Too dry for lizards: short-term rainfall influence on lizard microhabitat use in an experimental rainfall manipulation within a piñon-juniper

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Summary

1. Ectotherms such as lizards are expected to alter their behaviour and microhabitat use and experience population declines in response to rising temperatures. But the role of changing rainfall patterns on lizard behaviour and microhabitat use is not understood.

2. We used a 5-year rainfall manipulation experiment in a piñon pine-juniper woodland in central New Mexico to study how a lizard species' microhabitat use varies in four different rainfall treatments.

3. We examined ground temperatures in the sun and shade, and daily rainfall, within each treatment, during lizard activity periods, to address how lizards used sun or shade microhabitats on a daily basis. Our small-scale rainfall and temperature measurements indicate that rainfall, not temperatures, predict lizard microhabitat use.

4. Lizards showed a strong preference for shaded microhabitats during dry periods and used sunny microhabitats following rainfall events, regardless of treatment type. Lizards remained active during dry periods, foraging in the shade of trees.

5. Our study shows that rainfall can influence lizard microhabitat use more than temperature in a piñon pine-juniper woodland and the trees provide important refugia. The loss of piñon pine and juniper trees from prolonged drought threatens to limit the amount of shade available to lizards in the future.

Key-words: climate change, lizard, microhabitat use, piñon-juniper woodland, rainfall, temperature

Introduction

Understanding the abiotic factors that influence habitat use and behaviour is crucial for predicting species extinction risk, or how they will respond to climate change (Suttle, Thomsen & Power 2007; Smith, Knapp & Collins 2009; Scheffers *et al.* 2014). Species extinction risk from climate change is multifarious and includes physiological stresses, temporal mismatches and decreased food availability (Cahill *et al.* 2012). In ectotherms such as lizards, climate warming and thermal niche shifts have been hypothesized to increase extinction risk by reducing activity periods, which limits foraging times and fecundity, potentially leading to extinction (Sinervo *et al.* 2010). But the causal mechanisms driving extinction risk remain unclear (Cahill *et al.* 2012; Kearney 2013). The relationship between altered thermal niche regimes and lizard declines is complex, and factors such as water, food and microhabitat availability may act as proximate drivers for extinction risk (Brook, Sodhi & Bradshaw 2008; Cahill *et al.* 2012; Buckley, Eherenberger & Angilletta 2015). Additionally, lizards may avoid thermal stress by increasing their use of shade under future warming conditions (Huey & Tewksbury 2009; Kearney, Shine & Porter 2009). These potentially synergistic interactions and behavioural adaptations have called into question the thermal niche change explanation as the primary driver of lizard extinctions (Kearney 2013).

One way ectotherms can contend with increased thermal stress in temperate arid and semi-arid environments is by increasing use of shade or burrow microhabitats (Huey &

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Tewksbury 2009; Kearney, Shine & Porter 2009). Micro-habitat use has significant physiological consequences on lizard ecological performance (Huey 1991), and behavioural adjustments may enhance fitness if animals have access to appropriate microhabitats as local temperatures increase with global warming (Clusella-Trullas, Blackburn & Chown 2011; Callion *et al.* 2014). Changing temperatures are an obvious trigger for behavioural change, but the effects of changing rainfall patterns on ectotherm behaviour and habitat use are largely unknown (Clusella-Trullas, Blackburn & Chown 2011) and may elicit similar responses.

In semi-arid environments, water availability is a key driver of plant productivity (Collins *et al.* 2014), and changes in this resource can negatively impact trophic interactions and animal activity (Voigt *et al.* 2003; Suttle, Thomsen & Power 2007). Chronic water stress can result in bottom-up trophic effects that alter trophic interactions and behaviours, disrupting ecosystem and community dynamics (Voigt *et al.* 2003; Suttle, Thomsen & Power 2007; Smith, Knapp & Collins 2009; McCluney *et al.* 2012). For example, cricket and spider foraging decisions are based on water needs rather than nutrition during dry conditions, with spiders consuming more water-rich resources, increasing predator–prey interactions when water is limiting (McCluney & Sabo 2009). During seasonally dry periods the lizard *Heloderma suspectum* becomes inactive and spends more time in below-ground burrows than foraging at the surface with no apparent temperature effect (Davis & DeNardo 2009), suggesting water availability has a strong influence the behaviour of this species. Finally, reptile reproductive output, activity patterns, and foraging peak during wet periods (Pianka 1970; Duda, Krzysik & Freillich 1999; Shine & Brown 2008).

To maintain optimal body temperatures, lizards and other terrestrial ectotherms behaviourally regulate body temperature by altering their daily or seasonal use of shaded or sunny microhabitats (Huey 1991; Adolph & Porter 1993). Despite their dry, relatively impermeable skin, lizards have to manage their water balance or risk becoming dehydrated, especially in hot and arid environments (Munsey 1972). Symptoms of thermal stress in lizards include decreased locomotor performance, activity time, and prey acquisition; water-stressed lizards experience similar functional problems (Crowley 1987; Wilson & Havel 1989; Davis & DeNardo 2009). Desiccation and heat stress are highly correlated because thermally stressed lizards cannot forage or obtain water from prey, and hydrically stressed lizards cannot properly thermoregulate (Crowley 1987). Lizards balance the physiological interaction between thermal stress and water loss by shuttling across warm exposed and cool shaded microhabitat gradients (Stevenson 1985; Huey & Tewksbury 2009). But, for shade-to-sun shuttling to be an effective strategy there must be stability in the abundance and quality of available microhabitats (Kearney 2013; Sears & Angilletta 2015).

