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# Precipitation quantity and timing affect native plant production and growth of a key herbivore, the desert tortoise, in the Mojave Desert

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## Abstract

**Background:** Deserts may be disproportionately vulnerable to changes in precipitation that accompany global climate change due to complex evolutionary relationships of species to historical conditions. Based on current and projected climate scenarios for the southwestern United States, we manipulated rainfall timing and quantity and measured the response by plants and the growth and behavior of the desert tortoise (*Gopherus agassizii*) to precipitation in the eastern Mojave Desert.

**Results:** We found that winter-dominant rain – the current prevailing pattern in the eastern Mojave Desert – and greater total rainfall correlated with greater cover and species richness of plants. Winter-dominant rain also correlated with a higher proportion of native plants flowering relative to invasive plants. Juvenile tortoises grew more rapidly when they were subjected to rainfall treatments that associated with increased plant abundance and species richness, while their behavior appeared more driven by water availability.

**Conclusions:** Our results suggest that precipitation timing may be as important as rainfall quantity when considering total effects of climate change on arid-adapted systems. Further research should explore how the timing of rainfall may interact with aridity or temperature to influence total effects due to climate change on arid communities.

**Keywords:** Activity, Arid ecosystems, *Gopherus agassizii*, Rainfall, Trophic levels

## Background

In terrestrial systems, temperature and moisture are among the most important drivers of productivity [1]. Water availability can affect many aspects of ecological communities, from primary productivity to activity patterns in wildlife [1, 2]. Through the effects of rainfall on reproduction and recruitment, precipitation patterns can influence population structure and inter- and intra-species interactions [3, 4]. In arid ecosystems, where water is the primary limiting factor for most species [5], community structure may be particularly susceptible to perturbations in precipitation. Inhabitants of arid regions

have life histories and behaviors that are often tightly coupled to the prevailing conditions for which they are adapted. Xeric plants, for example, have physiological traits that prevent germination until narrow hydric and thermal conditions are met [6, 7]. As a result, precipitation strongly affects plant productivity seasonally and annually in arid environments [7, 8], which in turn affects herbivore populations [9]. Water-limited ecosystems are thus potentially useful models for studying effects of climate-mediated alterations of precipitation on ecological communities.

Southwestern North America has been identified as a regional climate change hotspot, which is an area that will show some of the greatest response to climate change [10, 11]. Climate projections for the southwest generally predict mean increases in annual temperature and increasing aridity [12, 13]. Precipitation patterns are

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also expected to become increasingly variable, with frequent and longer droughts and possible shifts from winter- to spring-dominant rainfall [10, 12]. Both total rainfall and the timing of rainfall are expected to change under future climate scenarios.

Abundant winter rainfall is linked to growth and reproduction in many vertebrates of southwestern North America, including rodents, lizards, and tortoises [9, 14, 15]. Arid-adapted animals can supplement their water intake by foraging on plants [16, 17], but germination of winter annuals also depends on adequate winter precipitation [18]. Thus, droughts are likely to co-occur with food shortages, thereby negatively affecting growth rates and causing other demographic effects [19, 20]. Among Agamid lizards, for example, wet years were associated with increased vegetation that resulted in community interactions that increased lizard populations [21]. Reduced precipitation or a loss of winter rain may cumulatively affect vertebrate populations through negative effects on growth and recruitment or changes in community interactions.

Ectotherms and long-lived species appear to be particularly sensitive to changing climate conditions [22–24]. Prolonged droughts or exposure to extreme heat can cause high mortality [25, 26], to which populations with low intrinsic growth rates are especially susceptible [27]. We used the Mojave desert tortoise (*Gopherus agassizii*) – a long-lived ectothermic herbivore native to the Mojave Desert – to examine potential effects of climate-mediated changes in precipitation on species in arid systems. Desert tortoises obtain much of their annual energy budget from short, intensive foraging seasons during the spring and late summer when seasonal plants flower and fruit [15, 28]. Outside of those seasons or during droughts, tortoises must withstand prolonged resource scarcity [2, 29], relying on behavioral and physiological traits to survive [2, 30, 31]. Overall, the natural history and ecology of desert tortoises are closely tied to rainfall—see Ernst and Lovich [32] for an extensive review.

