

Thermoregulation during the summer season in the Goode's horned lizard *Phrynosoma goodei* (Iguania: Phrynosomatidae) in Sonoran Desert

Rafael Alejandro Lara-Resendiz^{1,*}, Tereza Jezkova², Philip C. Rosen³,
Fausto Roberto Méndez-de La Cruz¹

Abstract. Reptiles in desert environments depend on habitat thermal quality to regulate their body temperature and perform biological activities. Understanding thermoregulation with respect to habitat thermal quality is critical for accurate predictions of species responses to climate change. We evaluated thermoregulation in Goode's horned lizard, *Phrynosoma goodei*, and measured habitat thermal quality at the Reserva de la Biosfera El Pinacate y Gran Desierto de Altar, Sonora, Mexico, during the hottest season of the year. We found that field-active body temperature averaged $38.1 \pm 0.38^\circ\text{C}$, preferred body temperature in laboratory averaged $34.9 \pm 0.18^\circ\text{C}$ and preferred body temperature range was $32.5\text{--}37.3^\circ\text{C}$. Operative temperature (i.e. environmental temperature available to the lizards) averaged $43.0 \pm 0.07^\circ\text{C}$, with maximum temperature being near 70°C , and 62.9% of operative temperatures were above preferred body temperature range of *P. goodei*. Microhabitat thermal quality occupied by the lizards was high in the morning (7:00-10:30) and afternoon (5:50-dusk). We found that despite strong thermal constraints *P. goodei* was highly accurate and efficient in regulating its body temperature and that it presented a bimodal thermoregulatory pattern, being active in the mornings and in the evenings in order to avoid high mid-day environmental temperatures. Despite its thermoregulatory ability, *P. goodei* may be vulnerable to climate warming.

Keywords: arid zone, climate change, hot season, operative temperature, phrynosomatid, Sonora, thermal efficiency, thermal quality.

Introduction

Ectothermic animals depend on the availability and distribution of thermal habitat resources to efficiently regulate their body temperatures (T_b) and perform daily biological activities (e.g., feeding, digestion, growth, reproduction; Huey, 1982). Desert species must maintain adequate T_b during their activity period, despite living in habitats with extremely high environmental temperatures (Cowles and Bogert, 1944; Avery, 1982). Therefore, thermoregulatory behaviour is critical to maintain their T_b within a preferred body temperature (T_p) range to avoid overheating,

and to optimize the net benefit of activity in harsh environments (Vickers, Manicom and Schwarzkopf, 2011).

High environmental temperatures restrict the activity periods of lizards in warm environments (Dunham, 1993; Kearney, 2013). This occurs because the lizards are exposed to operative environmental temperatures (T_e) above their T_p range, thus restricting activity in both time and space. When the net energy gain becomes insufficient for females in their reproductive and active season, the population declines and may eventually head to local extinction (Huey, Losos and Moritz, 2010; Sinervo et al., 2010, 2011). Previous reports had shown that species in desert ecosystems have high extinction risk due to increases of environmental temperatures and consequent decrease of activity periods (e.g., Ballesteros-Barrera, Martínez-Meyer and Gadsden, 2007; Barrows, 2011; Gadsden et al., 2012). Therefore, it is necessary to understand and monitor the thermal requirements and thermoregulatory behaviour of reptiles in harsh en-

1 - Laboratorio de Herpetología, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán, A.P. 70515, C.P. 04510, Distrito Federal, México

2 - School of Life Sciences, University of Nevada, Las Vegas, 4505 S. Maryland Pkwy, Las Vegas, NV 89110, USA

3 - School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, USA

*Corresponding author; e-mail: rafas.lara@gmail.com

Table 1. Metrics and indices of thermal ecology used in this study.

Symbol	Description
T_b	The field active body temperatures of a representative sample of free-ranging animals. This temperature measured with cloacal probes or telemetry.
T_p	Preferred or selected temperature represents the range of core temperature within which an ectothermic animal seeks to maintain itself by behavioural means (IUPS Thermal Commission, 2003). Typically measured in thermal gradients and represented by central 50% of body temperatures.
T_{p25}	Lower limit of T_p , computed from the interquartile 25% of all body temperatures in the thermal gradient.
T_{p75}	Upper limit of T_p , computed from the interquartile 75% of all body temperatures in the thermal gradient.
T_e	Environmental operative temperatures describe the available equilibrium body temperatures, which an animal will experience in a specific habitat in the absence of thermoregulation. This temperature measured with cooper models, taxidermies, or PVC models, located in the microhabitats occupied by small ectotherms (Bakken, 1992; Dzialowski, 2005).
d_b	Accuracy of thermoregulation, measured as mean absolute deviation of T_b from T_p range (Hertz, Huey and Stevenson, 1993).
d_e	Thermal quality of habitat, measured as mean absolute deviation of T_e from T_p range (Hertz, Huey and Stevenson, 1993).
$d_e - d_b$	Effectiveness of thermoregulation of Blouin-Demers and Weatherhead (2001).
E	Effectiveness of thermoregulation of Hertz, Huey and Stevenson (1993); $E = 1 - d_b/d_e$.

vironments in order to assess their extinction risk in face of climate change (Deutsch et al., 2008; Kearney, Shine and Porter, 2009; Paranjpe et al., 2012).

