



Thermal ecology of two sympatric saxicolous lizards of the genus *Phymaturus* from the Payunia region (Argentina)

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ABSTRACT

We evaluated the thermal biology of two sympatric saxicolous species of the genus *Phymaturus*, endemic from the Argentine Payunia region. Taking into account that the distributional range of *Phymaturus roigorum* (the largest species) is greater than the range of *P. payuniae*, we evaluated the habitat (type of rocks) used by these species. We recorded body temperature and operative temperatures in different habitats, and we determined the preferred body temperature in the laboratory. We compared the thermal quality of habitats occupied and not occupied by *Phymaturus payuniae*, and the accuracy and effectiveness of thermoregulation between species.

P. roigorum was found on many different kinds of rocks, but *P. payuniae* was found mainly on two types of rocks and not found on dark basalts. No differences were found in habitat thermal quality or in preferred temperatures when comparing among populations or between species. Although both species are thermoregulators, *P. payuniae* demonstrated better accuracy and effectiveness. This is the first study to assess thermal biology in coexisting species of the genus *Phymaturus* and provides the first data on effectiveness of thermoregulation for the genus. The results obtained have importance from a conservation perspective, since both endemic species are vulnerable and no data on habitat or thermal requirements were available up till now.

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1. Introduction

Biotic and abiotic components, as well as historical factors, may influence the geographic range of species (MacArthur, 1972; Soberón and Peterson, 2005). Since temperature has a significant impact on the physiology of ectotherms, availability of a micro-habitat appropriate for thermoregulation is one of the most important factors that influence activity pattern, habitat selection and spatial distributions (Wilms et al., 2011).

The main costs of thermoregulation are predation risk and the reduction in time for other non thermoregulatory activities such as foraging (Gregory et al., 1999; Huey, 1982; Huey and Slatkin, 1976; Pianka and Pianka, 1970). When thermal availability is outside of the preferred body temperature range, lizards may face two different scenarios: if thermal availability is below the preferred temperature, the cost for thermoregulation may be high, and the habitat could be considered non-optimal for the establishment of the species. However, if thermal availability is above the preferred

body temperature, lizards must retreat to cool refuges to avoid overheating (Sinervo et al., 2010), thus increasing the number of hours of restriction and consequently limiting foraging (constraining metabolic functions like growth and reproduction).

The genus *Phymaturus* comprises saxicolous lizards that are distributed in Argentina and Chile. This genus is considered conservative in several of its features, due to the fact that all species are herbivorous and viviparous (Scolaro et al., 2008). Thermal biology and niche requirements were postulated as conservative as well within the genus (Cruz et al., 2009; Debandi et al., 2012). However, species of different size could exhibit different thermal requirements or thermoregulatory behavior. Moreover, species that have different ranges are likely to also 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) and/or amplitude in preferred temperatures (difference between maximum and minimum values).

In the Argentine Payunia region, two endemic species of *Phymaturus* coexist: *P. roigorum* (the largest, belonging to the *palluma* group), and *P. payuniae* (belonging to the *patagonicus* group) (Debandi et al., 2012). We observed that the distribution of the smaller *P. payuniae* is included within the distributional range

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of *P. roigorum*, and it has always been found in sympatry (syntopy) with the latter. *Phymaturus roigorum*, instead, was found to be either in allopatry or in sympatry with *P. payuniaie*. When coexisting, they share microhabitats for basking and refuge, and show similar patterns of daily activity (Corbalán and Debandi, unpub. data). Basking behavior in these species was recently reported by Corbalán and Debandi (2013). Rock surface temperature has a direct influence on the thermoregulatory behavior, and postural adjustments are similar in both species during cloud covered conditions (Corbalán and Debandi, 2013). Thus, both species exhibit thigmothermic and heliothermic thermoregulation, depending on environmental conditions.

The purpose of this study was to evaluate habitat use and thermal biology of *P. roigorum* and *P. payuniaie*. Specifically, the objectives were: (1) to know the distribution of both species in the region and the habitat (type of rocks) used by each one, (2) to determine the preferred body temperature range or set-point range (T_{set}) of both species, and (3) to determine the accuracy of body temperature in the field relative to the set-point range and the effectiveness of thermoregulation.

