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Temperature and Precipitation Interact to Predict Size Responses to Climate Change in Fence Lizards

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Abstract.—**Body size is known to vary with temperature, and in the past decades has been shown to vary with anthropogenic climate change. Many species have exhibited size declines in conjunction with warming temperatures, but some groups, such as reptiles, remain under-studied. We tested whether body size changes of the Eastern Fence Lizard (*Sceloporus undulatus*) species complex across their U.S. range were related to temperature and precipitation over 115 y. We measured snout-vent length (SVL) of more than 600 adults collected from 1899–2014 and extracted mean annual temperature, temperature of the warmest quarter, total annual precipitation, and elevation for the latitude, longitude, and year of collection for each specimen. We found that over time, temperature increased while precipitation decreased at our sampled sites, and size of males and females increased. Size was predicted by a marginally significant interaction between temperature and precipitation, indicating that as temperatures warmed, individuals became larger in dry areas and smaller in wet areas, supporting the desiccation resistance hypothesis (larger in dry environments). Our data suggest that precipitation may be an overlooked factor influencing size, warranting further examination in other taxa.**

Key Words.—body size; clines; global warming; museum collections; *Sceloporus*; reptiles

Introduction

The impact of climate change on organism size has been well-documented in the literature (Sheridan and Bickford 2011; Gardner et al. 2019; Weeks et al. 2020). Numerous studies across all major taxonomic groups of animals have demonstrated that a majority of species get smaller in response to climate change (Gardner et al. 2011). This has implications for heat tolerance (Buckley 2021; Peralta-Maraver and Rezende 2021), survival (Roff 2002), reproductive output (Roff 2002), and, in turn, population size. Within this body of literature, exceptions to size decline have been observed (Chamaille-Jammes et al. 2006; Tryjanowski et al. 2006; Gerard et al. 2020), raising questions as to which species are likely to decline with climate change and which may increase in size or remain largely unaffected. Though most taxonomic groups have received at least some attention in this field, reptiles remain the least-studied, despite the potential for this group to be one of the most heavily impacted.

Based on experimental and natural populations, body sizes of some ectotherms are smaller at warmer temperatures (Bizer 1978; Desai and Singh 2009), likely due to the impact of temperature on both metabolism and growth rate. We refer to latitudinal and elevational clines in ectotherm size (smaller at warmer temperatures) as geographic size clines. Further, the temperature-size rule states that as developmental temperatures increase, rate of development increases, but the rate of growth does not often increase proportionally, so organisms are smaller at a given age or stage class when reared at warmer temperatures compared to those reared in colder temperatures (Atkinson 1996). Thus, ectothermic organisms are expected to be heavily impacted by global warming due to the combined impacts of increased temperature on growth and development, metabolism, and heat regulation.

Reptiles provide an interesting group of study because many squamates have been shown to follow the inverse of predicted geographic size clines or to lack latitudinal patterns in size (Ashton and Feldman 2003; Rodrigues et al. 2018). Thus, squamates provide the opportunity to test whether observed geographic size clines predict a response of species to climate change. To date, only three studies have explicitly examined the response of reptile size to climate change (Chamaille-Jammes et al. 2006; Lopez-Calderon et al. 2017; Stanley et al. 2020). Data on biogeographic size clines are not available for all six of the reptile species examined to date, and the two for which such data are readily available show mixed ability of biogeographic patterns to reliably predict responses to climate change. The Side-blotched Lizard (*Uta stansburiana*) for example, follow an inverse geographic size cline (larger at warmer temperatures; Parker and Pianka 1975), and have been shown to become larger in response to anthropogenic warming (Stanley et al. 2020). The Western Fence Lizard (*Sceloporus occidentalis)* also follow an inverse geographic size cline (larger at warmer temperatures; Sinervo et al. 1991) but have been shown to become smaller in response to anthropogenic warming (Stanley et al. 2020). Thus, questions remain as to whether reptile responses to climate warming may be predicted by geographic size clines of individual species.

