996 both sides of the road were surveyed. In addition to notching the carapace with identification codes, epoxy tags were applied to first right and fourth left pleural scutes on the carapace with the corresponding tortoise identification number. When shells of dead tortoises were found, observers painted them with yellow paint. During the course of studies, transects were conducted with groups of observers that varied in size (Table 1).

After the surveys of Freilich et al. (2000), studies of female reproductive output were conducted both on and near the Plot by Lovich et al. (1999) from 1997 to 1999. Although they did not conduct systematic surveys as done both before and after their research, they did note recaptures of animals from Freilich et al. (2000) and marked previously unregistered tortoises as they were encountered. The next surveys were conducted in 2004–2005 on only the north side of road (Bacon and Fesnock, 2005). At that time, dead tortoises were marked with green paint, including those marked earlier with yellow paint by Freilich and his team.

In 2012, 34 years after the first survey in 1978 (Barrow, 1979), surveys were conducted on fourteen different occasions from 22 April to 21 June, 2012 which largely coincided with months of peak activity levels in *G. agassizii* (Freilich et al., 2000; Woodbury and Hardy, 1948). We walked transects from 0530 to 1100 h when surface air temperatures were above the regional lower activity level threshold of about 18 °C (Lovich et al., 2012) and below the thermal maximum (35 °C) for handling desert tortoises stipulated in our permit from the U.S. Fish and Wildlife Service. To efficiently survey the Plot it was subdivided into 16 equal size (201.2 m²) sub-plots and all corners were established in the field with precision Trimble Global Positioning System (GPS) equipment, and marked with orange flagging to facilitate relocation and proper positioning on the day transects were conducted. Immediately prior to surveying a sub-plot, five 1.27 cm diameter, white marker sticks, each ≈3 m long, were vertically spaced at equal intervals along opposite sides of the sub-plot and flagged with orange tape to increase their visibility.

Sub-plots were surveyed by slowly walking individual transects with groups of 3–5 equally-spaced investigators (Table 1). The

white marker sticks were used to mark transect starting and ending points and to keep investigators properly aligned when they walked transects across the individual sub-plots. We looked for tortoises and tortoise burrows both in the open spaces between shrubs and under the canopies of shrubs where they often seek shade. Although we endeavored to walk straight lines, sinusoidal deviations of approx. ±2 m were necessary to avoid large desert shrubs and cacti along each transect. While we did not utilize line distance sampling techniques (Swann et al., 2002) in our study, Anderson et al. (2001) demonstrated that similar sinusoidal deviations along single line distance sampling transects with three observers (one on the line and two walking parallel 20 m on either side of the line) yielded underestimates on and immediately adjacent to the transect while the majority of tortoise detections occurred within 15–25 m of the line. The spacing of our transects, 12.5–25 m apart, generally allowed visual search overlap between adjacent observers walking parallel transects, but it is very likely that some tortoises were undetected during all surveys at the Plot, including ours. When tortoise burrows were located, we recorded their location using GPS and attempted to determine burrow occupation by living tortoises. Investigators checked burrows to the extent possible with flash lights, mirrors, and elongated sticks (Medica et al., 1986) to find hidden tortoises, but some burrows were too deep or curved to determine if they were occupied.

In 2012, when three people typically surveyed a sub-plot, they would position themselves 25 m apart between two of the flagged white marker sticks (i.e., one investigator at each flagged marker, and one in the middle), and then walk straight transects parallel to one another to the opposite side of the sub-plot where the corresponding markers were set. To stay on line when poles were obscured by terrain or vegetation, at least two people carried a compass to maintain a consistent heading. Investigators repeated this process until the sub-plot was completely examined. With four or five surveyors we used a similar protocol, however people were spaced approximately 17 or 12.5 m apart, respectively (Table 1). In a majority of cases (48 out of 80 transects) some lines in a sub-plot were surveyed twice to maintain proper spacing as the surveyors moved across the sub-plot. Repeated sampling has been shown to provide a statistically robust method for censusing small populations in another species of *Gopherus* (Stober and Smith, 2010).

Upon capture, live tortoises were weighed, measured, photographed, and their locations were documented with a Trimble GPS (accurate to ±3 m). Unmarked tortoises were notched as indicated above with identification numbers starting at 300, to avoid numbers previously assigned to marked tortoises at the site. When dead tortoises were encountered an effort was made to determine if they were marked previously as shown by notches on the carapace or the presence of yellow and/or green paint. If tortoise remains were disarticulated, they were reassembled (when feasible) to determine approximate straight-line carapace (CL) and/or plastron length (PL) and sex, and to gather potential information on cause of death including predation as suggested by shells that are cracked away from sutures or scarred by carnivore tooth marks (Woodbury and Hardy, 1948). When remains allowed only measurements of PL, CL was estimated using least squares linear regressions based on data from live Barrow tortoises. Unpublished criteria for aging the remains of Agassiz's desert tortoise were given in Woodman and Berry (1984) (cited in Berry, 1986). They identified four categories, based on disarticulation state and bone weathering, for estimating the approximate time since death: less than one year, one to two years, two to four years and more than four years. We were interested in recent deaths since the last survey before ours was in 2005 so we excluded remains that were estimated to be four or more years old. The accuracy of the criteria we used to estimate time of death for recently deceased tortoises

Table 1

Summary of different studies conducted on Agassiz's desert tortoise (*Gopherus agassizii*) at the 2.59 km² Barrow Plot, Joshua Tree National Park, California, USA. Abbreviations are as follows: N designates surveys performed north of Black Eagle Mine Road (area = 1 × 1.6 km) and B designates studies conducted both north and south (1.6 × 0.64 km) of the road. Data for skeletal remains in years marked with an asterisk include all skeletons found in that year plus skeletons counted in preceding years. Some years may include tortoises from multiple investigators at the site. In 2012, numbers in parentheses signify individuals included in the survival analysis since not all individuals were marked that year.

Year	Region of plot surveyed	# Of searchers	Person hours	Survey days	Transects (meters apart)	Live individuals captured ^{a,b,c}	Female ^a	Male ^a	Juvenile ^b	Reported skeletal remains
1978	B	1	–	25	45	51	19	22	10	39
1991	N	3–10	199	10	15	47	21	21	5	–
1992	N	3–13	237	9	15	59	28	20	11	11
1993	B	4–17	360	11	15	108	43	39	26	3
1994	B	4–13	293	10	15	42	20	19	3	3
1995	B	4–8	303	10	15	58	21	22	15	4
1996	B	4–8	245	11	15	35	18	13	4	5
1997*	B	2	–	–	–	19	11	4	4	2
1998*	B	2	–	–	–	23	9	10	4	5
1999*	B	2	–	–	–	5	3	1	1	9
2004	N	4+	491	11	15	42	3	6	33	59
2005	N	4+	724	23	15	28	1	5	22	8
2012	B	2–5	137	14	12.5–25	14	4(3)	5(3)	3	64

* Data from this period are based on both those individuals that were being tracked via radio telemetry and other individuals found serendipitously during radio tracking.