Thermoregulation of small ectotherms can be evaluated by the protocol proposed by Hertz, Huey and Stevenson (1993), through employment of three biophysical indices: habitat thermal quality (d_e), thermoregulation accuracy (d_b), and thermoregulation efficiency (E ; table 1). These indices are calculated using three thermal variables: body temperatures during activity period in the field (T_b), preferred temperature range in a thermal gradient (T_p), and operative temperatures in the microhabitat occupied by the lizard (T_e ; see more details in Materials and methods). This protocol has shown advantages over previous methods and it has been used widely for desert lizards (Kearney and Predavec, 2000; Blouin-Demers and Nadeau, 2005).

Here we evaluate thermoregulation of Goode's horned lizard (*Phrynosoma goodei* Stejneger, 1893). *Phrynosoma goodei* inhabits the northern Sonoran Desert; which provides an opportunity to examine thermoregulation of a desert-adapted lizard in one of the driest and hottest places in North America (Ezcurra and Rodrigues, 1986). Previous stud-

ies have examined thermal biology of species in the genus *Phrynosoma* (e.g., Cowles and Bogert, 1944; Heath, 1964, 1965; Pianka and Parker, 1975; Powell and Russell, 1985; Christian, 1998; Woolrich-Piña, Smith and Lemos-Espinal, 2012; also see Avery, 1982 and references therein); however, few studies have evaluated the detailed regulation of temperature in this genus using T_b , T_p , and T_e to determine the effectiveness of thermoregulation and habitat thermal quality (e.g., Vázquez-Urzúa, 2008; Arias-Balderas, 2011; Lara-Resendiz, 2013b; Arenas-Moreno, 2014). Therefore, the objectives of the present study are to: (1) examine the field (T_b) and preferred (T_p) body temperature of the desert horned lizard *P. goodei* and quantify available operative environmental temperature (T_e); and (2) evaluate the accuracy and effectiveness of thermoregulation and thermal quality in one of the hottest and most arid habitats in North America. Additionally, we compare our results with data available for other phrynosomatid lizards.

Materials and methods

Species and study site

Phrynosoma goodei, Goode's horned lizard, has recently been elevated from a subspecies of *P. platyrhinos* to a sep-

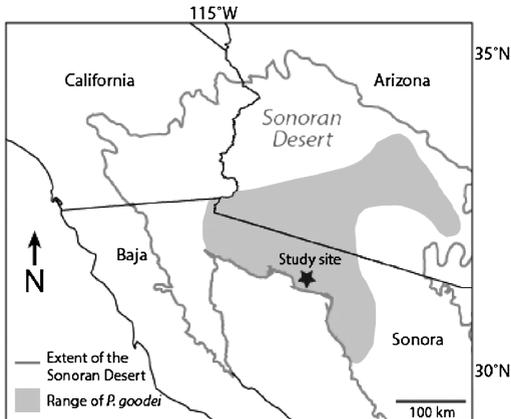


Figure 1. Distribution of *P. goodei* in Sonoran Desert.

arate species, based on mitochondrial DNA and morphological data (Mulcahy et al., 2006). *Phrynosoma goodei* is an oviparous horned lizard that occurs south of Gila River, from Avra Valley west of Tucson to near Yuma, Arizona, and in coastal deserts of Sonora, Mexico (fig. 1). It is partially sympatric with *P. mcallii* (Jezkova, 2010), though largely allopatric and parapatric on regional (Rosen, 2007) and local (Rorabaugh, Palermo and Dunn, 1987; Young, 2010) scales. To the north and west, it is replaced by allopatrically distributed *P. platyrhinos*. *Phrynosoma goodei* has a snout vent length (SVL) averaging about 72 mm, paired dorsal spots, coloration variable with background habitat, sparse flecking on the venter, three enlarged temporal horns, and occipital horns orientated dorsally (upward), and posteriorly (Klauber, 1935; Smith and Taylor, 1950; Pianka, 1991; Mulcahy et al., 2006). Within its narrow range, it is associated with woody shrubs and cacti in arid habitats on gravelly and loamy bajadas, lava flows, in valleys, and, primarily outside the distribution of *P. mcallii*, on dunes and sand fields (Baur and Montanucci, 1998; Sherbrooke, 2003; Young, 2010).

