

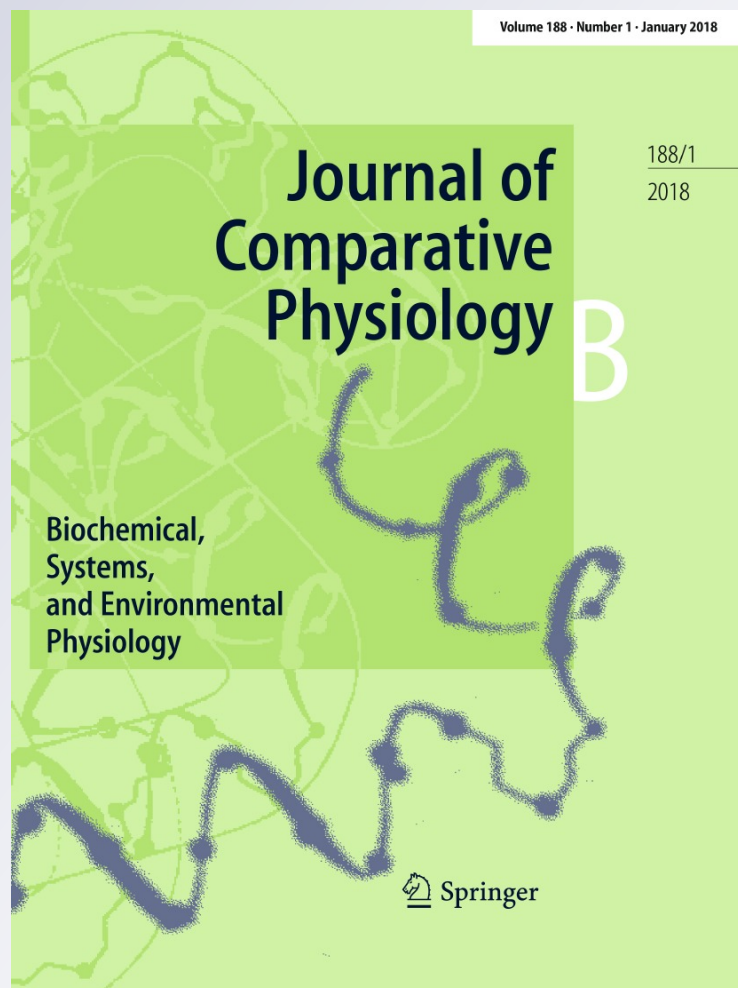
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**Journal of Comparative Physiology B**  
Biochemical, Systems, and  
Environmental Physiology

ISSN 0174-1578  
Volume 188  
Number 1

J Comp Physiol B (2018) 188:141-152  
DOI 10.1007/s00360-017-1116-3



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# Thermal physiology of three sympatric and syntopic Liolaemidae lizards in cold and arid environments of Patagonia (Argentina)

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Received: 7 December 2016 / Revised: 6 July 2017 / Accepted: 11 July 2017 / Published online: 19 July 2017  
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**Abstract** The thermal physiology determines the whole biology of ectotherm organisms, by limiting their acquisition and allocation of resources. Herein, we aim to add knowledge on how different species use the thermal resources when they coexist in a habitat, studying the thermal physiology of three sympatric and syntopic liolaemid lizards, *Phymaturus querque*, *Phymaturus zapalensis*, and *Liolaemus elongatus* during the summer season. We measured the body temperatures at capture places, the operative microenvironmental temperatures in the field, and the preferred body temperature in an experimental thermal gradient in the laboratory. We found that the three species are thermoregulators, selecting cooler thermal microenvironments than the ones expected by chance, and even cooler than the temperatures they selected in a laboratory environment. *Liolaemus elongatus* is a more efficient thermoregulator ( $E=0.671$ ) than the two *Phymaturus* species, *P. querque* ( $E=0.441$ ) and *P. zapalensis* ( $E=0.471$ ), which are moderate thermoregulators and, apparently, specialists in finding specific types of shelters, since they seem to select certain types of rock crevices. Herein, we found that during the summer season, although individuals have access to warm microenvironments, they spend time on cool refuges, probably to prevent overheating. This highlights the importance of an adequate spatial distribution of operative temperatures ( $T_e$ ), more than just a mere availability of appropriate temperatures.

**Keywords** *Phymaturus querque* · *Phymaturus zapalensis* · *Liolaemus elongatus* · Thermoregulatory physiology

## Introduction

The principal factors that drive all aspects of physiology, ecology, and evolution of ectotherms are the environmental factors (e.g., temperature, solar radiation, wind speed, humidity, availability of shade, and refuge), as well as the animal properties (e.g., size, shape, color, and reflectance; Huey 1982; Angilletta 2009; Smith et al. 2016). Often, physiological processes are optimized within a relatively narrow body temperature range (Huey 1982; Angilletta 2009) that could vary between coexisting species. Different species can adopt different thermoregulatory strategies in similar environments and, in consequence, a change in the environmental temperatures would not affect all organisms equally (Angilletta 2009). This highlights the importance of studying how different species use their thermal resources when they coexist in syntopy. Syntopic species can compete for thermoregulatory opportunities if they are limited in space and time (Magnuson et al. 1979), being the thermal niche partitioning a potential mechanism allowing the coexistence of similar species (Pateron and Blouin-Demers 2016). Species could partition thermal resources by altering their habitat use in space or time, since these are the dimensions along which thermal resources vary (Magnuson et al. 1979; Pateron and Blouin-Demers 2016).

Resource partitioning can occur between any species in the same community, but it is more likely to occur between closely related species, because they are more likely to overlap in their fundamental niches (Pateron and Blouin-Demers 2016). The study of resources

Communicated by H.V. Carey.

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segregation in daily activity patterns and food consumption of the sympatric lizards *Phymaturus roigorum* (from the *palluma* phylogenetic group of *Phymaturus* genus) and *Phymaturus payuniaie* (from the *patagonicus* phylogenetic group), in the central-west of Argentina, showed that selectivity towards different plant species and the time schedule for foraging are the primary mechanisms that allow the coexistence of these lizards, who spend similar amounts of time basking (Corbalán and Debandi 2014). The evaluation of habitat suitability of the genus *Phymaturus* using ecological niche models has revealed that the ecological differences between the *palluma* and *patagonicus* groups are more likely to occur due to habitat availability in their respective regions than to differences in habitat preferences (Debandi et al. 2012). Although thermal biology and niche requirements within the genus *Phymaturus* seem to be highly conservative (Ibargüengoytía et al. 2008; Cruz et al. 2009; Debandi et al. 2012; Corbalán et al. 2013), some traits are different between phylogenetic groups. In the *palluma* group, all species studied up to today exhibit prolonged biannual female cycles, greater snout–vent length, and larger head size in males than in females, and interspecific differences in male reproductive cycles (Habit and Ortiz 1996; Boretto and Ibargüengoytía 2006, 2009; Boretto et al. 2007; Cabezas Cartes et al. 2010), whereas the *patagonicus* group exhibited annual–biannual female reproductive cycles, greater snout–vent length in females than males, and similar male reproductive cycles (Ibargüengoytía 2004; Boretto and Ibargüengoytía 2009; Boretto et al. 2014a). The sympatric *P. roigorum* and *P. payuniaie* showed that, despite the differences in body mass and size and the long time of divergence between clades, the preferred temperatures were similar between them (Corbalán et al. 2013). In contrast, in Patagonian environments, the syntopic lizards *Phymaturus tenebrosus* and *Liolaemus elongatus* evidence differences in the microhabitat used, in the accuracy in thermoregulation, and in activity timetables (Ibargüengoytía 2005).

In the present work, we study the thermal physiology of three sympatric and syntopic lizards, *Phymaturus querque*, *Phymaturus zapalensis*, and *Liolaemus elongatus*, in Patagonian environments, during the summer season, by measuring the body temperature at capture, the operative microenvironmental temperatures in the field, the preferred body temperatures in an experimental thermal gradient in the laboratory, and so determining the effectiveness of the thermoregulation. We expect *Phymaturus* species to thermoregulate differently than *L. elongatus*, based on the selective microhabitat that each one occupies. The present result could contribute in future studies to predict how this coexisting species would respond in a scenario of climate change and their potential re-distributions, a

topic especially sensitive considering that *P. querque* is the southernmost species of the *palluma* group, and the vulnerable status of the genus *Phymaturus* (Abdala et al. 2012).