Here, we artificially modified precipitation patterns in natural enclosures. We measured productivity of winter annuals and herbaceous perennials in response to four rainfall treatments. We concurrently measured growth and activity of the desert tortoises in the treatment pens. Demographic and population changes are critical indicators of climate response [33]. Although precipitation likely affects multiple life stages and aspects of life history, ranging from reproductive success to adult mortality [26, 34], these data can be difficult to obtain for long-lived species. Juvenile tortoises, however, can experience rapid, resource-dependent growth that is tied to rainfall [15, 35]. Survival and recruitment of juvenile tortoises also affects population persistence [36]. We thus focused on juvenile growth as a proxy for

understanding possible demographic responses to altered climate because, it responds more quickly to changing resources and habitat quality than many other demographic metrics [37]. Desert tortoises also exhibit behavioral plasticity, which allow them to alter metabolic expenditures based on water availability [2]. Thus, by measuring tortoise activity in addition to growth, we studied behavioral plasticity that may reduce challenges posed by future climate scenarios. The primary objective of this study was to measure whether rainfall quantity and timing could each affect plant productivity and herbivore growth. Secondarily, we sought to determine whether tortoises can mitigate for different precipitation patterns through behavioral plasticity. Although we measured both juvenile tortoise growth and response of annuals and herbaceous perennials to precipitation, this study was not designed to measure foraging patterns of desert tortoises or long-term changes in vegetative structure.

## Methods

### Study site

We used two outdoor enclosures divided into nine pens (each pen was 81 m<sup>2</sup>) that were open to natural conditions. Enclosures excluded predators of juvenile desert tortoises, including ravens, coyotes, and ground squirrels. The enclosures were located at the Ivanpah Desert Tortoise Research Facility (IDTRF), which is a “head-starting” facility in which juvenile tortoises are temporarily reared in captivity. IDTRF is located in the northeastern portion of Mojave National Preserve at an elevation of 900 m (35° 27'0 N, 115°23'2 W CA, USA). Maximum annual rainfall across the Mojave Desert for elevations below 1,000 m rarely exceeds 250 mm/year (typically 90 – 120 mm/year), but the Mojave Desert is characterized by extremely high inter-annual and spatial variation [38]. Ivanpah Valley is situated east of 117°W meridian and experiences a bimodal precipitation pattern that can be categorized into autumn-winter-spring (“cool-season”; October–April/May) and summer (“warm-season”; July–September) rainfall [7, 39]. Although warm-season rainfall is often of high intensity, much of the biological activity in the Mojave Desert is generally believed to occur during the cool-season [7].

### Rainfall and supplemental treatments

Our experimental treatments supplemented natural rainfall using an aquifer-fed sprinkler system. Rain treatments were supplemental in order to meet the conservation objectives of the larger head-start project, which was an experimental program aimed at improving juvenile desert tortoise survival and recruitment. Due to the presence of cool-season rainfall across the Mojave and its importance for biological activity [7, 39], we focused our supplemental water treatments on rainfall during the cool-season. We

divided cool-season precipitation into two, 4-month periods: 1) winter (October-January) and 2) spring (February-May) rain. Over two years, we measured the effect of rainfall quantity and timing on seasonal plants and juvenile tortoises. To do so, we assigned one enclosure as ‘LOW’ (9 pens) and one as ‘HIGH’ (9 pens) rain treatments. We watered HIGH enclosures with sprinklers twice as often as LOW enclosures (Table 1) from October 2011 – May 2013. We exaggerated the natural ratio of winter-to-spring, cool-season precipitation between years to measure the effects of precipitation timing. The LOW and HIGH treatments were nested within two seasonal treatments. The “spring-dominant” treatment received 30% of cool-season supplemental rain during October–January, with the remaining 70% added during February–May. The “winter-dominant” treatment, in contrast, received 65% of cool season supplemental rain during October–January, with the remaining 35% added during February–May. We conducted timing treatments across two years due to logistical constraints (Table 1). Total differences between the seasonal rainfall treatments reflected natural variation over the two years of our study and the supplemental additions (Table 1). We calculated total supplemental rainfall by measuring the flow rate at sprinkler heads, which was 9.96 L/min. We then used the minutes watered to calculate the total amount of supplemented water added and converted that to mm of precipitation using the standard metric of 1 mm of rain is equal to 1 L/m<sup>2</sup>. We downloaded climate data from WestMap for the coordinates provided for IDTRF to calculate natural rainfall and mean annual temperatures at IDTRF during the two years of study, as well as an average for the 10 years leading up to the study for comparison to

historical patterns (October 2001 – September 2011). Natural rainfall at our study site likely varied from the downloaded data. However, the pens were confined to a <0.2 ha area and natural variance between pens should be negligible, such that treatments were the primary cause of differences in precipitation.