Existing evidence also suggests that for reptiles and other species, females and males may differ in their response to climate changes (Tryjanowski et al. 2006; Sheridan et al. 2018; Wilson et al. 2019; Stanley et al. 2020; Wonglersak et al. 2020). Size of females and males are likely subject to different selection pressures, so examination of sex-specific responses to climate change will help determine proximate and ultimate mechanisms driving size changes, and ultimately improve predictions of how ongoing climate change will impact populations and communities. Collectively, theory and existing evidence suggest that: (1) reptiles are likely to respond strongly to anthropogenic climate change due to the temperature-size rule and the relationship between temperature and metabolism; (2) geographic size clines may be a predictor of size responses to climate change in reptiles; and (3) reptiles may exhibit sex-specific responses to climate change. To further our knowledge in these three key areas, we examined size of females and males from the *Sceloporus undulatus* species complex, using museum specimens collected from 1899–2014. We used specimens from 1899–1960 to establish whether this group exhibits geographic size clines, and then examined how climate and size changed over the study period, as well as whether size is predicted by temperature and precipitation. We expected that if this group exhibited geographic size clines, they would become smaller with warming temperatures across the range of sampled sites.

Materials and Methods

Study species.—We examined the Eastern Fence Lizard (*Sceloporus undulatus*) species complex as these lizards are abundant in museum collections, with more than 100 y of collected specimens. We recognize that *S. undulatus* represents a species complex, but due to the taxonomic uncertainty of species boundaries noted in Leaché and Reeder (2002), and hybridization at putative species boundaries (Leaché and Cole 2007), we chose to follow current naming by the housing institution. The Reptile Database (https://reptile-database.reptarium.cz/) acknowledges that taxonomy of this species group needs updating but continues to list all states within our study as part of the range of *S. undulatus.* Numerous other museums such as American Museum of Natural History and Smithsonian continue to list *S. undulatus* as the species name for holdings from each of the states in our study. Further, Leaché and Reeder (2002) note that morphological variation within each of their proposed species is as great or greater than variation between species, so we have chosen to examine the influence of climate on size of individuals from this species complex, rather than for individual purported species from this group whose boundaries remain uncertain.

Body size.—We examined all specimens labeled *Sceloporus undulatus* at the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA, and selected for our dataset adults (> 41 mm SVL; see below) with data on latitude, longitude, and year of collection. A single researcher (CJ) measured all individuals for snout-vent length (SVL) to avoid inter-individual measurement bias (Lee 1982). This person measured all specimens with calipers, and all specimens were manually and gently flattened to be straight if they were not already so. We excluded from our study any specimens that could not be laid flat and straight. Our dataset contained SVL of 672 individuals (328 females; 344 males) collected from 1899–2014 (Fig. 1). Previous work has demonstrated that this species group varies in size across their range, with hatchlings ranging from 21–30 mm SVL (Tinkle and Dunham 1986) and minimum SVL of mature females ranging from 47–66 mm (Tinkle and Dunham 1986). To avoid biasing our dataset towards larger individuals, however, we only used the minimum size of sexually mature males (based on the presence of enlarged anal pores or everted hemipenes) across all locations (41 mm SVL; unpubl. data) as the threshold for inclusion in our dataset. We classified individuals with enlarged anal pores or everted hemipenes as male, and individuals > 41 mm SVL that lacked enlarged anal pores or everted hemipenes as female.

Environmental data.—For each specimen, we extracted mean annual temperature (˚C, Tm) and total annual precipitation (mm) for its specific latitude, longitude, and year of collection from the PRISM dataset (http://prism.oregonstate.edu), which has a 30 arc-second resolution, in ArcGIS Pro v2.5.2 (Esri, Redlands, California, USA). We also downloaded mean temperature for June, July, and August (the three warmest months of the year) using the PRISM dataset and calculated mean temperature of the warmest quarter (°C, TWQ) in ArcGIS Pro using raster calculator. For each specimen, we extracted mean temperature of the warmest quarter for its specific latitude, longitude, and year of collection in ArcGIS Pro. Elevation was extracted in ArcGIS Pro,