Our study area was located within the La Reserva de la Biosfera El Pinacate y Gran Desierto de Altar – referred to subsequently as the RBP – in northwestern Sonora, Mexico (31°32'14"N, 113°27'10"W, 60 m elev., fig. 1). The Pinacate region belongs to the driest and hottest places in North America (Ezcurra and Rodrigues, 1986). This area is delimited by the Gulf of California and is characterized by typical very dry semi-stabilized sand dunes and volcanic fields with low cover of vegetation. The major geologic units are composed of volcanic, metamorphic, plutonic, and sedimentary units (Kasper-Zubillaga et al., 2008). Average annual temperature is 22°C, although air temperature is very high in summer, often reaching 49°C in the shade (Búrquez and Castillo, 1994). In winter, freezing temperatures occur regularly and this phenomenon has been long recognized as important for Sonoran Desert vegetation (Búrquez and Castillo, 1994; Weiss and Overpeck, 2005). Average annual precipitation is 125 mm, and varies from 52 to 164 mm, with the rainfall pattern being highly unpredictable (Ezcurra

and Rodrigues, 1986; Búrquez and Castillo, 1994; Sánchez-Flores, 2007). In this region, half or more of annual precipitation falls during the July–October hot season as monsoonal storms (Felger, 2000), as is characteristic for the Sonoran Desert. This marked seasonality is critical for foraging and reproduction of reptiles (e.g., Huey and Pianka, 1977; Angilletta, Sears and Winters, 2001; García-De la Peña et al., 2007; Navarro-García, García and Méndez-de la Cruz, 2008). Annual potential evapotranspiration rates exceed 2500 mm (Sánchez-Flores, 2007). The most representative woody perennial plants are *Larrea tridentata*, *Ambrosia dumosa*, *A. deltoidea*, *Hilaria rigida*, *Encelia farinosa*, *Jatropha cuneata*, *Fouquieria splendens*, *Opuntia bigelovii*, *Parkinsonia microphylla*, *Olneya tesota*, and *Carnegiea gigantea* (Ezcurra, Equihua and López-Portillo, 1987; Búrquez and Castillo, 1994; Felger, 2000).

Fieldwork

Fieldwork was conducted during July and August of 2011, the hottest months of the year (Ezcurra and Rodrigues, 1986; Ezcurra, Equihua and López-Portillo, 1987). We searched for lizards between 6:00 and 22:00 h. We collected 40 *P. goodei* and measured their T_b with a digital thermometer (Fluke model 51-II) with a K thermocouple ($\pm 0.1^\circ\text{C}$). We placed the thermometer one centimetre into the cloaca and recorded the lizard's T_b within the first 20 seconds after capture. We recorded time of capture, snout-vent length (SVL; mm), sex, and location using a hand-held GPS unit.

Operative temperature (T_e) represents the equilibrium temperature of inanimate objects with their environment and permits us to explore the thermic environment at the same spatial scale as experienced by the lizards; furthermore, it can be replicated easily to measure multiple spatial-temporal thermal conditions (Bakken, 1992). Previous studies used various materials to measure the T_e (see Dzialowski, 2005). Recently, T_e has been validated with polyvinylchloride (PVC) pipe models for T_b of small ectotherms (Dzialowski, 2005, see also supporting online material in Sinervo et al., 2010).

Thermal models were designed to mimic lizard thermal properties; they were made of PVC, resembled *P. goodei* in shape and size, painted in grey 33 to approximate the reflectivity of phrynosomatids (Adolph, 1990; Sinervo et al., 2010), and previously calibrated (see below). Twelve models were connected to 12 data-logger sensors (HOBO® Pro V2) and T_e was recorded every 30 minutes during July and August of 2011. Only T_e in the possible lizard activity period were analysed from 7:00 to 22:30 due to possible crepuscular activity (Harris, 1958; Williams, 1959; Lara-Resendiz, Gadsden and Méndez-de la Cruz, 2013). The models were placed in the following microhabitats: (1) stabilized sand dunes: two in shade and two sunlit; (2) transition between sand dunes and lava flows: two in shade and two sunlit; (3) lava flows: two in shade and two sunlit. All models were placed in the same orientation relative to sunrise; at each site one model was in a microhabitat with direct sun all the time and the other model in a microhabitat always

completely in the shade under natural vegetation; these represent the extremes of temperature in each site. We justify these microhabitat types as potential refuges and places of activity based on the life history, previous observations during fieldwork, and literature (Baur and Montanucci, 1998; Sherbrooke, 2003; Lara-Resendiz, 2013a).

The PVC models were calibrated with a lizard in the field. We took the temperatures of the lizard and the PVC model every 3 minutes during 3 hours, in both sunny and shaded microhabitats. In this calibration, we found a highly significant linear correlation between field T_b and T_e ($r = 0.98$, $n = 51$, $P < 0.001$; $T_b = 7.4582 + 0.8207T_e$). Thus, we assumed the lizard models accurately measured the available T_e for the horned lizard in this study.