## Materials and methods

### Study area

The study was carried out in the Laguna Blanca National Park in Zapala, Occidental District (Neuquén Province, Argentina 39°1'16" S and 70°24'33" W, 824–1312 m asl). The Patagonian Phytogeographic Province seasonal climate is dry and cold, with strong winds from the west, and snow in the winter months with freezing temperatures occurring throughout most of the year (Cabrera 1976). The Laguna Blanca lagoon can be partially frozen during the winter months (pers. obs.), and the mean annual precipitation is 176 mm (Cabrera 1976). In consequence, Liolaemidae lizards that inhabit the Laguna Blanca N.P. are inactive and take refuge in the rock crevices during the cold season, from mid-autumn (May) to early spring (October; Boretto and Ibargüengoytía 2009). At the study site, the landscape is characterized by plateaus with steppe vegetation, mostly *Mulinum spinosum* Persoon 1805, *Haplopappus pectinatus* Philippi 1862, *Senecio filaginoides* Pyrame de Candolle 1837, and *Senecio subulatus* Hooker and Arnott 1841 growing in sandy soil (Cabrera 1976).

### Study species

In the Laguna Blanca N.P., the species *Liolaemus elongatus*, *Phymaturus querque*, and *Phymaturus zapalensis* live in sympatry and syntopy. The genus *Liolaemus* comprises more than 230 species with a high diversity in their life history traits, and a wide latitudinal, altitudinal, and climatic distribution from the Andean mountains in Peru and Bolivia, to Tierra del Fuego Province in Argentina, from the Pacific Islands to Brazil, and from sea level to as high as 5000 m asl (Cei 1986; Schulte 2013). The genus *Phymaturus*, the sister clade to *Liolaemus*, is a monophyletic genus that comprises saxicolous, viviparous, and mostly herbivorous species of lizards that inhabit cold environments of the Andean highlands in Argentina and Chile, and the volcanic plateaus of Patagonia, Argentina (Cei 1986). In the genus *Phymaturus*, two groups have been recognized based on morphological traits (Etheridge 1995): the *palluma* group (=flagellifer, sensu Cei 1993; Cei and Scolaro 2006), and the *patagonicus* group (Cei 1993; Etheridge 1995). *Phymaturus querque*, from the *palluma* group, is only known to be found on rocky outcrops near the southern shore of the Laguna Blanca lake (Neuquén, Argentina; Lobo et al. 2010), and up to today, there are no studies



about its biology. In addition, while initially, *P. zapalensis*, from the *patagonicus* group, was considered endemic in the area of the Laguna Blanca N.P. (Cei and Castro 1973), its distribution is wider. This species is found around basalt gaps 40 km west of Zapala (Neuquén), and from this locality is distributed to the south, always in volcanic rocky outcrops near the Limay River (Piedra del Águila City), approximately between 39° and 40° S, and between 1000 and 1300 m asl (Cei 1986; Scolaro 2005). Studies on reproductive biology (Boretto and Ibarzüengoytía 2009), field thermal biology (Ibarzüengoytía et al. 2008), and thermal preferences (Cruz et al. 2009) of *P. zapalensis*, in populations outside the Laguna Blanca N.P., have been realized. *Liolaemus elongatus* is a viviparous, insectivorous lizard, widely distributed on rocky outcrops in the steppe from Neuquén to Chubut, in the western and south–central regions of the Río Negro Province, Argentina (Minoli et al. 2013). The reproductive biology (Ibarzüengoytía and Cusac 1998) and thermal preference (Ibarzüengoytía 2005; Kubisch et al. 2016) of *L. elongatus* have been described.

### Field and laboratory work

We captured a total of 32 specimens of *P. querque*, 16 specimens of *P. zapalensis*, and 10 specimens of *L. elongatus* from the 15th to the 17th of January of 2015, corresponding to the summer season of the Southern Hemisphere. During this field trip, all the specimens were captured on granite rock outcrops using a slipknot, and each one was georeferenced, so that they could be released back to the capture site after the experiments were finished. The number of specimens used in this study is necessarily small because of the protected conservation status of the species. Genus *Phymaturus* is unique within the herpetofauna of Argentina, since all the species are vulnerable (Abdala et al. 2012), based on their highly specialized biology, mode of life (saxicolous), reproduction (viviparous), with prolonged female reproduction, and low mean annual

reproductive output, and an herbivore diet. The populations of most *Phymaturus* species are scarce, and there is a high degree of endemism (Abdala et al. 2012). We followed the ASIH/HL/SSAR Guidelines for the Use of Live Amphibians and Reptiles as well as the regulations detailed in the Argentinean National Law #14346.

Immediately after capture, the body temperature ( $T_b$ ) was measured using a catheter probe TES TP-K01, 1.62 mm diameter introduced inside the cloaca, connected to a TES 1302 digital thermometer (TES Electrical Electronic Corp., Taipei, Taiwan,  $\pm 0.01$  °C). Individuals were grabbed by the head, and the temperature measurements were performed within a period of 10 s after capture, to prevent heat transfer from the operator's hands. We also registered the substratum temperature ( $T_s$ ) and the air temperature 1 cm above the ground ( $T_a$ ) of the microenvironment where the lizards were captured. All specimens were captured active from 9:00 to 20:50 h, except two individuals of *P. zapalensis* that were found early in the morning, inactive in crevices, and with lower body temperature, which were used only in the experiments of preferred body temperatures ( $T_{pref}$ ), and were not considered in the rest of the analysis. We recorded if the specimens were captured inside or outside the rock crevices, and the time of the day. Lizards were taken to the laboratory where the snout–vent length (SVL, digital gauge  $\pm 0.02$  mm, CA-01, Lee Tools, Guangzhou, Guangdong, China), sex (by the presence of precloacal pores in males), and body mass (BM, 100 g spring scale  $\pm 0.5$  g; Pesola AG, Baar, Switzerland) were measured and recorded (Table 1). During the captivity, which lasted 5 days, each lizard was placed individually in cloth bags at ambient room temperature (20–23 °C) or in  $T_{pref}$  terrariums with water ad-libitum, to minimize stress and to prevent dehydration. Each lizard was released back to the capture site after the experiments were finished.

To determine the adult or juvenile condition of each specimen, we used the minimum adult size previously determined for *L. elongatus* (males = 57.26 mm SVL;

**Table 1** Mean and standard error (SE), range values and sample size ( $n$ ) of body mass (BM, g), and snout–vent length (SVL, mm) of adult males, adult females, and juveniles of *Phymaturus querque*, *Phymaturus zapalensis*, and *Liolaemus elongatus*

Species	BM $\pm$ SE (range)	SVL $\pm$ SE (range)
<i>Phymaturus querque</i>		
Males ( $n=13$ )	42.80 $\pm$ 1.19 (33.50–48.00)	100.97 $\pm$ 1.13 (90.83–106.44)
Females ( $n=17$ )	38.91 $\pm$ 1.60 (27.00–49.00)	97.45 $\pm$ 1.10 (88.12–104.43)
Juveniles ( $n=2$ )	13.00 $\pm$ 2.00 (11.00–15.00)	68.35 $\pm$ 2.07 (66.28–70.42)
<i>Phymaturus zapalensis</i>		
Males ( $n=8$ )	23.25 $\pm$ 1.02 (18.00–26.00)	84.95 $\pm$ 1.43 (77.95–90.70)
Females ( $n=5$ )	22.50 $\pm$ 1.87 (19.00–29.00)	86.49 $\pm$ 2.86 (78.75–96.05)
Juveniles ( $n=3$ )	12.33 $\pm$ 1.59 (10.50–15.50)	68.66 $\pm$ 4.33 (64.25–77.32)
<i>Liolaemus elongatus</i>		
Males ( $n=5$ )	14.50 $\pm$ 0.63 (13.00–16.00)	76.70 $\pm$ 1.15 (74.27–80.54)
Females ( $n=5$ )	13.50 $\pm$ 0.59 (11.50–15.00)	74.46 $\pm$ 2.10 (69.17–82.03)

females = 53.74 mm SVL; Ibargüengoytía and Cusac 1998) and *P. zapalensis* (males = 75.66 mm SVL; females = 79.02 mm SVL; Boretto and Ibargüengoytía 2009). We considered the published data of the minimum adult size for other *Phymaturus* species of the *paluma* group (Habit and Ortíz 1996; Boretto and Ibargüengoytía 2009; Cabezas Cartes et al. 2010) to estimate a mean value of the minimum SVL for adults of *P. querque* (males = 83.70 mm SVL; females = 81.77 mm SVL).