**Plant community**

Annually, we maintained three research enclosures without tortoises in each of the HIGH and LOW treatments to control for changes in the plant community that may have resulted from grazing by tortoises. We used these tortoise-free enclosures to quantify the response of winter annual and herbaceous perennial plants (hereafter plants), to rainfall (natural + supplemental) quantity and timing. In April 2012 and 2013, we collected data on flowering plants by dividing each enclosure into a grid of 1-m<sup>2</sup> plots. Within each enclosure, we randomly selected five plots each year, which represented approximately 6% of the area. We documented species richness of plants and visually estimated their ground cover (%) using a 1-m<sup>2</sup> quadrat frame subdivided into 20 x 20 cm cells. We also calculated the proportion of invasive species out of the total number of species documented in each plot.

Plant data were heteroskedastic and not normally distributed. Thus, we implemented generalized linear models with a Poisson distribution using the mean quadrat values for cover, species richness, and proportion of invasive species in each enclosure. We ran three separate models for each of the above three plant metrics: species richness, ground cover, and proportion of non-natives. For all three models, we included rainfall quantity and timing as fixed

**Table 1** Natural and supplemental rainfall distributions during the cool-season (October–May) rainfall treatments

	Spring-dominant rainfall (2011–2012)					Winter-dominant rainfall (2012–2013)				
	Natural	Supplemental				Natural	Supplemental			
		LOW	HIGH	LOW	HIGH		LOW	HIGH		
	mm	mm	%	mm	%	mm	mm	%	mm	%
OCT	16.0	14.8	19	29.5	19	17.3	14.8	21	29.5	21
NOV	11.9	1.2	8	2.5	6	0.0	14.8	10	29.5	13
DEC	17.3	1.2	11	2.5	8	27.4	7.4	22	14.8	18
JAN	1.3	1.2	1	2.5	2	17.0	7.4	16	14.8	14
FEB	4.1	11.1	9	22.1	11	6.1	7.4	9	14.8	9
MAR	16.0	14.8	19	29.5	19	6.1	7.4	9	14.8	9
APR	25.1	14.8	24	29.5	23	0.5	7.4	5	14.8	7
MAY	0.0	14.8	9	29.5	12	5.3	7.4	8	14.8	9
SUM		73.8		147.6		79.7	74.0		147.8	
Total	91.7	165.6		239.3		153.7			227.5	

The spring-dominant treatments occurred during autumn 2011 through spring 2012. Winter-dominant rainfall treatments occurred during autumn 2012 through spring 2013. Percentages show the total percentage of cool-season rain that fell in a given month, including natural and supplemental rain. Totals represent the total amount of cool-season rain, including natural and supplemental rain in each treatment. Natural rainfall was obtained from WestMap for coordinates 35° 27'0 N, 115°23'2 W at [http://www.cefa.dri.edu/Westmap/Westmap\\_home.php](http://www.cefa.dri.edu/Westmap/Westmap_home.php) on 17 March 2017

effects in the same model. We used program R version 3.1 [R Core Team (2013), Vienna, Austria], assessed significance at  $\alpha = 0.05$ , and we present descriptive statistics as mean ( $\pm 1$  SE).

### Tortoise growth

We obtained hatchling tortoises from free-ranging adult females approximately 12 km south of IDTRF. In May 2011 and 2012, we brought gravid females into separate nesting enclosures and released them after they laid eggs or 30 d had passed. Eggs incubated in nests that were constructed by their mothers. Beginning on 31 July 2011 and 2012, we searched for neonatal tortoises. We removed neonates and uniquely marked them with temporary non-toxic nail polish so that they could be distinguished without handling.

We assigned neonates to research enclosures in a stratified block design so that no more than one tortoise from a given mother resided in each enclosure. In September 2011, we divided 39 neonates among three LOW ( $n = 20$ ) and three HIGH ( $n = 19$ ) enclosures. In September 2012, we divided 48 neonates among three additional LOW ( $n = 24$ ) and HIGH ( $n = 24$ ) enclosures. We measured mid-line carapace length (MCL) of the neonates in September 2011 and 2012 and again in May 2012 and 2013 to determine growth rates during the first eight months post-hatching. During the winter and early spring of 2012, two carcasses were found and another four animals from the 2012 cohort were suspected to have died. Mortality largely occurred within clutches, was likely primarily a result of maternal resource allocation to offspring, and has previously been reported by Nafus et al. [40]. Treatments appeared to have negligible effects on mortality and thus mortality is not discussed further.

We examined the effect of rainfall treatment on tortoise growth rates using linear-mixed effect models in the 'nlme' package [41] in program R. We normalized tortoise growth data using square root transformations prior to analysis. We included rainfall quantity and timing as predictors in the same model and blocked tortoises by enclosure and by mother to account for possible enclosure or maternal effects. Maternal effects on growth and survival for the juveniles used in this study were previously reported by Nafus et al. [40]. To reduce blocking factors, loss of degrees of freedom, and to minimize the effects of prior experience (e.g. forage quality in the first year) and changes in growth rate across time, we avoided repeated measures of individuals across years. In other words, we only analyzed one 8-month growth period for each cohort of juvenile tortoises.

