

This article was downloaded by: [Valeria Corbalán]

On: 05 June 2013, At: 11:26

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Basking behaviour in two sympatric herbivorous lizards (Liolaemidae: Phymaturus) from the Payunia volcanic region of Argentina

Valeria Corbalán^a & Guillermo Debandi^a

^a Instituto Argentino de Investigaciones de las Zonas Áridas IADIZA, CONICET, Mendoza, Argentina

Published online: 26 Mar 2013.

To cite this article: Valeria Corbalán & Guillermo Debandi (2013): Basking behaviour in two sympatric herbivorous lizards (Liolaemidae: Phymaturus) from the Payunia volcanic region of Argentina, *Journal of Natural History*, 47:19-20, 1365-1378

To link to this article: <http://dx.doi.org/10.1080/00222933.2012.759291>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Basking behaviour in two sympatric herbivorous lizards (Liolaemidae: *Phymaturus*) from the Payunia volcanic region of Argentina

Valeria Corbalán* and Guillermo Debandi

Instituto Argentino de Investigaciones de las Zonas Áridas IADIZA, CONICET, Mendoza, Argentina

(Received 21 August 2012; final version received 20 November 2012; first published online 26 March 2013)

We studied several aspects of the thermal biology of two coexisting saxicolous species of the genus *Phymaturus* (Liolaemidae) at the Payunia, a volcanic region in Argentina where harsh conditions prevail. We marked individuals in grids and assessed the environmental conditions when the individuals showed their maximum activity (i.e. when more than 50% of marked individuals were active), the time spent basking, and the postural behaviour in relation to different cloudiness conditions. We found that temperatures recorded when the species exhibit their peaks of activity were higher for *Phymaturus payunia*, the smaller species, during the summer at one of the three studied sites. *Phymaturus roigorom* exhibited the longest basking periods, but during these longer periods cloudy conditions prevailed. Both species adopted a head-up posture when conditions were sunny and a head-down posture when under cloudy conditions. This is the first contribution where thermal aspects of two sympatric species of *Phymaturus* are evaluated.

Keywords: activity peaks; coexistence; postural adjustments; rock lizards

Introduction

Thermal biology is a widely studied topic in reptiles because temperature influences physiological and ecological features of organisms, as well as their fitness (Avery 1982; Huey 1982; Huey and Bennett 1987; Martin-Vallejo et al. 1995; Bauwens et al. 1996, 1999; Seebacher and Franklin 2005). Reptiles living at high latitudes and altitudes are faced with low temperatures and harsh environments (Spellerberg 1976). Hibernation throughout the winter, daily activity patterns, selection of thermally appropriate microhabitats, and postural adjustments, are some of the mechanisms used by lizards for thermoregulation in these environments (Porter and Gates 1969; Huey and Slatkin 1976; Dunham et al. 1989; Adolph 1990; Adolph and Porter 1993; Hertz et al. 1993; Melville and Schulte 2001). However, these mechanisms may depend on intrinsic characteristics of species, such as body size, since smaller lizards heat up faster than larger ones (Carothers 1983; Seebacher and Shine 2004). So, differences in heating and cooling rates, as well as in time spent basking, could be expected for different-sized species.

The genus *Phymaturus* includes Argentinean and Chilean lizard species that inhabit rocky promontories along the Andes and Patagonia. Studies indicate that the genus is conservative in several aspects of its life history (such as reproduction, habitat,

*Corresponding author. Email: corbalan@mendoza-conicet.gob.ar

and diet; Cei 1986; Scolaro et al. 2008), including thermal biology (Cruz et al. 2009). Mean field body temperatures of eight studied species ranged from 22.5 to 32.3°C (Cruz et al. 2009; Vidal et al. 2010), the maximum being reported for *Phymaturus tenebrosus* (37°C; Ibargüengoytía et al. 2008). Critical thermal maxima ranged from 39.9°C to 44.6°C, whereas critical thermal minima ranged from 5.2°C to 11.8°C (Cruz et al. 2009). Despite the conservatism in thermal biology within the genus, some differences were reported among species. Differences in body temperature were found between *Phymaturus zapalensis* and *Phymaturus punae* (Ibargüengoytía et al. 2008). Also, different modes of heat transfer were suggested for some species: thigmothermy in Patagonian species such as *P. tenebrosus* and *P. zapalensis* (Ibargüengoytía et al. 2008), and heliothermy in Andean species such as *P. punae* and *Phymaturus palluma* (Ibargüengoytía et al. 2008; Vidal et al. 2010). It was proposed that these behaviours are strongly influenced by the local environment (availability of radiation; Ibargüengoytía et al. 2008). Ibargüengoytía et al. (2008) also suggested that *P. punae* and *P. tenebrosus* are active thermoregulators, whereas *P. zapalensis* behaves almost as a thermoconformer, as also demonstrated for *P. palluma* (Vidal et al. 2010).