^a Number of individuals is based only on tortoises with identification numbers (notched or epoxied).

^b Juveniles were defined as <18 cm carapace length.

^c Number of males and females may disagree with previously reported because we do not include recaptures in the same year.

was validated by comparisons with carcasses of tortoises that were known to be alive in 2005 but died sometime thereafter. During surveys, scat samples from coyotes were also collected opportunistically and then examined in the lab to determine if they contained tortoise remains.

We acquired yearly estimated winter precipitation data (October–March) from WestMap (Fig. 1), a fine-scale (~1–4 km) climate mapping program that uses PRISM (Parameter–elevation Regressions on Independent Slopes Model) data to project regional climate. PRISM uses a digital elevation model of topography and nearest point measurements of climate data to generate estimates of monthly weather parameters (precipitation, temperature, and dew point: (http://www.cefa.dri.edu/Westmap/Westmap_home.php)). To test hypotheses about the effects of multiyear drought on survival we calculated covariates based on average estimated winter precipitation in the prior year (ppt), the prior 2 years (ppt2) and the prior 3 years (ppt3).

2.2. Survivorship modeling

Only marked adult tortoises ≥ 18 cm carapace length (Ernst and Lovich, 2009) were used in our survival analyses because there were only a few recaptures of smaller (sub-adult) tortoises, a situation previously noted by Freilich et al. (2000). We used only data collected from 1991 to 2012 in the survivorship analysis because investigators in 1991–1996 were unable to confidently identify tortoise marks attributed to the 1978 survey by Barrow. As a result of shallow identification notches (deeper notches persist on turtle shells for decades) applied to tortoises by Barrow, only six tortoises found from 1991 to 1996 bore marks suggesting they were marked in 1978. Although we were primarily interested in survival and its relationship to estimated precipitation patterns, it was necessary to model movement between the northern and southern portions of our study area to properly incorporate information from all years. We modeled movement between the two portions using a multistate generalization of the Cormack–Jolly–Seber model (Neil Arnason, 1972; Williams et al., 2002) in which the three biological states were defined as dead or permanently immigrated (state 0), alive and located in the northern portion of the study area (state 1), or alive and located in the southern portion (state 2). Changes in the state of an individual can be characterized generally using

state transition parameters, ϕ_t^{lm} , reflecting the probability that an individual in true state l at time t is in state m at time $t + 1$. For the purposes of our study, we decomposed ϕ_t^{lm} into (apparent) survival, S_t , and movement between sites ψ_t^{lm} . In all five models, S_t was modeled using a logit link and either 0 or 1 covariates. Observed capture history suggested that movement was rare, bidirectional, and did not vary over time, so we estimated only a single parameter, τ , indicating the probability of moving between portions of the study region within a year. Thus

$$\psi_t = \begin{bmatrix} 1 - \tau & \tau \\ \tau & 1 - \tau \end{bmatrix}$$

for all t and for all transitions not including state 0.

Tortoise surveys are characterized by imperfect detection (e.g., a tortoise may be in the study area but located deep within a burrow and thus unavailable for capture), and as a result, states are not observed perfectly (except in the case of radio-tagged individuals, see below). In particular, an individual that was not captured in a particular survey could be in any one of the 3 states. The imperfect detection process was modeled using parameters p_t^l , indicating the probability that an individual in true state l in year t was detected. In years where surveys only occurred in the northern portion of the study region p_t^1 was set to zero and in all other years $p_t^1 = p_t^2 = p_t$. Sampling effort varied from full surveys to incidental captures during a radio telemetry study. Moreover capture probabilities are known to vary greatly from year to year in desert tortoises independent of effort. Detection of tortoises above ground depends on temperature, the timing and amount of rainfall, and food plant availability (Duda et al., 1999; Freilich et al., 2000). Wet years with good germination of annual food plants are the best years to look for active *G. agassizii*. The majority of previous transect-based studies were conducted in wet years, but two years (1994 and 1996) had estimated winter precipitation substantially below the long-term mean and the most recent survey (2012) was conducted during another dry period (Fig. 1).

In addition to weather-related effects on detection, the people conducting the surveys varied over the three decade time span of the studies, as did their experience, ranging from those with significant experience looking for desert tortoises and their burrows, to others that were volunteers with limited training. However, Freilich and LaRue (1998) and Anderson et al. (2001) found that

observer experience had no demonstrable effect on the ability to find tortoise models in controlled field trials. Because of the potential effect of precipitation and germination on tortoise detection, and the potential for differences in experience among teams of researchers, we estimated separate p_t 's for each survey year. For tortoises that were radio-tagged for a portion of the study period (see Table 1), we assumed initial capture equivalent to the p_t for the capture year and a capture probability equal to one for all subsequent years in which they were encountered using radio equipment.

We considered five models corresponding to different hypotheses about S_t . A priori we predicted that tortoise survival would be lower when there were multiple consecutive years of drought. Survival could be lowered either because tortoises are unable to meet their energetic needs, or because predators, like coyotes, prey switch to tortoises, or for a combination of these reasons (tortoises may take more risks to meet their energetic needs and predators may begin to actively search for them). Based on the research of Peterson (1994a) who observed drought-induced mortality of tortoises following two years of low precipitation and annual plant food shortages, we were unsure whether these declines in survival would be more closely linked to estimated winter precipitation over the preceding two or three years, so we included candidate models based on both quantities - $S(\text{ppt}2)$ and $S(\text{ppt}3)$: Fig. 1). We compared these two models to a model based only on estimated winter precipitation in the preceding year, $S(\text{ppt})$, and two alternative models that assumed either a constant survival, $S(\cdot)$, or a linear trend in survival $S(T)$. Model parameters were estimated using maximum likelihood and the optim function (with the "BFGS" method) in R statistical software (64 bit ver. 2.14.2). Models were compared using Akaike Information Criterion (AIC) (Burnham and Anderson, 1998) and confidence intervals were determined by estimating and solving the Hessian. Abundance estimates from the best model were determined for all years in which the whole area was surveyed and capture probability was greater than 0.1 using the Horvitz-Thompson method (McDonald et al., 2005).

3. Results

3.1. Precipitation patterns over the study period

The wettest three year period since tortoises were first surveyed in the Plot in 1978 occurred in 1991–1993 and the wettest year was 2005, which was near record setting (King et al., 2007). The driest year was 2002 and the driest three year period was 2000–2002. In the two decades prior to the first survey there

was an even drier three year period (1970–1972) and many years were relatively dry (Fig. 1). During the period of the survival analysis the average amount of estimated winter precipitation in the preceding three winters was greater than 2.5 cm in all years but one over the first part of the study, before declining to lower values from 1996 to 2004 and then increasing in all years but one after 2005 (Fig. 1).