2. Materials and methods

2.1. Study area

The study was carried out on the Payunia region, an area dominated by a volcanic landscape, in southern Mendoza Province, Argentina (approximately from 35° 40' to 36° 52' South latitude, and from 68° 20' to 69° 40' West longitude) (Fig. 1). Most of the surveyed areas are situated at La Payunia Reserve, which comprises a total of 259,000 ha. Within the Reserve, lies one of the largest volcanoes in the region, the Payún Matrú, whose summit reaches 3700 m asl. Outside the Reserve, we surveyed the Payún highland plain, and the Palauco and Nevado hills. The climate of the region is arid and cold, influenced by winds from the Pacific Ocean (Candia et al., 1993; Capitanelli, 1972). Winters are rainy and snowy, and summers are dry (Candia et al., 1993). Because of these harsh conditions, lizards remain inactive during cold months.

2.2. Species distribution in the area

Five sampling trips were conducted from February 2007 to November 2011, recording the presence/absence of *Phymaturus* species around the area. All records were georeferenced using a Garmin eTrex Vista HCx GPS. Additionally, notes were taken about the easiness of finding either species at each site as an indirect measure of relative abundance (low/high abundance). Because different types of rocks (and therefore with different mineral composition, color and welding degree) may reflect differences in the thermal quality of the habitat for thermoregulation by the saxicolous lizards, we classified the habitat used by each species based on the type of rocks. For this, we used the available geologic map of the Payún Matrú volcano and its surrounding area (Llambías, 2008).

2.3. Field and laboratory temperatures of lizards

We caught, by noosing, a total of 55 adult individuals of *P. roigorum* and 30 individuals of *P. payuniaie* from different rocky promontories of the region (Fig. 1). Most of them (81.18%) were captured within the Payunia Reserve from 4th to 10th November 2011, while the rest were captured outside the Reserve (Payún highland plain, and Nevado and Palauco hills) from 25th to 28th November 2011. In four of these sites both species were syntopic, whereas in another four only *P. roigorum* was present (allopatric

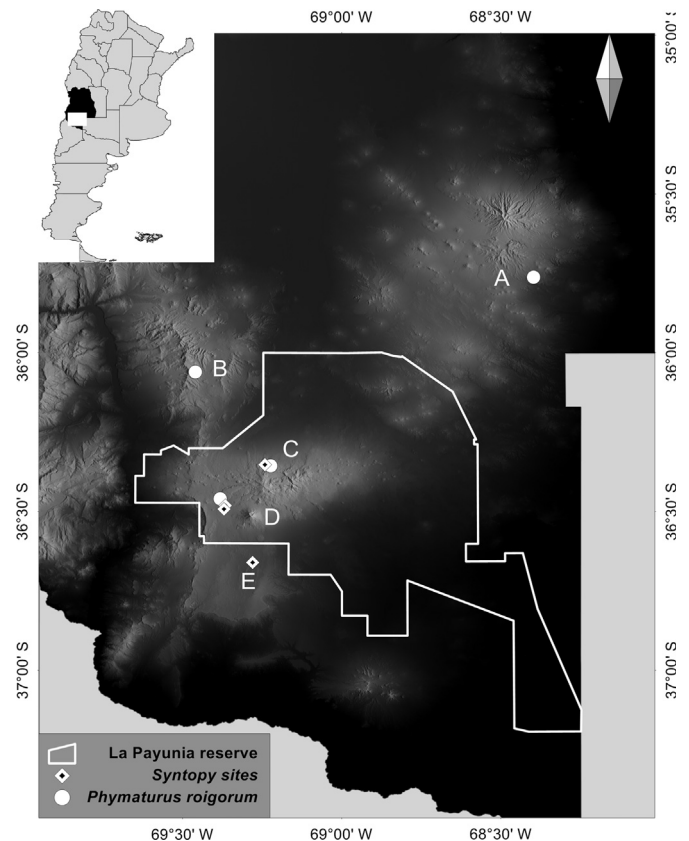


Fig. 1. Sites of capture of *Phymaturus roigorum* and *P. payuniaie* in the Payunia region for thermal experiments. Diamonds indicate those sites where both species were present (syntopy), and circles indicate those sites where only *P. roigorum* was present (allopatry). (A) Nevado hills; (B) Palauco hills; (C) Payún Matrú volcano; (D) Payún Liso volcano and (E) Payún highland plain.