### Operative temperatures ( $T_e$ )

The  $T_e$  equals the steady-state temperature of an organism in a particular microclimate in the absence of metabolic heating and evaporative cooling (Winslow et al. 1940; Bakken 1992). Thermal models were used to determine the availability of spatial and temporal heterogeneity of microenvironmental temperatures for thermoregulation ( $T_e$ ; *sensu* Hertz 1992; Bakken 1992; Angilletta 2009), allowing to characterize the thermal environment as perceived by the organism, independently of any physiological and/or behavioral thermoregulation (Angilletta 2009). The  $T_e$  was used to analyze the possibilities that lizards have to achieve temperatures within the optimal physiological temperature range (Bakken et al. 1985; Bakken 1992; Dzialowski 2005; Williams et al. 2008). We recorded the  $T_e$  in the field, during the sampling days, every 2 min, using 30 gray PVC plastic oval models of 35 × 10 mm and 120 mm long. Models were connected to a data-logger (3 Onset HOBO U23-003 Temperature Data Logger with 2 External Channels; 1000 Series Squirrel Meter/Logger GEN2 transmitters, 24 channel Data Loggers TM1033), with the thermocouple inside, and closed at the ends with silicone (Fastix®). The models were placed homogeneously within a range of about 30 m<sup>2</sup>, and fell randomly in different kind of microsites (e.g., in the sun, shade, in soil, on rocks, under vegetation...). Thus, we covered the spatial and temporal availabilities of microenvironmental temperatures for thermoregulation. The models were tested in the previous studies with calibration experiments (described in Boretto et al. 2014b for *Phymaturus*; Kubisch et al. 2016 for *Liolaemus*).

### Preferred body temperature

To measure the preferred body temperatures ( $T_{pref}$ ), lizards of *P. querque* ( $N=32$ ) and *P. zapalensis* ( $N=16$ ) were placed individually in an open-top terrarium (100 × 20 × 17 cm<sup>3</sup>) with a thermal gradient (20–50 °C) produced by an overhead lamp (75 W) placed at one end of the terrarium. The  $T_{pref}$  experiments were performed from 10 a.m. to 17 p.m. h, in the same hours when lizards of these species were capture active in their habitats. The substrate of the terrarium consisted of a layer of medium

density fibreboard (MDF) wood which has good conductivity to radiant heat, thus heating from the radiation of the lamp, giving the lizard a warm substrate from which it can also gain heat. The body temperature of each lizard was measured every second for 150 min using ultra-thin (1 mm) catheter thermocouples (Product code 5SC-TT-T-40-72; Omega Engineering Inc., Stamford, CT, USA) fastened in the belly of the lizard with an insulating material (to isolate the thermocouple from the substrate and be able to record the temperature of the body without the influence of the temperature of the air or the substrate) and an adhesive tape, connected to an 8-channel data-logger (Measurement Computing 1.2 kHz Data Acquisition Device, OMEGA TC-08 ± 0.5 °C, Stamford, USA). For each individual, we estimated the mean and the range of the  $T_{pref}$ . We also estimated the set-point temperature ranges ( $T_{set}$ ) identifying the interquartile range (middle 50% of the data) and the mean of the upper bound of  $T_{pref}$ . The preferred body temperature of *L. elongatus* was obtained from Kubisch et al. (2016) with the same methodology.

### Restriction hours estimation

We estimated the restriction hours, defined as the hours when lizards would be in their shelters due to temperatures exceeding their thermal preferences (Sinervo et al. 2010). The hours of restriction were calculated based on the data obtained during the first 2 days of capture (because on the third day sampling was performed until midday), as the daily number of hours when the temperature of at least 50% of the models exceeded the mean of the upper bound of  $T_{pref}$  considered as the threshold for activity restriction (Kubisch et al. 2016).

### Indexes of thermal quality of the habitat, and accuracy and effectiveness of thermoregulation

We followed Hertz et al. (1993) methodology to quantify the thermoregulatory behavior, using the information of the preferred body temperatures obtained in the thermal gradient, and the availability of operative temperatures in the natural environment. We determined the  $d_b$  (individual deviation) as an index based on the average extent to which each individual experienced  $T_b$  outside the set-point range of their  $T_{pref}$ . The  $d_b$  was estimated as the average of the absolute value of the deviations of  $T_b$  from  $T_{set}$  of each individual. Following, for each species, we calculated the  $d_e$  as an index of the mean thermal quality of the habitat from an organism's perspective. The  $d_e$  was estimated as the mean of the deviation of  $T_e$  from the  $T_{set}$  of each individual. Since in Patagonian environments there are high thermal amplitudes throughout the day, the  $T_e$  is highly dynamic. In consequence, we used the mean value of  $T_e$  from the whole

data registered from the previous hour and until the capture of each specimen. We have defined the effectiveness of thermoregulation as the existence of active selection of the thermal microhabitat, calculating the index  $E = 1 - (d_b/d_e)$ , which integrates the average degree to which each of the three studied liolaemids experienced  $T_b$  outside the set-point range ( $d_b$ ), and the corresponding  $d_e$ . When lizards' thermoregulation is not effective, the  $E$  index approaches zero and the species is considered to be thermoconformer, while, when lizards thermoregulation is effective, the  $E$  index gradually approaches a value of one. Finally, if the  $E$  index is close to 0.5, the species is considered to be a moderately effective thermoregulator (Hertz et al. 1993).

In addition, we calculated another index to estimate the effectiveness of thermoregulation, based on the difference between  $d_e$  and  $d_b$ , in agreement with several authors that propose that the magnitude of this difference is a measure of how much an animal departs from thermoconformity (Blouin-Demers and Weatherhead 2001, 2002; Corbalán et al. 2013). This  $d_e - d_b$  index provides an open-ended scale where negative numbers represent animals that avoid thermally favorable habitats, zero represents perfect thermoconformity, and positive numbers represent animals that thermoregulate up to some extent (Blouin-Demers and Weatherhead 2001).

### Statistical analyses

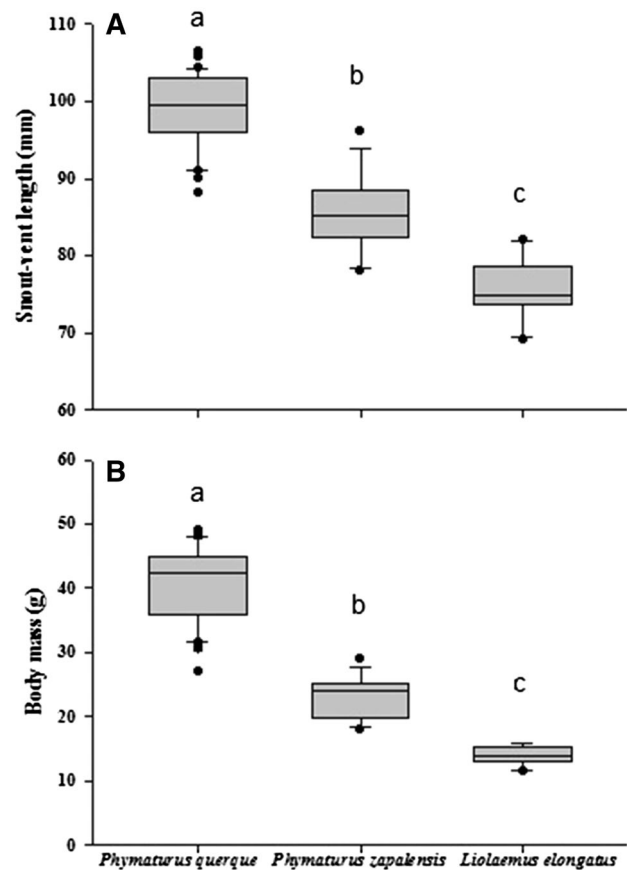
We used the statistical software Sigma Stat 3.5<sup>®</sup> (Systat Software Inc., Chicago, Illinois, USA), Sigma Plot 10.0<sup>®</sup> (Systat Software Inc., Chicago, Illinois, USA), and SPSS 17.0<sup>®</sup>. We used a  $t$  test to compare  $T_b$  and  $T_{pref}$  between adult males and females, and the  $T_b$  between lizards outside the crevices vs lizards inside them, for each species. We used a proportion test to analyze if the proportion of lizards of each *Phymaturus* species that was observed inside the crevice was significantly different from 0.5 or not. We used a two-sample test of proportions to analyze differences in the proportion of individuals of *P. querque* and *P. zapalensis* inside the crevice. When the assumptions of normality and/or homogeneity of variance were not fulfilled, we used the Mann–Whitney rank–sum test. We used a one-way analysis of variance (ANOVA) and the Holm–Sidak method for a posteriori comparisons of SVL and  $T_b$  between species. As the assumptions of normality and/or homogeneity of variance were not fulfilled, we used a Kruskal–Wallis test with Dunn's Method for a posteriori comparisons of BM and  $T_{pref}$  between the sympatric species studied. We performed linear regressions to estimate the relationship between  $T_b$  and SVL, BM,  $T_s$ , and  $T_a$ , and between  $T_{pref}$  and SVL or BM. We used paired  $t$  test to compare the  $T_b$  with the  $T_{pref}$  of each lizard within each species. Assumptions of normality and homogeneity

of variance were tested with the one-sample Kolmogorov–Smirnov test and with the Levene test, respectively. Means are given with a  $\pm$  standard error (SE).