Piñon pine-juniper woodland is the most common forest type in the southwestern United States, covering more than 36 million acres (Shaw, Steed & DeBlander 2005). It also is one of the most threatened forest types from direct and indirect climate change factors (Gutzler & Robbins 2010; Gaylord *et al.* 2013). Over the last century, warming and drying trends across the southwestern United States have dramatically shifted forests to more open and grassland habitats, and these climatic stressors are expected to become more severe in the coming decades (Williams *et al.* 2013; McDowell & Allen 2015). Both piñon pine and juniper trees are unequally vulnerable to drought stress, with piñon pines experiencing disproportionately higher mortality rates than juniper trees (Gaylord *et al.* 2013). This increased drought vulnerability and tree mortality is likely to lead to an ecological state transition from woodlands to more simplified juniper-grassland or grassland habitats (Allen & Breshears 1998; Breshears *et al.* 2005; Collins *et al.* 2014; McDowell & Allen 2015). Piñon pine-juniper woodlands provide a structurally heterogeneous mosaic of widely spaced and unevenly distributed shaded microhabitats that will be homogenized by massive reductions in tree cover, removing the relatively cool and humid physiological shade refuge available for ectotherms such as lizards (Chen, Saunders & Crow 1999; Gutzler & Robbins 2010; Kearney 2013; Sears & Angilletta 2015).

Although there is a rich body of work on lizard responses to increased temperatures (Sinervo *et al.* 2010; Huey *et al.* 2012; Kearney *et al.* 2013), little is known about lizard responses to water stress in nature. Studies of lizard responses to climate change have utilized sophisticated modelling at coarse spatial scales but their predictions may be biased by failing to incorporate habitat and thermal heterogeneity (Sears & Angilletta 2015). For example, the widespread use of coarse climatic layers from WORLDCLIM at 10-arc min resolution in climate change studies (Hannah *et al.* 2014) may create a mismatch between local abiotic conditions, microhabitat conditions, and expected organismal response *in situ* (Potter, Woods & Pincebourde 2013). Therefore, relating the temporally and spatially heterogeneous abiotic conditions that animals experience *in situ* can better inform species responses to future climate change (Hannah *et al.* 2014; Sears & Angilletta 2015).

Field experiments that manipulate rainfall and temperature are ideal for testing the effects of climate change on microhabitat use of free ranging ectotherms (Suttle, Thomsen & Power 2007; Davis & DeNardo 2009). Moreover, studies that incorporate a wide range of rainfall gradients can allow for testing a spectrum of species responses to climate change, which is needed to assess climate change related risks (Kayler *et al.* 2015). To assess the daily microhabitat use of a lizard species in an arid piñon pine-juniper woodland in central New Mexico (Pangle *et al.* 2012), we used four experimental rainfall treatments ranging from severe drought (~45% rainfall reduction) to above-average precipitation (~130% rainfall increase above

30 year mean). The study species, *Aspidoscelis exsanguis* (Chihuahuan spotted whiptail), is a thermoregulator that shuttles between open and shaded microhabitats while actively foraging (Echternacht 1967). Its daily activity is hydrically costly, and Bowker (1993) found that moisture, not temperatures govern their daily activity, because lizards may expend up to 63% of their water mass while active. Our experimental design allowed us to relate microhabitat use to real-time subhourly temperatures and rainfall experienced by hydrically sensitive free-living lizards, the first time to our knowledge this has been done. We asked which abiotic elements, ground temperature or short-term rainfall, best predicted *A. exsanguis'* microhabitat use within each treatment type. Because high tree mortality and canopy dieback have been reported in this study system (Gaylord *et al.* 2013), we suggest that the resulting reduction of tree shade may have a cascading effect on lizards' ability to buffer against future climate change impacts in piñon pine-juniper woodlands (Kearney 2013).

Materials and methods

STUDY SITE DESCRIPTION AND EXPERIMENTAL RAINFALL TREATMENTS

This study was conducted at the Sevilleta National Wildlife Refuge and Long Term Ecological Research (LTER) site on the eastern slope of the Los Pinos Mountains, Socorro County, New Mexico, United States (34°23′11″N, 106°31′46″W; elevation 1911 m). Two species of trees were dominant at the study site, piñon pine (*Pinus edulis*) and oneseed juniper (*Juniperus monosperma*). Typically, these trees occur in patchy clumps (2–10 m apart) in a matrix of bare ground, bunch grasses, cacti, and small shrubs between tree clumps. A nearby weather station (Cerro Montoso #42; http://sev.lternet.edu/) indicated that the 20-year mean (1989–2009) annual precipitation was 362·7 mm year^{-1}, with a mean annual temperature of 12·7 °C (maximum mean monthly of 31·0 °C in July; minimum mean monthly −3·3 °C in December). The site is strongly influenced by seasonal monsoons that occur between July and September (Pangle *et al.* 2012).

Study plots were 40 × 40 m and dispersed over 25 ha in a piñon-juniper woodland and were part of a large-scale rainfall manipulation experiment that began in 2007 (see Pangle *et al.* 2012 for details). There were four experimental rainfall treatments with three replicates per treatment (Fig. S1, Supporting information): (i) ambient treatment with no manipulation; (ii) irrigated treatment that received ambient rainfall plus six 19 mm irrigations between April and October; (iii) drought treatment that continuously removed ~45% of ambient rainfall using transparent polymer troughs; and (iv) cover control treatment that received ambient rainfall but had inverted transparent polymer covering. Irrigation events were applied from storage tanks via 16 equally spaced, 6·1 m tall, sprinklers (Pangle *et al.* 2012). The drought and cover control treatments had 29 parallel transparent polymer troughs (drought) or domes (cover control) covering approximately 45% of each plot allowing both unfiltered and filtered sunlight to reach the ground. This reduction in rainfall is modelled from future predictions (Pangle *et al.* 2012) and the extreme 2002-2003 drought that resulted in widespread tree mortality in the southwest (Breshears *et al.* 2005). The effect of each treatment influenced the amount of rainfall received within each plot during our sampling period, last week of May to first week of August, with irrigation plots receiving the highest rainfall (2011: 75·5 mm;

2012: 93·5 mm), followed by ambient and cover control (2011: 37·5 mm; 2012: 36·5 mm), and drought received the least (2011: 20·6 mm; 2012: 16·2 mm) for our sampling months.