sites). Body temperature (T_b) was recorded at the moment of capture using TES TP-K thermocouples connected to a TES 1312A digital thermometer (range: –50 to 1300 °C, resolution: 0.1/1 °C). To minimize the stress in the animals, a laboratory was placed in the scientific station sited near the Reserve in order to perform selected body temperature (T_{set}) experiments. Each day, captured individuals within the Reserve were transported to the laboratory and kept at ambient temperature 1–3 h before experiments began. Those individuals captured outside the Reserve were transported to Mendoza city and experiments were conducted at the Research Institute (IADIZA) between 1 and 5 days after capture.

Two wooden terrariums of 1 × 1 m with four separated lanes each were used for estimating the T_{set} (Pough and Gans, 1982) of lizards. At one end of each lane, a 75 W incandescent lamp was placed to generate a temperature gradient (from about 45 °C to 22 °C). A sheet of aluminum paper covered 2/3 of the terrarium above the lamps to keep the end warm and help maintain the gradient. An ultrafine thermocouple was taped to the belly of the lizard and connected to an 8-channel data-logger (Measurement Computing 1.2 kHz Data Acquisition Device). During experiments, each individual (of *P. roigorum* or *P. payuniaie*, indistinctly) was placed on a lane for 135 min.

Body temperature was recorded every 60 s, and data for the first 15 min were discarded from the analyses, allowing the animals to recognize the terrarium and to select their preferred temperature.

Once the experiments were finished, all individuals were sexed, weighed (with a Pesola micro-line spring scale, 100 g × 1 g), and snout-vent length and tail length were recorded (with a digital

calliper, 0.01 mm accuracy). Later, most individuals were released at the capture site, and some of them were deposited in the herpetological collection of IADIZA for further studies.

2.4. Operative temperature

During the time of capture of the lizards, we placed physical models at 4 sites (two syntopic and two allopatric sites) in order to make an estimation of the operative temperature (T_e) in the field. We also placed models at two other allopatric sites, but no captures were made there. Operative temperature represents the “null” distribution of T_b that non-regulating animals would achieve (Hertz et al., 1993). According to the literature, models should be placed in different microhabitats used by animals (Hertz, 1992; Hertz et al., 1993; Wilms et al., 2011). Considering that our studied species are saxicolous, we placed four models on the three microsites most frequently used by our lizards: two on sun-exposed rocks, one inside crevices, and one on shrub-shaded rocks. We averaged the values from the two models placed in the sun before calculating operative temperature.

Models were constructed using 3-layered propylene tubes filled with cryogel (see below), with the ends sealed with cork. A temperature probe connected to a 4-channel Onset HOBO logger passed through the cork into the tube. Temperature was recorded at 15 min intervals during the animals' time of activity (between 9:00 am and 7:00 pm).

Previously, we had tested two kinds of standard models used for lizards: a gray-painted plastic tube and a copper model. However, temperature achieved by these models did not fit very well with our species (*P. roigorum*: $R^2=0.09$, $P=0.66$ and $R^2=0.64$, $P<0.0001$, plastic and copper models respectively; *P. payunia*: $R^2=0.61$, $P<0.0001$ and $R^2=0.67$, $P=0.0002$, respectively). In order to obtain a better model for the studied species, we performed different trials with diverse materials. These models were calibrated using living and dead *Phymaturus* lizards that were tied to rocks and monitored in real time with a thermocouple taped to their bellies. These trials consisted in alternating animals and models between sun and shade conditions without surpassing the critical temperature of the species. We chose models made of 3-layered red propylene tubes (IPS, <http://www.ips-arg.com>), 15 cm long, and filled with cryogel, because the fit of the linear regression was better for both species ($R^2=0.93$, $P<0.0001$, $n=192$ for live *P. roigorum*, $R^2=0.75$, $P<0.0001$, $n=156$ for live *P. payunia*, and $R^2=0.93$, $P<0.0001$, $n=161$ for a dead *P. roigorum*). The advantage of tubes filled with cryogel used for lizards lies in the fact that heating and cooling rates are slower than in standard models, thus imitating more closely the actual rates in the body of *Phymaturus* lizards.

