

# Thermoregulation in a saxicolous population of the lizard *Urosaurus ornatus* from the northern Chihuahuan Desert, Mexico

Hector Gadsden<sup>1</sup>, Rafael A. Lara-Reséndiz<sup>2,3</sup>, Nallely F. Minjarrez-Flores<sup>4</sup>, Ana Gatica-Colima<sup>4</sup>,  
Geoffrey R. Smith<sup>5,\*</sup>

**Abstract.** Environmental temperatures often regulate the activity and physiological processes of ectotherms. Because environmental temperatures can vary significantly among seasons, lizards exposed to different thermal conditions in different months could differ in how they thermoregulate or behave. Here, we present a combination of field, laboratory, and modeling approaches to examine thermoregulation, habitat thermal quality, and hours of thermal restriction on activity in a saxicolous population of *Urosaurus ornatus* in two thermally contrasting months (June and October) in a micro-insular mountain system in the northern Chihuahuan Desert in Mexico. Both active and preferred body temperatures did not vary between months. In this population, *U. ornatus* is an active thermoregulator with highly accurate and efficient thermoregulation despite the thermal quality in both months. However, during the breeding season (June) activity is restricted (i.e., high number of hours of restriction) compared to the non-breeding season (October). Therefore, our results suggest that this saxicolous population of *U. ornatus* could be threatened by global climate change and it is essential to determine a conservation strategy for this population.

**Keywords:** arid environment, hours of thermal restriction, operative temperatures, preferred temperature, thermal quality, thermoregulatory efficiency.

## Introduction

Thermoregulation is a critical aspect of the biology of ectotherms, such as reptiles, because of the influence of body temperature on their ecology, physiology, evolution and behaviour (Avery, 1979; Huey, 1982; Angilletta, 2009).

Thermoregulation allows ectotherms to maintain relatively high body temperatures ( $T_b$ ) within or near their optimal thermal range, which determines their daily biological activities (Bartholomew, 1982). Ectotherms in environments with high temperatures have an increased risk of overheating which often results in decreased activity time to avoid high environmental temperatures (Avery, 1982; Huey, 1982) which can increase extinction risk, especially in a warming climate (Sinervo et al., 2010, 2018; Medina et al., 2016; Pontes-da-Silva et al., 2018). Therefore, studies on the thermoregulation of ectotherms that live in such environments are essential to evaluate the capacity of different species to minimize the effects of thermally extreme environments on body temperature (Kearney et al., 2009; Kubisch et al., 2016; Lara-Reséndiz et al., 2014, 2015; Kirchof et al., 2017).

In lizards, thermoregulatory behaviour can vary seasonally and change thermoregulatory

- 1 - Instituto de Ecología, A. C.-Centro Regional del Bajío, Av. Lázaro Cárdenas 253, C. P. 61600, Pátzcuaro, Michoacán, México
- 2 - Centro de Investigaciones Biológicas del Noroeste, Playa Palo de Santa Rita Sur, 23096 La Paz, Baja California Sur, México
- 3 - Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales. Centro de Zoología Aplicada. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto de Diversidad y Ecología Animal (IDEA), Rondeau 798, X5000AVP, Córdoba, Argentina
- 4 - Instituto de Ciencias Biomédicas, Departamento de Ciencias Químico-Biológicas, Programa de Biología. Anillo envolvente del PRONAF y Estocolmo s/n. C. P. 31310. Ciudad Juárez, Chihuahua, México
- 5 - Department of Biology, Denison University, Granville, OH 43023, USA

\*Corresponding author; e-mail: smithg@denison.edu

efficiency ( $E$ ) (Waldschmidt, 1980; Bustos Zagal et al., 2013) because the thermal environment can vary throughout the activity season with potential consequences for body temperature or thermal tolerances. For example, daily activity patterns and preferred body temperature ( $T_p$ ) of lizards can vary significantly among seasons (Angilletta, 2001; Hult and Germano, 2015) and their thermoregulatory efficiency can vary throughout the year (Stellatelli et al., 2018; Ortega et al., 2019; Ortega and Martin-Vallejo, 2019). In addition, some desert and tropical lizards show seasonal changes in activity time or habitat use (García, 2008; Siliceo-Cantero et al., 2016) with their patterns of daily activity sometimes being bimodal during spring and summer, but unimodal in autumn (Montgomery and Mackessy, 2003; García-de la Peña et al., 2007). Such shifts in activity patterns suggest that there are behavioral changes in thermoregulatory activity (Bauwens et al., 1996; Díaz and Cabezas-Díaz, 2004; Brewster and Beaupre, 2019), possibly related to changes in temperature preferences or tolerances (Domínguez-Guerrero et al., 2019). In addition to behavioral adjustments, reptiles may physiologically compensate for harsh thermal environments through plastic shifts in their thermal requirements or thermal tolerances which favor performance in sub-optimal conditions (Stellatelli et al., 2018; Domínguez-Guerrero et al., 2019).

Tree lizards of the genus *Urosaurus* live in a diversity of habitats ranging from xeric to mesic conditions (Wiens, 1993) and each habitat presents a unique thermal environment. However, differences in environmental temperatures among habitats may not necessarily lead to differences in body temperature of the lizards. For example, desert and mountain populations of *U. ornatus* in Arizona and New Mexico experienced different environmental temperatures, but lizards in the two populations did not differ in body temperature or thermal tolerance (Smith and Ballinger, 1994, 1995).

Our objectives are to examine habitat thermal quality, thermoregulatory accuracy, efficiency

of thermoregulation, and hours of thermal restriction of activity in two thermally contrasting months for *U. ornatus* in a population in the Chihuahuan Desert in northern Mexico. Of specific interest is that this particular population of *U. ornatus* uses rock microhabitats (i.e., saxicolous) compared to other populations of *U. ornatus* that occur primarily on trees (i.e., arboreal). First, we determined the relationship between  $T_b$  and environmental temperatures ( $T_a$  and  $T_s$ ; Huey and Slatkin, 1976). Second, we evaluated habitat thermal quality and the accuracy and efficiency of thermoregulation according to Hertz et al. (1993) and Blouin-Demers and Weatherhead (2001). Lastly, we evaluated the hours of thermal restriction during activity time, following Sinervo et al. (2010).