### Tortoise behavioral observations

We observed all juvenile tortoises in a pen for 30 consecutive minutes from 0700 to 1300 approximately

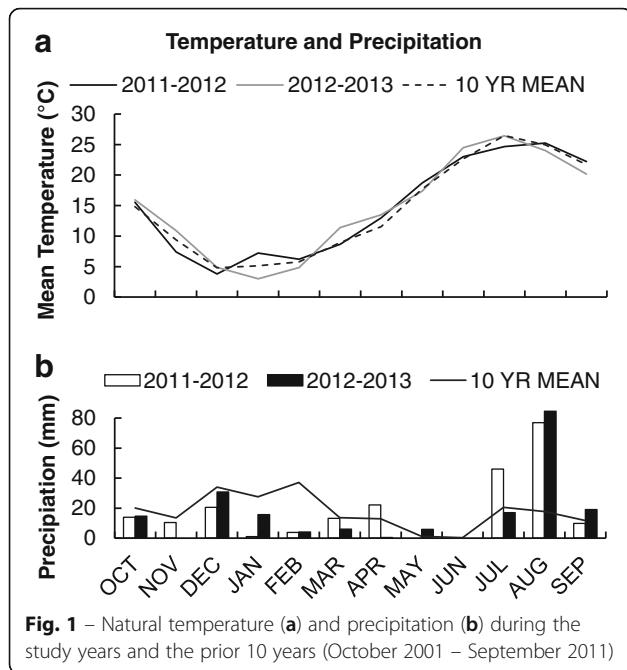
weekly from April–May 2012 and 2013, which yielded seven total observation periods for each enclosure (728 observations for 81 animals). We recorded the behavior of every animal in a pen as one of four categories: inactive (not visible, below ground), resting (visible and stationary in shade), basking (visible and stationary in sunlight), and foraging (biting, chewing, or walking) at 2-min intervals (16 behaviors per observation period). Desert tortoises are typically active during April and May, but activity tapers off rapidly in June as temperatures climb. We limited observations to air temperatures when adult tortoises are most active and discontinued observations when air temperatures exceeded 35 °C [42]. We measured shaded air temperature on a white surface approximately 0.5 m above ground at the beginning of each observation. We timed observations so as not to coincide with rainfall or watering, when tortoises emerge to drink.

To determine whether tortoise behavior differed based on rainfall treatments, we used a negative binomial logistic mixed-effect model in the 'lme4' package in R [43]. We quantified activity by calculating the percentage of the 30-min observation period that each animal spent active on the surface (resting, basking, and foraging). We included rainfall quantity, rainfall timing, and air temperature as fixed effects. Because we completed repeated observations of the same individuals across seven weeks, we included tortoise identity nested by enclosure and observation date as a random effect.

## Results

### Rainfall and supplemental treatments

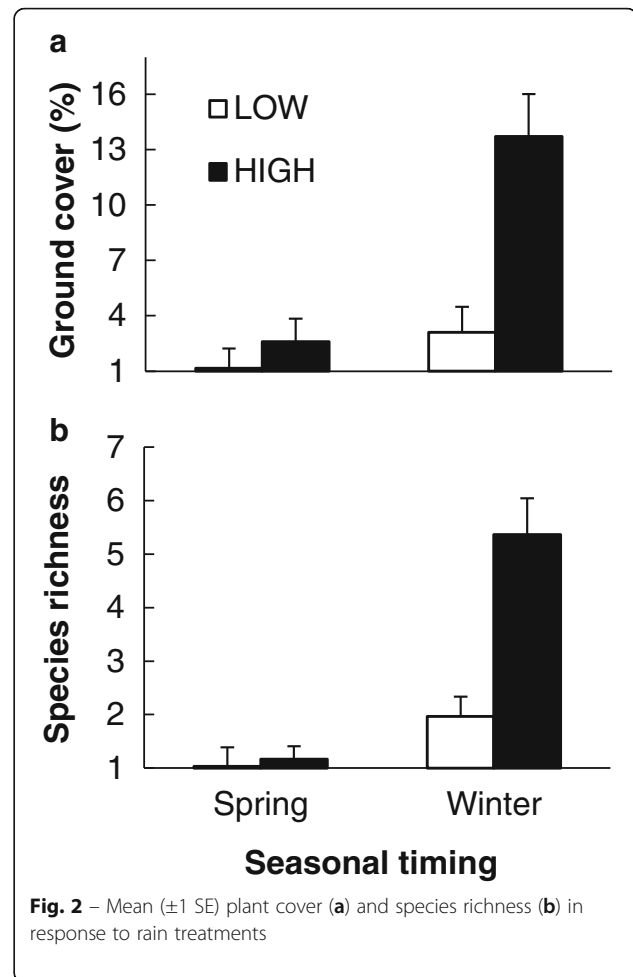
Mean monthly temperatures during the preceding decade tended to be cooler during winter months than during the study years. Mean annual temperature overall was similar across both study years (Fig. 1a). Natural annual rainfall between the two years differed by 7.3 mm during the cool season (October–May; Table 1) and by 19.5 mm overall (Fig. 1b), where 2012–2013 was naturally drier. Mean precipitation from October – May during 2001–2011 was 160 mm, which was 74 mm more than the minimum that occurred during our study years. Mean rainfall for the preceding 10 years showed greater total rainfall during cool-season months and less rainfall during warm-season months than the conditions observed during the period of study (Fig. 1b). During 2011–2012, 46.0 mm (54%) of natural rain that fell during the cool-season occurred during October–January (Table 1). During 2012–2013, 61.2 mm (79%) of natural rain that fell during the cool-season occurred during October–January (Table 1). Thus, cool-season rainfall was naturally winter-dominant during 2012–2013 and less so during 2011–2012; we accentuated this difference with our supplemental watering between years so that