2.5. Statistical analyses and indexes of accuracy and effectiveness of thermoregulation

We compared body mass and snout-vent length (SVL) between sexes for each species using *t*-test. As differences were found between males and females for *P. roigorum* (see Section 3.2), we compared T_{set} between sexes and species using Two-Way-ANCOVA with body mass as covariate. Furthermore, in order to evaluate whether individuals from different populations have different preferences according to the habitat where they live, we compared T_{set} of individuals of each species from different sites using One-Way-ANCOVA with body mass as covariate. For this, we chose 6 different sites for *P. roigorum* and 4 sites for *P. payunia*. These were chosen based on the number of individuals captured on each site, which was enough to make statistical comparisons. Since no differences in T_{set} were found among populations or between sexes (see Section 3.2), we pooled the data for all individuals of

each species for the remaining analyses. Then, mean values of T_{set} for each individual were averaged to estimate the T_{set} of the species as a whole. All tests were performed using InfoStat software (InfoStat, 2009).

Set-point temperature ranges (T_{set}) were estimated from T_{set} of each individual by identifying the interquartile range (middle 50% of the data). The amplitude of T_{set} values (difference between maximum and minimum) and T_{set} range were compared between species using *t*-test. Each set-point range was used to estimate the accuracy and effectiveness of thermoregulation (Hertz et al., 1993); afterwards all of them were averaged to obtain a mean value for each species.

In order to assess the accuracy of body temperatures (i.e. how successfully lizards achieve T_b within the target range), we also estimated the d_b index (Hertz et al., 1993). This index was calculated as the average of the absolute value of the deviations ($^{\circ}\text{C}$) of T_b from the lower or upper bound of the T_{set} of each individual (Hertz et al. 1993).

The deviations between T_e and T_{set} were also calculated for each individual. This index (d_e) represents the average thermal quality of a habitat from the organism's perspective. Both d_b and d_e indexes were compared between species using *t*-test.

The effectiveness of thermoregulation was calculated using two indexes. The first one was proposed by Hertz et al. (1993) as: $E=1 - (\text{Mean } d_b/\text{Mean } d_e)$. When animals do not thermoregulate, E will approach zero. When animals do thermoregulate carefully and successfully, E will approach one (Hertz et al., 1993). Blouin-Demers and Weatherhead (2001, 2002) argue that the index proposed by Hertz et al. (1993) is problematic because two species can 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. Several authors agree that, additionally to E , it is appropriate to calculate the difference between d_e and d_b , since the magnitude of the difference is a measure of how much an animal departs from thermoregulation, and thus represents an index of thermoregulation (Blouin-Demers and Weatherhead, 2001, 2002; Willms et al., 2011). These indexes were calculated for 20 individuals of *P. payunia* and 32 individuals of *P. roigorum*, for we had no data on T_e for all sites where individuals were captured.

Because physical models were set up on different dates (only on days when animals were caught) and only on some sites, we were unable to make comparisons among T_e from all different sites and assess their thermal quality. To solve this problem, we evaluated how much T_e departs from T_{set} at those sites where *P. payunia* is present compared to sites with absence of this species. This measure (d_e) may be an indicative of the thermal quality of habitats for *P. payunia* and may help to understand its absence from some sites. For this, we used the mean values of T_{set} obtained for the species, and T_e data on two sites where *P. payunia* was present, and four sites where it was absent. Then, we pooled the data for each situation (presence/absence) and compared them using *t*-test.