Laboratory work

In the laboratory, the lizards were separated by gender and maintained at 25°C in plastic containers with soil and logs, and hydrated with a sprinkler. Laboratory experiments were conducted two days after capture. We obtained T_p of 30 *P. goodei* in a thermal gradient, which was a wooden box of 100 × 100 × 45 cm (length, width, and height) divided into ten tracks with insulation barriers to prevent behavioural influence of adjacent lizards, and filled with 2-3 centimetres of sandy soil. The cold side was obtained by placing the box in room with constant temperature from 20 to 22°C, the opposite side was placed under three lamps of 100 W hanging at 30 cm to reach 50°C.

No food was offered to the lizards during the experiment but they were hydrated every morning. Prior to measuring T_p , all specimens were acclimatized in the thermal gradient for two hours. Preferred body temperatures were recorded using the digital thermometer each hour from 7:30 to 17:30 h (activity period) for one day. We computed T_p range according to interquartile of 25% to 75% (i.e., T_{p25} to T_{p75} ; sensu Hertz, Huey and Stevenson, 1993). After laboratory experiments, all lizards were released at their capture sites.

Thermoregulation indices and statistical analysis

The data on T_b , T_p , and T_e were used to calculate the accuracy index of thermoregulation (d_b) and habitat thermal quality (d_e) as follows: if T_b or $T_e < T_p$, then $d_b = T_b - T_{p25}$ and $d_e = T_e - T_{p25}$ respectively, and if T_b or $T_e > T_p$ then $d_b = T_b - T_{p75}$ and $d_e = T_e - T_{p75}$, respectively. When T_b or T_e values were within T_p range, d_b and d_e were considered equal to zero. High values of d_b and d_e indicate a low accuracy index and low thermal quality, while values equal to or near to zero indicate high accuracy of thermoregulation and represent thermally ideal environments. Subsequently, thermoregulation efficiency (E) was calculated using averages of d_b and d_e ($= \bar{d}_b$ and \bar{d}_e) using the following equation: $E = 1 - (\bar{d}_b/\bar{d}_e)$. An E index near to one is indicative of an organism that actively thermoregulates, because environmental temperature is far from its physiological requirements. These organisms are subject to thermal stress and must increase or decrease their T_b with respect to T_e . In contrast, an E value equal or near to

zero is indicative of a thermoconformer that is not regulating temperatures actively because environmental temperature is within its physiological requirements (Hertz, Huey and Stevenson, 1993). However, as recognized by Hertz, Huey and Stevenson (1993), a given value of E can result from a variety of d_b and d_e combinations. For example, two species can therefore face different thermal environments and exhibit different thermoregulatory strategies and still have the same value of E if their ratios between d_b and d_e are the same (see discussion in Blouin-Demers and Weatherhead, 2001). Thus, it is also important to consider the magnitude of d_b and d_e in interpreting E (Blouin-Demers and Nadeau, 2005). Following Blouin-Demers and Nadeau (2001) we measured the index of effectiveness of thermoregulation ($d_e - d_b$) to quantify the extent of departure from perfect thermoconformity.

T_b and T_p were only recorded for adult *P. goodei* (SVL > 66 mm; Tanner and Krogh, 1973). Data were excluded when temperature measurements were taken more than 20 seconds after the first sighting of the lizard in the field.

Assumptions of normality and homogeneity of variances were analysed using the Kolmogorov-Smirnov and Levene's tests, respectively. To explore possible differences between sexes in T_b we used Student's *t*-test or a corresponding non-parametric test. To test possible differences between T_p , we used an analysis of variance with repeated measures (ANOVA) with within-subjects factor with 11 levels (every hourly measure of T_p), between subjects factor with two levels (male and female). Also we used one-way ANOVA or nonparametric tests to explore possible differences between T_e and d_e between substrates and using the post-hoc method of Dunn. We used the R software (R Development Core Team, 2012) and SigmaPlot version 10 (Systat Software, San Jose, CA) for statistical analyses and graphing. The significance value in all statistical tests was $P < 0.05$ (Sokal and Rohlf, 2000). Figures and tables in the text show average \pm standard errors (mean \pm SE), sample size (n), and temperature range.

Results

We collected 40 *P. goodei* (16 females and 24 males) that were generally found on stabilized sand dunes and occasionally on lava flows, which usually had sand mixed in. The observed activity period was diurnal from 07:40 to 20:06 hours, when the first and the last lizards were observed in the field, respectively. Variation of T_b and T_e with respect to the hours of the day can be seen in fig. 2 and histograms of recorded values in fig. 3. Lizard activity began when T_e reached 32.8°C; activity ceased at noon around 40°C, and in the evening when