38% of combined natural and supplemental rainfall fell during the winter of 2011–2012, compared with 68% during winter 2012–2013 (Table 1).

### Seasonal plant productivity and richness

All of the species observed to occur within the research enclosures were also detected within our vegetation plots. Average plant cover increased significantly with total rainfall ( $z = 4.3$ ,  $P < 0.001$ ,  $CI_{95} = 0.76, 2.04$ ), such that they covered an average of  $8 \pm 3\%$  (range: 1–18%) of HIGH treatment quadrats compared to only  $2 \pm 1\%$  (range: 0–5%) in LOW treatments. Average plant cover was also higher following the winter-dominant treatment ( $z = 4.5$ ,  $P < 0.001$ ,  $CI_{95} = 0.85, 2.17$ ), with the average cover increasing to  $8 \pm 1\%$  (range: 1–18%) from  $2 \pm 1\%$  (range: 0–5%) after the spring-dominant treatment, irrespective of total rainfall. Species richness also increased significantly with total rainfall ( $z = 2.0$ ,  $P = 0.04$ ,  $CI_{95} = 0.04, 1.92$ ), with an average of  $3 \pm 1$  (range: 1–7) species flowering in HIGH enclosures compared to  $1 \pm 0$  (range: 0–3) species in the LOW treatments. Species richness increased significantly during the winter-dominant treatment ( $z = 2.7$ ,  $P = 0.006$ ,  $CI_{95} = 0.40, 2.60$ ) to  $3 \pm 1$  species from  $< 1$  species on average during the spring-dominant treatment, irrespective of total rainfall. Plant cover and species richness had the greatest response to HIGH rainfall during the winter-dominant treatment, and the lowest response to LOW rainfall during the spring-dominant treatment (Fig. 2). See Additional file 1: Table S1 for a description of species encountered and their abundances based on seasonal rainfall treatment. In sum, species richness and cover by plants increased



with more rain, especially when the majority of rain occurred prior to February.

Two invasive species were documented to occur in the research enclosures: *Erodium cicutarium* (Red-stem filaree) and *Schismus barbatus* (Mediterranean grass). Although the proportion of invasive plant species correlated with precipitation, only rainfall timing was significant ( $z = 2.1$ ,  $P = 0.003$ ,  $CI_{95} = 0.23, 1.29$ ), whereas total rainfall was not ( $z = 1.1$ ,  $P = 0.25$ ,  $CI_{95} = -0.22, 0.53$ ). The proportion of invasive winter annuals decreased to  $38 \pm 6\%$  of species detected during the winter-dominant treatment compared to  $82 \pm 9\%$  of species during the spring-dominant treatment. This was especially true for the relative abundance of Mediterranean grass, which comprised over 60% of all individual plants encountered in the spring-dominant treatment compared to only 20% in the winter-dominant treatment (Additional file 1: Table S1).