3. Results

3.1. Rock types used by species

We found that, in the Payunia area, different types of rocks were used in different ways by the studied species. Both lizard species are more abundant on ignimbrites (especially on those loosely welded) and vitreous trachytes. *Phymaturus roigorum* is also abundant on sites with basalt rocks (Table 1), but *Phymaturus payunia* is rarely found using this kind of rock. On those basalt

promontories where the latter species is present, its abundance is very low (Table 1).

3.2. Lizard temperatures

Body mass and SVL showed significant differences between sexes for *P. roigorum* (t -test, $t_{\text{body mass}, 52} = -3.69$; $P < 0.001$; $t_{\text{SVL}, 52} = -3.51$, $P < 0.001$), with males being larger than females (Table 2); even so, no differences were found for *P. payunia* (t -test, $t_{\text{body mass}, 28} = 0.52$, $P = 0.61$; $t_{\text{SVL}, 28} = 1.44$, $P = 0.16$). By comparing these variables, we can also demonstrate significant differences between species, with *P. roigorum* being larger than *P. payunia* (Two-Way ANOVA, $F_{\text{body mass}, 3, 83} = 75.98$, $P < 0.0001$; $F_{\text{SVL}, 3, 83} = 104.07$, $P < 0.0001$) (Table 2).

Field body temperatures (T_b) were lower for individuals of *P. roigorum* (28.17 ± 3.99 °C) compared to *P. payunia* (30.75 ± 4.74 °C) (t -test, $t_{81} = 2.64$, $P < 0.01$, $n_{P. roigorum} = 55$; $n_{P. payunia} = 30$). Results were similar when we compared only data for lizards that were lying in the sun at the moment they were captured (eliminating data on individuals that were in crevices) (t -test, $t_{43} = 2.34$, $P < 0.05$, $n_{P. roigorum} = 23$; $n_{P. payunia} = 22$). No differences in T_b were found between individuals of *P. roigorum* living in syntopy with *P. payunia* and individuals living in allopatry (t -test, $t_{47} = 1.22$, $P = 0.23$, $n_{\text{syntopy}} = 23$; $n_{\text{allopatry}} = 26$).

Selected temperature (T_{sel}) in the laboratory did not show significant differences between species or sexes (Two-way ANCOVA, $F_{4, 80} = 0.49$, $P = 0.74$; Table 3).

No differences were found among sites for T_{sel} of *P. roigorum* (ANCOVA, $F_{6, 51} = 1.04$, $P = 0.41$) or *P. payunia* (ANCOVA, $F_{4, 28} = 1.06$, $P = 0.40$). Then, all T_{sel} data obtained for each species were pooled for further analyses.

Although mean range between maximum and minimum T_{sel} values and T_{set} range were higher for *Phymaturus roigorum* than

for *P. payunia* (Table 3), there were no significant differences between the species at $P = 0.05$ rejection level (amplitude: t -test, $t_{83} = -1.64$, $P = 0.10$; T_{set} range: t -test, $t_{83} = -1.80$, $P = 0.07$, $n_{P. roigorum} = 55$; $n_{P. payunia} = 30$).

3.3. Accuracy and effectiveness of thermoregulation

Most of T_b records had values below T_{set} in both species (82% and 70% for *P. roigorum* and *P. payunia*, respectively) whereas 16% and 17% of T_b records fell within T_{set} . Despite the T_b of *P. payunia* being closer to its T_{set} ($d_b = 4$) than that of *P. roigorum* ($d_b = 5.53$) (Table 4), no differences were found between species (t -test, $t_{79} = -1.62$, $P = 0.11$, $n_{P. roigorum} = 51$; $n_{P. payunia} = 30$) indicating that accuracy of thermoregulation was similar in both species.

All T_e were below T_{set} for both species, but d_e was significantly different between them (t -test, $t_{49} = 2.57$, $P = 0.01$, $n_{P. roigorum} = 32$; $n_{P. payunia} = 20$; Table 4), indicating that the habitat thermal quality is better for *P. roigorum*. When the T_e and mean T_{set} of *P. payunia* (habitat quality) were compared between sites with presence and absence of this species, we found no significant differences (t -test, $t_5 = 0.71$, $P = 0.51$).