All previous studies on the genus *Phymaturus* comprise comparisons among species living at different latitudes, because most species are endemic and coexistence between pairs of species is rare (Debandi et al. 2012). The Payunia region is an extra-Andean volcanic system where it is possible to find two coexisting species, *Phymaturus payuniaie* and *Phymaturus roigorum*, that belong to different clades (Lobo and Quinteros 2005). As both clades have evolved independently and have only recently made secondary contact (Díaz Gómez 2009), these species are ideal for conducting comparative studies under similar environmental conditions.

In this study we compared some aspects of the thermal biology of these two coexisting species, specifically those related to basking behaviour. In the field, we evaluated the prevailing environmental conditions (substrate temperature and air temperature) when each species showed its peak of activity, the length of time spent basking during the day and relationships with environmental conditions, and the postural behaviour in relation to different cloudiness conditions.

Material and methods

The study was carried out at La Payunia Reserve, southern Mendoza Province, Argentina. Situated 140 km east of the Andes Cordillera, it is dominated by a volcanic landscape. The weather of the region is arid and cold, influenced by winds from the Pacific Ocean (Capitanelli 1972; Candia et al. 1993). Winters are rainy and snowy, and summers are dry (Candia et al. 1993). These conditions mean that lizards remain inactive during cold months. Both *Phymaturus* species present in the area are diurnal, saxicolous, viviparous and herbivorous. *Phymaturus payuniaie* is one of the 21 species that comprise the *patagonicus* group of the genus, whereas *P. roigorum* belongs to the *palluma* group, which comprises 17 species (Debandi et al. 2012 and recent descriptions by Lobo et al. 2012a, b; Troncoso-Palacios and Lobo 2012). Species belonging to the *palluma* group have spinier scales in the tail and are larger than those of the *patagonicus* group (Cei 1993). Measurements of individuals of the studied species taken for this and other studies in the region confirm that there are significant differences in snout-vent length (*P. payuniaie* adults, mean \pm SD = 84.31 \pm 5.04 mm, $n = 77$; *P. roigorum* adults, mean \pm SD = 99.97 \pm 5.85 mm, $n = 116$; $t_{191} = -19.23$, $p < 0.0001$).

Both species are endemic to the Payunia region of Argentina. The distribution of the smaller *P. payunia* is included within the distribution range of *P. roigorum*, and is always found in sympatry (syntopy) with this species. *Phymaturus roigorum*, instead, could be found in allopatry or in sympatry with *P. payunia*, and its distribution range is wider (Debandi and Corbalán 2012). Both species are diurnal and show a unimodal pattern of basking activity, with a slight decrease at the middle of the day in *P. roigorum* (Debandi and Corbalán 2009). Agonistic interactions between species in places where they coexist are rare, but when they occur, they involve chasing of *P. payunia* by *P. roigorum* (inter-sexual or intra-sexual encounters) (Corbalán and Debandi in preparation).

We chose three sites for sampling the activity of *P. payunia* and *P. roigorum*. Two (sites 1 and 2) are located on the northern slope of the Payún Matrú volcano (36°20' S, 69°14' W, 2372 m above sea level), and are 380 m apart. The rocks of these sites are ignimbrites and traquites, respectively, from the Pleistocene–Holocene (Llambías 1966, 2008). Site 3 is located in a yardang landscape at the base of the Payún Liso volcano (36°29' S, 69°22' W, 2111 m above sea level), 20 km away from sites 1 and 2. Yardangs are wind-moulded ignimbrites that tend to be unimodal in direction and form elongated parallel buckets. Illuminance (recorded with Luximeter Exttech model 401025) in the area is near to 800 lx in the middle of the day and 400 lx at sunset.

Phymaturus payunia is only present at sites 2 and 3, whereas *P. roigorum* is present at all three sites, so we refer to site 1 as allopatric, and sites 2 and 3 as sympatric. On each site we established a grid of 10 × 20 m, and all individuals present in the grid were captured with a loop, sexed, measured with a digital caliper (0.01 mm accuracy), weighed with a Pesola micro-line spring scale (100 × 1 g), and permanently marked with jewellery beads sutured through the tail (Fisher and Muth 1989), and then released at the capture site. Combinations of colours allowed us to identify each individual. A total of 22 adult individuals of *P. payunia* (16 females and six males) and 24 adult individuals of *P. roigorum* (15 females and nine males) were marked. Observations began at least 2 days after these procedures, performed by two observers placed at two fixed points, allowing complete vision of the grid. We used binoculars for the observations. Three days of sampling with similar weather conditions were conducted in November 2008 (spring) and January 2009 (summer) at sites 1 and 2, and for 4 days in January 2009 at site 3. The daily period of observation was from 09:00 h until the time when all individuals retreated to crevices, about 19:00 h. As this time is referred to official Argentinean time, which corresponds to longitude 45°W, we estimated the mean local time (or solar time) of the sampling sites located approximately at 69°20' W, as being 1:37 h earlier than the official time. Hence, our period of observation was from 07:23 h to 17:23 h, mean local time. Throughout each day, we recorded activity behaviour during 10-minute intervals, separated by 5 minutes of resting.