Drought and cover control treatments (i.e. with polymer covers) displayed increased soil and air temperatures of 1–4 °C compared to non-covered treatments (Pangle *et al.* 2012), which is within the temperature increase predicted by year 2100 (IPCC 2007). Because of the similar temperature effects under drought and cover control treatments, the cover control treatment can be used as a control for the drought treatment (Pangle *et al.* 2012). This warming artifact of the plot design allowed us to examine lizard microhabitat use under different thermal and precipitation regimes that include current conditions, warmer and drier conditions, and warmer and wetter conditions.

By 2011, the fourth year of the rainfall manipulation study when lizard sampling began, significant tree mortality and canopy die-back had occurred in the drought treatments, particularly on hill slopes, and was attributed to a combination of simulated drought stress and insect attacks (Gaylord *et al.* 2013). For example, by 2010, 70% of piñon pines in the drought plots experienced whole-tree mortality, while juniper trees experienced up to 50% cumulative canopy browning or dieback. Within the other treatments (ambient, cover control and irrigation), piñon pines experienced 10% mortality and juniper canopy cover was reduced by 15–20% due to naturally occurring drought conditions (Gaylord *et al.* 2013).

ABIOTIC VARIABLES

We defined short-term rainfall as the cumulative amount of ambient rainfall 7-days prior to lizard sampling as measured from a weather station located on-site (Pangle *et al.* 2012). For the irrigation treatments, we added any administered 19 mm rainfall events to the 7-day ambient rainfall amount and for drought treatment plots we reduced ambient rainfall by 45%. We used mean and maximum air and ground temperature measurements from 0630 to 1230 h for the dates we recorded lizard behaviours. We used this time range for temperature measurements because it covered the fluctuation in temperatures to which the lizards were exposed immediately prior to- and during lizard sampling. We obtained, at 15-min intervals, soil temperature measurements from 12 temperature sensors buried 5 cm deep and air temperature from 12 temperature sensors 10 cm above the ground (Pangle *et al.* 2012). Six temperature sensors were placed under tree canopies and six were placed in exposed intercanopy areas allowing us to calculate 6-h mean soil temperatures in shade and sun microhabitats. We used the temperature measurement from 1230 h for daily mean maximum soil temperature. Data sets of the abiotic variables can be accessed from the LTER Portal (Pockman & McDowell 2014).

LIZARD SAMPLING AND BIOLOGY

Lizard sampling took place in 2011 and 2012, during the fourth and fifth years of the rainfall manipulation. Plots were 1600 m^2 and sampling boundaries were either delineated by treatment structures or flagging. Plots were not fenced and lizards could move freely in and out of plots and to adjacent plots (Fig. S1).

Seasonal activity of *A. exsanguis* occurs from April to September, and daily lizard activity is governed by ground temperatures and typically begins around 0630–0700 h when ground temperatures approach 26 °C and ceases mid-day when temperatures approach 50 °C (Echternacht 1967). By early afternoon *A. exsanguis* activity and observations decline, therefore to maximize lizard observations, daily sampling began between 0700 and 0800 h and ended no later than 1200 h during their peak activity time

(Echternacht 1967). We sampled plots weekly starting the last week of May and continued through the first week of August in 2011 and 2012, covering most of the species' seasonal active period. In 2011 each plot was sampled 10 times and in 2012 each plot was sampled 14 times.

We used the visual scanning method by walking slowly for approximately 35 min within plots to detect lizards (Heatwole 2012). We scanned the ground searching for lizards within the plot boundaries and recorded shade or sun microhabitat use. Data on lizard microhabitat use was recorded at the original location where the animal was observed. Double counting of individuals may be a concern with this method but is minimized with species that are continuously visible (Lovich *et al.* 2012), such as *A. exsanguis*. Because lizards were continuously visible we were able to limit potential double counts, and in instances of uncertainty we removed questionable data points. One potential confounding issue that could bias our observations is territoriality, but North American *Aspidoscelis* species are not known to exhibit territorial behaviours (Leuck 1985). We used short-focus binoculars to minimize observer disturbance as we observed lizard behaviour, and this field approach has been shown to work well with *A. exsanguis* (Cooper 2008). For each observation we recorded: (i) time of observation; (ii) microhabitat (open or under tree); (iii) sun or shade and (iv) behaviour (active foraging, digging or scratching, basking). We define microhabitat use as the specific patch of habitat, shade or sun, where a lizard was observed (Anderson 2007).

Surface air temperatures can co-vary with soil moisture and rainfall at monthly or annual time scales (Dai, Del Genio & Fung 1997), but not on a daily time scale. Dai, Trenberth & Karl (1999) found no relationship with daily diurnal surface air temperatures soil moisture at 5 cm depth and rainfall, but cloud cover had a strong relationship with surface air temperatures. Daily rainfall events show little impacts on air temperatures from evaporative cooling, and slight cooling effects last on the order of hours, especially during the warm season (Duda, Krzysik & Freillich 1999). To avoid any potential confounding effects between air and soil temperatures with rainfall events on our analyses we sampled lizards on sunny days at least 36 h following a natural rainfall event or irrigation event.