Both effectiveness indices showed that *P. roigorum* and *P. payunia* are thermoregulators, which is also demonstrated by the relationship between d_b and d_e (i.e., according to Hertz et al., 1993, if $d_b < d_e$, species are thermoregulators). The E index was lower for *P. roigorum*, and the magnitude $d_e - d_b$ was also lower for *P. roigorum* (Table 4) indicating that individuals of *P. payunia* are more efficient thermoregulators, as higher values indicate that animals depart more from thermoconformity.

4. Discussion

Thermal characteristics of *Phymaturus* and related species (*Liolaemus* species) have been evaluated by several authors (Carothers et al., 1997; Cruz et al., 2009; Ibargüengoytia, 2005; Ibargüengoytia et al., 2008; Labra, 1998; Labra et al., 2001; Marquet et al., 1989; Medina et al., 2009, 2011; Moreno Azócar et al., 2013; Valdecantos et al., 2013; Vidal et al., 2010). Some of these contributions compare the thermal biology of species from different latitudes, but in this work the thermal biology in coexisting species of the genus *Phymaturus* was assessed for the first time.

The average T_{sel} found for our studied species is within the range reported for other congeneric (31.1–36.3 °C, Cruz et al., 2009) or *Liolaemus* species (30–37 °C, Ibargüengoytia et al., 2010; Labra, 1998; Medina et al., 2009, 2011; Moreno Azócar et al., 2013;

Table 1

Presence of *P. roigorum* and *P. payunia* at sites with different rock types in the Payunia region. HA: high abundance; LA: low abundance.

Rock type	<i>P. roigorum</i>	<i>P. payunia</i>
Basalts	Present (Mostly HA)	Absent or present (LA)
Reoignimbrites	Present (LA)	Absent
Loosely welded ignimbrites	Present (HA)	Present (HA) or absent
Non-vitreous trachytes	Present (LA)	Present (LA)
Vitreous trachytes	Present (HA)	Present (HA)
Trachybasalts	Present (HA)	Absent

Table 2

Body mass (BM) and snout-vent length (SVL) for male and female *P. roigorum* and *P. payunia*.

		BM \pm SD (g)	SVL \pm SD (mm)
<i>P. roigorum</i>	Males ($n = 29$)	45.28 \pm 6.34	102.49 \pm 4.57
	Females ($n = 25$)	38.04 \pm 8.06	98.11 \pm 4.58
<i>P. payunia</i>	Males ($n = 18$)	21.5 \pm 1.87	81.92 \pm 4.06
	Females ($n = 12$)	22.25 \pm 4.75	84.24 \pm 4.68

Table 3

Selected temperature in the laboratory (T_{sel}) and set-point temperature ranges (T_{set}) for *P. roigorum* ($n = 55$) and *P. payunia* ($n = 30$). Values represent the Mean \pm SD of all individuals.

	T_{sel} (°C)				T_{set} (°C)		
	Mean	Min	Max	Amplitude	Lower limit	Upper limit	Range
<i>P. roigorum</i>	34.66 \pm 1.76	31.35 \pm 2.56	38.04 \pm 1.68	6.68 \pm 2.89	33.56 \pm 2.24	35.77 \pm 1.58	2.21 \pm 1.53
<i>P. payunia</i>	34.96 \pm 1.41	31.64 \pm 2.66	37.24 \pm 1.45	5.60 \pm 2.98	34.18 \pm 1.78	35.81 \pm 1.34	1.62 \pm 1.26

Table 4

Values of d_b , d_e , and thermoregulation efficiency indexes for *P. roigorum* and *P. payunia* from the Payunia region obtained in November 2011.

	d_b	d_e	E	$d_e - d_b$
<i>P. roigorum</i>	5.53 \pm 4.18 ($n = 51$)	9.15 \pm 4.12 ($n = 32$)	0.39	3.62
<i>P. payunia</i>	4 \pm 3.92 ($n = 30$)	11.35 \pm 2.01 ($n = 20$)	0.64	7.35