## Results

### Interspecific comparisons of body sizes

The three species showed differences in the body size of adult specimens (ANOVA,  $F_{2,52} = 113.340$ ,  $P < 0.001$ ; Fig. 1A). *Phymaturus querque* exhibited larger SVL than *P. zapalensis* (Holm–Sidak method,  $t_{P. querque vs P. zapalensis} = 8.914$ ,  $P < 0.001$ ,  $N_{P. querque} = 30$ ;  $N_{P. zapalensis} = 13$ ) and *L. elongatus* ( $t_{P. querque vs L. elongatus} = 14.117$ ,  $P < 0.001$ ,  $N_{P. querque} = 30$ ;  $N_{L. elongatus} = 10$ ); and *P. zapalensis* was larger in SVL than *L. elongatus* ( $t_{P. zapalensis vs L. elongatus} = 5.218$ ,  $P < 0.001$ ,  $N_{P. zapalensis} = 13$ ;  $N_{L. elongatus} = 10$ ; Fig. 1A). In addition, *P. querque* exhibited higher BM than *P. zapalensis* and *L. elongatus*



**Fig. 1** Box plots of interspecific differences of snout–vent length (mm; **A**) and body mass (g; **B**) of *Phymaturus querque*, *Phymaturus zapalensis*, and *Liolaemus elongatus*. Lowercase letters indicate the groups that were significantly different ( $P < 0.05$ ). The detailed statistical analyses are presented in the "Result" section

(Kruskal–Wallis,  $H_2=41.341$ ,  $P<0.001$ ; Dunn's Method,  $Q_{P. querque}$  vs  $P. zapalensis$  = 4.171,  $P<0.001$ ,  $N_{P. querque}$  = 30;  $N_{P. zapalensis}$  = 13,  $Q_{P. querque}$  vs  $L. elongatus$  = 5.846,  $P<0.001$ ,  $N_{P. querque}$  = 30;  $N_{L. elongatus}$  = 10; Fig. 1B), whereas  $P. zapalensis$  and  $L. elongatus$  did not exhibit differences in BM when the three species were analyzed together ( $Q_{P. zapalensis}$  vs  $L. elongatus$  = 1.782,  $P>0.05$ ,  $N_{P. zapalensis}$  = 13;  $N_{L. elongatus}$  = 10). However, when only  $P. zapalensis$  and  $L. elongatus$  were compared, they showed significant differences in BM, being  $P. zapalensis$  heavier (Mann–Whitney,  $U=130.000$ ,  $P\leq 0.001$ ,  $N_{P. zapalensis}$  = 13;  $N_{L. elongatus}$  = 10; Fig. 1B).

**Intra and interspecific comparisons of body temperature ( $T_b$ )**

None of the three species exhibited any relationship between  $T_b$  and SVL ( $F_{P. querque, 1, 31}$  = 0.825,  $P=0.371$ ;  $F_{P. zapalensis, 1, 13}$  = 0.780,  $P=0.395$ ;  $F_{L. elongatus, 1, 9}$  = 0.141,  $P=0.717$ ) or BM ( $F_{P. querque, 1, 31}$  = 0.096,  $P=0.759$ ;  $F_{P. zapalensis, 1, 13}$  = 0.911,  $P=0.359$ ;  $F_{L. elongatus, 1, 10}$  = 0.009,  $P=0.926$ ). In addition, there were no differences in the  $T_b$  between adult males and females ( $t_{P. querque, 28}$  = -0.881,  $P=0.386$ ;  $t_{P. zapalensis, 12}$  = 0.435,  $P=0.671$ ;  $t_{L. elongatus, 9}$  = 0.635,  $P=0.541$ ).

There were significant differences in the proportion of lizards of  $P. querque$  that were observed outside the crevices ( $N=9$ , 28%) and inside the crevice ( $N=23$ , 72%; proportion test,  $\chi^2=5.281$ ,  $N=32$ ,  $P=0.020$ ) prior capture. In contrast, in  $P. zapalensis$  there were no significant differences in the proportion of lizards outside ( $N=6$ , 43%) and inside the crevice ( $N=8$ , 57%; proportion test,  $\chi^2=0.071$ ,  $N=14$ ,  $P=0.791$ ). We did not find differences in the proportions of lizards of  $P. querque$  (71.9%) and  $P. zapalensis$  (57.1%) that were inside crevices (two-sample test of proportions,  $\chi^2=0.962$ ,  $df=1$ ,  $P=0.327$ ). In addition, there were no differences in the  $T_b$  between lizards of  $P. querque$  and  $P. zapalensis$  that were outside the crevices, and lizards that

were inside the crevices at the moment they were observed in the field prior the capture ( $t$  test,  $P. querque$ :  $t_{30}$  = 0.597,  $P=0.555$ ;  $\text{mean}_{\text{outside}}=30.367\pm 0.911^\circ\text{C}$ ,  $N=9$ ;  $\text{mean}_{\text{inside}}=29.691\pm 0.610^\circ\text{C}$ ,  $N=23$ ;  $t$  test,  $P. zapalensis$ :  $t_{12}$  = 1.160,  $P=0.269$ ;  $\text{mean}_{\text{outside}}=33.000\pm 0.938^\circ\text{C}$ ,  $N=6$ ;  $\text{mean}_{\text{inside}}=31.313\pm 1.041^\circ\text{C}$ ,  $N=8$ ). All specimens of  $L. elongatus$  were captured outside refuge.

We found interspecific differences in  $T_b$  (ANOVA,  $F_{2,55}=7.525$ ,  $P<0.001$ ), since  $L. elongatus$  and  $P. zapalensis$  showed higher  $T_b$  than  $P. querque$  (Holm–Sidak method,  $t_{L. elongatus}$  vs  $P. querque$  = 3.491,  $P=0.001$ ,  $N_{L. elongatus}$  = 10;  $N_{P. querque}$  = 32;  $t_{P. zapalensis}$  vs  $P. querque$  = 2.570,  $P=0.013$ ,  $N_{P. zapalensis}$  = 14;  $N_{P. querque}$  = 32). There were no differences in  $T_b$  between  $P. zapalensis$  and  $L. elongatus$  (Holm–Sidak method,  $t=1.066$ ,  $P=0.291$ ,  $N_{P. zapalensis}$  = 14,  $N_{L. elongatus}$  = 10).

**Microenvironmental temperatures at capture site and  $T_b$**

*Phymaturus querque* and  $P. zapalensis$  exhibited a positive relationship between  $T_b$  and  $T_s$ , and between  $T_b$  and  $T_a$  (Table 2). Nevertheless, the  $L. elongatus$  data did not show any relationship between  $T_b$  and  $T_s$ , or  $T_a$  (Table 2). Figure 2 illustrates the different relationships between  $T_b$  and microenvironmental temperatures at the moment of capture of each specimen of the three studied species.

**Intra and interspecific comparisons of preferred body temperature ( $T_{\text{pref}}$ )**

The  $T_{\text{pref}}$  did not show a relationship with SVL or BM in any of the three species (Linear Regression, SVL:  $F_{P. querque, 1, 31}$  = 0.096,  $P=0.759$ ;  $F_{P. zapalensis, 1, 15}$  = 1.839,  $P=0.197$ ;  $F_{L. elongatus, 1, 9}$  = 2.252,  $P=0.172$ ; BM:  $F_{P. querque, 1, 31}$  = 0.186,  $P=0.670$ ;  $F_{P. zapalensis, 1, 15}$  = 3.863,  $P=0.070$ ;  $F_{L. elongatus, 1, 10}$  = 1.010,  $P=0.344$ ), considering juvenile and adult specimens. In addition, there