ANALYSES

We used ANOVA to compare the mean abiotic variables between 2011 and 2012 to determine if there were significant differences between years. We found no difference in abiotic conditions between years (Table S1) and therefore analysed 2011 and 2012 together for all further analyses. We used ANOVA to determine if overall mean soil and air temperatures differed among treatments, and if soil and air temperature in shade and sun microhabitats differed among treatments. We used ANOVA to test if the mean percentage of green canopy cover of focal trees (Gaylord *et al.* 2013) had changed between 2007 and 2012 for each treatment. This was done to determine if the five-year experimental treatment affected canopy cover by the time of our lizard sampling. Green canopy cover change was recorded for 32 trees in the ambient treatment, 30 in cover control, 42 in drought and 34 in irrigation treatments.

We used a generalized regression with a zero-inflated poisson distribution to test whether the number of lizard observations (i.e. daily abundance) differed by treatment. This approach is appropriate for our count data because we had sampling periods with zero observation and the zero-inflated poisson allows for overdispersion when observations of zero are part of the data set (Crawley 2013).

We analyzed the frequency of lizards observed in shade or sun as a binomial response with logistic regression to test the null hypotheses of no relationship between short-term rainfall and/or

6 h mean and 1200 h maximum temperatures, and use of shade vs. sun habitats for each treatment (Crawley 2013). This approach allowed us to relate microhabitat use to real-time abiotic variables experienced by active lizards. We first ran the logistic regression with an interaction term between short-term rainfall and 6-h mean and 1200 h maximum soil temperatures. We used a Wald test to determine if the use of an interaction term is justified, where a non-significant Wald test indicates lack of evidence for an interaction, and that a simpler model with no interaction should be used (Crawley 2013). Based on the logistic regression results with the interaction term we then used a simple logistic regression model with rainfall as the only independent variable. We used the same approach with air temperatures and this yielded the same result. Because soil temperatures are more relevant to *A. exsanguis* (Bowker 1993) we present the air temperature results in the supplemental section (Table S2). All analyses were done in JMP-9 (SAS Institute Inc. 2010).

We used Bowker's (1993) linear regression equation (9.4×10^{-9}) (1.67^X) + 2.34; (X = soil temperature °C) to estimate total water loss for *A. exsanguis* over the 6-h morning active period (i.e. 0630–1230 h). Bowker (1993) calculated weight loss (g) per hour and assumed that weight loss represented water loss by the lizard. Since we do not have lizard field body temperature measurements we use the mean 6-h ground temperature measurements as a proxy (Echternacht 1967; Bowker 1993). We calculated water loss as grams/hour (g–h) for shade and sun habitats during wet (>4 mm rainfall previous 7-days) and dry periods (<4 mm rainfall previous 7-days).

Results

There were no significant differences in mean air temperature between 2011 and 2012 for any of the treatments (ANOVA: ambient: $P = 0.43$; $F = 2.46_{1,68}$; cover control: $P = 0.12$; $F = 0.79_{1,70}$; drought: $P = 0.09$, $F = 2.83_{1,70}$; irrigation $P = 0.06$; $F = 3.94_{1,70}$) or soil temperature (ANOVA: ambient: $P = 0.37$; $F = 0.79_{1,68}$; cover control: $P = 0.08$; $F = 3.14_{1,70}$; drought: $P = 0.16$, $F = 1.94_{1,70}$; irrigation $P = 0.33$; $F = 0.95_{1,70}$). Ambient and irrigation plots experienced lower temperatures than cover control and drought plots (Fig. 1). For each treatment maximum soil temperatures were significantly cooler in the shade compared to the sun habitats (Fig. 2; ANOVA: ambient: $P = 0.0001$; $F = 360.7_{1,138}$; cover control: $P = 0.0001$; $F = 740.0_{1,142}$; drought: $P = 0.0001$, $F = 434.0_{1,142}$; irrigation $P = 0.0001$; $F = 328.1_{1,142}$.). Drought treatments showed the largest difference between shade and sun temperatures and irrigation showed the smallest differences, with ambient and cover control being intermediate.

We had a total of 460 lizard observations (208 in 2011; 252 in 2012) across all treatments. For 2011 and 2012 combined we made 103 observations in the ambient, 63 in cover control, 94 in drought, and 200 in irrigation treatments. Our overall generalized zero-inflated poisson regression model indicates an effect of treatment on the daily lizard abundance ($P = 0.0001$, $\chi^2 = 41.12_{3,288}$). The treatment-level results from the generalized zero-inflated poisson regression model indicate that the irrigation treatment had significantly more lizards than all other treatments (ambient: $P = 0.012$, SE = 1.30, $\chi^2 = 6.3$, estimate = −3.27; cover control $P = 0.0001$, SE = 1.73, $\chi^2 = 32.93$,
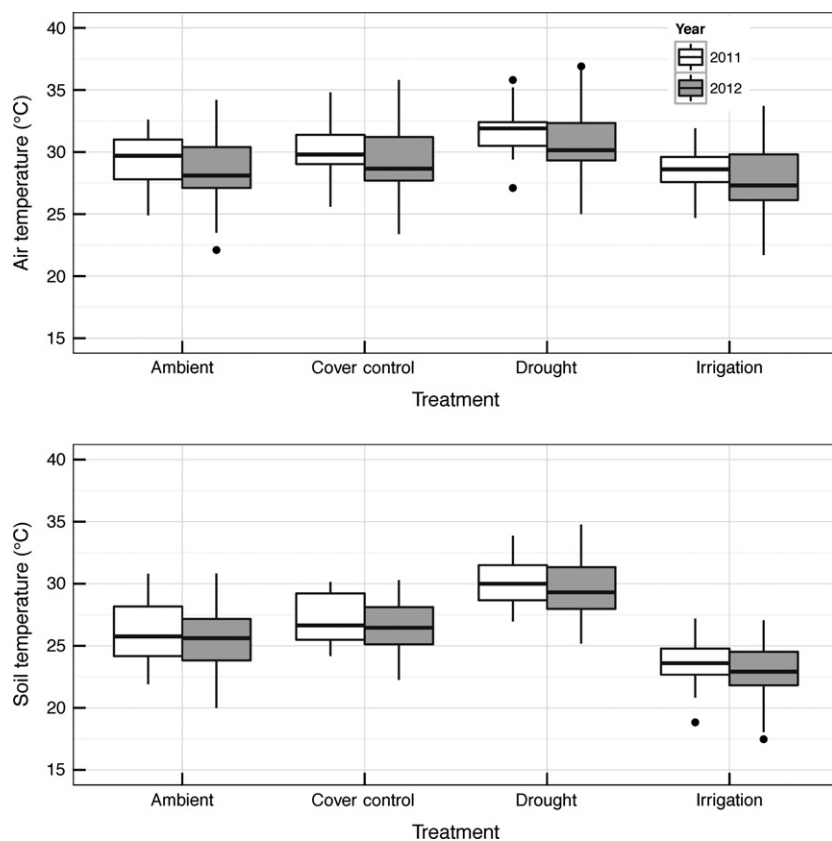
Fig. 1. Box plots of mean air and ground temperatures for each treatment type during the months (May–August) of lizard sampling 2011 and 2012.