We measured the temperature of rocks and air during lizard activity to investigate relationships among these parameters. Close to each grid we placed two temperature sensors for the entire sampling period. One of them was placed in a small rock hole to take surface temperature minimizing direct air contact, and the other at 2 cm above the soil surface to measure air temperature. Data were recorded every 5 minutes using an Onset HOBO weather micro-station. As the data-logger was located next to the grid, with similar environmental conditions (sun, exposure, wind, plant cover), we assume that the recorded temperatures are representative of the entire grid.

Activity peaks and environmental temperature

We assessed the environmental temperatures that occurred when the individuals showed their maximum activity. For this, we divided the entire daily sampling period into 30-minute intervals. Then, we counted all active individuals during these intervals, and chose only those intervals in which more than 50% of marked individuals of each species were active. For each of these intervals of maximum activity (activity peaks), we established rock temperature and temperature 2 cm above ground occurring at the time, by averaging data records obtained from the weather micro-station during these 30-minute intervals.

The values of each temperature variable (rock and air at 2 cm) recorded in these intervals were analysed with parametric analysis of variance to establish differences between species and sites, using INFOSTAT software (InfoStat 2009). One set of analyses used data from sites of sympatry (sites 2 and 3) to make comparisons between species at each site and date; a second analysis used only *P. roigorum* data to make comparisons among allopatric and sympatric sites (sites 1 and 2 for November and all three sites for January). For the last analyses, differences among the three sites were tested using Bonferroni correction, with a level of rejection of $\alpha = 0.016$, according to the number of multiple comparisons.

Basking time and environmental conditions

Basking comprised the lizard's behaviour of remaining quiet, taking heat from solar radiation or by contact with the rock surface (i.e. thermoregulating by heliothermy or thigmothermy). This behaviour excludes feeding and moving activities, but includes shuttling between sun and shade. We were interested to assess the time spent basking and its relationship with the temperature of rocks, cloudiness and wind velocity, as well as to quantify the use of shade during these periods.

Ibargüengoytía et al. (2008) reported that *P. tenebrosus* increases body temperature as substrate temperature rises. During field activity, body temperature remained around 30°C, but it decreased when substrate temperature exceeded 35°C. For our studied species, the upper limit of the set-point range (the interquartile range of the preferred temperature in the laboratory) is 35.81°C for *P. payunia* and 35.77°C for *P. roigorum* (Corbalán and Debandi, unpublished data). In view of the information reported by Ibargüengoytía et al. (2008) and the preferred body temperature of the species, we evaluated the environmental conditions prevailing during basking time of *P. payunia* and *P. roigorum* considering a substrate temperature threshold of 36°C. We classified data as above 36°C (+ 36°C), below 36°C (– 36°C), and basking periods in which rock temperature included temperatures above and below 36°C (\pm 36°C). Taking into account the amount of continuous observation periods where individuals were only basking, we established the following categories of basking time: *short*, when individuals remained basking for one to three consecutive time periods (equivalent to 10 to 40 min); *middle*, four to six time periods (55 min to 1:25 h); *long*, seven to 12 time periods (1:45–2:55 h); *very long*, 13 or more time periods (more than 3 h). In total, 336 records of consecutive basking periods were analysed. For this analysis we chose a total of 12 adult (eight females and four males) *P. payunia* individuals (nine from site 2 and three from site 3), and 14 adult (10 females and four males) *P. roigorum* individuals (five from site 1, five from site 2 and four from site 3). These individuals were

chosen because they had high frequency of occurrence in the grid, and their activity could be followed throughout the day. Three categorical variables were set: *temperature threshold* (+ 36°C, - 36°C, ± 36°C), *basking periods* (short, middle, long, very long), and *species* (*P. payunia*, *P. roigorum*). Generalized linear models (GLM) with Poisson errors and logarithms as link function (i.e. Logarithmic or Poisson Regression) were used to analyse data, and χ^2 test and Akaike's Information Criteria were used to assess goodness of fit of the models (Crawley 2007). This analysis was made with R statistical software, version 2.12 (R Development Core Team 2010). A mosaic plot was used to represent the counts of the three categorical variables, in which the area of tiles is proportional to the cell frequency (Friendly 1994). In addition, Pearson's standardized residuals printed in the plot were used to detect differences among categories, using the "VCD" and "VCDXTRA" packages running in R software (Meyer et al. 2006).

Additionally, with the data from the same individuals as before, we evaluated the association of basking periods of different length with environmental conditions like cloudiness, wind velocity (km/h), and proportion of shade use by lizards during basking. Cloudiness was categorized as *sunny*, when there were no interruptions of sunny conditions along the basking period; and *cloudy*, when clouds were partially or permanently interrupting sunlight during the basking period. Wind velocity (measured regularly along the day with a Kestrel 1000 pocket wind meter) was categorized as *moderate winds* (up to 15 km/h) and *strong winds* (more than 15 km/h). All these analyses were also made with GLM with Poisson errors using R statistical software. Finally, we evaluated the proportion of shade use during basking periods of different length (short, middle, long and very long). We categorized this variable as *shady*, when lizards used shade or alternated between sun and shade during the basking period; and *exposed*, when lizards were fully exposed to the sun over the whole time period. This variable was also analysed using GLM, but this time with binomial errors and logits as link function (i.e. Logistic regression) with R statistical software (Crawley 2007).