Our study is particularly relevant because this population of *U. ornatus* is in a relatively warm portion of the south-central range of this species in northern Chihuahua, and population extirpations are expected due to climate change in this geographical area (Sinervo et al., 2017). In addition, this population is strictly confined geographically within a small and isolated rocky, low-elevation mountain range, which does not allow potential migration to a cooler climate at higher elevations or latitudes with temperatures more suitable for survival (Parmesan, 2006; Guralnick and Pearman, 2010). Thus, this population of *U. ornatus* is potentially vulnerable to the increasing effects of global warming. The population of *U. ornatus* that we studied is further unique in that the rocky habitats in which it occurs there is little availability of shade. The relative lack of shade differs from that of typical populations of arboreal *U. ornatus* that are found in areas with trees. In its typical arboreal habitat, the chances of active thermoregulation by *U. ornatus* could be higher with lower thermoregulatory costs, since trees provide perches where lizards may cool down by convection, avoiding the conductive heat of substrates such as rocks or ground when temperatures are high (Bakken, 1989). For example, the presence of a diversity of bushes of different

heights allows the desert iguana *Dipsosaurus dorsalis* to thermoregulate by selecting a perch height that provides the appropriate air temperature and wind conditions to maintain an appropriate body temperature, thereby considerably extending the time available for activity (Porter et al., 1973). Consequently, studies of different thermoregulatory indices of this class of ectothermic animals in rocky and arboreal habitats are essential to determine specific conservation strategies for each type of population.

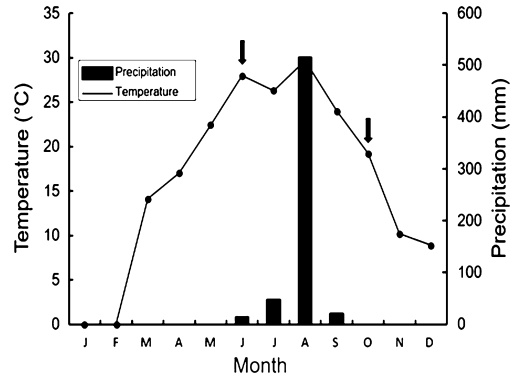
## Materials and methods

### Study species

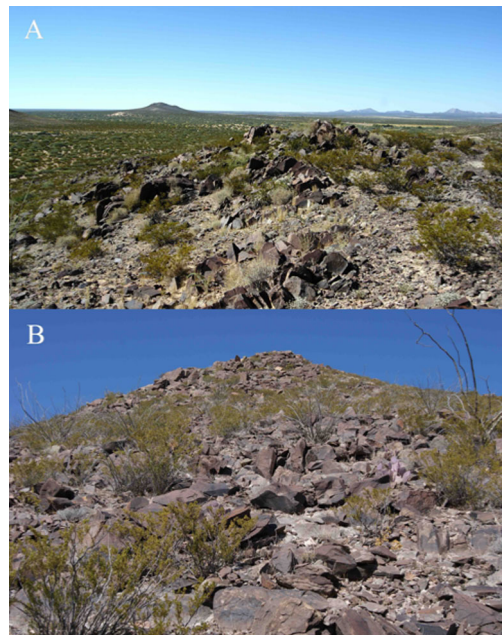
*Urosaurus ornatus* (Ornate Tree Lizard) is a relatively small, diurnal lizard (maximum SVL = 68 mm). This species is widely distributed from extreme southwestern Wyoming, western Colorado, southern Nevada, Utah, southeastern California, Arizona, New Mexico, and Texas in the United States to northeastern Baja California, Sonora, central Sinaloa, several islands in the Gulf of California, Chihuahua, northern Coahuila, and Tamaulipas in Mexico; and its elevational range extends from sea level to around 2770 m (Lemos-Espinal and Smith, 2007; Feldman et al., 2011). Our study population is located in the south-central portion of its range in northern Chihuahua. *Urosaurus ornatus* occupy two main structural habitats: trees (arboreal) or rocky outcrops and canyons (saxicolous) but it is rarely found in open habitats without structural hiding places (Miles, 1994; Herrel et al., 2001). *Urosaurus ornatus* is oviparous and can be observed in the field from April to late November (Lemos-Espinal and Smith, 2007; Goldberg, 2014), although the greatest reproductive activity is during the spring and summer (Goldberg, 2013, 2014).

### Study area

We conducted field work in the Sierra de Samalayuca, where *U. ornatus* is saxicolous. This site is a small, narrow, and isolated mountainous system (~13 km long and ~3 km wide) located within an endorheic basin of the northern Chihuahuan Desert to 45 km south of Ciudad Juarez, Chihuahua, Mexico (31°21'40.90"N, 106°34'12.65"W, elevational range: 1450-1750 m). The study area was located within the natural protected area of Médanos de Samalayuca. The climate of this region is dry, temperate, and seasonal; the highest temperature and rainfall occur in summer (July-September; fig. 1). Mean annual precipitation is 212 mm/year and mean annual temperature is 20.0°C, but it can vary between -16 and 41.2°C (Enríquez-Anchondo, 2003; Quiñones Martínez et al., 2018). The vegetation in Sierra Samalayuca is dominated by *Echinocactus parryi*, *Opuntia arenaria*, *Dasylirion acrotiche*, *Larrea tridentata* and grasses (Rzedowski, 1978; Enríquez-Anchondo, 2003), but arboreal forms are absent (fig. 2). Throughout the study site, rock faces with crevices are numerous.



**Figure 1.** Monthly mean temperature and precipitation (2010) from Ciudad Juárez, Chihuahua, Mexico (UACJ weather station, 2010). The arrow points to the average temperature of the two months (June and October) in which this study was conducted.



**Figure 2.** Photographs of the study site. A) A panoramic view; and B) highlighting the rocky elements of the landscape and the absence of arboreal vegetation.

### Field and laboratory work

We performed fieldwork in June and October 2010. We captured by noose or hand 18 and 17 adult lizards (>45 mm SVL) in June and October, respectively. Immediately after

capture, we recorded body temperature ( $T_b$ ) using a digital thermometer (Fluke™ model 51-II) with the thermocouple introduced one centimeter into the cloaca, air temperature ( $T_a$ ; thermometer 1 cm above substrate where individual was first observed), and substrate temperature ( $T_s$ ; thermometer touching substrate where individual was first observed). We also recorded time of capture, sex, SVL (mm), and location with a Garmin Etrex™ GPS receiver (Garmin Ltd., Olathe, Kansas, USA). We excluded lizards that required >45 seconds to capture from analysis and we took temperatures only from active lizards. Based on our observations, we define the activity period as the time the first lizard was observed in the morning to the end of activity in the afternoon. We subsequently transported all lizards to the laboratory and maintained them at 25°C in plastic containers with rocky soil and hydrated with a sprinkler.