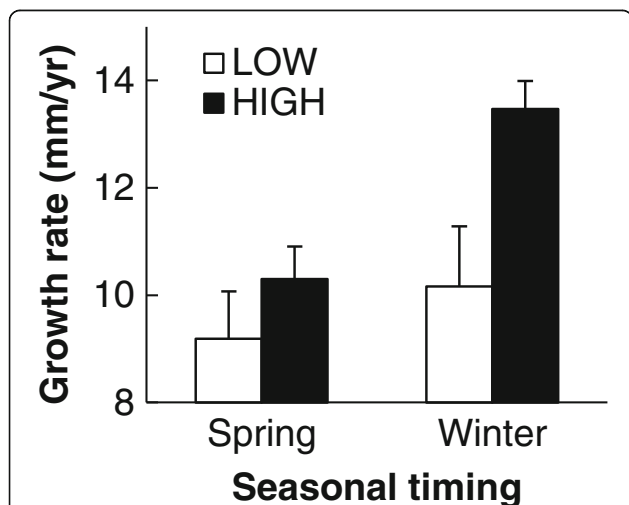
### Tortoise growth

Differences in neonatal tortoise growth across all rainfall treatments paralleled responses by the plant community, with both quantity and seasonal timing of rainfall

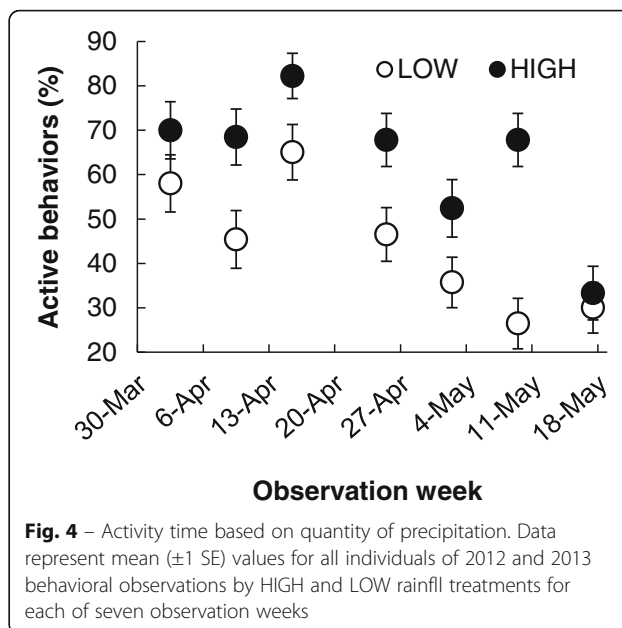
correlating significantly with annual growth ( $\beta = 0.2$ ,  $SE = 0.01$ ,  $DF = 56$ ,  $t = 25.5$ ,  $p < 0.001$ ). Tortoises reared in HIGH enclosures grew an average of 1.5 mm more than tortoises in LOW enclosures. This difference in total growth resulted from a growth rate that was 22% greater for tortoises in HIGH enclosures ( $11.9 \pm 0.7$  mm/year) compared to those in LOW enclosures ( $9.7 \pm 0.5$  mm/year) across both precipitation timing treatments ( $t = 2.4$ ,  $P = 0.01$ ,  $CI_{95} = 0.02, 0.46$ ). Tortoises raised in the winter-dominant treatment grew an average of 1.3 mm more than tortoises raised in the spring-dominant treatment, which resulted from an annual growth rate that was 19% greater ( $11.8 \pm 0.7$  mm/year versus  $9.6 \pm 0.8$  mm/year, respectively) across both HIGH and LOW treatments ( $t = 2.7$ ,  $P = 0.007$ ,  $CI_{95} = -0.03, 0.57$ ). Overall, growth rates were greatest for tortoises that experienced HIGH rainfall during the winter-dominant treatment, and least for tortoises in LOW rainfall during the spring-dominant treatment (Fig. 3).

**Tortoise behavior**

Juvenile tortoise activity differed based on total rainfall ( $z = 3.6$ ,  $P < 0.001$ ,  $CI_{95} = 0.18, 0.62$ ), but not rainfall timing ( $z = 0.3$ ,  $P = 0.75$ ,  $CI_{95} = -0.31, 0.41$ ). During a 30 min observation period, tortoises spent an average of 15 min active ( $53 \pm 2\%$  of behaviors), which did not differ significantly between the winter- and spring-dominant treatments. Across both study years, tortoises were active  $44 \pm 2\%$  of the observation period in LOW enclosures, compared to  $63 \pm 2\%$  of the observation period in HIGH enclosures. Differences in activity based on rainfall quantity were consistent across the majority of the spring activity season, but decreased in mid-May (Fig. 4). Tortoises in HIGH enclosures were more likely



**Fig. 3** – Tortoise growth in response to precipitation treatment. Rainfall quantity and seasonal timing had significant effects on mean ( $\pm 1$  SE) growth rates (mm/year) of neonatal desert tortoises



**Fig. 4** – Activity time based on quantity of precipitation. Data represent mean ( $\pm 1$  SE) values for all individuals of 2012 and 2013 behavioral observations by HIGH and LOW rainfall treatments for each of seven observation weeks

to be foraging than tortoises in LOW enclosures ( $17 \pm 1\%$  versus  $11 \pm 1\%$ , respectively), and spent twice as much time basking ( $14 \pm 2\%$  versus  $7 \pm 1\%$ , respectively). Tortoises in both treatments, however, rested a similar proportion of the time ( $\sim 40\%$ ). Air temperature below  $35^\circ C$  was not significantly correlated with activity ( $z = 0.9$ ,  $P = 0.32$ ,  $CI_{95} = -0.01, 0.03$ ). In summary, tortoises that experienced greater total rainfall spent more time foraging and basking than did those with less rainfall.