Valdecantos et al., 2013). Despite the differences in body mass and size, and the long time of divergence between clades, the preferred temperatures were similar between *P. roigorum* and *P. payunia*. Although male *P. roigorum* are larger than females, there were no differences in T_{sel} between sexes. Moreover, no differences were found in T_{sel} among individuals from different sites. Because of the conservative character of the genus (Debandi et al., 2012), these facts are not surprising, reinforcing the idea that evolutionary constraints play an important role in the thermal biology of *Phymaturus* (Cruz et al., 2009).

Although field body temperature was higher in *P. payunia* compared to *P. roigorum*, both species showed lower field body temperatures than the preferred temperatures in the laboratory. The same results were found for other species of high altitudes or latitudes (Ibargüengoytia, 2005; Ibargüengoytia et al., 2010; Marquet et al., 1989; Medina et al., 2009). Also, the d_e indices found in our species are similar to those found for most of the Patagonian and Punaean species (Ibargüengoytia et al., 2010; Medina et al., 2009, 2011; Moreno Azócar et al., 2013; Valdecantos et al., 2013). The high values of these indexes suggest that favorable thermal conditions do not predominate in these harsh environments (Marquet et al., 1989).

Our results indicate that both studied species are thermoregulators. Marquet et al. (1989) found that Andean *Liolaemus* lizards exposed to similar thermal environments thermoregulate in a similar way despite their differential use of microhabitats and different body sizes. Active thermoregulation was proposed also for other species of the genus such as *P. punae* and *P. tenebrosus* (Ibargüengoytia et al., 2008), whereas *P. zapalensis* and *P. palluma* were considered thermoconforming species (Ibargüengoytia et al., 2008; Vidal et al., 2010). However, these studies were based on the relationship between body and air or substrate temperatures, and therefore are not comparable to the present study, where operative temperatures from physical models were used.

Taking into account the d_e – d_b index of effectiveness, our results indicate that *Phymaturus payunia* thermoregulates more efficiently when compared to most Patagonian *Liolaemus* species (Ibargüengoytia et al., 2010; Medina et al., 2009, 2011; Moreno Azócar et al., 2013) or to syntopic species such as *L. cf. elongatus* (d_e – d_b =4.86; Kubisch, unpub. data), and *P. roigorum*. Instead, Punaean species of *Liolaemus* have similar or even higher values of d_e – d_b (ranging from 7.62 to 12.44) (Valdecantos et al., 2013). Willms et al. (2011) postulated that ectotherms thermoregulate more effectively when the thermal quality is low. The fact that *P. payunia* showed better thermoregulatory effectiveness than *P. roigorum* is consistent with the higher values of d_e found in this species, since higher values of d_e indicate lower thermal quality of habitats (Hertz et al. 1993). However, the comparison of d_e values between sites with presence and absence of *P. payunia* did not reveal differences in the thermal quality of habitats. Probably, the low number of sites and sampling dates used in these analyses did not allow us to find differences. Even in apparently similar habitats, lizards may use microhabitats hidden from our direct observation. Size of boulders, crevice depth, orientation and position within a boulder contribute to the complexity of the thermal environment in rock retreats (Huey et al., 1989; Clusella-Trullas et al., 2009). Payunia region (which represents the upper latitudinal limit of distribution of the patagonicus group of *Phymaturus*) could be a sub-optimal habitat for *P. payunia* and this could explain the absence of this species from some specific sites.

It is expected that species with wider geographic ranges will also show a wider thermal tolerance (Cruz et al., 2005) and/or amplitude in preferred temperatures (difference between maximum and minimum values). Preliminary studies about thermal tolerances indicated that the range between maximum and

minimum critical temperatures is wider in *P. roigorum* than in *P. payunia* (25.69 vs 23.37 °C) (Aguilar et al., 2010). In this study, no significant differences were found between species in amplitude (range between maximum and minimum T_{sel} values) or T_{set} range.