estimate = -9.98; drought: $P = 0.0001$, SE = 1.45, $\chi^2 = 18.56$, estimate -6.25).

During dry periods, lizards had a higher likelihood of being observed in tree shade whereas following a rainfall pulse event lizards were more likely to be found in the sun, irrespective of treatment. The logistic regression model incorporating rainfall, mean soil temperature and the interaction term between rainfall and mean soil temperature showed that short-term rainfall was the strongest predictor of lizard microhabitat use and soil temperature was a non-significant predictor in all treatments (Table 1). The same analyses with air temperature produced the same result (Table S2). The simplified, single variable rainfall logistic regression models showed the same results; rainfall better predicts microhabitat use than temperature (ambient: $P = 0.0001$, SE = 0.03, $\chi^2 = 10.72$, estimate = -0.11; cover control $P = 0.013$, SE = 0.05, $\chi^2 = 6.11$, estimate = -0.12; drought: $P = 0.0024$, SE = 0.10, $\chi^2 = 9.19$, estimate = -0.31; irrigation $P = 0.0034$, SE = 0.01, $\chi^2 = 8.57$, estimate = -0.05). The logistic regression model with all treatments combined was also significant for short-term rainfall predicting habitat use ($P = 0.0001$, SE = 0.012, $\chi^2 = 22.10$, estimate = -0.05; Fig. 3). Thus, there was a strong effect of rainfall and no effect of temperature on shade vs. sun habitat use, even for the warmest and driest treatments.

Since rainfall manipulation started in 2007, the mean percentage of green canopy cover has decreased, regardless of treatment type (Fig. 4). Between 2007 and 2012, green

canopy cover decreased on average by 25% in the ambient treatment (ANOVA: $P = 0.0001$; $F = 35.68_{1,61}$), by 30% in the cover control treatment ($P = 0.0001$; $F = 68.20_{1,58}$), by 68.9% in the drought treatment ($P = 0.0001$, $F = 125.85_{1,71}$), and by 24.1% in the irrigation treatment ($P = 0.0001$; $F = 33.10_{1,63}$).

The water loss proxy model predicts that lizard water loss should be greater in the sun compared to shade, and this difference was accentuated during dry periods (Fig. 5). The total estimated lizard water loss for the 6-h morning active period differed significantly between shade and sun habitats during dry (ANOVA: $P = 0.0001$, $F = 47.38_{1,370}$), and wet periods (ANOVA: $P = 0.0001$, $F = 24.77_{1,196}$) for all treatments combined.