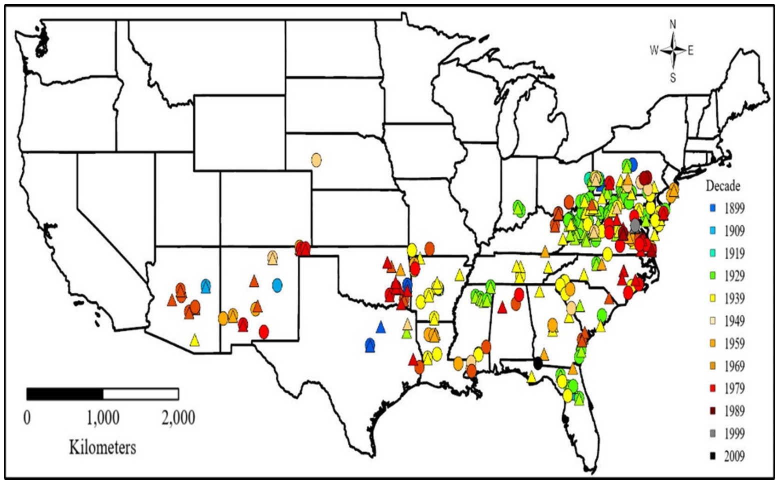

Figure 1. Collection localities of the Eastern Fence Lizard (*Sceloporus undulatus*) species group specimens (circles: females; triangles: males) used in the present study.

from the U.S. Geologic Survey (USGS) EarthExplorer (https://earthexplorer.usgs.gov/) digital elevation model map at 30 m resolution, based on latitude and longitude of collection of each specimen.

Data preparation and analyses.—We scaled annual mean temperature, mean temperature of the warmest quarter, total annual precipitation, elevation, latitude, and year of collection in R (R Core Team 2020) using the scale function, for use in models exploring the impact of environment on size. We used the natural log (ln) of SVL in analyses to meet assumptions of normality. To account for differences in climate across latitude, we grouped individuals into latitudinal quartiles. We rounded values of latitudes to a single decimal place (e.g., 28.9), and we divided unique values into quartiles.

To establish whether the *S. undulatus* complex exhibited geographic size clines, we analyzed change in lnSVL with Mixed Effect models (Zuur et al. 2009) containing scaled values for latitude and elevation as fixed effects, and sex as a random effect (random intercept; Table 1). This analysis contained only data from 1960 and earlier, given that 1960 is generally acknowledged as the onset of rapid climate warming (Girvetz et al. 2009). To determine how climate at sampled locations has changed over time, we analyzed changes in scaled values of temperature, temperature of the warmest quarter, and precipitation over time separately, with Mixed Effect models containing scaled values of elevation and year as fixed effects, and latitudinal quartile as a random effect (random intercept; Table 2). To determine how size has changed over time, we analyzed change in lnSVL with Mixed Effect models containing scaled values for elevation and year as fixed effects, and latitudinal quartile as a random effect (random intercept; Table 3). This test was performed in part to make our results comparable with other studies on this subject, which separately examined change in climate over time, and change in size over time, but did not directly examine the link between climate and size (Yom-Tov and Yom-Tov 2004; Okamiya et al. 2021). Finally, to determine enviornmental drivers of observed changes, we tested whether size (lnSVL) of each sex was predicted by scaled values of temperature (Tm and TWQ, separately), precipitation, or their interaction, using these as fixed effects and latitudinal quartile as a random effect (random intercept; Table 4). We perfomed all analyses in R (R Core Team 2020).

Table 1. Estimates of fixed effects from the Generalized Linear Mixed Model quantifying changes in body size (lnSVL) of the Eastern Fence Lizard (*Sceloporus undulatus*) across latitude and elevation from 1899–1960. Model 1 (model structure: lmer(lnSVL~Lat_cs*Elev_cs + (1|Sex))) based on 405 size, latitude, and elevation values. Latitude and elevation were scaled in R prior to analyses to meet assumptions of linear modeling. The abbreviations SE = standard error and df = degrees of freedom.