Two days after capture, we recorded the preferred body temperature ( $T_p$ ) in a laboratory thermal gradient consisting of a wooden box with  $1.5 \times 1.0 \times 0.5$  m ( $l \times w \times h$ ) dimensions divided into 10 15-cm wide tracks using insulation barriers to prevent behavioral interactions between adjacent lizards (Lara-Resendiz et al., 2015; Gadsden et al., 2015, 2018). The box was housed in a room maintained at a constant temperature of 20°C by air conditioning. We placed lamps at one end and the center of the box at different heights to generate a thermal gradient from 20–50°C. This type of thermal gradient has been widely used with lizards (Camacho and Rusch, 2017). Lizards remained in the gradient from 0700 to 1800 h. We recorded  $T_b$  every hour starting at 0900 h with the same digital thermometer used in the field. We consider the extreme  $T_p$  values reached by lizards in the thermal gradient as voluntary thermal minimum ( $VT_{\min}$ ) and maximum ( $VT_{\max}$ ) (Camacho and Rusch, 2017). We used the percentiles 25 and 75 of the  $T_p$  for each month ( $T_{p25}$  and  $T_{p75}$ ) as the  $T_p$  interquartile range (Hertz et al., 1993). All lizards were released at their capture sites at the conclusion of the laboratory trials.

We recorded operative temperature ( $T_e$ ) using four datalogger sensors connected to previously field calibrated PVC models of *Sceloporus maculosus* (Rodríguez-Muñoz, 2015), similar in length and cylindrical shape to *U. ornatus* ( $48 \times 15$  mm, mean SVL and body diameter respectively of an adult tree lizard). Rodríguez-Muñoz (2015) found a highly significant relationship between  $T_b$  of restrained lizards of *S. maculosus* and  $T_e$  of PVC models during calibration ( $r = 0.98$ ,  $n = 56$ ,  $P < 0.001$ ;  $T_b = 11.278 + 0.5706T_e$ ). Thus, we assumed the lizard models accurately measured the available  $T_e$  for the tree lizards in this study, especially during hours of activity ( $T_b > 26^\circ\text{C}$ ). Models were sealed with silicone at each end and painted with reflective spray paint (Rustoleum™ gray primer) to approximate the reflectivity of phrynosomatids (Adolph, 1990; Lara-Resendiz et al., 2015). In each month the models were placed in two rocky microsites occupied by the lizards (two in sunny sites and two in shade; Dzialowski, 2005; Sinervo et al., 2011). We recorded temperatures every 30 min from 0800–1900 h for 2 days to estimate the distribution of  $T_e$  throughout the potential daily activity period observed in the field.

### Thermoregulation indices

Because mean  $T_e$  differed between months (see Results), we calculated thermoregulation indices and hours of restriction in activity separately for each month. We used data on field ( $T_b$  and  $T_e$ ) and laboratory ( $T_p$ ) to calculate indices for thermoregulatory accuracy ( $d_b$ ) and habitat thermal quality ( $d_e$ ) (Hertz et al., 1993). If  $T_b$  or  $T_e < T_p$  interquartile range ( $T_{p75}-T_{p25}$ ), then  $d_b = T_{p25}-T_b$  and  $d_e = T_{p25}-T_e$ , respectively. If  $T_b$  or  $T_e > T_p$  interquartile range then  $d_b = T_b-T_{p75}$  and  $d_e = T_e-T_{p75}$ , respectively. We used the value of  $T_b-T_p$  and  $T_e-T_p$  deviations. When  $T_b$  or  $T_e$  values were within the  $T_p$  interquartile range,  $d_b$  and  $d_e$  were considered equal to zero. Therefore, when  $d_b$  or  $d_e$  has values close to zero, it indicates that lizards are accurately maintaining temperatures within their preferred range and a high thermal quality of the habitat, respectively. Subsequently, thermoregulatory efficiency ( $E$ ) was calculated in June and October using the equation:  $E = 1 - (d_b \text{ mean}/d_e \text{ mean})$ . An  $E$  index near to one is indicative of an actively thermoregulating organism. In contrast, an  $E$  value equal or close to zero is indicative of a thermoconformer that is not regulating temperatures actively (see more details in Hertz et al., 1993).

Given that the  $E$  index has been shown to produce spurious representation of reptile thermoregulation (Blouin-Demers and Nadeau, 2005), we also use the alternative  $E$  index proposed by Blouin-Demers and Weatherhead (2001), and calculated as  $d_e - d_b$ . In this case, thermoregulatory efficiency represents the magnitude of departure from thermoconformity of an ectotherm in which a value of 0 indicates perfect thermoconformity; a high value of this index indicates active thermoregulation and a negative value corresponds to avoidance of preferred temperatures.

Sinervo et al. (2010) estimated the number of hours per day potentially available for activity ( $h_a$ ) as the time when  $T_e$  was within the  $T_p$  interquartile range, and the hours of thermal restriction ( $h_r$ ), also known as the forced inactivity hours, as the time when  $T_e$  exceeded mean  $T_p$  (also see Sinervo et al., 2011; Lara-Resendiz et al., 2015). However, in this study, we estimated  $h_a$  as the time during which at least one model registered a  $T_e$  higher than the lower bound of  $T_p$  and lower than the upper bound of  $T_p$  (also called voluntary thermal minimum [ $VT_{\min}$ ] and voluntary thermal maximum [ $VT_{\max}$ ], respectively; Camacho and Rusch, 2017), while  $h_r$  was calculated when the  $T_e$  exceeded  $VT_{\max}$ . According to our measurements in the field and laboratory, the lowest voluntary active  $T_b$  of *U. ornatus* was 26°C and the maximum voluntary active  $T_b$  was 38°C, both values was assumed to be the thermal threshold for activity and restriction. This range represents a broader thermal threshold of activity ( $VT_{\min}-VT_{\max}$ ), because we consider that lizards could still be active in contrast with Sinervo et al (2010), who consider the threshold when  $T_e$  exceeded mean  $T_p$ . The  $VT_{\min}-VT_{\max}$  range as a threshold to calculate  $h_a$  and  $h_r$  has been used in recent studies on the extinction risk of lizards (e.g., Lara-Resendiz et al., 2019; Kubisch et al., 2016; Yuan et al., 2018). Here we calculated and compared  $h_a$  and  $h_r$  for each season (June and October).