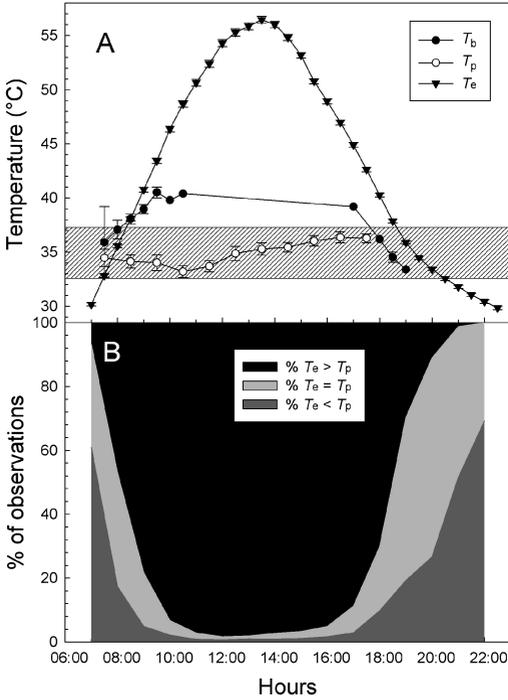


Figure 2. (A) Variation of body temperature (T_b) and preferred temperature (T_p) of *P. goodei* and operative temperature (T_e) during summer season, related to the percentage of observations. The horizontal shaded area identifies the preferred temperature range in thermal gradient. (B) Proportion of environmental temperature (T_p) measurements that were less than, equal to, or greater than preferred body temperature (T_p).

T_e dropped below 35.8°C (fig. 2A). The highest T_b recorded during activity was 42.8°C. Results of T_b , T_e , and T_p are summarized in table 2. Field body temperature was not significantly different between sexes ($t_1 = -0.823$; $P = 0.415$). Laboratory T_b was significantly different (lower) for the entire activity period in comparison with field T_b (ANOVA; Wilk's $\lambda = 0.339$; $F_{10,328} = 3.71$; $P = 0.007$). There was no significant effect found in T_p between sexes (Wilk's $\lambda = 0.526$; $F_{1,328} = 1.71$; $P = 0.15$). Operative temperatures were significantly different between substrates ($H_5 = 501.929$; 501.929 ; $P < 0.001$) Dunn's method formed four groups (see fig. 4).

Thermoregulatory indices suggest that *P. goodei* exhibits accurate thermoregulation ($d_b = 1.5$). T_b was within the T_p range in

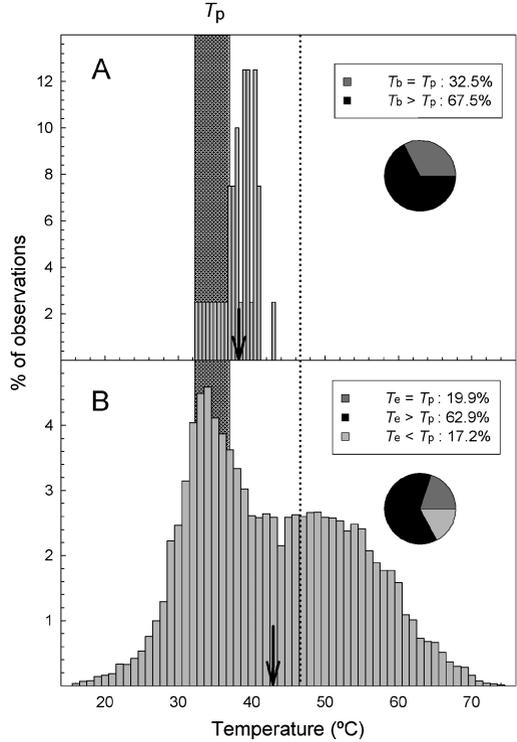


Figure 3. (A) Distribution of body temperature (T_b) for *P. goodei* and (B) operative temperature (T_e) from biophysical models for the day during summer season; vertical shaded area identifies the preferred temperature range in thermal gradient (T_p). Pie charts show the percentage of T_e above, within, and below T_p range. The arrow points to the average of the temperatures. Critical maximum temperature (CT_{max} ; from the literature) is depicted by the dashed line.

only 32.5% cases; T_b was above T_p range in 67.5% cases, and T_b was never below T_p during the summer season. Thermal quality index d_e was statistically different between substrates ($H_5 = 523.013$; $P < 0.001$): thermal quality was highest in the shade on lava flows and sand dunes, and lowest in sunlit condition on sand dunes and transitions between sand dunes and lava flows (see table 3; fig. 4). Operative temperature was within the T_p range in 19.9% of cases, below T_p range in 17.2% of cases, and above the T_p range in 62.9% (see fig. 3B). The highest percentage of T_e within the T_p range occurred from 07:00 to 10:30 hours and from 15:30 to 22:00. During the observed activity period of *P. goodei*, only 30.9% of T_e cases were within the T_p range (fig. 2B). Finally, thermal efficiency

Table 2. Field body temperature (T_b), operative temperature (T_e), preferred temperature in laboratory (T_p), and T_p range (quartiles 25 and 75%) in Celsius degrees, and accuracy in thermoregulation (d_b), habitat thermal quality (d_e), and thermoregulatory efficiency (E and $d_e - d_b$) in summer season for *Phrynosoma goodei*. Showing mean \pm SE and in parenthesis sample size and minimum-maximum.