3.2. Summary of 2012 results

During our 2012 survey, we encountered only 14 live adult and sub-adult tortoises and the remains of 64 dead tortoises. Of the latter, 33 (51.5%) were marked with yellow or green paint from earlier studies and did not represent recent mortalities but rather the long-term persistence of shell remains (e.g., Dodd, 1995). Based on criteria for estimating time since death, 19 (29.7%) of the carcasses were attributed to deaths in the previous four years (e.g., 2008–2012). Of these 19, 12 (63%) were found upright under the canopy of creosote bushes with mostly articulated shells as if they died in place (i.e., they were not moved to the location by predators).

Living and dead tortoise body sizes (CL) were not appreciably different. The 14 living tortoises ranged from 11.8 to 27.3 cm CL (mean = 21.7, sd = 5.6). Carcass CL in 2012 (including estimates based on rearticulating skeletons) ranged from 13.5 to 31.2 cm (mean = 20.6, sd = 3.9). Linear regressions relating the \log_{10} of CL across years for live tortoises showed no significant change in body size for males ($r^2 = 0.009$; $F = 1.802$; $df = 1, 189$; $P = 0.181$) or females ($r^2 = 0.005$; $F = 1.028$; $df = 1, 199$; $P = 0.312$).

3.3. Modeling survival

We fit and compared five models, three were based on precipitation in the preceding 1, 2 and 3 winters. The best model of survival was based on the average estimated winter precipitation over the preceding three winters (Table 2) and estimates a mean annual (apparent) survival rate of 0.87. Values below the mean, some substantially so, occurred in 1991, 1997–2004 and 2008 (Fig. 2). All five models also included an estimate of the probability of moving between north and south portions of the study site within a year (τ), which was estimated at 0.12 (SE=0.02) in the best model. Estimates of capture probabilities were also generally high in the beginning of the study corresponding to a time when search effort was high and germination of food plants was generally favorable for tortoises (Table 1, Fig. 3). Estimates of capture probabilities had higher uncertainty for the last two surveys, in part because of the large gaps in survey coverage in the latter half of the study

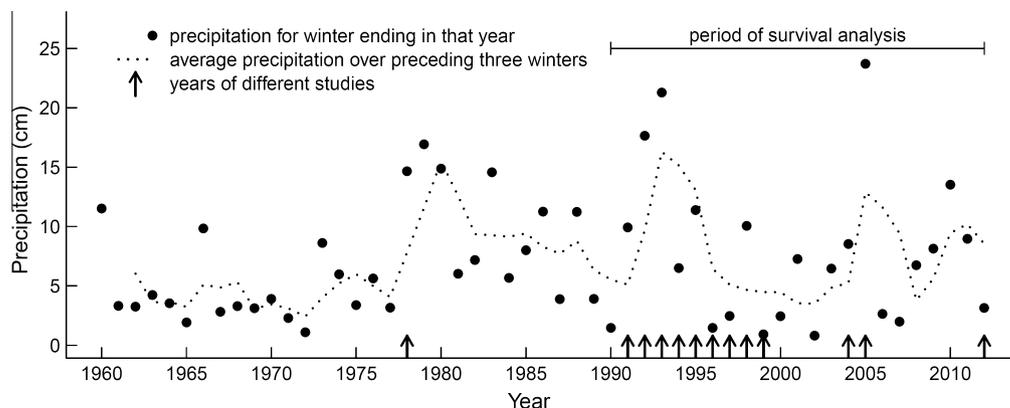


Fig. 1. Estimated winter precipitation (1960–2012) and average of preceding three years at an Agassiz's desert tortoise study site in Joshua Tree National Park, California, USA based on WestMap data (refer to text for details).

Table 2

Models of Agassiz's desert tortoise survival based on preceding winter estimated precipitation from one [S(ppt)] to three [S(ppt3)] years. Model S(.) assumed a constant survival rate and model S(T) assumed a linear trend in survival. All models assumed τ was constant and p_t varied for each year. Model comparison provides overwhelming support for model where survival is a function of average estimated winter precipitation (October–March) over three preceding years.

Model	Number of parameters	Negative log likelihood	Difference in AIC from best model	Akaike weight
S(ppt3)	14	470.8	0	0.9995
S(ppt2)	14	474.6	7.7	0.0005
S(ppt)	14	477.0	12.4	0
S(T), τ (.)	14	477.8	14	0
S(.), τ (.)	13	481.7	19.8	0

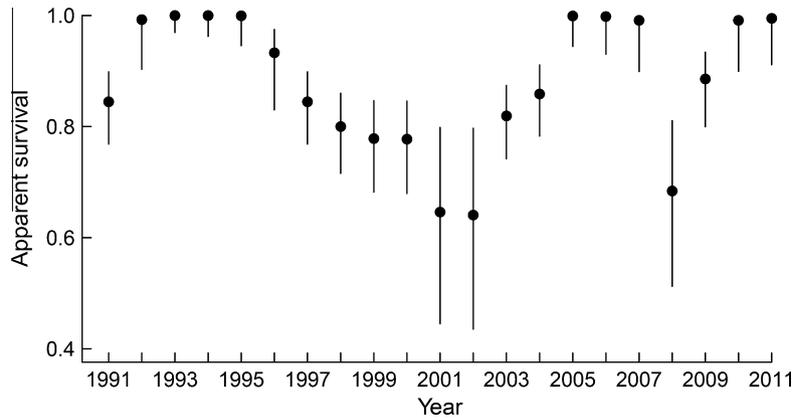


Fig. 2. Estimates, and 95% confidence intervals, of apparent survival of Agassiz's desert tortoises over study period based on model S(ppt3) that assumes survival is a function of precipitation in preceding three years.

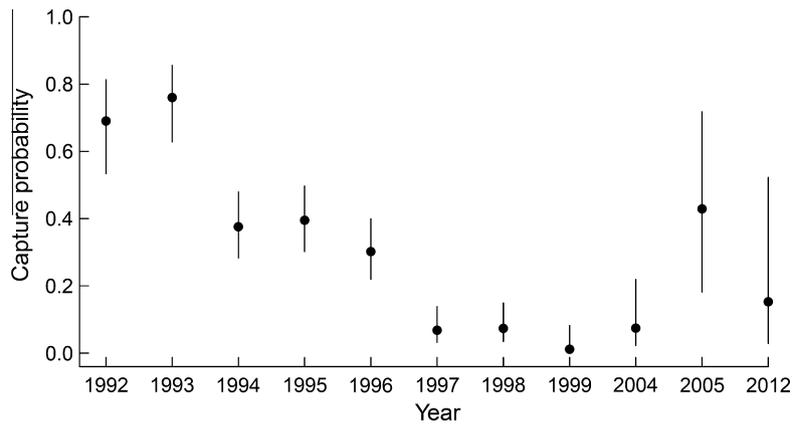


Fig. 3. Estimates of capture probability (p_t), and 95% confidence intervals, of Agassiz's desert tortoises for each survey year.

period. We estimated adult abundances as a derived parameter in years where the whole study area was surveyed and capture probabilities were greater than 0.1 using the Horvitz–Thompson estimator for open population models (page 241 in McDonald et al., 2005). In agreement with the survival analysis, abundances declined greatly between 1996 and 2012 (Fig. 4).