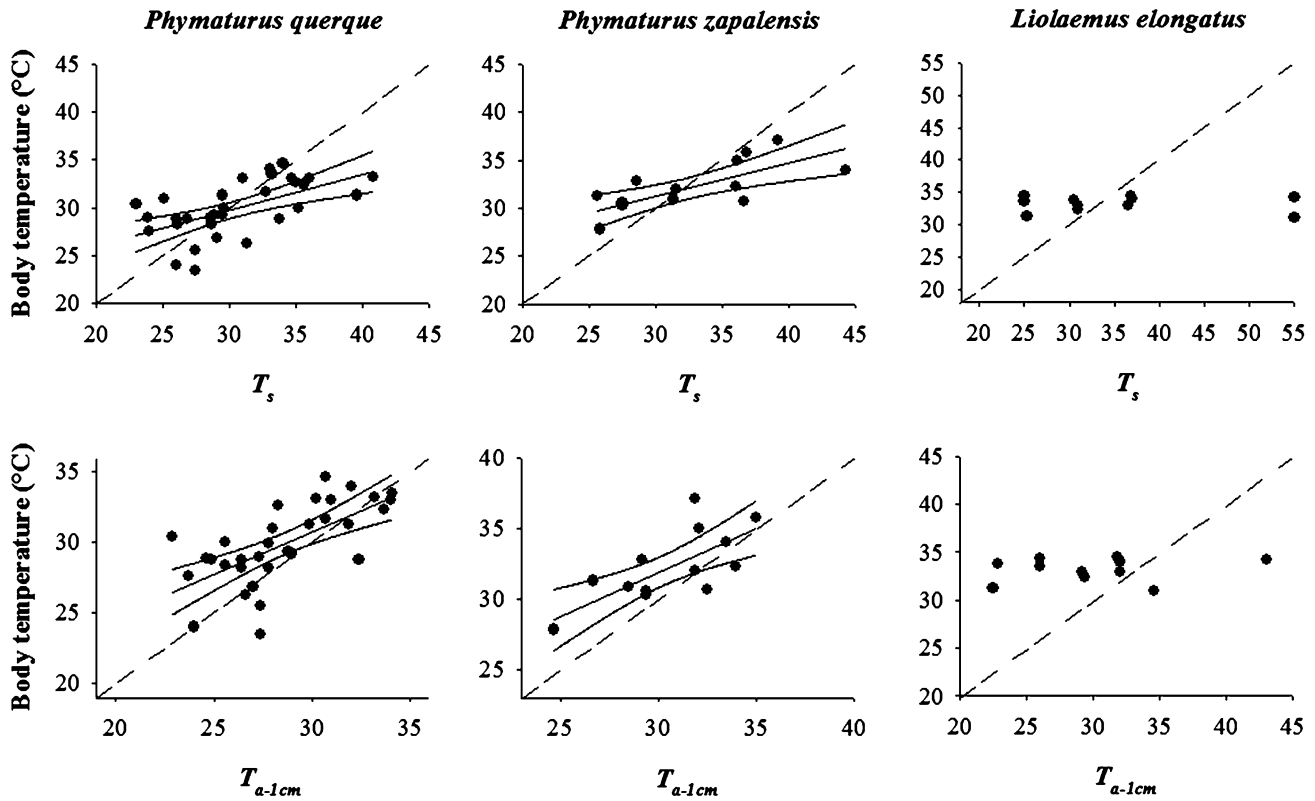
**Table 2** Descriptive data of field body temperature ( $T_b$ ) at capture of *Phymaturus querque*, *Phymaturus zapalensis*, and *Liolaemus elongatus* and descriptive data of microenvironmental temperatures at the

moment of capture of each specimen:  $T_s$  substratum temperature;  $T_a$  air temperature 1 cm above the ground at capture

Species	Mean $T_b \pm$ SE (range)	Mean $T_s \pm$ SE (range)	Mean $T_a \pm$ SE (range)	Linear regression model	F	P value	$r^2$
<i>Phymaturus querque</i>	29.88 ± 0.50 (23.5–34.6)	30.44 ± 0.80 (23.0–40.8)	28.54 ± 0.56 (22.9–34.1)	$T_b = 18.36 + 0.38 \times T_s$ $T_b = 12.76 + 0.60 \times T_a$	$F_{1,31} = 16.77$ $F_{1,31} = 23.99$	<0.001 <0.001	0.359 0.444
<i>Phymaturus zapalensis</i>	32.04 ± 1.16 (27.8–37.1)	32.33 ± 1.57 (25.6–44.3)	30.25 ± 0.88 (24.7–35.0)	$T_b = 20.89 + 0.34 \times T_s$ $T_b = 12.94 + 0.63 \times T_a$	$F_{1,13} = 14.73$ $F_{1,13} = 16.58$	0.002 0.002	0.551 0.580
<i>Liolaemus elongatus</i>	33.16 ± 0.37 (31.0–34.5)	35.26 ± 3.24 (25.0–55.0)	29.94 ± 1.76 (22.5–43.0)	$T_b = 33.60 - 0.01 \times T_s$ $T_b = 32.14 + 0.03 \times T_a$	$F_{1,10} = 0.11$ $F_{1,10} = 0.25$	0.751 0.630	0.012 0.027

Mean ± standard error (SE) and range (between parentheses) are indicated. The linear regression models between  $T_b$  and microenvironmental temperatures are presented with its corresponding F, P value, and  $r^2$  value





**Fig. 2** Relationship between body temperature ( $T_b$ ), substratum temperatures ( $T_s$ ), and air temperatures 1 cm above the ground ( $T_a$ ) recorded at capture of individuals of *Phymaturus querque*, *Phymaturus zapalensis*, and *Liolaemus elongatus* during activity. Dashed lines

indicate  $Y=X$  relationships. When the linear regression was significant, the least-squares line and 95% confidence intervals were indicated. The detailed statistical analyses are presented in Table 2

were no differences in the  $T_{pref}$  between adult males and females ( $t$  test,  $t_{P. querque, 28} = 0.363$ ,  $P = 0.719$ ;  $t_{P. zapalensis, 12} = 0.701$ ,  $P = 0.498$ ; Mann–Whitney,  $U_{L. elongatus, 9} = 20.000$ ,  $P = 0.151$ ). In consequence, we used all the captured individuals of the three sympatric liolaemids to perform interspecific comparisons. We did not find any differences in  $T_{pref}$  between the species studied ( $H_2 = 4.240$ ,  $P = 0.120$ ,  $N_{P. querque} = 32$ ,  $N_{P. zapalensis} = 16$ ,  $N_{L. elongatus} = 10$ ; Table 3).

**Restriction hours**

Considering that the upper bound of  $T_{pref}$  for *P. querque* and *P. zapalensis* was 38.6°C and for *L. elongatus* it was 39.2°C, the restriction hours estimated during the first 2 days of capture were 6.40 and 8.10 h for *P. querque* and *P. zapalensis*, and 6.23 and 7.83 h for *L. elongatus*.

**Accuracy and effectiveness of thermoregulation**

The  $T_b$  was significantly lower than the  $T_{pref}$  in the three species (paired  $t$  test,  $t_{P. querque, 31} = -10.912$ ,  $P < 0.001$ ;

**Table 3** Thermal preferences and efficiency of thermoregulation of *Phymaturus querque*, *Phymaturus zapalensis*, and *Liolaemus elongatus*

Species	N	Mean $T_{pref}$	Lower set-point of $T_{pref}$	Upper set-point of $T_{pref}$	$d_b$	$d_e$	E	$d_e - d_b$
<i>Phymaturus querque</i>	32	35.66 ± 0.20 (33.16–37.90)	34.79 ± 0.25 (31.05–37.56)	36.87 ± 0.16 (34.73–39.21)	4.971	8.891	0.441	3.925
<i>Phymaturus zapalensis</i>	16	35.84 ± 0.22 (34.34–37.35)	35.02 ± 0.25 (32.67–36.30)	36.80 ± 0.21 (35.91–38.26)	3.282	6.207	0.471	2.925
<i>Liolaemus elongatus</i>	10	36.41 ± 0.48 (33.80–38.00)	35.28 ± 0.62 (31.55–37.58)	37.58 ± 0.39 (35.08–38.88)	2.285	6.953	0.671	4.668

The mean, standard error, and lower and upper values of preference of body temperature ( $T_{pref}$ ), the lower and upper set-point of  $T_{pref}$ , and the mean of the absolute value of the deviations of  $T_b$  from  $T_{set}$  of each individual ( $d_b$ ), the mean of absolute value of the deviation of  $T_e$  from the  $T_{set}$  of each individual ( $d_e$ ), and the effectiveness of thermoregulation (E) are presented

$t_{P. zapalensis, 13} = -4.659$ ,  $P < 0.001$ ;  $t_{L. elongatus, 9} = -6.06$ ,  $P < 0.001$ ). In addition, most of the  $T_b$  measurements had values below  $T_{set}$  in all species: 96.9% of *P. querque*, 78.6% of *P. zapalensis*, and 90% of *L. elongatus* presented  $T_b$  values below the lower  $T_{set}$  (Fig. 3). In *P. zapalensis*, 7.1% of the individuals presented  $T_b$  values above upper  $T_{set}$ , but this result represents a single individual from a total sample of 14, and therefore, it is not representative.