Species	T_b	T_e	T_p	T_p range (25-75%)	d_b	d_e	$d_e - d_b$	E
<i>Phrynosoma goodei</i>	38.1 \pm 0.38 (40; 32.6-42.8)	43.0 \pm 0.07 (19 294; 13.2-74.2)	34.9 \pm 0.18 (30; 26.9-41.8)	32.5-37.3	1.5 \pm 0.23 (40; 0-5.5)	8.3 \pm 0.06 (19 294; 0-36.9)	6.8	0.82

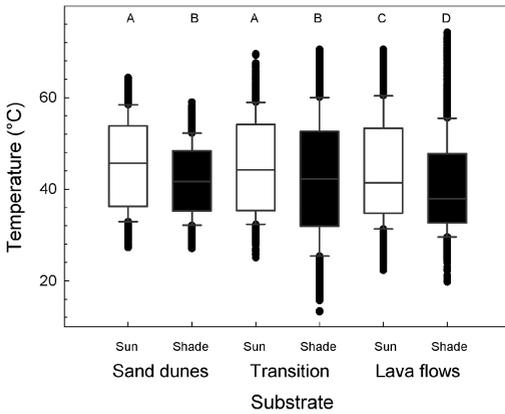


Figure 4. Operative temperatures for *P. goodei* in three substrates (sand dunes, transition, and lava flows). Same letters identify same statistical groups.

indices E and $d_e - d_b$ indicate that *P. goodei* was efficient in regulating its body temperature on different substrates (0.75-0.85 and 4.62-8.43, respectively; table 3).

Discussion

For ectothermic animals, the ability to thermoregulate is essential for performance of daily biological activities, such as feeding, digestion, growth, and reproduction and therefore directly influences species distributional limits and ability to resist extinction in face of climate change (Sinervo et al., 2010). In this study, we measured several thermoregulatory indices in *P. goodei* in order to evaluate thermophysiology of the species.

Field T_b (38.1°C) and laboratory T_p (34.9°C) of *P. goodei* were above and close to, respectively, averages of other lizards of the Phrynosomatidae reported by Sinervo et al. (2010), who determined that T_b for this family ranges from

26.8 to 41.5°C, with an average of 35.2 \pm 0.20°C. Field and thermal gradient body temperature averages in our study are broadly similar to those reported for the closely related *P. platyrhinos* and other *Phrynosoma* species occupying desert conditions (Cowles and Bogert, 1944; Brattstrom, 1965; Pianka and Parker, 1975; Woolrich-Piña, Smith and Lemos-Espinal, 2012), which is unsurprising given that closely related species tend to retain their ecological niche over evolutionary time scales (i.e. niche conservatism; Wiens and Graham, 2005). Thus, close relatives often share similarities in their morphology, ecology, life history, and ecological niche, as well as in their physiology (Scolaro, Ibarguengoytía and Pincheira-Donoso, 2008; Cooper, Jetz and Freckleton, 2010; Díaz de la Vega-Pérez et al., 2013; Grigg and Buckley, 2013). Based on morphological and molecular genetic analyses, Mulcahy et al. (2006) found that *P. goodei* appears morphologically intermediate between *P. mcallii* and *P. platyrhinos*, and speculated on a potential ancient hybrid origin for *P. goodei*. Our results support this prediction as *P. goodei* retain similarities in their thermophysiology with *P. platyrhinos* (Tanner and Krogh, 1973; Pianka and Parker, 1975) and *P. mcallii* (Norris, 1949; Heath, 1965; Pianka and Parker, 1975). Although our thermal gradient results were broadly similar to field and gradient results for related species, as expected, our observed field T_b was higher than reported for other phrynosomatid species, including other *Phrynosoma* (Woolrich-Piña, Smith and Lemos-Espinal, 2012; Lara-Resendiz, 2013b), pointing toward significant T_e con-

Table 3. Operative temperatures (T_e) in Celsius degrees, available thermal quality (d_e), and thermal efficiency (E and $d_e - d_b$) during summer season in different substrates for *P. goodei* in the Reserva de la Biosfera El Pinacate y Gran Desierto de Altar, Sonora, Mexico. Showing mean \pm SE and in parenthesis sample size, minimum and maximum. Same letters identify same statistical groups.