3.4. Known or suspected causes of mortality in 2012

Only one live tortoise was observed with symptoms (Berry and Christopher, 2001) consistent with upper respiratory tract disease (URTD – e.g., mucous exudate bubbling from the nares). Signs of attempted predation were seen on two (16.6%) living tortoises. In contrast, 19 (29.7%) of tortoise carcasses detected had signs of predation or scavenging (including missing heads or limbs, carapace or plastron bones that were broken away from sutures, or scat piles of carnivores on or near the remains). The relative proportions of

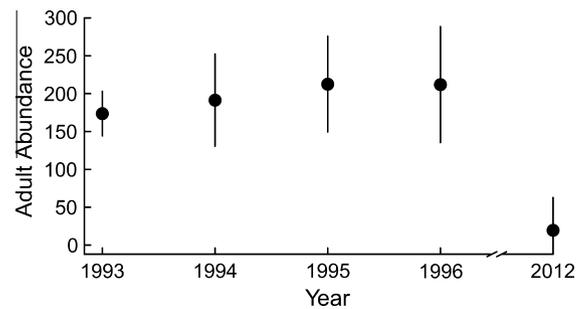


Fig. 4. Abundance, and 95% confidence intervals, of Agassiz's desert tortoises over the study period (estimates only plotted for years when capture probability was greater than 0.1 and the whole study area, both north and south of Black Eagle Road, was surveyed).

live versus dead tortoises with evidence of predation or scavenging were not statistically different (two-tailed Fisher's exact test summing small P values, $P = 0.33$). Suspected or confirmed predators or scavengers included coyotes and kit foxes (*Vulpes macrotis*), although mountain lions (*Felis concolor*) occur in the area and are known predators (Medica and Greger, 2009; Riedle et al., 2010) of desert tortoises. Sightings or signs of both canid species were frequently observed during our studies. Unpublished data from radio-telemetry studies conducted at the site in 1996–1999 (Lovich et al., 1999) confirmed coyotes as predators or scavengers at that time. Of 15 tortoises alive in 1996, 3 were predated or scavenged in 1997, 5 in 1998 and 5 in 1999. Hairs found on the remains of these tortoises were from coyotes as shown by DNA and microscopic analysis. In 2012, we found the remains of as many as seven tortoises in four coyote scats examined. One scat contained the remains of at least two individual tortoises as shown by a detached juvenile foot, forelimb scales and toe nails of an adult, and shell scutes of various sizes. It is not known if the tortoise remains were a result of predation or scavenging.

3.5. Other observations based on data from all surveys

The number of live individual tortoises found each year fluctuated greatly, as did estimated population numbers, in large part due to whether both sides of the road were surveyed or not (Table 1; Fig. 4). Standardizing search time, the number of hours required per live tortoise found increased dramatically from 2.97 to 5.43 person hours/live tortoise found in the 1990s to 12.32–14.75 person hours/live tortoise in later years (Table 1), whether including full or partial Plot surveys. Sex ratios, defined as the number of live males divided by the number of females, ranged from unity, to male biased (5:1), to female biased (0.22:1) across years with no trend in any one direction (Table 1).

4. Discussion

Our study empirically demonstrates the long-term effects of climate variation, specifically persistent and recurrent droughts, on survivorship in free-living Agassiz's desert tortoises over more than a generation time. The fact that the overall effect has been a slow decline of the population, despite its protection inside the boundaries of a national park, underscores the challenges faced by resource managers responsible for recovery of conservation-reliant species under a changing climate.

Primary productivity and thus availability of food for herbivorous desert consumers is tightly linked to the amount and timing of precipitation. Germination and persistence of annual food plants for tortoises are strongly correlated with the timing and amount of winter precipitation (Beatley, 1967, 1974; Medica et al., 2012). In turn, survival of tortoises is associated with availability of food plants. For example, annual female survivorship of a desert tortoise population near Palm Springs, California, approximately 87 km from the Plot, was 92% from 1997 to 2010 (Lovich et al., 2011). The Palm Springs site is characterized by greater rainfall (long-term mean winter precipitation is about 11.4 cm, Ennen et al., 2012) and consistently higher productivity of winter annual plants than the Plot (Lovich et al., 1999). During the same time period, the range of point estimates of apparent survival of tortoises at the drier and less productive Plot ranged from only 0.64 to 1.0 with a mean of 0.87. Farther to the east in Arizona, survival of the closely-related and demographically similar *G. morafkai* ranged from 0.87 to 0.97 with a mean of 0.92 at 15 locations over 22 years (1987–2008) (Zylstra et al., 2012). It is difficult to say what “normal” rates of survival are for desert tortoises, but their combination of life history traits suggests that survival of adults is

important for population persistence as a means of compensating for late maturity and high rates of nest failure, something that has been validated with modeling (Doak et al., 1994). Adult survivorship rates reviewed by Ernst and Lovich (2009) for both desert tortoise species ranged from about 0.75 to 0.97, with 0.98 considered an “optimistic estimate of tortoise survival in undisturbed areas” according to Doak et al. (1994).

Some of the variation in survivorship observed among studies is attributed to the response of desert tortoises to regional differences in precipitation with variable life-history strategies tailored to the particular circumstances (Curtin et al., 2009). In the eastern and southern portions of the ranges of both *G. agassizii* and *G. morafkai* (respectively), summer rain during the monsoon is an important factor in the ecology of desert tortoises (Averill-Murray et al., 2002a,b). However, the strength of the monsoon diminishes from east to west, and in the western portion of the Sonoran Desert where our study site is located, the percentage of warm season precipitation is negligible (Lovich and Beaman, 2007). In the western portion of the range of *G. agassizii*, precipitation is delivered primarily as a result of winter storms with little summer inputs. Lack of consistent and significant summer precipitation at the Plot may partially explain the lower survivorship values we observed in comparison with all but the westernmost populations reported by Zylstra et al. (2012). In the populations studied by Zylstra et al. survival rates rebounded after a few years of drought. Survival in our population increased following the droughts prior to 1978 and after the drought in the late 1990s, but the sharp decline in estimated number of tortoises on the Plot after 1996 (Fig. 4) suggests that the potential for full recovery of the population to its former abundance is now seriously compromised.

Although it is difficult to determine the exact cause of death in tortoises without detailed necropsies (Berry et al., 2002; Homer et al., 1998), the results of our analysis confirm previous studies demonstrating that recurring drought has a strong effect on apparent survival of adult *G. agassizii*. Indeed, the upright posture and location of many of the carcasses we found outside of their burrows is consistent with the behavior of tortoises dying from dehydration and starvation (Berry et al., 2002), although alternative explanations are possible.