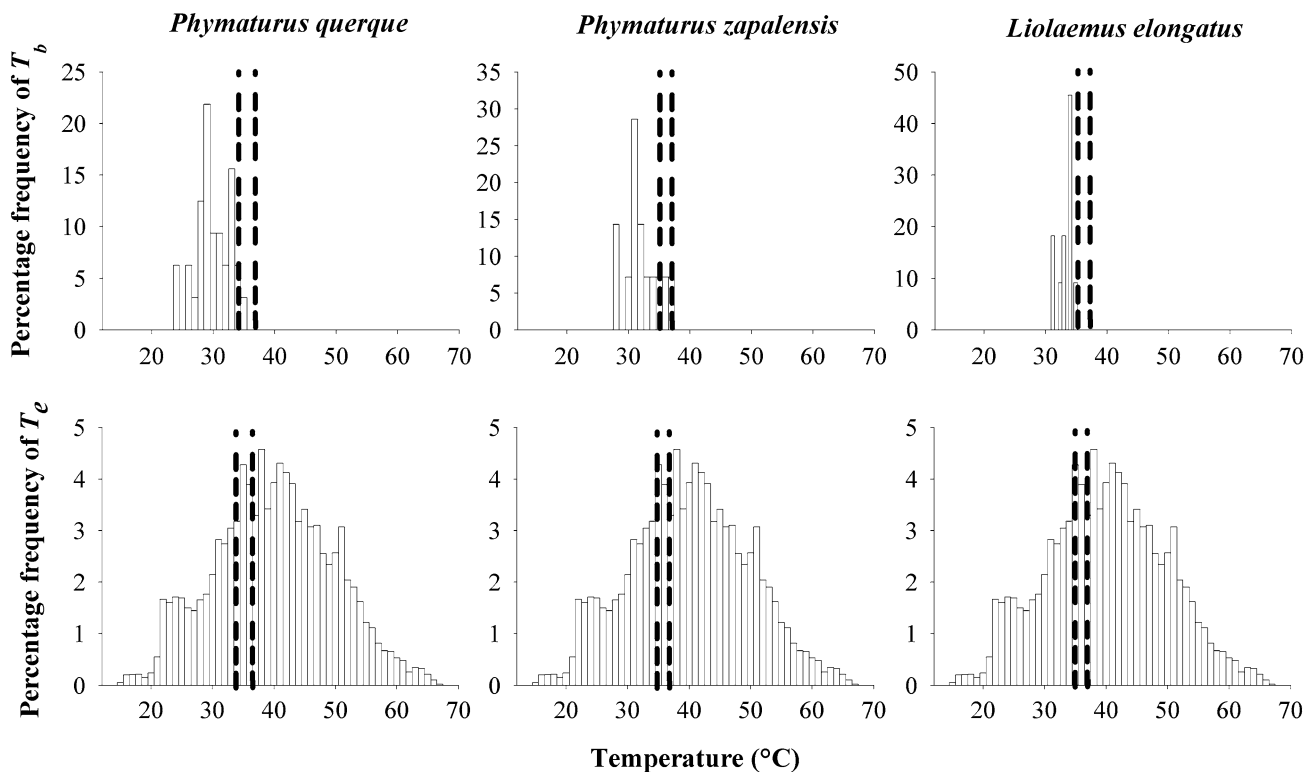
The effectiveness of thermoregulation of *P. querque* ( $E = 0.441$ ) and *P. zapalensis* ( $E = 0.471$ ) was lower than *L. elongatus* ( $E = 0.671$ ; Table 3). The magnitude of the difference  $d_e - d_b$  was greater in *L. elongatus*, and the lowest difference  $d_e - d_b$  was exhibited by *P. zapalensis* (Table 3).

### Discussion

In the present work, we studied the thermal biology of sympatric and syntopic species of the genus *Phymaturus* and *Liolaemus*, in the Laguna Blanca National Park, Neuquén (Patagonia, Argentina), which represents the southernmost distribution of the *Phymaturus palluma* group. Knowledge of the thermal requirements and the effectiveness of thermoregulation in these species provides useful information

that could contribute to predict how sympatric and syntopic species would respond in a scenario of climate change. Herein, we found that, considering the  $E$  index proposed by Hertz et al. (1993), *L. elongatus* is an effective thermoregulator ( $E = 0.671$ ), while *P. querque* ( $E = 0.441$ ) and *P. zapalensis* ( $E = 0.471$ ) are moderate thermoregulators.

Blouin-Demers and Weatherhead (2001, 2002) have described cases of species that experience different climatic conditions and present different thermoregulatory behavior, but have similar  $E$  values (Blouin-Demers and Weatherhead 2001). In consequence, we calculated the  $E$  index, and also we considered the magnitude of the difference of  $d_e - d_b$  in interpreting  $E$ , since the magnitude of this difference indicates how much an animal departs from thermoconformity (Blouin-Demers and Weatherhead 2001, 2002). In our study, the magnitude of the difference of  $d_e - d_b$  was positive and greater in *L. elongatus* (4.668), strengthening its definition as an efficient thermoregulator, better than *P. querque* and *P. zapalensis*. At the same time, *P. querque* (3.925) showed being a more efficient thermoregulator than *P. zapalensis* (2.925). The magnitude of the difference of  $d_e - d_b$  puts in evidence that these two sympatric and syntopic *Phymaturus* have different efficiency in thermoregulation, and this difference was not showed by the  $E$  index.



**Fig. 3** Distribution of body temperature ( $T_b$ ) at capture, of *Phymaturus querque*, *Phymaturus zapalensis*, and *Liolaemus elongatus* (bars; upper graph), and thermal availability distribution (operative temper-

atures:  $T_e$ ; bars, below graph). The dashed lines indicate the lower and upper set-points of the preferred body temperature ( $T_{pref}$ )

Differences in the efficiency of thermoregulation were also found in other sympatric species of *Phymaturus*, *P. roigorum* (*palluma* group;  $d_e - d_b = 3.62$ ), and *P. payuniaie* (*patagonicus* group;  $d_e - d_b = 7.35$ ; Corbalán et al. 2013). Similarly, the  $E$  index showed differences in the accuracy of thermoregulation between *P. roigorum* ( $E = 0.39$ ) and *P. payuniaie* ( $E = 0.64$ ), indicating that individuals of *P. payuniaie*, from the *patagonicus* group, are more efficient thermoregulators (Corbalán et al. 2013). A recent study showed that *Phymaturus palluma*, from the *palluma* group, is a better thermoregulator than the rest of congeners ( $E = 0.79$ , Vicenzi et al. 2017). The difference of  $d_e - d_b$  between sympatric *Phymaturus* studied here showed that *P. querque*, from the *palluma* group, is a better thermoregulator than *P. zapalensis*, from the *patagonicus* group, although the difference between these species is smaller than between *P. roigorum* and *P. payuniaie*. These results show that the geographically southernmost species of the *palluma* group *P. querque*, and the geographically northernmost species of the *patagonicus* group *P. payuniaie* are better thermoregulators than their sympatric species *P. zapalensis* and *P. roigorum*, respectively.

The thermoregulation efficiencies of the studied species are in accordance with the relationship of  $T_b$  to the microenvironmental temperatures. *Phymaturus querque* and *P. zapalensis* exhibited a positive relationship between  $T_b$  and  $T_s$ , and  $T_a$ ; in contrast with *L. elongatus* that did not show any relationship between  $T_b$  and  $T_s$ , and  $T_a$ . In this sense, other *Phymaturus* have been defined, based on the relationship of  $T_b$  and microenvironmental temperatures, as thermoregulators like *Phymaturus punae* and *Phymaturus tenebrosus*, while *P. zapalensis* has been proposed as a thermoconformer (Ibargüengoytía et al. 2008).

The mean preferred temperatures ( $T_{pref}$ ) obtained in the laboratory were similar between *P. querque*, *P. zapalensis*, and *L. elongatus*, although they exhibited significant interspecific differences in SVL and body mass. Intrinsic factors such as body size, body mass, sex, or reproductive condition have been showed in several studies to affect  $T_b$  (Mathies and Andrews 1997; Angilletta 2009). Nevertheless, none of the three liolaemids studied here exhibited a relationship between  $T_b$  or  $T_{pref}$  and SVL, or body mass, and none exhibited differences in  $T_b$  or  $T_{pref}$  between adult males and females, so intraspecific differences must be interpreted cautiously, since the sample size is low. Similar results were found in the sympatric *P. roigorum* and *P. payuniaie* (Corbalán et al. 2013), and in the sympatric species *Liolaemus sarmientoi* and *Liolaemus magellanicus* (Ibargüengoytía et al. 2010), as in others *Phymaturus* studied (Ibargüengoytía 2005; Ibargüengoytía et al. 2008; Cruz et al. 2009). We found that, even though lizards studied here had access to warm microenvironments ( $T_e$ ), they selected cooler environments. Indeed, most of the field  $T_b$

records had values below the lower  $T_{set}$  in the three species: 96.9% of *P. querque*, 78.6% of *P. zapalensis*, and 90% of *L. elongatus*. Thermoregulation has a cost that depends on the biological and physical environmental circumstances, like predation risk (Huey and Slatkin 1976; Huey 1982; Gregory et al. 1999), competition (Huey and Slatkin 1976; Labra 1995), and the spatial distribution of operative environmental temperatures in the habitat ( $T_e$ ; Withers and Campbell 1985; Clusella-Trullas and Chown 2011; Sears and Angilletta 2015). During the period of our study in the Laguna Blanca N. P., we found that lizards had microhabitats with  $T_e$  that were within the preferred range of  $T_b$ , but they also had a high availability of microhabitats with values of  $T_e$  well above the  $T_{pref}$ .