Relationships between postural behaviours and light exposure

Based on McConnachie et al. (2009), we recorded two postural behaviours of individuals during basking: *upper body raised* (head or head and front of body raised, without contact with substrate), and *prostrate* (head and body flat on the rock surface). We assessed whether these postures were related to *light exposure* for each species using a GLM with Poisson error as explained above. Three categories of *light exposure* were considered: sunny, cloudy and semi-cloudy (when both sunny and cloudy conditions were recorded during the 10-min observation period).

Results

Activity peaks and rock and air temperature

We detected a total of 58 intervals when more than 50% of marked *P. payunia* were active, and a total of 78 and 44 intervals when more than 50% of *P. roigorum* were active in sympatry and allopatry, respectively (Tables 1 and 2). At sympatric sites, both measured temperatures were always higher at times when *P. payunia* showed its peaks of activity than when over 50% of *P. roigorum* individuals were active. Analyses of

Table 1. Comparisons of rock and air at 2 cm above ground temperatures ($^{\circ}\text{C}$, mean \pm SE) recorded during those periods of time at which *Phymaturus payunia* and *Phymaturus roigorom* showed activity peaks at sympatric sites (S2 and S3) in the Payunia region.

Sites	Temperatures	<i>Phymaturus payunia</i>	<i>Phymaturus roigorom</i>	<i>F</i>	<i>df</i>	<i>p</i>
S2–November	Rock	39.30 \pm 1.02 (<i>n</i> = 28)	39.07 \pm 1.39 (<i>n</i> = 19)	0.02	1, 45	0.89
	Air at 2 cm	31.05 \pm 0.71 (<i>n</i> = 28)	30.71 \pm 1.02 (<i>n</i> = 19)	0.08	1, 45	0.78
S2–January	Rock	39.46 \pm 0.87 (<i>n</i> = 25)	37.69 \pm 0.82 (<i>n</i> = 41)	1.97	1, 64	0.16
	Air at 2 cm	35.91 \pm 0.90 (<i>n</i> = 25)	34.69 \pm 0.83 (<i>n</i> = 41)	0.93	1, 64	0.34
S3–January	Rock	44.89 \pm 2.14 (<i>n</i> = 5)	38.30 \pm 1.16 (<i>n</i> = 18)	7.10	1, 21	<0.05
	Air at 2 cm	42.45 \pm 2.25 (<i>n</i> = 5)	37.05 \pm 0.70 (<i>n</i> = 18)	9.56	1, 21	<0.01

Significant *P* values are given in bold.

Table 2. Comparisons between allopatric (S1) and sympatric (S2 and S3) sites of rock and air at 2 cm above ground ($^{\circ}\text{C}$, mean \pm SE) recorded during those periods of time at which *Phymaturus roigorom* showed activity peaks in each sampling period in the Payunia region.

	Temperatures	S1	S2	S3	<i>F</i>	<i>df</i>	<i>p</i>
November	Rock	31.77 \pm 0.53 (<i>n</i> = 27)	39.07 \pm 1.39 (<i>n</i> = 19)		30.39	1, 44	<0.001
	Air at 2 cm	30.95 \pm 0.60 (<i>n</i> = 27)	30.71 \pm 1.02 (<i>n</i> = 19)		0.05	1, 44	0.83
January	Rock	32.88 \pm 0.77 (<i>n</i> = 17) a	37.69 \pm 0.82 (<i>n</i> = 41) b	38.30 \pm 1.16 (<i>n</i> = 18) b	7.23	2, 73	0.001
	Air at 2 cm	33.05 \pm 1.46 (<i>n</i> = 17)	34.69 \pm 0.83 (<i>n</i> = 41)	37.05 \pm 0.70 (<i>n</i> = 18)	2.83	2, 73	0.06

Significant *P* values are given in bold, differences among sites are indicated by lower case letters (a \neq b).

variance indicated that differences were significant only at site 3 during January for both temperatures assessed (Table 1).

When we compared *P. roigorom* among sites to assess a possible effect of allopatry/sympatry, we found significant differences in rock temperatures at which most individuals were active (Table 2). During November, site 1 (where only *P. roigorom* was found) showed the lowest rock temperature (31.7 $^{\circ}\text{C}$) at maximum activity. The same occurred during January, with rock temperature being lowest at site 1 (Table 2). Air temperature at 2 cm above ground did not differ among sites during November or January (Table 2).

Basking time and environmental conditions*Rock temperature*

Generalized linear models indicated that there is a significant three-way interaction between temperature threshold, basking time, and species ($\chi^2_6 = 18.13$, $p < 0.01$). To visualize differences in frequencies, we computed the value of Pearson's standardized residuals (3.07) for the adjusted rejection level ($\alpha = 0.0021$, the value of $\alpha = 0.05$ adjusted for 24 multiple comparisons). According to this calculation, *P. roigorum* had a significantly higher frequency of long periods than *P. payuniaie* when temperature was rising, given by the higher than expected frequencies of long periods at + 36°C, and of very long periods at $\pm 36^\circ\text{C}$ (Figure 1). Also, there were no *very long* records of basking periods for either species when the temperature of rocks was below 36°C (Figure 1).