	Estimate	SE	df	*t*	*P*
Model 1					
Intercept	4.0728	0.035	1.00	115.96	0.005
Lat_cs	0.0651	0.007	400.09	8.906	< 0.001
Elev_cs	-0.0184	0.007	400.03	-2.590	< 0.001
Lat_cs:Elev_cs	0.0015	0.008	400.31	0.180	0.857

Results

We found no interaction between latitude and elevation (Table 1), and found that the lnSVL of the *S. undulatus* group varied with latitude as predicted by the temperature-size rule (smaller at lower latitudes; fixed effect estimate = 0.065, standard error = 0.007, $P < 0.001$), but size was inversely related to elevation (-0.018, 0.007, $P < 0.001$). Mean annual temperature (0.18, 0.019, $P < 0.001$) and mean temperature of the warmest quarter (0.24, 0.026, P < 0.001) were positively related to an interaction between

Table 2. Estimates of fixed effects from the Generalized Linear Mixed Model quantifying changes in annual mean temperature (Model 2), temperature of the warmest quarter (Model 3) and total annual precipitation (Model 4) in the sampled areas of the USA. Models 2 (model structure: lmer(Temp_cs~Year_cs*Elev_cs+(1|LatQuart))), 3 (model structure: lmer(TempWQ_cs~Year_cs*Elev_cs+(1|LatQuart))), and 4 (model structure: lmer(Precip_cs~Year_cs*Elev_cs+(1|LatQuart))) are based on 672 temperature, precipitation, and elevation values spanning 115 y (1899–2014). Year and elevation were scaled in R prior to analyses to meet assumptions of linear modeling. The abbreviations SE = standard error and df = degrees of freedom.

	Estimate	SE	df	*t*	*P*
Model 2					
Intercept	0.0545	0.473	3.00	0.115	0.915
Year_cs	0.0254	0.016	665.18	1.557	0.120
Elev_cs	-0.6205	0.017	665.16	-36.32	< 0.001
Year_cs:Elev_cs	0.1810	0.019	665.07	9.582	< 0.001
Model 3					
Intercept	0.0143	0.391	3.00	0.037	0.973
Year_cs	0.0615	0.023	665.48	2.709	< 0.001
Elev_cs	-0.6837	0.023	665.44	-28.81	< 0.001
Year_cs:Elev_cs	0.2427	0.026	665.19	9.249	< 0.001
Model 4					
Intercept	0.0045	0.121	3.03	0.037	0.973
Year_cs	0.0012	0.030	667.42	0.040	0.968
Elev_cs	-0.7062	0.032	667.42	-22.30	< 0.001
Year_cs:Elev_cs	-0.0911	0.035	667.47	-2.596	< 0.010

elevation and year indicating that for a given elevation, temperature has increased over time at our sampled sites (Table 2). Precipitation was negatively related to an interaction between elevation and year (-0.091, 0.035, $P < 0.01$), indicating that for a given elevation, precipitation decreased over time for our sampled sites (Table 2).

Female size was positively related to an interaction between year and elevation (0.021, 0.01, $P < 0.05$; Table 3), indicating that for a given elevation, female size increased over time. The same was true for male size (0.018, 0.01, P = 0.03; Table 3). The interaction between elevation and year also indicates that size increased more at high elevations than at low elevations (Fig. 2).

We tested whether there was an interaction between scaled values of precipitation and both mean annual temperature and mean temperature of the warmest quarter, for female and male size (lnSVL) separately. For both males and females, there was a marginally significant interaction between temperature (Tm and TWQ) and precipitation (Table 4). These data indicate that as temperatures warm, individuals will increase in size in dry areas, but decrease in size in wet areas (Fig. 2). This supports the above data showing that over the

Table 3. Estimates of fixed effects from the Generalized Linear Mixed Model quantifying changes in size (lnSVL) of the Eastern Fence Lizard (*Sceloporus undulatus*) in the USA. Model 5 is based on 328 female size values spanning 103 years (1899–2002). Model 6 is based on 344 male size values spanning 155 years (1899–2014). Model structure for both is lmer(lnSVL~Year_cs*Elev_cs + (1|LatQuart)). Year and elevation were scaled in R prior to analyses to meet assumptions of linear modeling. The abbreviations SE = standard error and df = degrees of freedom.