It has been described that, if thermal availability ( $T_e$ ) is above the upper bound of  $T_{pref}$ , lizards should retreat to cool refuges to avoid overheating (Sinervo et al. 2010). The time spent in thermoregulation, or waiting for conditions that allow thermoregulation, cannot be used for other activities, increasing the number of hours of restriction of activities (Sinervo et al. 2010). In our study, the estimated restriction hours were from 6.40 to 8.10 h for *P. querque* and *P. zapalensis*, and from 6.23 to 7.83 h for *L. elongatus*. In the Andean highlands, the lizard *Phymaturus palluma* (from the *palluma* group) currently have daily average restriction hours of 2–6 h during the activity season. Relating restriction hours with physiological variables, Vicenzi et al. (2017) predicted a reduction in the potential distribution between 35 and 65% of its original distributional range by the year 2050. Using similar methodology, for *L. elongatus* it has been predicted that 26.5% of populations could become extinct by the year 2080 (Kubisch et al. 2016). These results suggest that the sympatric *P. querque*, *P. zapalensis*, and *L. elongatus* lizards could be in the future at risk of reducing their populations due to the forecast increase in the environmental temperatures by the global climatic change, since they currently exhibited a higher amount of restriction hours than *P. palluma* (Vicenzi et al. 2017), and other Patagonian populations of *L. elongatus* (Kubisch et al. 2016). Besides, viviparous lizards are especially vulnerable to the increment of environmental temperatures (Sinervo et al. 2010), and the three sympatric species studied here present a viviparous reproductive mode. Particularly, the genus *Phymaturus* exhibited low frequency of reproduction and low mean annual reproductive output (Habit and Ortiz 1996; Ibargüengoytía 2004; Boretto and Ibargüengoytía 2006, 2009; Boretto et al. 2007, 2014a; Cabezas Cartes et al. 2010) which are important risk factors for this species.

Our observations during the sampling days evidence that the *Phymaturus* species were inside the rock crevices more frequently than the *Liolaemus* species. In addition, the proportion of individuals of *P. querque* that were observed

inside crevice prior to capture was higher than outside them, whereas the proportion of individuals of *P. zapalensis* seen outside and inside crevices was not different. This is in agreement with the fact that *P. zapalensis* and *L. elongatus* exhibited higher  $T_b$  than *P. querque*, probably due to differences in thermal habits, body size, and thermal inertia, since we found interspecific differences in body size between species, *P. querque* being greater in terms of SVL and body mass than *P. zapalensis* and *L. elongatus*, and *P. zapalensis* showed a greater SVL than *L. elongatus*. While the  $T_b$  of lizards of *P. querque* and *P. zapalensis* outside the crevices was not different from the one of lizards inside them, this preliminary result must be interpreted carefully due to the low sample size. Current studies about microhabitat use, home range, and times of daily activities of these *Phymaturus* species with a higher sample size will allow us to discuss these preliminary results with greater support.

Similarly to our findings of interspecific differences in body size in the sympatric species studied, in the sympatric *P. roigorum* (*palluma* group) and *P. payunia* (*patagonicus* group), there were also differences in body size and  $T_b$ , since *P. roigorum* exhibited a larger SVL and a lower  $T_b$  than *P. payunia* (Corbalán et al. 2013). In relation to the  $T_{pref}$ , we found no interspecific differences, and in *P. querque* (35.7°C) and *P. zapalensis* (35.8°C), the  $T_{pref}$  was inside the range found in other *Phymaturus* species (31.1–36.3°C, Cruz et al. 2009), only slightly higher than those previously found in *P. zapalensis* (33.1°C; sample size  $n=5$ , Cruz et al. 2009), *P. roigorum* (34.7°C), *P. payunia* (34.9°C, Corbalán et al. 2013), and *P. palluma* (35.15°C; Vicenzi et al. 2017). A weak association between  $T_b$  and  $T_{pref}$  has been found in other *Phymaturus*, suggesting that the species may experience ecological constraints for thermoregulation (Cruz et al. 2009). This, along with the similar thermal conditions at the localities where the *Phymaturus* species inhabit, may have driven the lack of variation in thermal biology as well as in other ecological traits like the viviparous reproductive mode, the prolonged female reproductive cycles, the herbivorous diet, and saxicolous habits, among others. Ectothermic animals with similar traits may use microhabitats differently to regulate their body temperature (Magnuson et al. 1979; Huey et al. 1989; Paterson and Blouin-Demers 2016). In addition, species with different body sizes may have different thermal requirements or thermoregulatory behavior. Moreover, species that have different distributional ranges are also likely to have different thermal requirements, and it is expected that those species with wider geographic ranges will show a wider thermal tolerance (Cruz et al. 2005). As seen in our study, the three sympatric and syntopic species showed differences in their body size, shape, and color, and different thermoregulatory efficiency, distributional range,

and other components of their life history traits too, especially between the *Phymaturus* species and the *L. elongatus*. Under the cost–benefit model, thermoconformity is expected when climatic extreme conditions would make a precise thermoregulation too costly (Huey and Slatkin 1976). These costs and benefits of thermoregulation in different thermal landscapes, with a specific heterogeneity and spatial structure, should induce organisms to thermoregulate differently, with different strategies ranging from thermoconformity to precise thermoregulatory (Sears and Angilletta 2015). Present results, along with the previous studies of thermal physiology of *Phymaturus* (Ibargüengoytia 2005; Cruz et al. 2009; Corbalán et al. 2013; Vicenzi et al. 2017), show that the physiological optimal temperature (*sensu* Huey and Slatkin 1976; Hertz et al. 1993) is not always the ecological optimal temperature, probably because of the high cost of thermoregulation. We found that the three species look for microenvironments to obtain body temperature differently than what would be expected by chance, indicating that they thermoregulate, selecting cold microenvironments, even cooler than the temperature they preferred in the laboratory. *Liolaemus elongatus* is a more efficient thermoregulator than the two *Phymaturus* species, who are better specialized in finding shelters (only certain kinds of rock crevices; Cabezas Cartes et al. 2014). Even if individuals have access to warm microenvironments they spend time in cool refuges, probably to prevent overheating (a high cost of thermoregulation), highlighting the importance of an adequate spatial distribution of  $T_e$ , more than just the mere availability of appropriate temperatures.

**Acknowledgements** We thank D. Fernández for his help on field trips and N.R. Ibargüengoytia for his insightful comments. We would also like to thank to three anonymous reviewers for their insightful comments and contributions for the improvement of this manuscript. We also thank the Delegación Regional de Parques Nacionales de la Patagonia for granting permits for researching, and the people at Laguna Blanca N.P. for their logistical support. This research was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 00033), Agencia Nacional de Promoción Científica y Tecnológica (PICT 2578), and Universidad Nacional del Comahue (04/B196).

## References

- Abdala CS, Acosta JL, Acosta JC, Alvarez B, Arias F, Avila L, Blanco G, Bonino M, Boretto JM, Brancatelli G, Breitman MF, Cabrera M, Cairo S, Corbalán V, Hernando A, Ibargüengoytia N, Kakoliris F, Laspiur A, Montero R, Morando M, Pellegrin N, Perez CHF, Quinteros S, Semhan R, Tudesco ME, Vega L, Zalba SM (2012) Categorización del estado de conservación de los lagartos de la República Argentina. Cuad Herpetol 26:215–247
- Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford



- Bakken GS (1992) Measurement and application of operative and standard operative temperatures in ecology. *Am Zool* 32:194–216. doi:[10.1093/icb/322194](https://doi.org/10.1093/icb/322194)
- Bakken GS, Santee WR, Erskine DJ (1985) Operative and standard operative temperatures: tools for thermal energetics studies. *Am Zool* 25:933–943 doi:[10.1093/icb/254933](https://doi.org/10.1093/icb/254933)
- Blouin-Demers G, Weatherhead PJ (2001) Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82:3025–3043
- Blouin-Demers G, Weatherhead PJ (2002) Habitat-specific behavioral thermo-regulation by black rat snakes (*Elaphe obsoleta obsoleta*). *Oikos* 97:59–68
- Boretto JM, Ibagüengoytía NR (2006) Asynchronous spermatogenesis and biennial female cycle of the viviparous lizard *Phymaturus antofagastensis* (Liolaemidae): reproductive responses to high altitudes and temperate climate of Catamarca, Argentina. *Amphib-Reptilia* 27:25–36
- Boretto JM, Ibagüengoytía NR (2009) *Phymaturus* of Patagonia, Argentina: reproductive biology of *Phymaturus zapalensis* (Liolaemidae) and a comparison of sexual dimorphism within the genus. *J Herpetol* 43:96–104
- Boretto JM, Ibagüengoytía NR, Acosta JC, Blanco GM, Villavicencio HJ, Marinero JA (2007) Reproductive biology and sexual dimorphism of a high-altitude population of the viviparous lizard *Phymaturus punae* from the Andes in Argentina. *Amphib-Reptilia* 28:427–432
- Boretto JM, Cabezas Cartes F, Tappari F, Méndez-De la Cruz F, Sinervo B, Scolaro JA, Ibagüengoytía NR (2014a) Reproductive biology of *Phymaturus spectabilis* (Liolaemidae): females skip reproduction in cold and harsh environments of Patagonia, Argentina. *Herpetol Conserv Biol* 9:170–180
- Boretto JM, Cabezas Cartes F, Kubisch EL, Sinervo B, Ibagüengoytía NR (2014b) Changes in female reproduction and body condition in an endemic lizard, *Phymaturus spectabilis*, following the Puyehue volcanic ashfall event. *Herpetol Conserv Biol* 9:181–191
- Cabezas Cartes F, Boretto JM, Acosta JC, Jahn GA, Blanco G, Laspiur A, Ibagüengoytía NR (2010) Reproductive biology of *Phymaturus cf. palluma*: a vulnerable lizard from the highlands of the Andes, San Juan, Argentina. *Herpetol Conserv Biol* 5:430–440
- Cabezas Cartes F, Kubisch E, Ibagüengoytía NR (2014) Consequences of the deposition of volcanic ashes on locomotor performance of *Phymaturus* lizards from Patagonia, Argentina. *J Exp Zool A* 321A:164–172
- Cabrera AL (1976) Regiones Fitogeográficas de la República Argentina. In ACME (ed) *Enciclopedia Argentina de Agricultura y Jardinería* 2. ACME, Buenos Aires
- Cei JM (1986) Reptiles del centro, centro-oeste y sur de la Argentina: Herpetofauna de las zonas áridas y semiáridas. Monografía IV. Museo Regionale di Scienze Naturali, Torino
- Cei JM (1993) Reptiles del Noroeste, Nordeste y Este de la Argentina. Herpetofauna de las Selvas Subtropicales, Puna y Pampas. Monografía XIV. Museo Regionale di Scienze Naturali, Torino
- Cei JM, Castro LP (1973) Taxonomic and serological researches on the *Phymaturus patagonicus* complex. *J Herpetol* 7:237–247
- Cei JM, Scolaro JA (2006) The neotype of the type species of the Neotropical iguanian genus *Phymaturus*: a critical commentary on a recent opinion of the International Commission on Zoological Nomenclature. *Zootaxa* 1297:17–22
- Clusella-Trullas S, Chown SL (2011) Comment on “erosion of lizard diversity by climate change and altered thermal niches”. *Science* 332:537. doi:[10.1126/science.1195193](https://doi.org/10.1126/science.1195193) (PMID:21527699)
- Corbalán V, Debandi G (2014) Resource segregation in two herbivorous species of mountain lizards from Argentina. *Herpetol J* 24(4):201–208
- Corbalán V, Debandi G, Kubisch E (2013) Thermal ecology of two sympatric saxicolous lizards of the genus *Phymaturus* from the Payunia region (Argentina). *J Therm Biol* 38:384–389
- Cruz FB, Fitzgerald LA, Espinoza RE, Schulte JA (2005) The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *J Evol Biol* 18:1559–1578
- Cruz F, Belver L, Acosta JC, Villavicencio HJ, Blanco G, Cánovas MG (2009) Thermal biology of *Phymaturus* lizards: evolutionary constraints or lack of environmental variation? *Zoology* 112:425–432
- Debandi G, Corbalán V, Scolaro JA, Roig-Juñent SA (2012) Predicting the environmental niche of the genus *Phymaturus*: are *palluma* and *patagonicus* groups ecologically differentiated? *Aust Ecol* 37:392–400
- Dzialowski EM (2005) Use of operative temperature and standard operative temperature models in thermal biology. *J Therm Biol* 30:317–334. doi:[10.1016/j.jtherbio.2005.01.005](https://doi.org/10.1016/j.jtherbio.2005.01.005)
- Etheridge R (1995) Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the taxonomy of Liolaeminae (Reptilia: Squamata: Tropiduridae). *Am Mus Novit* 3142:1–34
- Gregory PT, Crampton LH, Skebo KM (1999) Conflicts and interaction among reproduction, thermoregulation and feeding in viviparous reptiles: are gravid snakes anorexic? *J Zool* 248:231–241
- Habit EM, Ortiz JC (1996) Ciclo reproductivo de *Phymaturus flagellifer* (Reptilia, Tropiduridae). *Boletín de la Sociedad Biológica de Concepción* 67:7–14
- Hertz PE (1992) Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology* 73:1405–1417
- Hertz PE, Huey RB, Stevenson R (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am Nat* 142:796–818
- Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: C Gans and FH Pough (ed) *Biology of the Reptilia*, vol 12. Academic Press, London, pp 25–91
- Huey RB, Slatkin M (1976) Cost and benefits of lizard thermoregulation. *Q Rev Biol* 51:363–384
- Huey RB, Peterson CR, Arnold SJ, Porter WP (1989) Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70:931–944
- Ibagüengoytía NR (2004) Prolonged cycles as a common reproductive pattern in viviparous lizards from Patagonia, Argentina. Reproductive cycle of *Phymaturus patagonicus*. *J Herpetol* 38:73–79
- Ibagüengoytía NR (2005) Field, selected body temperature and thermal tolerance of the syntopic lizards *Phymaturus patagonicus* and *Liolaemus elongatus* (Iguania: Liolaemidae). *J Arid Environ* 62:435–448
- Ibagüengoytía NR, Cussac VE (1998) Reproduction of the viviparous lizard *Liolaemus elongatus* in the highlands of Patagonia: plastic cycles in *Liolaemus* as a response to climate? *Herpetol J* 8:99–105
- Ibagüengoytía NR, Acosta JC, Boretto JM, Villavicencio HJ, Marinero JA, Krenz JD (2008) Field thermal biology in *Phymaturus* lizards: comparisons from the Andes to the Patagonian steppe in Argentina. *J Arid Environ* 72:1620–1630
- Ibagüengoytía NR, Medina SM, Fernández JB, Gutiérrez JA, Tappari F, Scolaro A (2010) Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. *J Therm Biol* 35:21–27
- Kubisch E, Corbalán V, Ibagüengoytía NR, Sinervo B (2016) Local extinction risk of three species of lizard from Patagonia as a result of global warming. *Can J Zool* 94:49–59. doi:[10.1139/cjz-2015-0024](https://doi.org/10.1139/cjz-2015-0024)

- Labra A (1995) Thermoregulation in *Pristidactylus* lizards (Polycridae): effects of group size. *J Herpetol* 29:260–264
- Lobo F, Abdala C, Valdecantos S (2010) Taxonomic studies of the genus *Phymaturus* (Iguania: Liolaemidae): description of four new species. *S Am J Herpetol* 5(2):102–126
- Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. *Am Zool* 19(1):331–343
- Mathies T, Andrews R (1997) Influence of pregnancy on the thermal biology of the lizard, *Sceloporus jarrovi*: why do pregnant females exhibit low body temperatures? *Funct Ecol* 11:498–507
- Minoli I, Medina CD, Frutos N, Morando M, Avila LJ (2013) A revised geographical range for *Liolaemus elongatus* Koslowsky, 1896 (Squamata: Liolaemini) in Argentina: review of reported and new-data based distribution with new localities. *Acta Herpetol* 8(2):159–162
- Paterson JE, Blouin-Demers G (2016) Do ectotherms partition thermal resources? We still do not know. *Oecologia* 183:337–345
- Schulte JA (2013) Undersampling taxa will underestimate molecular divergence dates: an example from the South American lizard clade Liolaemini. *Int J Evol Biol* 2013:628467. doi:10.1155/2013/628467
- Scolaro JA (2005) Reptiles Patagónicos: Sur. Una Guía de Campo. Universidad Nacional de la Patagonia San Juan Bosco, Trelew
- Sears MW, Angilletta MJ (2015) Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. *Am Nat* 185(4):E94–E102
- Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, Gadsden H, Ávila LJ, Morando M, De la Riva IJ, Sepúlveda PV, Duarte Rocha CF, Ibargüengoytía N, Aguilar Puntriano C, Massot M, Lepetz V, Oksanen TA, Chapple DG, Bauer AM, Branch WR, Clobert J, Sites JW Jr (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328:894–899. doi:10.1126/science.1184695 (PMID:20466932)
- Smith KR, Cadena V, Endler JA, Kearney MR, Porter WP, Stuart-Fox D (2016) Color change for thermoregulation versus camouflage in free-ranging lizards. *Am Nat* 188:668678
- Vicenzi N, Corbalán V, Miles D, Sinervo B, Ibargüengoytía N (2017) Range increment or range detriment? Predicting potential changes in distribution caused by climate change for the endemic high-Andean lizard *Phymaturus palluma*. *Biol Conserv* 206:151–160
- Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol* 6:2621–2626 (PMID:19108608)
- Winslow CE, Gagge AP, Herrington LP (1940) Heat exchange and regulation in radiant environments above and below air temperature. *Am J Physiol-Leg Content* 131(1):79–92
- Withers PC, Campbell JD (1985) Effects of environmental cost on thermoregulation in the desert iguana. *Physiol Zool* 58:329–339