Cloudiness

When analysing cloudiness in relation to basking periods, both species had higher frequencies of active individuals spending a short time basking, independent of cloudiness (non-significant three-way interaction, $\chi^2_1 = 0.20$, $p = 0.65$). Also, there was no significant interaction between species and cloudiness ($\chi^2_1 = 0.77$, $p = 0.38$), indicating that both species had more individuals when sunny conditions prevailed. *Phymaturus roigorum* took longer basking periods more frequently than *P. payuniaie* (highly significant interaction between species and basking periods, $\chi^2_1 = 768.3$, $p < 0.0001$), especially when cloudiness prevailed (significant interaction between species and cloudiness, $\chi^2_1 = 8.29$, $p < 0.01$).

Wind velocity

When taking wind into account, GLM indicated no relationship between species, wind velocity and duration of basking periods, because there was no significant three-way interaction ($\chi^2_3 = 0.47$, $p = 0.92$). Moreover, wind did not show any significant interactions with the other two categorical variables.

Shade use

The proportion of periods in which individuals used shade was similar in both species, with this proportion growing larger as basking periods became longer ($\chi^2_2 = 13.506$, $p < 0.01$). We made comparisons between species only for *short* to *long* periods, because *P. payuniaie* had no records of *very long* basking periods. There were no differences between species ($\chi^2_1 = 0.24$, $p = 0.62$) and the species–period interaction was not significant ($\chi^2_2 = 2.91$, $p = 0.23$).

Relationships between postural behaviours and light exposure

Both species showed similar postural behaviour when exposed to different light conditions. There was no significant three-way interaction ($\chi^2_2 = 0.20$, $p = 0.90$), or two-way interaction between light exposure and species ($\chi^2_2 = 0.40$, $p = 0.81$). There was

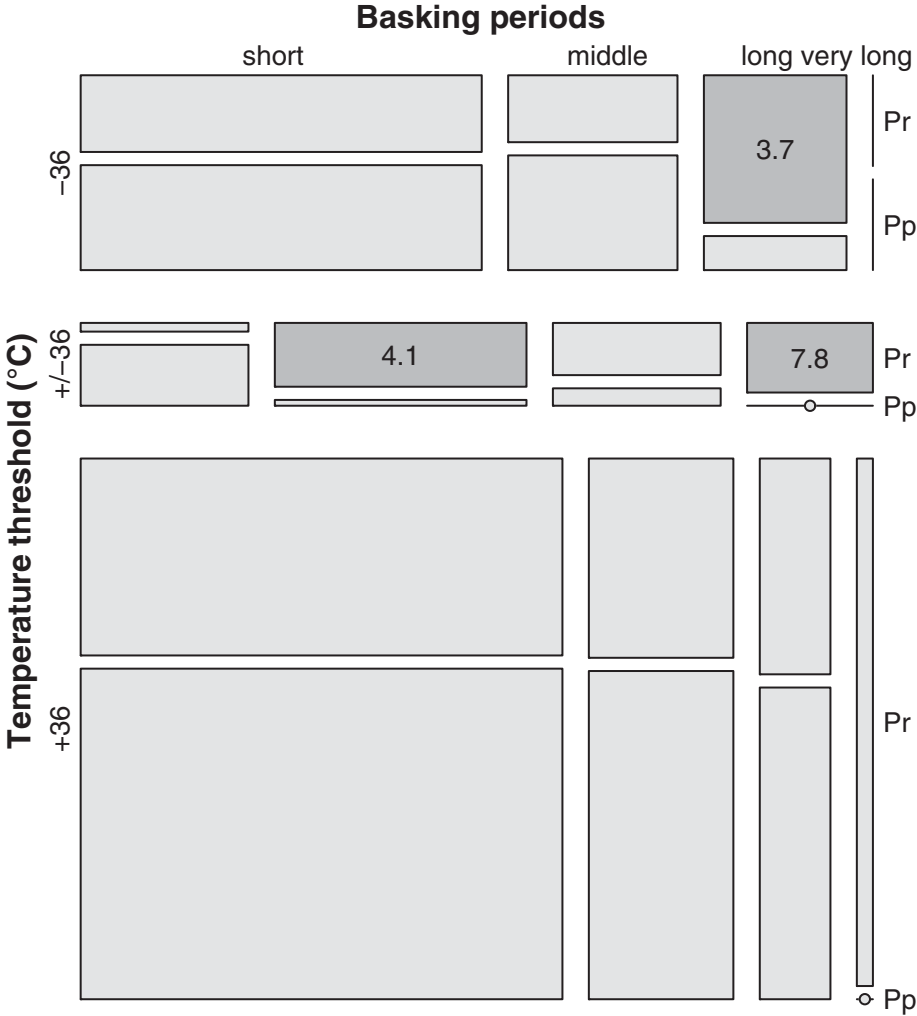


Figure 1. Mosaic plot showing frequency of records of *Phymaturus payunia* (Pp) and *Phymaturus roigorum* (Pr) for each category of basking periods (short, middle, long and very long), at different rock temperature thresholds. In the graph, the area of tiles is proportional to the cell frequency, and values of Pearson's standardized residuals are printed in the plot to assess differences among categories (see text for a more detailed procedure). Dark grey indicates categories that show significantly higher or lower than expected frequencies according to the adjusted rejection level.

a highly significant interaction between behaviour and light exposure ($\chi^2_2 = 83.60$, $p < 0.0001$), indicating that when sunny conditions prevailed, both species adopted an upper body raised posture, whereas when conditions were cloudy or semi-cloudy both adopted a prostrate posture (Figure 2).