From 1991 to 1996 Freilich et al. (2000) found that the tortoise population at the Plot was relatively stable, although the animals were much more difficult to locate in dry years. Our survival model agrees with his observations predicting relatively high survival from 1991 to 1996 followed by declines (Fig. 2). Moreover, estimates from the model (Fig. 3) suggest high capture probabilities in the wet years of 1991 and 1992 and lower capture probabilities in the three subsequent drier years (Fig. 1). It is important to point out that our estimates are of apparent survival, and thus are unable to disentangle permanent emigration from death. However, available evidence supports a high rate of site fidelity in tortoises. For example, Freilich's research at the Plot from 1991 to 1996 demonstrated that in dry years, recaptures were rare, presumably due to the animals' ability to shelter in burrows during drought where they were more difficult to detect. Some of the undetected tortoises had neither died nor emigrated as demonstrated by the fact that once rain returned, 73% of recaptures made on animals that had not been captured for >1 year were made within 300 m and 22% within 100 m of their previously known location. Site fidelity is also supported by our low estimate of the probability of movement from one side of the plot to the other (0.12).

Our study is the only detailed survivorship investigation to examine data from over a generation time for free-living *G. agassizii* (see also Medica et al., 2012 for survival of semi-wild tortoises in an enclosed habitat), providing a long-term perspective on mortality rates. That the effect can best be observed over a multi-decadal time span is not unexpected as tortoises of many species are

often able to buffer the effects of environmental variation over shorter time periods with relatively large body size and longevity (Blake et al., 2012), low metabolism (Peterson, 1994b), behavioral modifications such as remaining in burrows and retaining wastes (McCoy et al., 2011), and an ability to tolerate anhomeostasis (Henen et al., 1998; Peterson, 1996).

However, short-term research projects occasionally document drought-induced tortoise mortality events, due in large measure to the serendipitous timing of those studies relative to drought cycles. Significant mortality events, attributed to drought-induced physiological stress resulting from dehydration and starvation, are well-documented at various locations across the ranges of the two species of desert tortoises (Berry et al., 2002; Longshore et al., 2003; Peterson, 1994a). All previously reported events of high adult tortoise mortality occurred in relatively dry years (Peterson, 1994a). Collectively, this research shows the important effect of drought duration to tortoise survivorship. After 2–3 years of drought and low germination of food plants, tortoise populations experience die offs, a finding reflected in the results we observed using three year moving average winter precipitation as a determinant of survival. Drought conditions also affect desert tortoise populations with decreased reproductive output (Lovich et al., 1999) and changes in clutch phenology (Lovich et al., 2012), both of which can affect populations.

Other long-term studies show similar effects of drought on tortoise populations (Medica et al., 2012). Drought severity reduced survival in 15 populations of *G. morafkai* in Arizona from 1987 to 2008, a time period broadly coincident with our 1991–2012 studies. The effect of drought was greatest for populations in the most arid regions, especially those closest to our study site (Zylstra et al., 2012). Periods of low precipitation and higher tortoise mortality they noted coincided with ours.

Interestingly, despite their common name, Agassiz's desert tortoises are not necessarily well-adapted to the desert environment, but rather appear to possess exaptations acquired from their distant ancestors that allow them to tolerate arid ecosystems. Modern desert conditions developed only during the most recent 1% of the evolutionary history of *G. agassizii* as a distinct species (Morafka and Berry, 2002) and this scenario may explain their sensitivity to persistent drought. In turn, the phenomenon of persistent drought tied to large mortality events has been advanced to explain the patchy and fragmented distribution of *G. agassizii* through its influence on population persistence (Morafka, 1994).

Although our research, and that of others, demonstrates that changes in apparent survivorship of desert tortoises are strongly associated with variation in winter precipitation, drought is not the only possible explanation for mortality. Disease has been implicated as a factor in the decline of tortoise populations (Berry et al., 2006) and the one tortoise we found with symptoms of URTD suggests that disease is present on the Plot. One of us (Freilich, pers. obs.) rarely observed symptoms consistent with disease during his surveys. However, in the period from 1997 to 1999 we observed a small number of tortoises with URTD symptoms. This may explain the decline in apparent survival observed after 1997 (Fig. 2). It is also possible that there is a synergistic interaction between drought and disease in *G. agassizii*. Lederle et al. (1997) observed that in above average rainfall years, a lower percentage of tortoises show symptoms of URTD. Thus, it is possible that drought-induced stress lowers the resistance of tortoises to infection (Peterson, 1994a).

It is also possible that some of the mortality experienced by the tortoise population was caused by Black Eagle Mine Road. Roads are known to contribute to tortoise mortality (von Seckendorff Hoff and Marlow, 2002) and population density effects so it is possible that some of the tortoises that were marked and never relocated were killed by vehicle strikes and consumed, or carried off by

predators without our knowledge. Maintained dirt roads like Black Eagle Mine Road also increase the probability of tortoise detection by passing motorists and this can lead to increased illegal collection of these popular animals (Grandmaison and Frary, 2012), another source of “mortality” that we could not detect.

Tortoise predators include coyotes and other desert carnivores (Ernst and Lovich, 2009; Medica et al., 2012) and they may be responsible for elevated mortality rates in drought years (Esque et al., 2010). Predation also appeared to play a role in mortality at the Plot, but 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 the Plot from 1997 to 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.

There can be synergistic interactions between predators, prey species and precipitation. Small mammal prey species of desert carnivores are known to fluctuate with rainfall and annual plant biomass, skipping reproduction in dry years sometimes with an annual lag effect (Beatley, 1969; Chew and Butterworth, 1964). Woodbury and Hardy (1948) may have been the first to notice that predation rates on *G. agassizii* covary with the abundance of rabbits (*Sylvilagus audubonii* and *Lepus californicus*), major prey items (as are rodents) of coyotes and other carnivores in the range of the tortoise. Later, Peterson (1994a) elaborated their observation by suggesting that drought contributed indirectly to increased mortality in *G. agassizii* populations because it triggered “prey switching” by predators. When “typical” desert carnivore prey populations (rabbits and rodents) decline due to the effect of reduced precipitation and the concomitant reduction in annual plant germination, predators may shift their hunting to tortoises and other species. A similar conclusion was offered to explain rangewide declines of *G. agassizii* in the Mojave Desert during a drought period in 2006 and 2007 (Esque et al., 2010) but the authors pointed out that future studies should include rigorous quantification of the prey base.

5. Conclusions

It appears that the Agassiz's desert tortoise population at the Plot has declined rapidly since 1996 and that the decline is related to the effects of persistent drought and its possible interaction with predation rate on tortoises by mammalian carnivores. Still, our most recent survey in 2012 was conducted in a year when estimated winter precipitation was low enough to make detection of tortoises difficult, (Duda et al., 1999; Freilich et al., 2000) but not impossible, as shown by the fact that we found tortoises. The decline in apparent survivorship appeared after 1996, even continuing through the El Niño year of 1998 when germination on the Plot was extensive. That year saw extensive flowering of annual plants on the Plot, including desert dandelion (*Malacothrix glabrata*), an important food plant for tortoises (Oftedal, 2002). Despite the productive conditions, estimated capture probability in 1998 was low (Fig. 3) underscoring the likelihood that the decline we observed was real and not due to sampling problems in what would otherwise be predicted to be a good year for finding tortoises.