Substrate	T_e average	d_e	$d_e - d_b$	E
Sand/sun	45.3 \pm 0.18 (2658, 27.2-64.4) A	9.21 \pm 0.16 A	7.71	0.84
Sand/shade	41.9 \pm 0.14 (2658, 27.0-58.9) B	6.12 \pm 0.11 C	4.62	0.75
Transition/sun	44.9 \pm 0.19 (2848, 25.0-69.5) A	9.12 \pm 0.16 AB	7.62	0.83
Transition/shade	42.4 \pm 0.20 (3904, 13.2-70.5) B	9.93 \pm 0.14 D	8.43	0.85
Lava flows/sun	43.9 \pm 0.19 (3320, 22.2-70.5) C	8.6 \pm 0.16 B	7.1	0.83
Lava flows/shade	40.7 \pm 0.16 (3906, 19.7-74.2) D	6.5 \pm 0.12 C	5	0.77

straints on activity in our very hot study system despite the high T_p of *Phrynosoma*.

Phrynosoma goodei showed a bimodal daily activity pattern with distinct morning and late afternoon-early evening activity periods (fig. 2A, B). According to Barrows and Allen (2009) and Wone and Beauchamp (2003), during summer days, horned lizards found refuge in their burrows from otherwise lethal surface temperatures (see also Grant, 1990). In this study, *P. goodei* retreated into burrows to escape the heat during large portions during summer days, when T_e exceeded 40°C. Even while active, *P. goodei* in our study were often operating at body temperatures above the T_p range (25-75%), to such an extent that mean field T_b actually fell outside the estimated T_p range. This highlights the extent to which *P. goodei* surface activity was strongly constrained by T_e .

Previously, experimental techniques have been used to establish critical thermal maxima (CT_{max}) in desert horned lizards (Cowles and Bogert, 1944; Ballinger and Schrank, 1970; Prieto and Whitford, 1971; Ballinger, Lemos-Espinal and Smith, 1998); these studies generally confirm that diurnal desert lizards are more heat tolerant, which is reflected in their thermal activity ranges and heat resistance. Together these studies report CT_{max} , with an average of 46.5°C (44.1-48.1°C). Typically, T_e in RBP was greater than calculated CT_{max} , (38.9%) espe-

cially between 11:00 to 16:00 hours. Therefore, high T_e ultimately caused decline in summer daily activity time for *P. goodei*. Higher T_b (near CT_{max}) results in high metabolic and water loss rates and potentially lower capacity to escape from predators (Cowles and Bogert, 1944), and frequent extremely hot microhabitats place the lizards at greater risk of lethal thermal stress (\approx 46°C). In this study, some lizards were active at T_b values that were much higher than T_p ; this observation could be attributed to the lizards' lack of time to complete daily activities (i.e. foraging, breeding, feeding, social interactions, etc.) when T_e forces lizards to retreat (Vickers, Manicom and Schwarzkopf, 2011 and their references). There is evidence that phrynosomatid lizards display crepuscular activity (Harris, 1958; Williams, 1959; Lara-Resendiz, Gadsden and Méndez-de la Cruz, 2013; Martínez-Méndez, Lara-Resendiz and Blair, 2013); this behaviour could serve as a behavioural response to minimize the risk of overheating stress during diurnal foraging (Huey, 1982). This strategy was not documented in this study, but future studies will help to determine whether shifts towards crepuscular activity may occur in primarily diurnal lizard species that are sensitive to climate change.

During summer, environmental thermal quality was considered relatively low ($d_e = 8.3$), despite different d_e values between different sub-

strates (table 2). This indicates that there is a higher variability in T_e (fig. 4) and consequently greater proportion of available T_e within the T_p range, especially early and late in the day (fig. 2A). It is evident that reptile thermoregulation is related to the distribution of available T_e and habitat thermal quality (Grant, 1990; Hertz, Huey and Stevenson, 1993). In our study, low thermal quality was associated with high levels of accuracy and efficiency in thermoregulation (see table 3). This is consistent with the extended cost-benefit model for thermoregulation in high temperature environments by Vickers, Manicom and Schwarzkopf (2011), which proposes that lizards thermoregulate more accurately and efficiently when T_e is high and habitat thermal quality is low. Moreover, in thermally heterogeneous environments, such as deserts, there is an increment of thermoregulatory effort when habitat thermal quality declines, gaining the fitness benefits of optimal T_b and maximizing the net benefit of activity (Vickers, Manicom and Schwarzkopf, 2011). RBP provides short periods of high thermal quality, which *P. goodei* exploits in summer to sustain activity at T_b close to the T_p range.