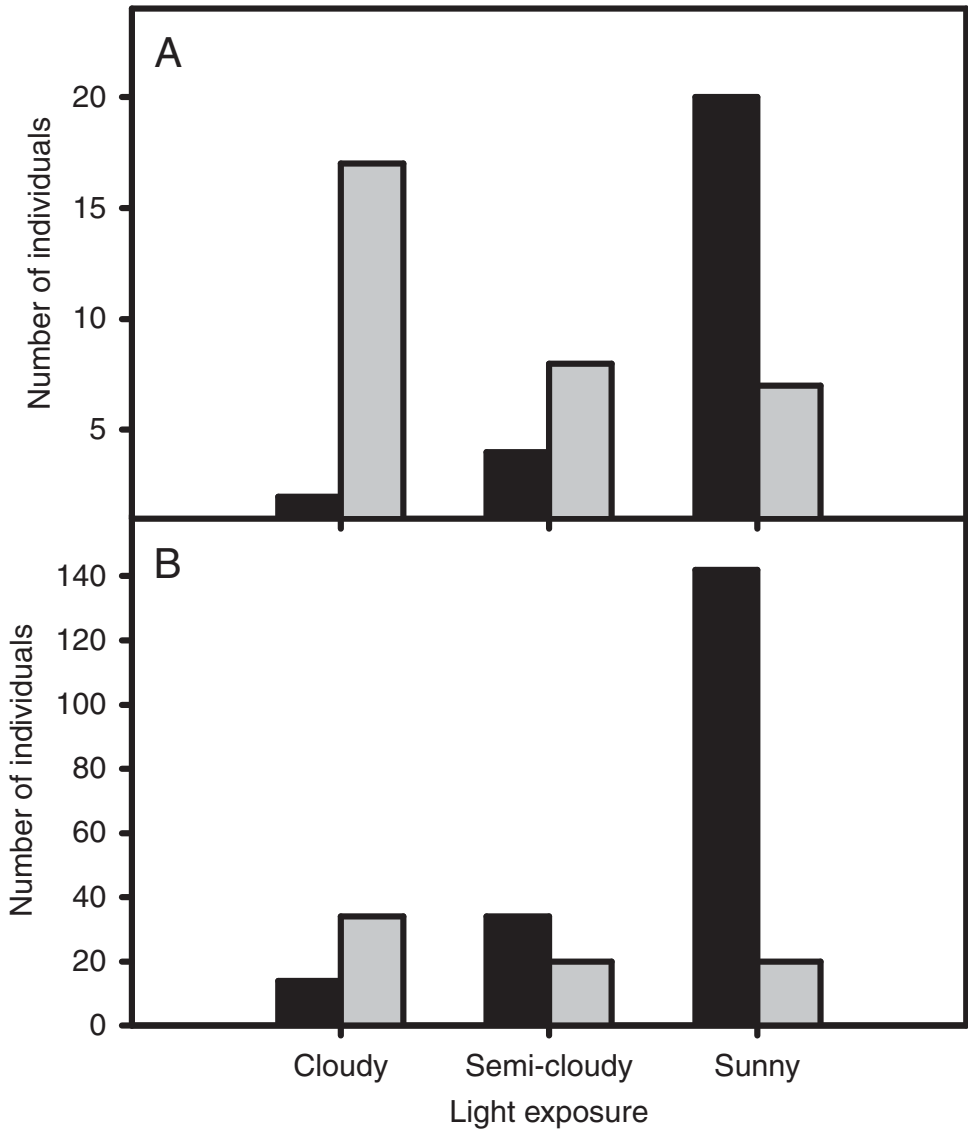


Figure 2. Frequency of postures exhibited by *Phymaturus payuniaie* (A) and *Phymaturus roigorum* (B) during different light exposures. Black bars represent head-up postures and grey bars represent prostrate postures.

Discussion

Bogert (1959) postulated that phylogeny has a role in the expression of body temperature among species. The genus *Phymaturus* is considered conservative in several characteristics, including thermal biology (Cruz et al. 2009). Recent studies demonstrated

that there are some differences in ecological niche between groups of species of the genus (i.e. the *patagonicus* and *palluma* groups) (Debandi et al. 2012). Whereas species belonging to the *patagonicus* group were positively associated with mean annual temperature, temperature seasonality, mean temperature of the driest quarter of the year and to a compound topographic index, species belonging to the *palluma* group were positively related to sunny days during the year, bare soil, isothermality and slope. However, this study also revealed that it is more likely that these differences are the result of habitat availability in their respective regions rather than of differences in habitat preferences (Debandi et al. 2012), reinforcing the conservative characteristics of the genus.