Deaths of desert tortoises due to drought are considered natural to the extent that they are not influenced by anthropogenically-induced climate change. The same can be said for predation and disease if they are under natural regulation. In the case of predation, several predators of desert tortoises (ravens and coyotes) actually benefit from human subsidies including garbage and artificial water sources (Boarman, 2003; Boarman et al., 2006; Esque et al.,

2010). In addition, incidence of disease increases in tortoises with proximity to concentrations of human activity (Berry et al., 2006) while survivorship shows an inverse relationship (Zylstra et al., 2012). At our study site, human effects on the environment are limited, especially since the area is designated as Wilderness with additional protections. However, consistent, and perhaps increasing, human access to the area is facilitated by the Black Eagle Mine Road. We found ample evidence of recent human activity on the Plot.

Of additional concern is the fact that modeling the potential effects of increasing temperatures (+2 °C) and decreasing annual precipitation (−5 cm) under a projected climate change scenario suggests that the Plot will be unsuitable for desert tortoise populations if these changes occur (Barrows, 2011). Given the high velocity of climate change in desert ecosystems (Loarie et al., 2009) such a scenario is not implausible. There is increasing evidence that the southwest United States is experiencing protracted dryness (Seager et al., 2007) and increasing temperatures (Weiss and Overpeck, 2005). Depleted soil moisture events (derived from a Variable Infiltration Capacity hydrological model) occur for durations of 4–10 years, based on the available historical record, but climate simulations into the 21st century suggest they might increase to durations of 12 years or more (Cayan et al., 2010).

Over a decade ago, a review of the effects of global warming concluded that the anomalous climate of the last century had already affected the physiology, distribution and phenology of some species (Hughes, 2000), and evidence continues to grow in support of that conclusion (Sinervo et al., 2010). It is possible that our results provide evidence of an early signal of the projected response of Agassiz's desert tortoise populations to increasing frequency and persistence of drought. On the other hand, the 1960s and 1970s appeared to be relatively dry and the population survived through those years, increasing dramatically during later periods of greater precipitation. However, if drought duration and frequency increase, they will likely have wider and more significant impacts on Agassiz's desert tortoise survivorship, particularly in the low Sonoran Desert portion of their range in California (Barrows, 2011), and it will be difficult or impossible for resource managers to mitigate their effects.

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References

- Anderson, D.R., Burnham, K.P., Lubow, B.C., Thomas, L., Corn, P.S., Medica, P.A., Marlow, R.W., 2001. Field trials of line transect methods applied to estimation of desert tortoise abundance. *Journal of Wildlife Management* 65, 583–597.
- Averill-Murray, R.C., Martin, B.E., Bailey, S.J., Wirt, E.B., 2002a. Activity and Behavior of the Sonoran Desert Tortoise in Arizona. University of Arizona Press and the Arizona-Sonorora Desert Museum, Tucson.
- Averill-Murray, R.C., Woodman, A.P., Howland, J.M., 2002b. Population Ecology of the Desert Tortoise in Arizona. University of Arizona Press and the Arizona-Sonorora Desert Museum, Tucson.
- Bacon, K.T., Fesnock, A.L., 2005. Long-term population monitoring of desert tortoises at the Barrow Site, Joshua Tree National Park. In: Unpublished Report, Joshua Tree National Park. pp. 1–13.
- Barrow, J., 1979. Aspects of ecology of the desert tortoise *Gopherus agassizi*. In: Joshua Tree National Monument, Pinto Basin, Riverside County, California. Proc. Symp. Desert Tortoise Council, pp. 105–131.
- Barrows, C.W., 2011. Sensitivity to climate change for two reptiles at the Mojave–Sonoran Desert interface. *Journal of Arid Environments* 75, 629–635.
- Beatley, J.C., 1967. Survival of winter annuals in the Northern Mojave Desert. *Ecology* 48, 745–750.
- Beatley, J.C., 1969. Dependence of Desert Rodents on Winter annuals and precipitation. *Ecology* 50, 721–724.
- Beatley, J.C., 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55, 856–863.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15, 365–377.
- Berry, K.H., 1986. Incidence of gunshot deaths in desert tortoise populations in California. *Wildlife Society Bulletin* 14, 127–132.
- Berry, K.H., Bailey, T.Y., Anderson, K.M., 2006. Attributes of desert tortoise populations at the National Training Center, central Mojave Desert, California, USA. *Journal of Arid Environments* 67, 165–191.
- Berry, K.H., Christopher, M.M., 2001. Guidelines for the field evaluation of desert tortoise health and disease. *Journal of Wildlife Diseases* 37, 427–450.
- Berry, K.H., Spangenberg, E.K., Homer, B.L., Jacobson, E.R., 2002. Deaths of desert tortoises following periods of drought and research manipulation. *Chelonian Conservation and Biology* 4, 436–448.
- Blake, S., Yackulic, C.B., Cabrera, F., Tapia, W., Gibbs, J.P., Kümmeth, F., Wikelski, M., 2012. Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients. *Journal of Animal Ecology* (n/a–n/a).
- Boarman, W.I., 2003. Managing a subsidized predator population: reducing common raven predation on desert tortoises. *Environmental Management* 32, 205–217.
- Boarman, W.I., Patten, M.A., Camp, R.J., Collis, S.J., 2006. Ecology of a population of subsidized predators: common ravens in the central Mojave Desert, California. *Journal of Arid Environments* 67, 248–261.
- Bowers, J.E., 2007. Has climatic warming altered spring flowering date of Sonoran Desert shrubs? *The Southwestern Naturalist* 52, 347–355.
- Brown, J.H., Valone, T.J., Curtin, C.G., 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences* 94, 9729–9733.
- Burnham, K.P., Anderson, D.R., 1998. *Model Selection and Inference: A Practical Information – Theoretic Approach*. Springer-Verlag, New York.
- Bury, R.B., Corn, P.S., 1995. Have desert tortoises undergone a long-term decline in abundance? *Wildlife Society Bulletin* 23, 41–47.
- Cagle, F.R., 1939. A system of marking turtles for future identification. *Copeia* 1939, 170–173.
- Callahan, J.T., 1984. Long-term ecological research. *BioScience* 34, 363–367.
- Cayan, D.R., Das, T., Pierce, D.W., Barnett, T.P., Tyree, M., Gershunov, A., 2010. Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences* 107, 21271–21276.
- Cayan, D.R., Kammerdiener, S.A., Dettinger, M.D., Caprio, J.M., Peterson, D.H., 2001. Changes in the Onset of Spring in the Western United States. *Bulletin of the American Meteorological Society*, 399–415.
- Chew, R.M., Butterworth, B.B., 1964. Ecology of rodents in Indian cove (Mojave desert), Joshua tree national monument, California. *Journal of Mammalogy* 45, 203–225.
- Congdon, J.D., Dunham, A.E., Van Loben Sels, R.C., 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7, 826–833.
- Congdon, J.D., Dunham, A.E., van Loben Sels, R.C., 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *American Zoologist* 34, 397–408.
- Corn, P.S., 1994. Recent trends of desert tortoise populations in the Mojave Desert, In: *Biology of North American Tortoises*. In: Bury, R.B., Germano, D.J. (Eds.), United States Department of the Interior, National Biological Survey. Fish and Wildlife Research, vol. 3, pp. 85–93.
- Curtin, A.J., Zug, G.R., Spotila, J.R., 2009. Longevity and growth strategies of the desert tortoise (*Gopherus agassizii*) in two American deserts. *Journal of Arid Environments* 73, 463–471.
- Doak, D., Kareiva, P., Klepetka, B., 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. *Ecological Applications* 4, 446–460.
- Dodd Jr., C.K., 1995. Disarticulation of turtle shells in north-central Florida: how long does a shell remain in the woods. *American Midland Naturalist* 134, 378–387.
- Duda, J., Krzysik, A.J., Freilich, J.E., 1999. Effects of drought on desert tortoise movement and activity. *Journal of Wildlife Management* 63, 1181–1192.