To estimate the percentage of time  $T_e$  exceeds the critical thermal maximum ( $CT_{\max}$ ) in *U. ornatus* for each month,

we used the  $CT_{Max}$  found by Gilbert and Miles (2017). However, it would be necessary to obtain more field data on  $T_b$  covering the complete activity cycle of this population to confirm the true minimum activity  $T_b$  (Angert et al., 2011).

We evaluated the assumptions of normality and homogeneity of variances using Kolmogorov-Smirnov and Levene's tests, respectively. Since the assumptions of parametric tests were not met, we used non-parametric analyses. We first used a Kruskal-Wallis Test to compare  $T_b$  and  $T_p$  among the four possible combinations of sex and month (e.g., June males vs. June females vs. October males vs. October females) to approximate a two-way ANOVA. Since these tests were not significant (see Results), we compared the different thermoregulation indices ( $T_b$ ,  $T_p$ ,  $T_c$ ,  $d_b$ ,  $d_c$ ,  $h_r$ , and  $h_a$ ) between months (with sexes pooled) and sexes (with month pooled) using non-parametric Mann-Whitney tests. We used a simple regression analysis to determine the relationship between  $T_b$  and environmental temperatures ( $T_a$  and  $T_s$ ). We calculated means and standard errors of  $E$  and  $d_c-d_b$  for June and October using a bootstrapping resampling method, using the average  $d_b$  for each month and 1000 iterations of  $d_c$  (see Lara-Resendiz et al., 2015), and then in both cases ( $E$  and  $d_c-d_b$ , respectively) we applied a Kruskal-Wallis test on the bootstrapped values to analyze the difference between months. Finally, field  $T_b$  observations that fell above or below the  $T_p$  interquartile range were used to define the direction of the  $T_b$  deviation with respect to the  $T_p$  interquartile range, as well as the percentage of  $T_b$  maintained within the  $T_p$  interquartile range (Hertz et al., 1993).

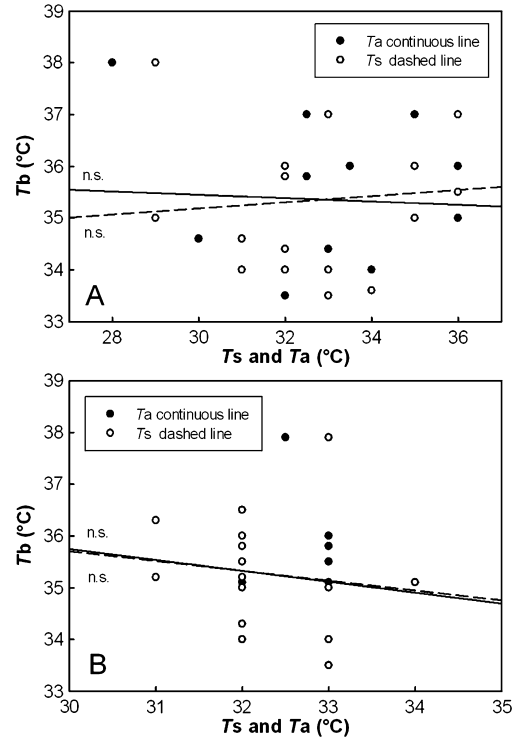
We used XLSTAT-Ecology ([www.xlstat.com/es/soluciones/ecology](http://www.xlstat.com/es/soluciones/ecology)) and SigmaPlot 12 for statistical analyses and graphing. The significance value for all statistical tests was  $P \leq 0.05$  and  $P$  values are two-tailed. Means are given  $\pm 1$  SE.

## Results

### Field $T_b$ and $T_p$

There was no significant difference in  $T_b$  among June males, June females, October males, and October females (Kruskal-Wallis Test  $H = 0.73$ ,  $df = 3$ ,  $P = 0.87$ ).

In June, mean  $T_b$  (females and males pooled) was  $35.3 \pm 0.3^\circ\text{C}$  (range:  $33.5-38.0^\circ\text{C}$ ;  $n = 18$ ). Mean  $T_s$  was  $32.9 \pm 0.5^\circ\text{C}$  and mean  $T_a$   $33.0 \pm 0.5^\circ\text{C}$ . There was no significant difference in mean  $T_b$  between females ( $35.3 \pm 0.6^\circ\text{C}$ ; range:  $33.6-37.0^\circ\text{C}$ ) and males ( $35.5 \pm 0.4^\circ\text{C}$ ; range:  $33.5-38.0^\circ\text{C}$ ; Mann-Whitney  $U = 26.5$ ,  $n_{females} = 7$ ,  $n_{males} = 11$ ,  $P = 0.7$ ). Body temperature was not related to  $T_s$  ( $n = 18$ ,  $r^2 =$



**Figure 3.** Relationship between body temperature ( $T_b$ ) and air temperature ( $T_a$ ) and substrate temperature ( $T_s$ ) of *Urosaurus ornatus* at Sierra de Samalayuca, Chihuahua, Mexico in A) June and B) October.

$0.009$ ,  $df = 16$ ,  $P = 0.7$ ) or  $T_a$  ( $n = 18$ ,  $r^2 = 0.003$ ,  $df = 16$ ,  $P = 0.8$ ) (see fig. 3A).

In October, mean  $T_b$  (females and males pooled) was  $35.2 \pm 0.2$  (range  $33.5-37.9^\circ\text{C}$ ;  $n = 17$ ). Mean  $T_s$  was  $32.4 \pm 0.2^\circ\text{C}$  and mean  $T_a$   $32.3 \pm 0.2^\circ\text{C}$ . There was no significant difference in mean  $T_b$  between females ( $35.6 \pm 0.6^\circ\text{C}$ ; range  $34-37.9^\circ\text{C}$ ) and males ( $35.0 \pm 0.2^\circ\text{C}$ ; range  $33.5-36.5^\circ\text{C}$ ; Mann-Whitney  $U = 19$ ,  $n_{females} = 7$ ,  $n_{males} = 10$ ,  $P = 0.3$ ). Body temperature was not related to  $T_s$  ( $n = 17$ ,  $r^2 = 0.024$ ,  $df = 15$ ,  $P = 0.5$ ) or  $T_a$  ( $n = 17$ ,  $r^2 = 0.018$ ,  $df = 15$ ,  $P = 0.6$ ) (see fig. 3B).

