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Field and laboratory responses to drought by Common Side-blotched Lizards (*Uta stansburiana*)

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ABSTRACT

Starting in 2012, and peaking in 2013, drought conditions in the Great Basin Desert persisted for almost four years. By studying a meta-population of Common Side-blotched Lizards in the wild, we found that a failure of spring rains correlated with a marked reduction of body condition in female, but not male, lizards. Likewise, rainfall correlated with reproductive scores of females such that a failure of spring rains in 2013 resulted in a cessation of the breeding season. By 2014 it was apparent that the drought had caused a general failure of recruitment into the population, which affected the body-size distribution of lizards for several subsequent years. To disentangle the effects of both water and food availability during a drought, we next conducted a laboratory experiment by imposing a drought on breeding animals, but not otherwise limiting food. Results indicate that the absence of drinking water alone tends to delay the breeding season as well as cause reproductive failure in females even as body condition was maintained. Our combination of field and laboratory data reveal that body condition and reproductive responses to drought are not strictly about food limitations, but are also caused by a lack of available drinking water.

1. Introduction

Water, including precipitation, is typically the limiting factor for plant productivity in desert environments (Hadley and Szarek, 1981; Noy-Meir, 1973), which in turn can regulate higher trophic levels (Dunham, 1982; Noy-Meir, 1974). Thus, during extreme weather events, such as during a drought, a suite of food-web responses is anticipated amongst the species that comprise desert ecosystems (Noy-Meir, 1979; Schwinning and Sala, 2004). However, because of the multivariate nature of an ecosystem's responses, determining which specific aspects of the environment limit higher trophic levels in nature can be a challenge. Moreover, much of the previous research of the effects of drought on desert ecosystems took advantage of fortuitous drought conditions during ongoing long-term studies (e.g., Dunham, 1978; Hoddenbach and Turner, 1968; Miriti et al., 2007). Thus, statistical control of the different variables affected by drought was typically lacking (but see Allen et al., 2013). Similar to many previous studies, the present study developed out of a fortuitous set of observations on a natural meta-population of desert lizards during an extended drought event in north-central Nevada that occurred from 2012 through 2016, but was followed with a laboratory study for comparison.

The previously-demonstrated effects of long-term drought on desert lizards include reduced survival (Whitford and Creusere, 1977), reduced food availability (Germano et al., 1994; Mayhew, 1966a), shorter breeding seasons (Mayhew, 1966a), fewer offspring per reproductive bout (Hoddenbach and Turner, 1968; Zweifel and Lowe, 1966), and reduced juvenile recruitment (Whitford and Creusere, 1977). Generally, the previous research on drought suggests that rainfall, particularly during the winter, positively correlates with reproduction in lizards (e.g., Mayhew, 1966a, 1966b; Zweifel and Lowe, 1966). However, the potential confounding of variables related to both moisture and food in response to natural variation in rainfall makes it difficult to disentangle the effects of these variables using natural observations alone. For example, a recent experimental study on desert ecosystems indicated that surface water additions had a greater positive effect than food additions related to groundwater across trophic levels, including in insectivorous lizards (Allen et al., 2013).

Although the relationship between food and reproduction has been established in certain model organisms, such as lizards (e.g., Guyer, 1988a, 1988b; Mayhew, 1966a, 1966b), less clear is the causal link between water and reproduction (e.g., Dickman et al., 1999; Smith, 1996). For example, Jones et al. (1987) reported that water stress, but not food abundance, affected reproduction in lizards from western Nebraska. Specifically, a lack of rainfall appeared to cause a reduction in body water content, but an increase in egg water content, which may

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represent an attempt by females to allocate resources to reproduction as part of a life-history trade-off (Jones et al., 1987). Such individual effects appear to scale up to population-level responses as well. For example, Stapley et al. (2015) reported that a long-term decline in a tropical lizard's abundance was related to intermittent dry periods in the rainforest caused by La Niña events. Similarly, an experimental manipulation altering water availability via rainfall in tropical forest plots during both wet and dry seasons revealed a complex set of responses in a lizard that included a positive relationship between moisture and population density due to increased recruitment (Andrews and Wright, 1994). Together, the previous studies on the effects of water availability alone suggest that population and ecosystem responses to events such as droughts remain to be identified. Yet many of these studies did not report on the reproductive responses of individuals leaving a gap in our understanding of such responses as they scale up to populations (but see Abell, 1999; Goldberg, 1975).

To better understand the reproductive impacts of drought in desert ecosystems, we combined observations on a meta-population of lizards from eight years spanning an extended drought in Nevada with a laboratory experiment imposing water, but not food, limitations on individuals. Both aspects of this study address a single hypothesis related to the lack of reproduction and recruitment in the population related to drought conditions. That is, we tested the hypothesis that lack of water alone was sufficient to affect body condition as well as reproductive success of lizards and that food limitations were not be the primary causal agent in the natural population-level drought responses reported previously.