- Edwards, T., Schwalbe, C., Swann, D., Goldberg, C., 2004. Implications of anthropogenic landscape change on inter-population movements of the desert tortoise (*Gopherus agassizii*). *Conservation Genetics* 5, 485–499.
- Ennen, J.R., Meyer, K., Lovich, J., 2012. Female *Agassiz's* desert tortoise activity at a wind energy facility in southern California: the influence of an El Niño event. *Natural Science* 4, 30–37.
- Ernst, C.H., Lovich, J.E., 2009. *Turtles of the United States and Canada*, Second ed. Johns Hopkins University Press, Baltimore.
- Esque, T.C., Nussear, K.E., Drake, K.K., Walde, A.D., Berry, K.H., Averill-Murray, R.C., Woodman, A.P., Boarman, W.I., Medica, P.A., Mack, J., Heaton, J.S., 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. *Endangered Species Research* 12, 167–177.
- Freilich, J.E., Burnham, K.P., Collins, C.P., Garry, C.A., 2000. Factors affecting population assessments of desert tortoises. *Conservation Biology* 14, 1479–1489.
- Freilich, J.E., LaRue Jr., E.L., 1998. Importance of observer experience in finding desert tortoises. *J. Wildlife Manage.* 62, 590–596.
- Germano, D.J., 1992. Longevity and age size relationships of populations of desert tortoises. *Copeia* 1992, 367–374.
- Germano, D.J., 1994. Growth and age at maturity of North American tortoises in relation to regional climates. *Canadian Journal of Zoology* 72, 918–931.
- Germano, D.J., Bury, R.B., 1994. Research on North American tortoises: a critique with suggestions for the future. In: Bury, R.B., Germano, D.J. (Eds.), *National Biological Survey, Fish and Wildlife Research*, 13.
- Grandmaison, D.D., Frary, V.J., 2012. Estimating the probability of illegal desert tortoise collection in the Sonoran Desert. *The Journal of Wildlife Management* 76, 262–268.
- Griffiths, R.A., Sewell, D., McCrear, R.S., 2010. Dynamics of a declining amphibian metapopulation: survival, dispersal and the impact of climate. *Biological Conservation* 143, 485–491.
- Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* 142, 14–32.
- Henen, B.T., Peterson, C.C., Wallis, I.R., Berry, K.H., Nagy, K.A., 1998. Effects of climatic variation on field metabolism and water relations of desert tortoises. *Oecologia* 117, 365–373.
- Hobbie, J.E., Carpenter, S.R., Grimm, N.B., Gosz, J.R., Seastedt, T.R., 2003. The US long term ecological research program. *BioScience* 53, 21–32.
- Homer, B.L., Berry, K.B., Brown, M.B., Ellis, G., Jacobson, E.R., 1998. Pathology of diseases in wild desert tortoises from California. *Journal of Wildlife Diseases* 34, 508–523.
- Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15, 56–61.
- Ihlow, F., Dambach, J., Engler, J.O., Flecks, M., Hartmann, T., Nekum, S., Rajaei, H., Rödder, D., 2012. On the brink of extinction? How climate change may affect global chelonian species richness and distribution. *Global Change Biology* (n/a–n/a).
- Karl, A.E., 1988. Investigations of the status of the desert tortoise, *Gopherus agassizii*, in Joshua Tree National Monument, In Cooperative National Park Resources Studies Unit, University of Nevada, Las Vegas. Report number 040/02. pp. 1–61 + Appendices.
- King, N.E., Argus, D., Langbein, J., Agnew, D.C., Bawden, G., Dollar, R.S., Liu, Z., Galloway, D., Reichard, E., Yong, A., Webb, F.H., Bock, Y., Stark, K., Barseghian, D., 2007. Space geodetic observation of expansion of the San Gabriel Valley, California, aquifer system, during heavy rainfall in winter 2004–2005. *Journal of Geophysical Research* 112, B03409.
- Knowles, N., Dettlinger, M.D., Cayan, D.R., 2006. Trends in snowfall versus rainfall in the Western United States. *Journal of Climate* 19, 4545–4559.
- Lederle, P.E., Rautenstrauch, K.R., Rakestraw, D.L., Zander, K.K., Boone, J.L., 1997. Upper respiratory tract disease and mycoplasmosis in desert tortoises from Nevada. *Journal of Wildlife Diseases* 33, 759–765.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. *Nature* 462, 1052–1055.
- Longshore, K.M., Jaeger, J.R., Sappington, J.M., 2003. Desert tortoise (*Gopherus agassizii*) survival at two eastern Mojave Desert sites: death by short-term drought? *Journal of Herpetology* 37, 169–177.
- Lovich, J., Agha, M., Meulblok, M., Meyer, K., Ennen, J., Loughran, C., Madrak, S., Bjurlin, C., 2012. Climatic variation affects clutch phenology in *Agassiz's* desert tortoise *Gopherus agassizii*. *Endangered Species Research* 19, 63–74.
- Lovich, J.E., Bainbridge, D., 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. *Environmental Management* 24, 309–326.
- Lovich, J.E., Beaman, K.R., 2007. A history of Gila Monster (*Heloderma suspectum cinctum*) records from California with comments on factors affecting their distribution. *Bulletin, Southern California Academy of Sciences* 106, 39–58.
- Lovich, J.E., Ennen, J.R., Madrak, S., Meyer, K., Loughran, C., Bjurlin, C., Arundel, T., Turner, W., Jones, C., Groenendaal, G.M., 2011. Effects of wind energy production on growth, demography, and survivorship of a Desert Tortoise (*Gopherus agassizii*) population in Southern California with comparisons to natural populations. *Herpetological Conservation and Biology* 6, 161–174.
- Lovich, J.E., Medica, P., Avery, H., Meyer, K., Bowser, G., Brown, A., 1999. Studies of reproductive output of the desert tortoise at Joshua Tree National Park, the Mojave National Preserve, and comparative sites. *Park Science* 19, 22–24 (Reprinted in *Tortuga Gazette* [Newsletter of the California Turtle and Tortoise Club] 1999, 35(7), pp. 1–2, 4).
- Magnuson, J.J., 1990. Long-term ecological research and the invisible present. *BioScience* 40, 495–501.
- McCoy, E.D., Moore, R.D., Mushinsky, H.R., Popa, S.C., 2011. Effects of rainfall and the potential influence of climate change on two congeneric tortoise species. *Chelonian Conservation and Biology* 10, 34–41.
- McDonald, T.L., Amstrup, S.C., Regehr, E.V., Manly, B.F., 2005. Examples. In: Amstrup, S.C., McDonald, T.L., Manly, B.F. (Eds.), *Handbook of Capture–recapture Analysis*. Princeton University Press, Princeton, p. 241.
- Medica, P.A., Greger, P.D., 2009. *Gopherus agassizii* (desert tortoise). Predation by mountain lion. *Herpetological Review* 40, 75–77.
- Medica, P.A., Lyons, C.L., Turner, F.B., 1986. “Tapping”: a technique for capturing tortoises. *Herpetological Review* 17, 15–16.
- Medica, P.A., Nussear, K.E., Esque, T.C., Saethre, M.B., 2012. Long-term growth of desert tortoises (*Gopherus agassizii*) in a Southern Nevada population. *Journal of Herpetology* 46, 213–220.
- Morafka, D.J., 1994. Neonates: missing links in the life histories of North American tortoises. In: Bury, R.B., Germano, D.J. (Eds.), *Biology of North American Tortoises*. United States Department of the Interior, National Biological Survey. *Fish and Wildlife Research*, vol. 13, pp. 161–173.
- Morafka, D.J., Berry, K.H., 2002. Is *Gopherus agassizii* a desert-adapted tortoise, or an exaptive opportunist? Implications for tortoise conservation. *Chelonian Conservation and Biology* 4, 263–287.
- Morris, W.F., Pfister, C.A., Tuliapurkar, S., Haridas, C.V., Boggs, C.L., Boyce, M.S., Bruna, E.M., Don, R.C., Coulson, T., Doak, D.F., Forsyth, S., Gaillard, J.-M., Horvitz, C.C., Kalisz, S., Kendall, B.E., Knight, T.M., Lee, C.T., Menges, E.S., 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89, 19–25.
- Murphy, G.I., 1968. Pattern in life history and the environment. *The American Naturalist* 102, 391–403.
- Neil Arnason, A., 1972. Parameter estimates from mark–recapture experiments on two populations subject to migration and death. *Researches on Population Ecology* 13, 97–113.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25–51.
- Oftedal, O.T., 2002. *Nutritional Ecology of the Desert Tortoise in the Mohave and Sonoran Deserts*. University of Arizona Press and The Arizona-Sonora Desert Museum, Tucson.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Peterson, C.C., 1994a. Different rates and causes of high mortality in two populations of the threatened desert tortoise *Gopherus agassizii*. *Biological Conservation* 70, 101–108.
- Peterson, C.C., 1994b. Physiological ecology of the desert tortoise, *Xerobates agassizii*. In: Brown, P.R., Wright, J.W. (Eds.), *Herpetology of the North American Deserts*. Southwestern Herpetological Society, pp. 213–225.
- Peterson, C.C., 1996. Anhomeostasis: seasonal water and solute relations in two populations of the desert tortoise (*Gopherus agassizii*) during chronic drought. *Physiological Zoology* 69, 1324–1358.
- Riedle, J.D., Averill-Murray, R.C., Grandmaison, D.D., 2010. Seasonal variation in survivorship and mortality of desert tortoises in the Sonoran Desert, Arizona. *Journal of Herpetology* 44, 164–167.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60.
- Schaffer, W.M., 1974. Optimal reproductive effort in fluctuating environments. *The American Naturalist* 108, 783–790.
- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A., Lau, N.-C., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181–1184.
- Service, U.S.F.a.W., 1990. *Desert Tortoise (Mojave population) Recovery Plan*. (73 pp. + appendices).
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Rocha, C.F.D., Ibarguengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., Sites, J.W., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899.
- Stober, J.M., Smith, L.L., 2010. Total counts versus line transects for estimating abundance of small gopher tortoise populations. *Journal of Wildlife Management* 74, 1595–1600.
- Stott, P.A., Tett, S.F.B., Jones, G.S., Allen, M.R., Mitchell, J.F.B., Jenkins, G.J., 2000. External control of 20th century temperature by natural and anthropogenic forcings. *Science* 290, 2133–2137.
- Swann, D.E., Averill-Murray, R.C., Schwalbe, C.R., 2002. Distance sampling for Sonoran Desert tortoises. *Journal of Wildlife Management* 66, 969–975.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Zagarodnov, V.S., Howat, I.M., Mikhailenko, V.N., Lin, P.-N., 2013. Annually resolved ice core records of tropical climate variability over the past ~1800 years. *Science* 2, 1–5.
- Tinkle, D.W., 1979. Long-term field studies. *BioScience* 29, 717.