There was no significant difference in mean  $T_b$  (females and males pooled) between months (June  $35.4 \pm 0.3^\circ\text{C}$ , range:  $33.5-38.0^\circ\text{C}$ ,  $n = 18$ ; October  $35.2 \pm 0.2^\circ\text{C}$ , range:  $33.5-37.9^\circ\text{C}$ ,  $n = 18$ ; Mann-Whitney Range Sum Test  $t =$

0.4,  $df = 32$ ,  $P = 0.6$ ). There was no significant difference in mean  $T_b$  between females (both months pooled,  $35.2 \pm 0.3^\circ\text{C}$ ; range:  $33.6\text{--}37.0^\circ\text{C}$ ) and males (both months pooled,  $35.2 \pm 0.2^\circ\text{C}$ ; range:  $33.5\text{--}38.0^\circ\text{C}$ ; Mann-Whitney Range Sum Test  $t = -0.107$ ,  $df = 31$ ,  $P = 0.9$ ).

There was no significant difference in  $T_p$  among June males, June females, October males, and October females (Kruskal-Wallis Test  $H = 2.67$ ,  $df = 3$ ,  $P = 0.44$ ).

Mean  $T_p$  of females (both months pooled) was  $33.7 \pm 0.2^\circ\text{C}$  ( $n = 13$ , range  $27.0\text{--}38.4^\circ\text{C}$ ), and in males it was  $33.1 \pm 0.2^\circ\text{C}$  ( $n = 14$ , range  $26.0\text{--}38.0^\circ\text{C}$ ). Mean  $T_p$  did not significantly differ between the sexes (Mann-Whitney Range Sum Test  $U = 7906$ ,  $df = 25$ ,  $P = 0.2$ ).

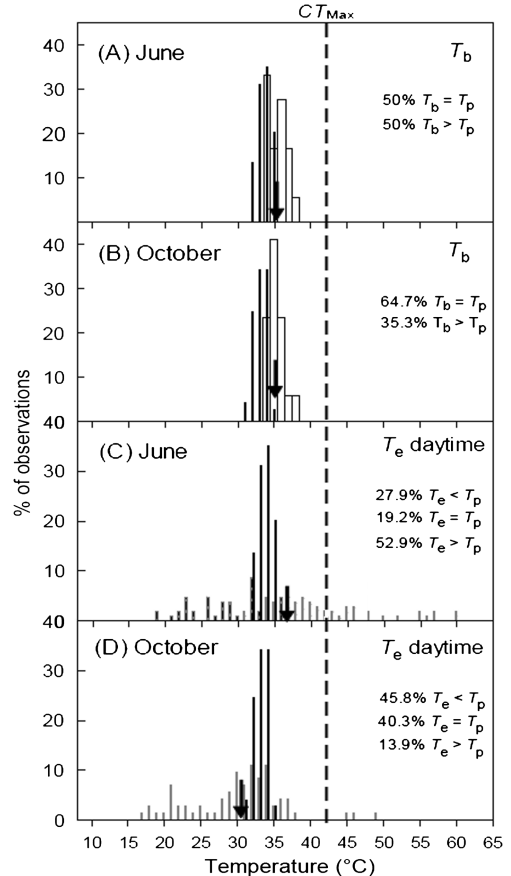
There was variation (both months pooled) of  $T_p$  throughout day (Kruskal-Wallis Test  $H = 32.2$ ,  $df = 23$ ,  $P = 0.001$ ). Therefore, we considered all data of the individuals to assess possible differences of  $T_p$  between months. In June, mean  $T_p$  (females and males pooled) was  $33.2 \pm 0.1^\circ\text{C}$  (fig. 4A,  $n = 14$ , range  $26.0\text{--}38.4^\circ\text{C}$ ), and in October it was  $33.1 \pm 0.2^\circ\text{C}$  (fig. 4B,  $n = 13$ , range  $26.0\text{--}37.0^\circ\text{C}$ ). Mean  $T_p$  did not significantly differ between months (Mann-Whitney Range Sum Test  $U = 10182.5$ ,  $df = 25$ ,  $P = 0.9$ ). Therefore, for this population of *U. ornatus* the general  $T_p$  interquartile range is  $32.0\text{--}35.0^\circ\text{C}$ .

#### Operative temperatures ( $T_e$ )

Mean operative temperature in June was  $36.2 \pm 0.8^\circ\text{C}$  (fig. 4C;  $n = 104$ , range  $19.4\text{--}59.9^\circ\text{C}$ ), and in October it was  $30.1 \pm 0.7^\circ\text{C}$  (fig. 4D;  $n = 72$ , range  $16.7\text{--}49.0^\circ\text{C}$ ). Mean  $T_e$  was higher in June than in October (fig. 5; Mann-Whitney Range Sum Test  $U = 5308.5$ ,  $df = 174$ ,  $P < 0.0001$ ).