	Estimate	SE	df	*t*	*P*
Model 5					
Intercept	4.101	0.039	3.003	106.0	< 0.001
Year_cs	-0.0001	0.009	323.70	-0.011	0.991
Elev_cs	0.0075	0.009	323.50	0.828	0.408
Year_cs:Elev_cs	0.0212	0.011	322.00	1.974	0.049
Model 6					
Intercept	4.044	0.034	2.957	119.3	< 0.001
Year_cs	0.026	0.007	339.57	3.768	< 0.001
Elev_cs	-0.011	0.008	339.49	-1.345	0.180
Year_cs:Elev_cs	0.018	0.008	338.46	2.225	0.027

past 115 y, temperatures have increased, precipitation has decreased, and body size of individuals in our study group has increased.

Discussion

We demonstrate that the *Sceloporus undulatus* species complex are larger at higher latitudes. We therefore predicted that as temperatures increased, size of individuals would decline. Our results demonstrate that temperature has increased and precipitation has declined at sampled sites, and sizes of both males and females have increased over the past 115 y. We also found that size is predicted by an interaction between temperature and precipitation for both males and females, indicating that as temperatures warm, members of this species group will get larger in dry areas and smaller in wet areas, in accordance with the Desiccation Resistance Hypothesis, which states that individuals are larger in dry conditions than in wet conditions to reduce desiccation risk (Nevo 1973; Bujan et al. 2016). Our results were similar for males and females, indicating a lack of sexual dimorphism in size response to climate change.

While many squamates exhibit reverse-geographic size clines (larger in warmer environments; Ashton and Feldman 2003), we found that individuals in the *S. undulatus* species complex are smaller at lower latitudes, similar to earlier results for *Sceloporus undulatus* (*sensu lato*; Angilletta et al. 2004). Thus, we expected to see size declines associated with warmer temperatures; however, we found that individuals increased in size over the last century, in conjunction with increases in temperature and

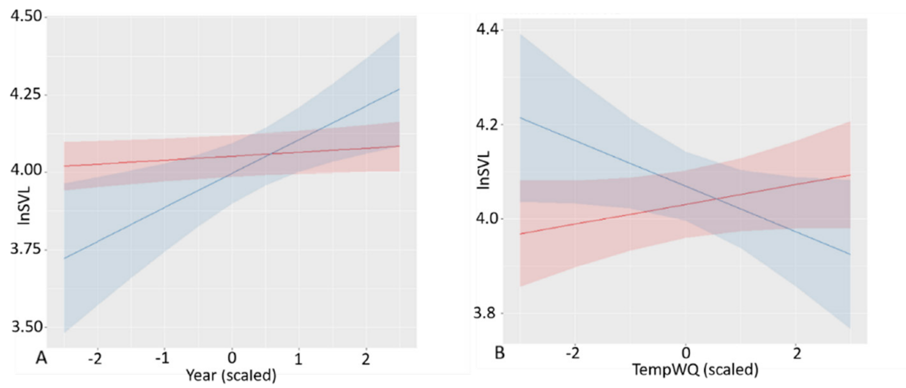

Figure 2. Predicted values of lnSVL of male the Eastern Fence Lizard (*Sceloporus undulatus*) as a function of (A) scaled year for high (blue) and low (red) elevations, and (B) scaled temperature of the warmest quarter for high (blue) and low (red) levels of precipitation. Shading shows 95% confidence intervals.

declines in precipitation. *Sceloporus occidentalis* follows a reverse geographic size cline (Sinervo et al. 1991), but was found to decrease in size from 1995–2016 (Stanley et al. 2020). Thus, there is no evidence that geographic size clines accurately predict responses to climate change