- Turner, R.M., 1990. Long-term vegetation change at a fully protected sonoran desert site. *Ecology* 71, 464–477.
- van Loben Sels, R.C., Congdon, J.D., Austin, J.T., 1997. Life history and ecology of the Sonoran mud turtle (*Kinosternon sonoriense*) in southeastern Arizona: a preliminary report. *Chelonian Conservation and Biology* 2, 338–344.
- Vieites, D.R., Min, M.-S., Wake, D.B., 2007. Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. *Proceedings of the National Academy of Sciences* 104, 19903–19907.
- von Seckendorff Hoff, K., Marlow, R.W., 2002. Impacts of vehicle road traffic on desert tortoise populations with consideration of conservation of tortoise habitat in southern Nevada. *Chelonian Conservation and Biology* 4, 449–456.
- Walther, G.-R., 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 2019–2024.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Weiss, J.L., Overpeck, J.T., 2005. Is the Sonoran Desert losing its cool? *Global Change Biology* 11, 2065–2077.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US Forest wildfire activity. *Science* 313, 940–943.
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego.
- Willis, C.G., Ruhfel, B., Primack, R.B., Miller-Rushing, A.J., Davis, C.C., 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences* 105, 17029–17033.
- Woodbury, A.M., Hardy, R., 1948. Studies of the desert tortoise, *Gopherus agassizii*. *Ecological Monographs* 18, 145–200.
- Woodman, A.P., Berry, K.H., 1984. A description of carcass deterioration for the desert tortoise and a preliminary analysis of disintegration rates at two sites in the Mojave Desert, California. In: Berry, K.H. (Ed.), *The Status of the Desert Tortoise (Gopherus agassizii) in the United States*. Desert Tortoise Council Rep. to the US Fish and Wildl. Serv. on Purchase Order No. 11310-0083-81. pp. A6-1–A6-31.
- Zylstra, E., Steidl, R., Jones, C., Averill-Murray, R., 2012. Spatial and temporal variation in survival of a rare reptile: a 22-year study of Sonoran desert tortoises. *Oecologia*, 1–10.