**Discussion**

In our enclosures, greater rainfall and winter-dominant rain positively affected plant productivity and species richness, effects which coincided with increased somatic growth in juvenile tortoises relative to lower rainfall and spring-dominant rain, respectively. It is important to note that although we sampled a reasonable portion of our research enclosures (6%) and focused on the season that most comprehensively reflects rain across the Mojave Desert, the Mojave Desert is large and localized adaptations may affect how plants and animals respond to precipitation aberrations. For instance, winter rain is suggested to be critical for blooms in the eastern Mojave, but large blooms have been documented in the western Mojave with very little winter rain following large storms in the spring [7, 44]. Because historical climate conditions in the western Mojave Desert are distinct from those in the eastern Mojave, biotic response to the scenarios we tested may vary depending on location. Moreover, in the prior 10 years cool-season rainfall was twice the amount that occurred during our study, with more monsoon rain occurring during our study. Monsoon rains in July and August that occur in many

parts of the Mojave Desert— especially east of the 117° meridian — [39] may have a rescue effect for lost winter rainfall, if summer rains provide reliable sources of food and water. Again, this effect, if present, is likely to be regionally variable. How biotic response to precipitation varies throughout the Mojave Desert warrants continued exploration.

The extent to which the effects we observed would be magnified under true increases in aridity is also yet uncharacterized. We were unable to decrease natural rainfall during the years of study due to limitations created by ethical constraints owing to the protected status of the desert tortoise, related conservation objectives, and the availability of enclosures. Therefore, our high water supplementation treatment reflected an above average year and our low water treatment reflected a more average year. Even without increased aridity and staying within historically normal conditions, however, we observed significant changes in plant productivity and tortoise growth. Although biotic response to rainfall is not linear, it is unlikely that even greater reductions in precipitation would have a positive effect relative to our results. Plant productivity in the Mojave Desert, for instance, is suggested to have critical thresholds of 50 mm of rainfall, below which there is little to no growth [18]. The present study suggests that changes in precipitation patterns in arid environments independently or in addition to temperature effects, require further study to better predict biotic response to climate change.

The novelty in our results arises especially from the finding that a departure from the prevailing winter-dominant precipitation patterns may magnify the effects of total changes in precipitation. Limited sample sizes of animals and available enclosures required sequential analysis of the effect of rainfall timing across two years rather than concurrently within a single year. This limitation inherently confounds the interpretation of the effects of shifts in rainfall timing with year, temperature, or other unmeasured variables. Fortunately, however, our treatments magnified natural rainfall patterns and our results are supported by prior studies: adequate winter rain is critical for flowering and is tightly coupled to the production of winter annuals in the eastern Mojave [7, 15, 45]. Moreover, laboratory studies suggest even when precipitation is abundant and continuous, few plants germinate after February 01, suggesting that rains that arrive after this date may not stimulate seedling response [46]. Observations of flowering annuals outside of our pens indicated they were absent in the spring of 2012, and abundant during the spring of 2013, even though 2012 had a wetter cool-season overall. As noted above, however, observations in the western Mojave have reported large blooms following dry winters and heavy

spring rain [44]. Thus, the relationship between precipitation and biotic response in arid ecosystems is complex and requires consideration of a number of factors, including region, rainfall pulses, seasonality, and quantity, as well as the effects of perennial shrub structure on recruitment of annuals [7, 47, 48]. Despite the sheer complexity of rain effects on biotic response, we think our results provide meaningful impetus to consider shifts in the timing of rainfall arrival as an important topic of study for measuring future climate change impacts in arid ecosystems.

One notable impact of rainfall timing in this study was that native plants were scarcer when the majority of cool season rain fell after January than when the majority of rain fell earlier. In the northeastern Mojave, water supplementation during the cool-season has been shown to have positive effects on native plant richness [49]. Generally, however, long-term increases in aridity may favor native species [50]. Of note, however, was our finding that outside of total rainfall, non-native annual plants had greater apparent plasticity in flowering in response to when rainfall arrived compared with native species. Invasive annual plants in our study responded to both spring- and winter-dominant cool-season rainfall. Greater trait plasticity is one characteristic generally thought to enhance invasion potential of species [51], so this finding is not materially surprising. The importance of native winter annuals relative to some non-natives to many desert herbivores [9, 15, 52] makes changes in the ratio of native to invasive plants an important consideration for evaluating the impacts of climate change on ecological communities and declining species in particular.