Discussion

Detailed studies of microhabitat use under such rainfall manipulations are sorely needed to understand the consequences of change (Bernardo 2014; Kayler *et al.* 2015), and to our knowledge such a field study has not been done until now on vertebrates (but see Suttle, Thomsen & Power 2007 for an invertebrate example). Our work confirms that climate change studies on ectotherms such as lizards must consider both temperature and rainfall (Clusella-Trullas, Blackburn & Chown 2011; Lovich *et al.* 2014), fine-grained variation in abiotic conditions (Hannah *et al.* 2014), and habitat heterogeneity (Sears & Angilletta 2015). We have presented a hierarchical connection between
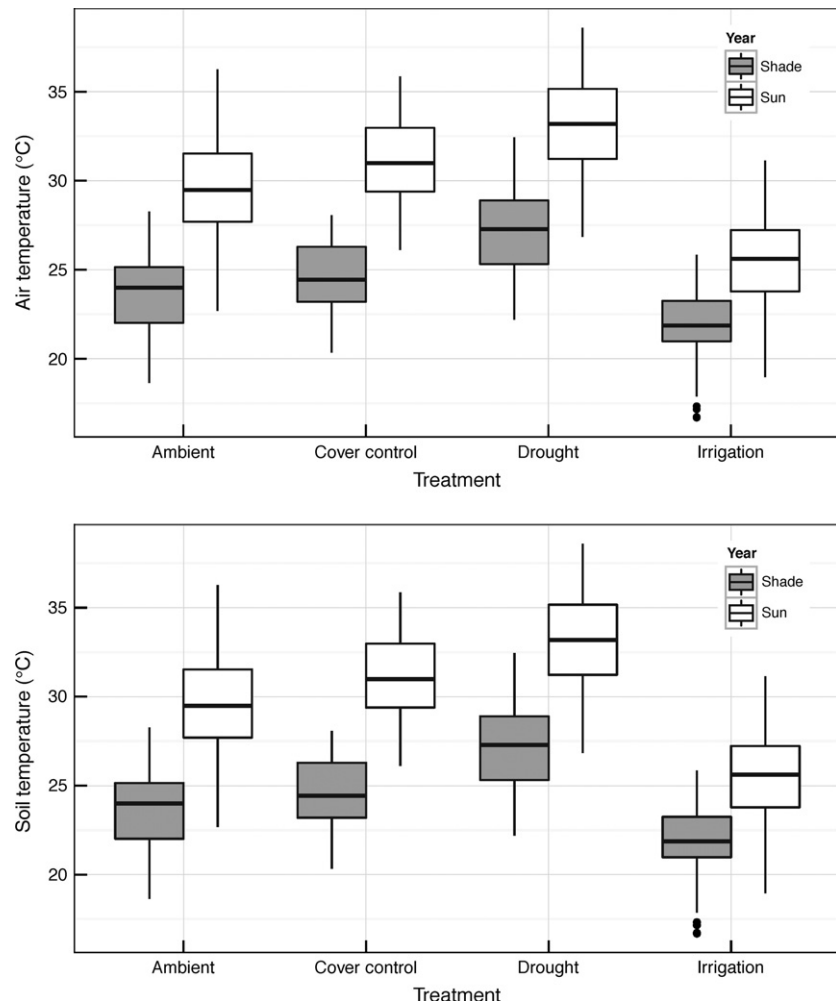
Fig. 2. Box plots of mean 6-h soil temperatures in shade and sun microhabitats for each treatment type. Soil temperatures were significantly lower in shade across all treatments. The 6-h time period covers the time of day lizards were active and represents the conditions lizards were exposed to during observation periods.

current and predicted climate change rainfall scenarios, tree mortality and lizard microhabitat use in the southwestern Unites States. By quantifying lizard microhabitat use within the framework of a field-based rainfall experiment we were able to investigate how real-time, subhourly temperature and rainfall influences free-living lizard microhabitat use under exposure to different and extreme rainfall scenarios.

Our most striking finding is that short-term rainfall, rather than soil or air temperatures, influenced daily lizard microhabitat use, even in the warmest drought treatments. The greater effect of rainfall relative to temperature on microhabitat use contradicts previous findings of lizard responses to climate change (Kearney, Shine & Porter 2009). During periods with low rainfall, lizards were more often observed in shade than sun and during periods with >4 mm of rainfall lizards were more often observed in the sun (Fig. 3). These findings reinforce the complexity of predicting species responses to climate change and confirm that fine scale autecological-environmental interactions are needed to best predict individual species responses (Clusella-Trullas, Blackburn & Chown 2011; Hannah *et al.* 2014). Any behavioural response to either rainfall or temperature change depends on the availability of shade

microhabitat refugia (Figs 3 and 5). Much of the southwestern United States is experiencing extreme droughts and long-term drying trends that are causing high rates of tree mortality (Breshears *et al.* 2005; Williams *et al.* 2013), which should have cascading, deleterious impacts on shade-using lizards (Kearney 2013; Clusella-Trullas & Chown 2014).

We propose that two drivers explain the rainfall-associated shift in lizard microhabitat use. First, lizards may simultaneously minimize water loss and thermal stress when active in the shade during harsh dry periods. Rate of evaporative water loss in lizards is positively associated with both arid conditions and higher temperatures (Claussen 1967; Munsey 1972). Lizards near their dehydration threshold prefer lower temperatures than those preferred by hydrated animals (Crowley 1987; Angilleta 2011); and the behavioural solution to this dilemma is to move from sun to shade, which can decrease a lizard's body temperature by up to 5 °C (Stevenson 1985). Bowker (1993) found water loss in *A. exsanguis* increased exponentially as substrate temperature increased beyond 37 °C, and suggested that water may be the most important factor limiting activity and determining microhabitat use in these lizards. In our study, the use of shade microhabitats during dry periods

Table 1. Logistic Regression model results of shade/sun habitat use by rainfall and mean maximum soil temperatures at 1200 h and 6-h mean soil temperature. Wald test determined that adding a rainfall × temperature parameter was uninformative and over-parameterized the model

Treatment	P	$\chi^2_{d.f.,n}$	Estimate ± SE	Wald test P
Tsoil @1200 h				
Ambient				
Whole model	0·001*	12·56$_{2,102}$		
Rainfall	0·001*	10·64	−0·13 ± 0·04	0·0004*
TsoilMax	0·15	2·07	−0·13 ± 0·09	0·15
Cover control				
Whole model	0·007*	9·71$_{2,63}$		
Rainfall	0·03*	3·89	−0·10 ± 0·05	0·04*
TsoilMax	0·17	1·84	0·16 ± 0·12	0·17
Drought				
Whole model	0·0003*	16·55$_{3,94}$		
Rainfall	0·0064*	7·42	−0·28 ± 0·10	0·008*
TsoilMax	0·25	1·29	0·09 ± 0·08	0·25
Irrigation				
Whole model	0·009*	9·30$_{3,200}$		
Rainfall	0·01*	6·50	−0·04 ± 0·01	0·009*
TsoilMax	0·50	0·45	0·04 ± 0·07	0·49
$\bar{x}$ Tsoil 6-h				
Ambient				
Whole model	0·002*	11·92$_{2,102}$		
Rainfall	0·001*	9·93	−0·12 ± 0·03	0·001*
Tsoil $\bar{x}$	0·22	1·45	−0·12 ± 0·1	0·22
Cover control				
Whole model	0·01*	9·14$_{2,63}$		
Rainfall	0·03*	4·47	−0·11 ± 0·05	0·03*
Tsoil $\bar{x}$	0·25	1·31	0·17 ± 0·15	0·25
Drought				
Whole model	0·0005*	15·33$_{3,94}$		
Rainfall	0·002*	9·30	−0·32 ± 0·10	0·002*
Tsoil $\bar{x}$	0·74	0·11	0·03 ± 0·12	0·74
Irrigation				
Whole model	0·011*	8·90$_{3,200}$		
Rainfall	0·01*	6·37	−0·04 ± 0·01	0·01*
Tsoil $\bar{x}$	0·80	0·05	0·02 ± 0·08	0·81

*Denotes significance.