#### Thermoregulation indices

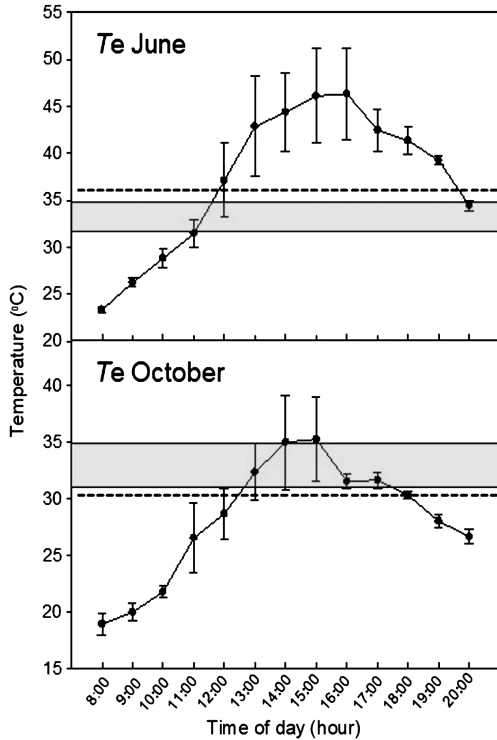
Mean  $d_b$  was  $0.7 \pm 0.2$  ( $n = 18$ ) in June and  $0.5 \pm 0.1$  ( $n = 17$ ) in October, which were not significantly different (Mann-Whitney



**Figure 4.** Distribution of field body temperatures ( $T_b$ ) of *Urosaurus ornatus* and operative temperatures ( $T_e$ ) at Sierra de Samalayuca in Chihuahua, México (June and October). The arrow points to the average of the field body temperatures (A, B) and operative temperatures (C, D). The preferred temperatures range ( $T_p$ ) in thermal gradient ( $32.0\text{--}35.0^\circ\text{C}$  and  $31.0\text{--}34.5^\circ\text{C}$ ; in June and October, respectively) is represented by black bars and field body temperatures is represented by white bars. The operative temperatures range is represented by gray bars. Maximum critical temperature ( $CT_{Max}$ ) of *U. ornatus* ( $42.3^\circ\text{C}$ ; Gilbert and Miles, 2017) is depicted by the dashed line.

Range Sum Test  $U = 161$ ,  $df = 33$ ,  $P = 0.7$ ). Thus, lizards maintained their  $T_b$  within its  $T_p$  interquartile range with similar accuracy in both months. In June, 50% of  $T_b$  records were within the  $T_p$  interquartile range, and 50% above (fig. 4A). In October, 64.7% were within the  $T_p$  interquartile range, and 35.3% above the preferred interquartile range (fig. 4B).

In June, 27.9% of  $T_e$  observations were below the  $T_p$  interquartile range, 19.2% within



**Figure 5.** Daytime variation in  $T_e$  of biophysical models in June and October at Sierra de Samalayuca, Chihuahua, Mexico. Points indicate mean  $\pm$  2 SD, dotted line indicates the average  $T_e$  from 8:00 to 20:00, and horizontal gray areas indicate  $T_p$  in the thermal gradient for *Urosaurus ornatus* (32.0–35.0°C). Notice the difference of scales.

the range and 52.9% above (fig. 4C). For this month a considerable percentage (26.9%) of  $T_e$  exceeded the  $CT_{Max}$  for *U. ornatus* of 42.3°C (Gilbert and Miles, 2017). In October, 45.8% of  $T_e$  observations were below the  $T_p$  interquartile range, 40.3% within the range and 13.9% above (fig. 4D). Nevertheless, in this month only a low percentage (4.1%) of  $T_e$  exceeded the  $CT_{Max}$  of this species.

The thermal quality index ( $d_e$ ) was estimated separately for each month (June and October) due to significant between-month differences in  $T_e$ . Mean  $d_e$  for *U. ornatus* was significantly higher in June ( $6.0 \pm 5.7$ ) than in October ( $3.9 \pm 0.5$ ) (Mann-Whitney Range Sum Test  $U = 1007$ ,  $df = 2$ ,  $P = 0.009$ ), suggesting thermal quality was lower in June than October.

Finally, the effectiveness of thermoregulation indices  $E$  and  $d_e - d_b$  indicate that *U. ornatus* was effective in regulating its body temperature. On the one hand, the  $E$  showed similar, but significantly different, values between months (BootStat June  $E = 0.88 \pm 0.01$ , and BootStat October  $E = 0.87 \pm 0.01$ ; Kruskal-Wallis Test  $H = 99.68$ ,  $df = 999$ ,  $P < 0.001$ ). On the other hand,  $d_e - d_b$  showed significantly greater thermoregulatory effectiveness in June (BootStat  $d_e - d_b = 5.2 \pm 0.01$ ) than in October (BootStat  $d_e - d_b = 3.4 \pm 0.01$ ) (Kruskal-Wallis Test  $H = 5636.36$ ,  $df = 999$ ,  $P < 0.001$ ).

#### Hours of restriction and hours of activity

June was the least suitable month due to high  $T_e$ , with an average  $h_r$  of  $6.4 \pm 0.3$  hours per day, whereas in October average  $h_r$  was  $<1$  hour per day (mean:  $0.8 \pm 0.8$  h) (Mann-Whitney Range Sum Test  $U = 130$ ,  $df = 2$ ,  $P = 0.002$ ). June was the least suitable month for activity with an average  $h_a$  of  $4.6 \pm 0.1$  h per day, compared to October which was the most suitable month for activity with an average  $h_a$  of almost eight hours per day (mean:  $7.9 \pm 0.2$  h) (Mann-Whitney Range Sum Test  $U = 142$ ,  $df = 2$ ,  $P = 0.01$ ).

#### Discussion

Our results are typical of a rocky environment with little availability of shade, unlike a “classic” tree environment, which *U. ornatus* generally inhabits. Bakken (1989) found that arboreal perches affect operative temperature as can the posture of the lizards and their location on a tree trunk relative to sun and shade. Populations of *U. ornatus* that inhabit rocks, like the one we studied, may be thermally disadvantaged if the rock habitat presents a more restricted range of thermal opportunities compared to the perches found in trees. Indeed, rocky habitats with little shade differ from typical arboreal populations of *U. ornatus* (Bakken, 1989). Despite

this, the cracks in rocks where these lizards have been observed, are a potentially important refuge to cope with the effects of high operative temperatures. However, in a typical arboreal habitat, the possibility to actively thermoregulate could be greater, representing lower thermoregulatory costs, since the thermal properties of tree perches can change greatly. Nevertheless, this is only a hypothesis that could be tested later by comparing operative temperature variation for *U. ornatus* populations in both habitat types. The models of Sears et al. (2016) showed that the spatial structure of landscape can qualitatively affect the responses of ectotherms to climate, with lizards thermoregulating more precisely when thermal resources are dispersed through space than when these are grouped together. Therefore, also it is necessary to consider spatially explicit simulations to predict the impacts of climate change at local scales.