Table 4. Estimates of fixed effects from mixed-effect models quantifying changes in size (lnSVL) of female and male the Eastern Fence Lizard (*Sceloporus undulatus*) in the USA. Models 7 (model structure: lmer(lnSVL~ Temp_cs*Precip_cs + (1|LatQuart))) and 8 (model structure: lmer(lnSVL~ TempWQ_cs* Precip_cs + (1|LatQuart))) were both run for females (n = 328) and males (n = 344) separately. Temperature, temperature of the warmest quarter, and precipitation were scaled in R prior to analyses to meet assumptions of linear modeling. The abbreviations SE = standard error and df = degrees of freedom.

	Estimate	SE	df	*t*	*P*
Model 7 (female)					
Intercept	4.113	0.032	2.41	128.6	< 0.001
Temp_cs	-0.005	0.013	130.98	-0.416	0.678
Precip_cs	-0.018	0.009	321.33	-2.045	0.042
Temp_cs:Precip_cs	-0.015	0.008	289.17	-1.766	0.078
Model 8 (female)					
Intercept	4.111	0.030	2.670	135.6	< 0.001
TempWQ_cs	-0.012	0.011	239.50	-1.101	0.272
Precip_cs	-0.018	0.008	321.78	-2.190	0.029
TempWQ_cs:Precip_cs	-0.016	0.008	305.77	-1.923	0.056
Model 7 (male)					
Intercept	4.050	0.034	2.64	119.6	< 0.001
Temp_cs	-0.007	0.013	154.24	-0.521	0.603
Precip_cs	0.007	0.008	336.77	0.857	0.392
Temp_cs:Precip_cs	-0.012	0.007	330.02	-1.611	0.108
Model 8 (male)					
Intercept	4.049	0.032	2.775	126.2	< 0.001
TempWQ_cs	-0.013	0.011	266.53	-1.190	0.235
Precip_cs	0.008	0.007	339.00	1.083	0.280
TempWQ_cs:Precip_cs	-0.014	0.007	335.79	-1.926	0.055

in *Sceloporus*, and it may be that precipitation, not temperature, is a stronger factor in explaining body size of squamates.

Of the three studies (covering six species) that have explicitly examined the link between body size and climate change in reptiles (Chamaille-Jammes et al. 2006; Lopez-Calderon et al. 2017; Stanley et al. 2020), only one (Stanley et al. 2020) tested the effects of temperature and precipitation on four species of reptiles. They found that precipitation had a more consistent impact on size than temperature. Precipitation was positively related to size in all cases where it was included in the best model, while temperature had a positive effect in two cases and a negative effect in one case (Stanley et al. 2020). This, combined with our results, suggests that for reptiles, precipitation is an important factor predicting size, and warrants further attention as studies continue to examine the impacts of climate change on size. We encourage researchers examining the impacts of climate change on body size to include precipitation, and the interaction of precipitation with temperature, in their analyses. Further, observational studies of *S. undulatus* from multiple parts of their range have suggested that latitudinal size may be driven by predation (Tinkle 1972; Tinkle and Ballinger 1972; Tinkle and Dunham 1986). Thus, it is possible that changes in predation pressure also may be contributing to observed size changes in this species group. Changes in predation pressure are impossible to determine from museum specimens, however, so long term field studies would be required to determine the influence of predation on observed size changes over time.

Reptiles represent the least-studied vertebrate group in the field of body size responses to climate change yet are among the most threatened globally (Lovich et al. 2018). Without sufficient data to predict how reptiles will respond to continued climate change, populations are likely to continue to be impacted. We recommend additional studies examine squamate size responses to climate change, as well as studies examining turtle size responses. No data directly examining turtle size responses to climate change exist, but turtles are known to follow geographic size clines (Ashton and Feldman 2003) and are the most threatened vertebrate group (Rhodin et al. 2018). Thus, understanding how turtles and other reptiles respond to climate change will aid in predicting future population trends for these taxa.

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