2. Materials and methods

2.1. Study subject

In order to determine the effects of water, especially drinking water, on reproductive responses, we studied Common Side-blotched Lizards, *Uta stansburiana*. Side-blotched lizards are small (maturing at ~40 mm; Zani and Rollyson, 2011) and abundant where they occur (densities > 25 adults per ha; Scoular et al., 2011), but have the potential to be long-lived in the absence of predators (Scoular et al., 2011) with a maximum life span in the wild of at least 7 years at higher latitudes (P.A.Z. pers. obs.). Side-blotched lizards have a geographic distribution that ranges from Baja California, north into Washington State, and from coastal California to western Texas and Oklahoma (Stebbins, 2003). Across their range, side-blotched lizards are likely to have experienced drought conditions, especially considering recent report of a 1000-year span of drought conditions ending ~1850 YBP across much of the northern Great Basin (Mensing et al., 2013).

2.2. Field animals

In 2010, we began studying lizards from two populations in north-central Nevada that both occur in salt scrub desert along the shoreline of ancient Lake Lahontan within the Great Basin Desert: Lovelock (LV) (40.22 °N, 118.54 °W, elev. 1255 m; Pershing Co., NV) is a tufa boulder field; Humboldt Sink (HS) (39.95 °N, 118.74 °W, elev. 1245 m; Churchill Co., NV) is a mixed tufa/lava boulder field. Because these two populations are only 30 km apart with a continuous expanse of tufa between them, for purposes of this study both sites (hereafter, LV and HS) were considered a single meta-population and combined to ensure sample sizes were sufficiently large for analyses. Anecdotal observations based on vegetative responses suggest that both sites experienced similar rainfall patterns and drought conditions throughout the study period.

Side-blotched-lizard reproductive phenology along the shores of ancient Lake Lahontan is focused on the early, wet spring season alone due to seasonal drying in the summer (average July rainfall is 2.2 mm). Consequently, lizards are active beginning in early March at which time mature females begin vitellogenesis for a first clutch typically in early- to mid-April. Immature females continue to grow and typically accomplish a first clutch by early- to mid-May. If conditions permit, females will attempt a second clutch in early May and at least a third clutch in June.

Lizards in the field were sampled annually over 8 years (from 2010–2017), which roughly corresponded to two years of pre-drought conditions, the four years of the drought, and two years of post-drought recovery. Sampling was typically done in late March or early April (early spring), and then again in late May through June (late spring/early summer). Lizard sampling was achieved by 1–3 researchers walking evenly-spaced transects back and forth through boulder-covered slopes at 5-m intervals using a handheld GPS device to avoid re-sampling previously searched areas. Individual lizards were caught using a slip-knot of surgical thread tied to an eyelet made from a paper clip inserted into a hollow kite pole. Animals were captured, measured, palpated for reproductive state, and released at the site of capture unharmed.

Measurements in the field for both sexes included: i) snout-to-vent length (SVL) to the nearest 0.5 mm using a linear rule, ii) mass to the nearest 0.01 g using a 10-g Pesola spring-loaded balance, and iii) lizard sex (male/female)(Zani and Rollyson, 2011). From these data we calculated lizard body condition using the scaled-mass index of Peig and Green (2009), which can be calculated by the formula:

Condition of individual X = avg. mass * (avg. SVL/SVL of individual X)^RMA-regression slope, where SVL = snout-vent length, and RMA-regression slope = the slope of the reduced major-axis regression between natural-log transformed length and mass data. Rather than compute body condition separately for each sampling period, scaled-mass index was calculated for all measurements simultaneously, but separately on males and females because of the different energetic and life-history responses of the two sexes to the breeding season.

We also scored reproductive condition of females via abdominal palpations as in previous studies from our laboratory (Zani et al., 2008; Scoular et al., 2011; Zani and Rollyson, 2011) as follows: 0) no follicles (NF) defined as lacking any discernible follicles, 1) unenlarged follicles (UF) as presence of cluster of small (< 1 mm), hard, round follicles, 2) enlarged follicles (EF) as presence of cluster of large (> 1 mm), hard, round follicles, 3) yolked follicles (YF) as presence of cluster of large (> 3 mm), soft, round eggs, 4) shelled eggs (SE) as presence of large (> 3 mm), firm, oblong eggs, 5) post reproductive (PR) as lacking any discernible follicles or eggs, but with presence of orange ventral coloration that occurs during ovulation (Zani et al., 2008). Assigning a reproductive score from these abdominal palpations was aided by consideration of that female's length (SVL) because large female side-blotched lizards reproduce two to three weeks earlier than smaller females (Zani and Rollyson, 2011). This scoring system was verified by its use previously to score > 1000 gravid females that then oviposited in the laboratory (e.g., see Zani and Rollyson, 2011). We further verified reproductive score by performing ultrasounds on 57 gravid side-blotched-lizard females pooled from five populations (P.A.A., S.S. French, and G. Smith, unpubl. data.). Ultrasound images were used to count and measure the length of each follicle, which were then summed to create a reproductive index based on follicle length (G. Smith, pers. comm.). This reproductive index was very highly correlated with reproductive score via palpations ($F_{1,55} = 110.69$, $P < 0.001$, $R^2 = 0.668$), suggesting that the use of reproductive scores is valid.

2.3. Laboratory animals

To separate the effects of lack of water from the confounding effects of lack of food potentially experienced in nature, we exposed individual side-blotched lizards to drought conditions in the laboratory. Animals for the laboratory drought experiment were obtained during the summer of 2014 from a population of side-blotched lizards at Three-Lizards Butte (TL) in eastern Oregon (43.7797 °N, 120.3878 °W, elev.