Our limited observations of  $T_b$  and  $T_p$  in the population of *U. ornatus* that we studied are within the ranges previously found in the genus *Urosaurus* (see also the supplementary online material of Sinervo et al. (2010) for additional information on  $T_b$  and  $T_p$  in the genus *Urosaurus*), despite using a different substrate (i.e., saxicolous rather than arboreal). In addition,  $T_p$  did not differ between June and October, suggesting there may be limited or no acclimation effects on  $T_p$ . These observations lend support to the conclusion of Grigg and Buckley (2013) that this genus of lizards is relatively conservative in its thermal physiology, although a phylogenetic comparative analysis is required (see Feldman et al., 2011). However, Gilbert and Miles (2019) found that the thermal ecology (body temperature, preferred temperature and critical thermal temperature) of *U. ornatus* varied among populations along an elevational gradient suggesting its thermal physiology (thermal sensitivity of physiological performance) may be less conserved than the similarities in  $T_b$  might indicate. In addition,

in some particular species, at least of phrynosomatids (e.g., *Sceloporus jarrovi*), significant differences have been found in the thermal requirements (e.g., preferred body temperatures of male and female lizards) of sexes or life stages (Beal et al., 2014), and reproductive status (Mathies and Andrews, 1997), which we did not study. Therefore, more detailed analysis of variation in aspects of the thermoregulation and thermal physiology are needed before definitive conclusions about the conservative nature of thermal physiology in this genus can be drawn.

Despite the potential differences in thermal ecology of *U. ornatus* indicated by Gilbert and Miles (2019), the mean  $T_b$  we observed in our study is similar to those observed in other populations of *U. ornatus* (34.5°C, southeastern Arizona-southwestern New Mexico, Smith and Ballinger, 1995; 34.5-37.4°C, central Arizona, Vitt et al., 1981; Congdon et al., 1982; also see Brattstrom, 1965) and *Urosaurus bicarinatus* from Guerrero (34.6°C; Lemos-Espinal et al., 1997). Mean  $T_p$  in the population that we studied falls within the range of  $T_p$ s determined for other populations of *U. ornatus*. For example, mean  $T_p$  of *U. ornatus* from an urban population in Phoenix, Arizona was 31.8°C and ranged from 25.4-37.4°C (Ackley et al., 2015), and mean  $T_p$  of *U. ornatus* from southeastern Arizona was 36.0°C (Gilbert and Miles, 2017).

The mean field  $T_b$  for *U. ornatus* in our population was essentially the same in June ( $35.3 \pm 0.3^\circ\text{C}$ ) as in October ( $35.2 \pm 0.2^\circ\text{C}$ ). Vitt et al. (1981) observed relatively little monthly variation in mean  $T_b$  in *U. ornatus* from central Arizona, but  $T_b$  in *U. ornatus* from southeastern Arizona and southwestern New Mexico varied from month to month with higher  $T_b$ s in summer and lower in the fall (Smith and Ballinger, 1995), which suggests that the thermal ecology of this species may be less conservative in its thermal physiology than previously thought (see also Gilbert and Miles, 2019). Therefore, we suggest extending these studies of  $T_b$  to other seasons and months of the year to explore



possible differences in  $T_b$ . This is particularly relevant because differences in estimated thermoregulation indices could modify the conclusions obtained in our study.

Body temperature ( $T_b$ ) in *U. ornatus* was not related to either  $T_s$  or  $T_a$ . According to Huey and Slatkin (1976) a species is a thermoregulator when the value of the slope of the linear regression of  $T_b$  on environmental temperature ( $T_a$  or  $T_s$ ) is close to zero (i.e., not significant). Mean  $T_b$  for *U. ornatus* in June and October were similar despite the fact that  $T_s$  and  $T_a$  were lower than  $T_b$  in both months and  $T_e$  registered in June was significantly higher than October. Therefore, *U. ornatus* in June face a more hostile thermal environment than in October, yet they were still able to display a relatively lower thermal accuracy in June than October (although this difference was not statistically significant). In addition, the index of thermoregulatory efficiency ( $d_e - d_b$ ) was higher in June than October, with June having an environment with a lower thermal quality ( $d_e = 6.0$ ) than October ( $d_e = 3.9$ ). Likewise, the observed  $E$  was 0.88 in June and 0.87 in October, suggesting they are thermoregulators since both of these values are near 1 (Hertz et al., 1993). On the other hand, in both June and October the  $T_b$  we observed for *U. ornatus* in the field was near to the upper limit (35.0°C) of the  $T_p$  interquartile range. Thus, this saxicolous population maintained its  $T_b$  close to its preferred temperature, despite the differences in thermal quality in both months. Thus, as has been found in arboreal populations of *U. ornatus* (see Gilbert and Miles, 2017), several pieces of evidence from our study suggest that lizards in the saxicolous population of *U. ornatus* are active thermoregulators.

The relatively low field  $T_b$  and  $h_a$  and the high  $h_r$  of *U. ornatus* in June may also reflect physiological responses to thermal constraints from a high  $T_e$ . In our study population, *U. ornatus* may reduce its activity time to keep the high thermoregulatory efficiency and potentially high associated costs of  $h_r$ . This small

tree lizard has low body mass that increases its heating rate and may require more cautious thermoregulatory behavior to reduce the risk of overheating (i.e. exceeding  $CT_{Max}$ ; Angilletta et al., 2004).

Current research suggests ectothermic organisms from desert environments have a high extinction probability under current rates of global warming because sufficiently rapid adaptive change in  $T_b$  is unlikely (Ballesteros-Barrera et al., 2007; Deutsch et al., 2008; Sinervo et al., 2010, 2018; Gadsden et al., 2012; Paranjpe et al., 2013; Lara-Reséndiz et al., 2015; Minoli et al., 2019). However, some species may be relatively resilient to changes in their thermal environment with climate change (e.g., *Dipsosaurus dorsalis*; Lara-Reséndiz et al., 2019). Nevertheless, impacts of rising environmental temperatures on populations depend on an ectotherm's capacity to compensate through acclimation, thermoregulatory behaviors, such as habitat selection; change in daily activity patterns; and shifts in the phenology of reproduction and activity (Deutsch et al., 2008; Huey et al., 2009; Kearney et al., 2009; Valenzuela-Ceballos et al., 2015). Species or populations can also potentially track their shifting climate-niche through dispersal (Chown et al., 2010). Likewise, according to Garcia-Porta et al. (2019) the current trend of fast increasing temperatures will probably modify the adaptations of preferred to environmental temperatures that have been molded through millions of years. The ability of species to mitigate these new circumstances across behavioral responses remains unresolved. However, given the apparent conservative nature of  $T_p$  and the apparent lack of acclimation effects on  $T_p$  in the population of *U. ornatus* that we studied, it seems unlikely that this population of *U. ornatus* would be able to compensate for rapid temperature changes and so would be very vulnerable to changes in global temperature.