Preliminary studies on preferred temperature in the laboratory for *P. payunia* and *P. roigorum* indicate that these species do not show differences in this parameter, and are included within the range reported for other species of the genus (Corbalán and Debandi unpublished data). However, several differences in basking behaviour between both sympatric species were found in this study. The most important difference was in the rock and air at 2 cm above ground temperatures recorded in summer at site 3 at the time when species exhibit their activity peak (i.e. when more than 50% of marked individuals were active), all being higher for *P. payunia*. Air and rock temperatures exceed by 5–7°C the critical maximum body temperature for the species (about 37.2°C; Aguilar et al. 2010). These results are surprising because *P. payunia* is smaller, and smaller lizards heat up faster than larger ones (Carothers 1983; Seebacher and Shine 2004), reaching lethal body temperatures in a short time. However, the amount of solar radiation absorbed by an organism is a product not only of body size but also of skin reflectance (Clusella-Trullas et al. 2009) and incidence of solar radiation on the body (i.e. orientation of dorsum or head towards the sun; Ribeiro et al. 2007; McConnachie et al. 2009), variables which were not assessed in this study. Nevertheless, we can conclude that in *P. payunia*, over-heating (and lethal consequences) seems to be avoided by having shorter basking periods, and using shade more when basking periods are longer.

Another important difference between the species is the exposure of *P. roigorum* during very long basking periods. Individuals of this species were observed in basking positions for over 3 h. This basking period is longer than that observed for *P. payunia* and other saxicolous species such as *Tropidurus torquatus*, which remains in the sun for 30 min until the temperature warms up, when it retreats to rock cracks or shaded areas (Ribeiro et al. 2007). However, we also observed that *P. roigorum* remained basking for these long periods mainly when cloudy conditions prevailed. As was recorded for *P. payunia* and *T. torquatus*, *P. roigorum* also used a higher proportion of shade when basking periods were longer. Then, cloudiness conditions and shade use during long basking periods probably help *P. roigorum* to avoid over-heating.

Basking for shorter periods could be advantageous for *P. payunia* not only to avoid over-heating but also to avoid predators. No studies on predation have been published for *Phymaturus* species, but Videla (1982) reported that *Agriornis* (Passeriformes) preys on *P. palluma* in Uspallata (Mendoza, Argentina). We observed individuals of *Agriornis montanus* trying to catch immature *Phymaturus* lizards in the Payunia region and therefore this species could be a potential predator on our studied lizards. Pianka and Vitt (2003) suggested that potential predators are limited by lizard size relative to predator size. Taking into account that *Agriornis* is a medium-sized bird

(21 cm), it is possible that the smaller species *P. payunia* would be more vulnerable to predation by this bird than *P. roigorum* at our study site (at adult stage).

Differences between sites of allopatry and sympatry were evident in *P. roigorum*. Rock temperature during the peak of activity of this species was lower at the allopatric site in spring and summer. Further studies taking into account the temperature of rocks at each site may help to understand the distribution of both species in the Payunia region. Although both species show similar preferred temperatures under laboratory conditions (Corbalán and Debandi, unpublished data), it is possible that *P. roigorum* can tolerate a wider temperature range than *P. payunia*, explaining the absence of *P. payunia* from several rocky promontories of the region where *P. roigorum* is present.

The thermal biology of many terrestrial squamates is dominated by the behavioural exploitation of solar radiative energy for the regulation of body temperature (Spellerberg 1972; Avery 1982). Lizards use solar radiation in two different ways, by basking in the sun (heliothermy) or by adressing parts of the body to a sun-warmed substrate (thigmothermy) (Withers and O'Shea 1993). The raised upper body posture (or head-up) recorded in individuals of both species in this study under sunny conditions is in keeping with the concept of heliothermy, whereas the prostrate posture is typically a thigmothermic behaviour. Vidal et al. (2010) observed that individuals of *P. palluma* from Chile exposed their body surface on rocks when basking, and suggested that this species has a predominantly thigmothermic behaviour. Ibarzüengoytía et al. (2008) proposed that lizards of the *Phymaturus* genus are mainly heliothermic at higher altitudes, and mostly thigmothermic at lower altitudes. Our results indicate that the coexisting species *P. roigorum* and *P. payunia* adopt both behaviours to thermoregulate, as has been demonstrated for other saxicolous lizards such as *P. palluma* (Videla 1982), *T. torquatus* (Ribeiro et al. 2007) and *Pseudocordylus melanotus* (McConnachie et al. 2009). When sunny conditions prevailed, both species adopted a heliothermic posture (head-up), but when cloudy conditions prevailed, both species adopted a thigmothermic posture (prostrate), indicating an opportunistic thermoregulatory behaviour. Ibarzüengoytía et al. (2010) also found an opportunistic behaviour for *Liolaemus sarmientoi* and *Liolaemus magellanicus*. These species show heliothermy when the air temperature is cold (during the morning), and thigmothermy in the warmest hours of the day (early afternoon). In contrast, Videla (1982) observed thigmothermic basking in *P. palluma* when it initiated activities after leaving crevices, turning to heliothermy after heat acquisition by thigmothermy. We observed a similar behaviour to that observed by Videla (1982) for *P. palluma*. Sherwood et al. (2005) and McConnachie et al. (2009) argue that lizards bask in sunlight on cold mornings and gain heat from radiation and conduction from warmed surfaces. Similarly, prostrate postures are frequent during winter and when it is overcast. During the hottest periods, more elevated postures avoid direct contact with the rock surface, minimizing heat gained from it, as well as increasing potential heat loss by exposing a greater surface area to the air (McConnachie et al. 2009).