Most studies of lizard thermoregulation have been performed during the summer months, seemingly providing only a partial view of lizard thermoregulation (Huey and Pianka, 1977). However, we believe that summer is the most important season for several reasons. First, diurnal lizards often maintain relatively high and constant T_b during their activity time. As a result, mean T_b of active lizards often varies relatively little despite daily, seasonal, and geographical variation in thermal environments (Avery, 1982; Adolph and Porter, 1993). Therefore, behavioural and physiological mechanisms for maintaining T_b within the T_p range are most critical during summer. Second, *Phrynosoma* lizards, including *P. goodei*, in the Sonoran Desert region are reproductively active from April to August (Howard, 1974; Goldberg, 2011), during the hottest time of the year. Pregnant or gravid females avoid extreme temper-

atures, which can have detrimental effects on adults or offspring (Cowles and Burleson, 1944; Cowles, 1945; Licht, 1965; Beuchat, 1988; Ji, Qiu and Diong, 2002; Olsson et al., 2004). Therefore, thermoregulatory accuracy and efficiency are essential in this season. Third, the Spring and Fall transitions between extended periods of winter cold and summer heat are relatively rapid, limiting the ability of lizards to compensate for rising temperatures by extending seasonal activity periods early and late in the warm season. Fourth, and most importantly, even though the lizards tolerate high T_b , deserts with high environmental temperatures restrict thermoregulatory options in breeding season, that is, increase h_r (see below). Then, lizards spend longer periods in refuges, reducing foraging time to the degree that the net energy gain becomes insufficient for reproduction, or they compensate behaviourally in ways likely entailing risk to survival (Dunham, 1993; Huey, Losos and Moritz, 2010; Sinervo et al., 2010). Annual activity time and thermoregulatory strategies can differ between seasons substantially (Adolph and Porter, 1993; Christian and Bedford, 1995; Diaz and Cabezas-Diaz, 2004; Navarro-García, García and Méndez-de la Cruz, 2008) as a result of a number of environmental factors, such as the variation of environmental temperature, precipitation and food availability, vegetation type, moisture, latitude, etc.

Global warming trends might further limit activity periods of *P. goodei* and cause population declines or even extinction. Recent research on lizards of the genus *Sceloporus* showed that 12% of 200 Mexican populations have become locally extinct since 1975 as result of warming environmental temperatures (Sinervo et al., 2010). This was attributed to lizards' exposure to environmental T_e greater than T_p , thus shortening activity time. Critical reduction in activity time was largely determined by hours of forced inactivity (i.e., hours of thermal restriction, h_r , sensu Sinervo et al., 2010) during the reproductive season. Consequently, net energy gain can

become insufficient for females, resulting in reduced reproductive rates (Dunham, 1993; Huey, Losos and Moritz, 2010; Sinervo et al., 2010, 2011). As such, h_r limits foraging, constraining costly metabolic functions like growth and maintenance, thereby undermining population growth rates and raising extinction risk.

In *P. goodei*, adults foraged from at least March–September and females carrying eggs have been found April through July (Howard, 1974). Although at least half of annual precipitation in our study region (Felger, 2000) and throughout the range of *P. goodei* (Turner and Brown, 1982) falls July–October, our results suggest that the thermal environment already strongly constrains the lizard's activity during this summer rain season when clouds and moisture often ameliorate the steady heat of the preceding two months of the hot-dry season. Climate warming of 2.6–4.8°C during the present century is projected for this region with a high degree of confidence (Garfin et al., 2013). This warming would further constrain *P. goodei* activity during July–August and may fully extend the thermal constraints through most of the warm season and reproductive period. Although Sinervo et al. (2010) predicted the most severe effects of climate warming in regions south and east of our study area, a recent critique (Kearney, 2013) pointed toward stronger effects of warming in our study region due to the very low amount of shade available for compensatory thermoregulatory behaviour. Climate models for our region (Garfin et al., 2013) do not predict increased rainfall, and thus predict reduced vegetation cover with increased temperature and evapotranspiration. Kearney's (2013) modelling suggests that *P. goodei* and other diurnal, terrestrial desert lizards may indeed be ecologically threatened as temperatures increase.

Phrynosoma goodei will have limited opportunity to shift its range northwards during climate warming, as it would have to compete with parapatric *P. platyrhinos*. To the east, and upward in elevation, *P. goodei* is faced with a rel-

atively steep rise in elevation into the less arid Arizona Upland Sonora Desert currently occupied by *P. solare*, or up the Gila and Santa Cruz river valleys where *P. goodei* is currently suffering from massive degradation of its habitat and changing vegetation (see Jackson and Comus, 1999). Our findings suggest that *P. goodei*, with its limited geographic distribution, might be severely threatened by combined forces of climatic and landscape change. This should be further validated in a global approach; future studies should extend seasonal, microhabitat, and geographic scope and provide explicit modelling for the potential risk of extinction due to global warming for this group of desert lizards.

In conclusion, the findings of this study demonstrate that *P. goodei* in summer is an active thermoregulator with a thermoregulatory pattern that allows effective use of available microhabitats. In addition, this horned lizard maintains high levels of accuracy and efficiency in its thermoregulatory behaviour to achieve and maintain its T_b near to the optimal preferred range despite the high environmental temperatures in one of the hottest and most arid habitats in the Sonoran Desert. Finally, this habitat offers low thermal quality, but provides spatio-temporal activity opportunities with optimal temperatures that *P. goodei* exploits successfully. Future climate change, however, might negatively impact this species.

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