Fig. 3. Logistic regression plot of short-term rainfall by probability of observation in shade (open circles = sun; black circles = shade) for all treatments combined. Points represent observations from sampling periods and short-term rainfall. See text for logistic regression results.

supported Bowker's assertion that water loss determines behaviour of *A. exsanguis*. This result also fits with Stevenson's (1985) behavioural solution of lizards using shade when ground temperatures may be up to 8·5 °C cooler than sunny microhabitats (Fig. 1). The use of shade microhabitats can be dependent on an organism's tolerance to water loss (Cohen & Alford 1996), and in the case of *A. exsanguis* use of shade can aid in water conservation during dry periods (Fig. 5). The use of shade during dry periods allows *A. exsanguis* to simultaneously remain active and foraging while conserving water in shade tree island refugia.

Second, trophic-level species interactions may influence lizard microhabitat use as invertebrate prey encounter rates may differ between open and shaded microhabitats in relation to water availability. Small invertebrates are particularly vulnerable to water loss (Chown & Gaston 1999) and thus may be more abundant in shaded areas during times of water stress, leading to more lizard predatory activity in
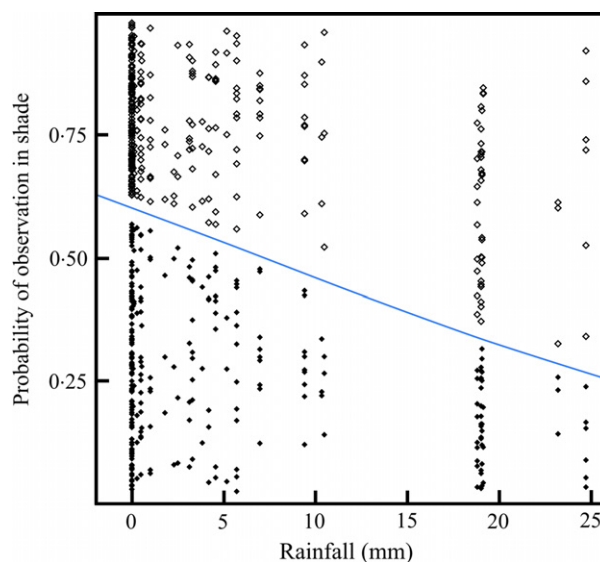
shaded areas when water is scarce. For example, Trotter, Cobb & Whitham (2008) found arthropod abundances and diversity in piñon pine-juniper woodlands decreased when drought stresses were high and Schowalter, Lightfoot & Whitford (1999) observed an increase in arthropod abundance and diversity following experimental watering in a creosote-grassland, indicating that arthropods respond quickly to moisture pulses. The ebb and flow of rainfall pulses driving invertebrate prey distribution may dictate lizard microhabitat use as lizards track their prey.

Increased temperatures have been identified as the greatest threat to lizard populations (Huey, Losos & Moritz 2010; Sinervo *et al.* 2010), and are predicted to influence lizard microhabitat use (Kearney, Shine & Porter 2009). The lack of an observed effect of soil temperature on *A. exsanguis'* preference for sun vs. shade habitat is in contrary with the predictions found in the literature. We hypothesize that the lack of a temperature effect on lizard microhabitat use and behaviour is rooted in the thermal biology of *A. exsanguis*. We did not collect field body temperatures for our lizards, but *A. exsanguis* has been shown to maintain a field body temperature of 38·5 °C at ground temperatures of 41·7 °C (Schall 1977; Bowker 1993). During our daily sampling periods mean ground temperatures were within the normal active range of *A. exsanguis,* even under the warmest drought and cover control treatments (Fig. 1). The lack of an effect in these warmer treatments was surprising and suggests that *A. exsanguis* may not be very vulnerable to future warming temperatures if rainfall remains stable and shaded microhabitats remain part of the landscape.