An explanation to the absence of the smaller species in basalts may be related to the higher temperatures that this rock type may achieve. According to satellite images, those sites where basalts are predominant have higher temperatures than sites with other rock types (Debandi and Corbalán, 2012). When the thermal availability of the habitat is above the preferred body temperature, individuals are forced to retreat to cool crevices, which consequently limits foraging and mating encounters (Sinervo et al., 2010). Aguilar et al. (2010) found that the value of critical maximum body temperature is lower in *P. payunia* (37.2 ± 1.05 °C vs 39 ± 0.63 °C for *P. roigorum*), and this species has a higher heating rate compared to *P. roigorum*, which is related to its smaller size. Thus, *P. payunia* may reach optimal temperatures in shorter spans of time, and therefore their activity periods (time spent basking) are shorter compared to *P. roigorum*, as was demonstrated by Corbalán and Debandi (2013). In extremely hot habitats, this could be disadvantageous for the species because of a higher reduction of its fitness-related activities.

Kearney et al. (2009) pointed out that higher air temperatures increase the required foraging rate because of the effect of metabolic demand. Moreover, in ectotherms living in desert areas, where thermoregulatory priorities are keeping cool rather than staying warm, the efficiency of thermoregulation is tied strongly to the availability of shade, and hence to the nature and extent of vegetation cover (Kearney et al., 2009). Shade use is an important component of the behavioral thermoregulation in both studied species (Corbalán and Debandi, 2013), but we have no data of the proportion of shade on different sites that can explain the absence of *P. payunia* from some sites.

Other explanations about the avoidance of basalt rocks by *P. payunia* may be related to cryptic coloration or inter-specific interactions. We observed that different populations of *P. roigorum* show color variations, which are closely associated with the substrate where they live. Individuals from basalt rocks are darker, whereas those from ignimbrites or trachytes are whitish or yellowish. However, no differences in coloration are evident in different populations of *P. payunia*, which is brownish with light spots. Higher plasticity in adopting different colors according to the substrate could allow *P. roigorum* to exploit different types of rocks more efficiently, *P. payunia* could benefit from living on light colored rocks because of their higher crypticity with respect to darker rocks. In relation to inter-specific interactions, they are likely not the cause of its absence, since no signs of competition were found between the studied species or with other coexisting species such as *Liolaemus cf. elongatus* and *L. austromendocinus* (unpub. data).

The data presented in this work are part of the study of the ecology of *P. roigorum* and *P. payunia* and the mechanisms that promote their coexistence. This is the first study where thermal biology in coexisting species of the genus *Phymaturus* are assessed and provides the first data on effectiveness of thermoregulation for the genus. The knowledge of thermal requirements and thermoregulatory efficiency is important not only as basis to understand the distribution of species in space, but also to predict the response of the species facing a climate change scenario. Because of their restricted distribution and reproductive mode, both species are considered within the category “vulnerable” in the Argentinean red list (Abdala et al., 2012). Data on all aspects of their life history (diet, time and space use, as well as thermal requirements) are important to implement conservation strategies.

Future studies evaluating T_e on different sites at the same time (and for longer periods), and taking availability of food and shade

into account must be the next step to understand the factors influencing the distribution of the species in the Payunia region.

5. Conclusions

Phymaturus roigorum and *P. payuniae* use the space in different ways. Both lizard species are more abundant on ignimbrites and vitreous trachytes, however, while *P. roigorum* is also abundant in basalts, *P. payuniae* avoids this kind of rocks.

Both species showed similar selected body temperatures, and within the range reported for other species of the genus. No differences in T_{sel} between sexes or among different populations were evident in this study. Thermal quality was similar in habitats with or without *P. payuniae*, therefore we cannot conclude that differences in habitat occupancy are related to thermal quality. As other related species, our studied species are thermoregulators and experience field body temperatures below the set-point range. Accuracy of thermoregulation (d_b) was similar in both species, but effectiveness was higher in *P. payuniae* (the d_e – d_b difference was two-fold in the latter species), constituting the first values of effectiveness of thermoregulation reported for *Phymaturus* species.

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