Our study demonstrates that this saxicolous population of *U. ornatus* inhabiting a desert

habitat may be vulnerable to changes in thermal habitat quality because they display relatively low field  $T_b$ , reflecting the high microclimate temperatures that increase risks of overheating and dehydration and shorten the time available for feeding and breeding activities, while also increasing temperature-related maintenance costs, potentially leading to local extinction. Further increases in  $T_e$  with global warming are likely to increase the risk of local extirpation and global extinction in other similar habitats (Lara-Resendiz et al., 2015).

According to the lizard extinction model developed by Sinervo et al. (2010), species are negatively affected when  $T_e$  rises above  $T_p$ , or when  $h_r > 3.8 \text{ d}^{-1}$  during the peak months of the reproductive period. At our study site, the hours of activity ( $h_a$ ) in *U. ornatus* were 4.6 and  $7.9 h_a \text{ d}^{-1}$  in June (within the reproductive period) and October, respectively; and the hours of restriction ( $h_r$ ) were  $6.4$  and  $0.8 h_r \text{ d}^{-1}$  in June and October, respectively. Despite the fact that we found a high number of  $h_r$  during the breeding season, we can consider that our approach is more conservative than that used in Sinervo et al., (2010), because we use the  $TV_{\min}-TV_{\max}$  range as threshold. Based on this, the thermal risk of this saxicolous population is likely greater than that estimated using Sinervo et al. (2010). In addition, such models may not adequately incorporate the various mechanisms by which lizards can respond to changing climates (see Taylor et al., 2020 for discussion).

Our observations would suggest this population may be at risk for extirpation. Indeed, in June, the  $h_r$  were higher than values previously calculated for phrynosomatid lizards based largely upon members of the genus *Sceloporus* (Sinervo et al., 2010, 2011) and similar to the average registered in two species of *Phrynosoma* (*P. cornutum* and *P. modestum*) from sites relatively close to our study site in the Chihuahuan Desert (Lara-Resendiz et al., 2015). However, additional data on  $h_r$  in contrasting populations throughout the distribution may be required to determine and compare how closely

*U. ornatus* approaches the extinction limit defined by Sinervo et al. (2010, 2011). In addition, additional data on  $h_r$  earlier in the spring reproductive period (e.g., April-May; Goldberg, 2014) may help refine the estimates of extinction probabilities for this population. The proximity of numerous rock crevices may provide microclimate refugia for these lizards, potentially allowing them more opportunity to persist in the face of climate warming (Sears et al., 2011, 2016; Jiménez-Robles and De la Riva, 2019). The presence of potential competitors, such as *Uta stansburiana* whose distribution and habitat overlap with *U. ornatus* (Hammerston, 2007a), could affect the ability of *U. ornatus* to thermoregulate and be active, and thus affect the estimated hours of activity for *U. ornatus*. In addition, we did not directly evaluate the activity budgets (e.g., time spent basking, foraging, resting, and non-foraging) of *U. ornatus* in our population. It is unknown whether this population can adequately complete all aspects of its activity budget in the 4.6 h of daily activity estimated here. Therefore, while suggestive, our limited data do not allow us to conclude with certainty if population viability is impaired due to climate change.

*Urosaurus ornatus* is found in a large number of protected areas, such as national parks, monuments and wilderness areas. In the northern portion of its distribution, no direct conservation measures are currently needed for its widespread and adaptable populations. However, populations that inhabit the southern portion of its geographical distribution in northern Mexico that are more likely to be affected by global warming, the projected consequences of global warming should be included in a conservation plan for this local population of lizard possibly threatened by climate change. Indeed, the area of sand dunes that surrounds the Sierra de Samalayuca is heating up drastically and rapidly (Lara-Resendiz et al., 2015; see also Cuervo-Robayo et al., 2020). *Uta stansburiana* near the Sierra de

Samalayuca have low thermoregulatory precision ( $d_b$ ), thermal quality ( $d_e$ ), operative temperature ( $T_e$ ) and hours of activity ( $h_a$ ) (Rivera-Hernández, 2012), which could indicate susceptibility to the consequences of warming temperatures. *Phrynosoma cornutum* and *Phrynosoma modestum* inhabiting the sand dunes that surround the Sierra de Samalayuca have higher environmental temperatures that restrict their activity periods. *Phrynosoma cornutum* maintained  $h_r$  values greater than 10 hours and in *P. modestum* the hours of restriction were above 7 (Lara-Reséndiz, et al., 2015). Based on these results, it appears the localities near Sierra de Samalayuca are thermally challenging for the lizard species studied so far. Indeed Lara-Reséndiz et al. (2015) found that if air temperature rises as predicted by climate models *P. cornutum* is projected to become locally extinct at 18% and *P. modestum* at 60% of localities by 2080, respectively. It is therefore critically necessary to develop extinction models for parapatric populations of *U. ornatus* and *U. stansburiana* to estimate their risk of extinctions and the extent of potentially viable areas for dispersal in the face of climate warming.

The fact that our study area is located within the Médanos de Samalayuca protected natural area could favor the creation and application of a conservation plan focused on *U. ornatus* located in the Sierra de Samalayuca. However, given the apparent susceptibility of this population of *U. ornatus* to global temperature increases, its presence in a protected area is unlikely to provide any protection from this global change. The probable extinction of some populations of this species along the southern limits of its distribution could reduce its range in that area, especially on rocky islands compared to tree areas where it normally inhabits. This due to the higher thermal challenges in those rocky habitats (e.g., Bakken, 1989). However, given the large geographic range of this lizard species, we expected that such potential contraction in its distribution range does not affect its international conservation status determined by IUCN

as Least Concern (Hammerson et al., 2007b), but probably might contribute to a change in its status in Mexico. Given this, the best conservation interventions might be maintaining or creating dispersal corridors for threatened populations, or even consideration of facilitated dispersal (i.e., translocation).

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