Growth by captive juvenile desert tortoises was greatest in the winter-dominant, high rain treatment and was comparable to growth of wild juveniles (14.7 mm/year) during good years in the eastern Mojave [53]. Although growth rates were lowest for tortoises in our spring-dominant, low rain treatment, they were still markedly higher than growth rates documented for wild juveniles during a drought (3.6 mm/year) in the eastern Mojave [53]. We found that growth rates between the winter-dominant, low rain treatment and the spring-dominant high water treatment were both roughly 11 mm/year. These results suggest interactive or additive effects between precipitation and plant productivity on juvenile growth that are independently influenced by how much and when rain arrives. For example, winter rain and annual vegetation were correlated with annual growth equally well across sequential years, with faster growth associated with years of high rainfall [15, 41]. Although we focused on neonatal growth, rainfall is also likely to affect other life stages of the tortoise. Females located in areas with more rain produce larger eggs, but their nests have lower hatching rates [34]. Adults may have more

flexibility in forage, and their forage preferences may change with water availability, but droughts can cause wide-spread adult mortality [25, 26, 54]. Overall, our results suggest that even during years in which mortality is not necessarily greater, changes in precipitation due to climate change are likely to cause subtle demographic effects, such as altering juvenile growth.

Behavioral plasticity may allow organisms to adaptively increase short-term survival during droughts or resource scarcity [55]. Neonatal tortoises that experienced less rainfall also decreased their time spent above ground. Reduced activity in response to lowered water availability has also been found in adult tortoises and other arid-adapted reptiles such as the Gila monster, *Heloderma suspectum* [2, 56]. Lowered activity can benefit arid-adapted species by reducing evaporative water loss and other metabolic expenditures when water is scarce [57, 58]. Although species such as the desert tortoise can escape some thermal or metabolic challenges created by water scarcity by retreating into burrows, not all arid tortoise species burrow and many species face substantial challenges in metabolic maintenance as habitat is degraded and temperatures increase [59, 60]. Reduced activity in juvenile tortoises in the present study also resulted in fewer foraging and basking behaviors even when green plants were available. In Lacertid lizards, reductions in activity in response to reduced water availability also corresponded to less growth [61]. In the long-term, episodic gains that neonatal tortoises acquire from lowered activity in response to reduced rainfall are thus likely to come with costs, such as lower growth rates [34, 42].

## Conclusions

Desert ecosystems, which are characterized by extreme water scarcity, are expected to be disproportionately affected by climate change [24, 62]. Desert inhabitants have many specialized traits that allow them to persist despite regular water deficits [63]. Because many arid-adapted species may be approaching thresholds of adaptability to extreme water shortages, they may be more susceptible to changes in precipitation than to changes in temperature [24]. Here, we provide evidence that the timing of precipitation could be as important as the quantity of precipitation in understanding potential effects of changing climate on terrestrial plants and herbivores. Herbivores were negatively affected by rain effects on the plant community even when water was abundant for drinking and some forage was available. Better understanding of the biotic response to predicted seasonal changes in precipitation patterns as a result of climate change may improve predictions of how ecological communities will be affected and merits additional study.

## Additional files

**Additional file 1:** Annual and herbaceous perennial plant species documented in plant quadrats by treatment (precipitation timing and quantity). (DOCX 26.9 kb)

## Abbreviations

IDTRF: Ivanpah desert tortoise research facility; MCL: Midline carapace length

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## Availability of data and materials

The datasets generated and/or analysed during the current study are not publicly available due to ongoing use in additional studies that are to be published in the future, but may be available from the corresponding author on reasonable request.

## Authors' contributions

TDT, MGN, KAB, and BDT contributed to conception, study design, and data collection. Analysis and interpretation were completed by MGN who drafted the initial manuscript. All authors contributed considerable revisions. All authors read and approved the final manuscript.

## Competing interests

The authors declare that they have no competing interests.

## Consent for publication

NA

## Ethics approval

Research followed protocols approved by the Institutional Animal Care and Use Committee through the University of California Davis (IACUC # 15997) and University of Georgia (A2010 04-059-Y3-A0), with full accordance to permits provided by US Fish and Wildlife Service (Permit # TE-17838A), California Department of Fish and Game (Permit # SC-11072), and Mojave National Preserve (Permit # MOJA-2011-SCI-0023).

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