Shifting microhabitat use is frequently cited as a strategy for countering the effects of climate change (Scheffers *et al.*
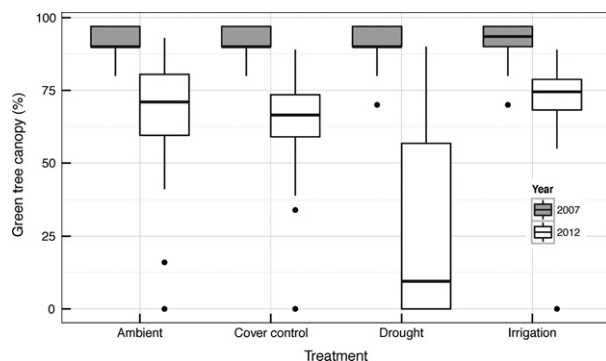
Fig. 4. Box plots of mean percent change in live, green canopy cover between 2007 (start of the rainfall manipulation) and 2012 (last year of lizard sampling) for each treatment. Percent of green canopy cover comes from focal trees monitored annually within the study plots. There was a significant decrease in green canopy cover for all treatments, and the drought plot showed the greatest change.
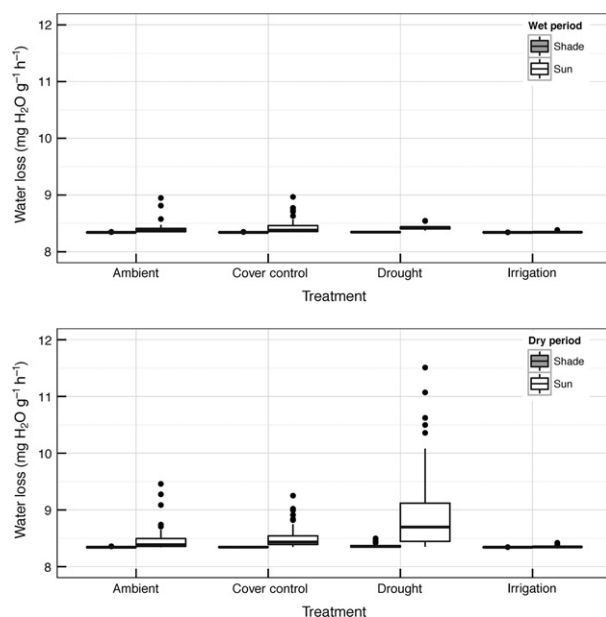

Fig. 5. Box plots of estimated lizard water loss (mg of water/h) within each treatment, and shade or sun microhabitats. The model predicts lizard water loss to be greatest during dry periods while lizards are in the sun, and that water loss is least when in the shade.

2014). However, we note that any behavioural response to either rainfall or temperature change depends on the availability of suitable shade refugia that may themselves be affected by climate change. In particular, in arid or semi-arid environments it is important to account for the concomitant impacts of climate change on trees, which provide critical shade microhabitats (Allen & Breshears 1998; Breshears *et al.* 2005; Kearney *et al.* 2013). The decline of piñon pine-juniper woodlands, including the decrease in canopy cover quality (i.e. green to brown canopy cover), poses serious dangers to animals that rely on this habitat (Fig. 4). We observed just such a decline in our study plots: there was a significant decrease in green

canopy cover for all treatments between 2007 and 2012, as well as high tree mortality (Fig. 4; Gaylord *et al.* 2013). Drought, fires and bark beetle outbreaks have reduced the coverage of piñon-juniper woodlands over the last few decades driving a shift to juniper and/or grassland dominated systems (Breshears *et al.* 2005; Williams *et al.* 2013). The loss of tree cover and decrease in canopy quality in this system may have severe consequences for *A. exsanguis* and other ectotherms even beyond the loss of protective microhabitat. For example, drought-stressed piñon pines support lower arthropod abundance and diversity than non-drought stressed trees (Stone, Gehring & Whitham 2010). This pattern suggests a bottom-up trophic cascade in this system.

During the course of sampling we observed many behaviours of *A. exsanguis* that helped to inform our interpretations. Foraging and microhabitat behaviours of *A. exsanguis* fluctuated with rainfall pulses, with foraging area expanding following rainfall pulses to include both sun or shade microhabitats. Over the course of our sampling lizards moved quickly and directly between the 3–10 m separating tree-shade islands during dry periods. During dry periods, *A. exsanguis* foraged by scratching and digging in the friable needle litter under tree canopies and fed on various below-ground invertebrate larvae and smaller prey including termites. During wetter periods lizards expanded their foraging area to sun microhabitats and foraging behaviours switched from scratching and digging to actively searching for above-ground prey. When lizards were foraging in sun microhabitats, we observed them feeding on above-ground prey such as moths, beetles, grasshoppers and cicadas. As conditions became drier, lizards once again became more common in the shade, emphasizing the role of rainfall not just on microhabitat use but also on the total area available for food acquisition. The shifts in microhabitat and foraging behaviours provided evidence that rainfall strongly affected where and how *A. exsanguis* located prey. Furthermore, lizards were active for at least 5 h per day after rainfall, with no evidence of restricted activity times in any treatment.

Our findings of short-term rainfall driven microhabitat use can likely be extrapolated to other ectotherms that occur in piñon pine-juniper woodlands, such as snakes and arthropods. Most ectotherms must cope with the same physiological stresses associated with warmer temperatures and drought (Deutsch *et al.* 2009; Dillon, Wang & Huey 2010). Similar to our lizard results, many invertebrates use shade microhabitats to avoid stressful abiotic conditions (Shepherd, Brantley & Tarleton 2002; Stone, Gehring & Whitham 2010). The loss of piñon pine and juniper trees due to climatic stresses will result in fewer and more widely spaced shade islands. In the short term, animals in this system will have to contend with several problems including possibly locating the increasingly rare shade islands and increases in competition. However, the likely consequence of an eventual shift to a juniper-grassland or grassland will be the extirpation of the lizard species that depend on the

current heterogeneous piñon pine-juniper habitat mosaic (Sears & Angilletta 2015).

Acknowledgements

Data accessibility

Lizard and abiotic data are deposited at the Sevilleta LTER Portal. The lizard data were collected at part of MJR's dissertation and are under embargo until 2019 and can be accessed at http://sev.lternet.edu/data/sev-249. Abiotic data have no embargo and can be accessed at: http://dx.doi.org/10.6073/pasta/a053a821b84c51356730b4ee05a10e3f (Pockman & McDowell 2014).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Photographs of the four treatment types where lizards were studied.

Table S1. ANOVA results comparing 2011 and 2012 air and ground temperatures for each treatment.

Table S2. Logistic Regression model results of shade/sun habitat use by rainfall and mean maximum air temperatures at 1200 h and 6-h mean air temperature.