This is the first study to evaluate the biological aspects of two coexisting species of *Phymaturus*. We found differences between species in the rock temperature during their activity peaks at site 3, as well as differences between species in the time spent basking. However, the duration of basking periods may vary depending on sex and pregnancy (gravid females may spend more time basking than males and non-gravid females; Shine 1980; Schwarzkopf and Shine 1991). Because the number of males and

gravid/non-gravid females at each site and on each date (November/January) was not sufficient to make comparisons, these aspects were not assessed in this study. Other factors such as coloration may influence heat absorption (Clusella-Trullas et al. 2009), and therefore basking duration. Unlike other *Phymaturus* species, neither of the studied species have black heads which could increase heat gain, but the pattern and size of spots and proportion of clear/dark colours on the back may vary between sexes, and among individuals from different populations (personal observation). Males of *P. roigorum* are yellowish or whitish, whereas females are brownish. These aspects should be evaluated in further studies to better understand thermoregulation in these species. This study represents a first step to the knowledge of the ecology, behaviour and resource segregation for these species that coexist in the same habitat, feeding on the same plant species and sharing refuge and microsites to thermoregulate.

Acknowledgements

We thank the Dirección de Recursos Naturales Renovables of Mendoza province for allowing us to carry out the study in La Payunia Reserve, UGAP (Unidad de Gestión Ambiental Payunia) for logistic support, and N. Horák for language revision. The research was financed by Agencia de Promoción Científica y Técnica (PICT 2122–2006) and CONICET (PIP 114-200801-00238).

References

- Adolph S. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology*. 7:315–327.
- Adolph S, Porter W. 1993. Temperature activity and lizard life histories. *Am Nat.* 142:273–295.
- Aguilar R, Corbalán V, Piña CI. 2010. Biología térmica de dos habitantes de la árida Payunia: *Phymaturus roigorum* y *Phymaturus payunia*. Poster session presented at: AHA 2010. XI Congreso Argentino de Herpetología; Buenos Aires, Argentina.
- Avery RA. 1982. Biology of reptilia. In: Gans C, Pough FH, editors. *Field studies of body temperatures and thermoregulation*. New York: Academic Press. p. 167–211.
- Bauwens D, Castilla AM, Mouton PFN. 1999. Field body temperatures, activity levels and opportunities for thermoregulation in an extreme microhabitat specialist, the girdled lizard (*Cordylus macropholis*). *J Zool (London)*. 249:11–18.
- Bauwens D, Hertz P, Castilla A. 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology*. 77:1818–1830.
- Bogert CM. 1959. How reptiles regulate their body temperature. *Sci Am.* 22:213–221.
- Candía R, Puig S, Dalmasso A, Videla F, Martínez Carretero E. 1993. Diseño del Plan de manejo para la Reserva Provincial La Payunia (Malargüe, Mendoza). *Multequina*. 2:5–87.
- Capitanelli R. 1972. Geología, geomorfología, climatología, fitogeografía y zoogeografía de la provincia de Mendoza. In: Roig FA, editor. *Geomorfología y clima de la provincia de Mendoza*. Buenos Aires: Boletín de la Sociedad Argentina de Botánica. p. 15–48.
- Carothers J. 1983. Size-related activity patterns in an herbivorous lizard. *Oecologia*. 57:103–106.
- Cei JM. 1986. Reptiles del centro, centro-oeste y sur de la Argentina: Herpetofauna de las zonas áridas y semiáridas. Torino: Mus. Reg. Sci. Nat. Torino: Monografía 4.
- Cei JM. 1993. Reptiles del noroeste, nordeste y este de la Argentina: Herpetofauna de las selvas subtropicales, Puna y Pampas. Torino: Mus. Reg. Sci. Nat. Torino: Monografía 14.
- Clusella-Trullas S, van Wyk JH, Spotila JR. 2009. Thermal benefits of melanism in cordylid lizards: a theoretical and field test. *Ecology*. 90:2297–2312.
- Crawley MJ. 2007. *The R Book*. Chichester (UK): John Wiley & Sons, Inc.

- Cruz F, Belver L, Acosta JC, Villavicencio HJ, Blanco G, Canovas 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.
- Debandi G, Corbalán V. 2009. Actividad diaria de dos especies coexistentes del género *Phymaturus* en Payunia (Mendoza). X Congreso Argentino de Herpetología (AHA).
- Debandi G, Corbalán V. 2012. Relación entre el tipo de rocas y la distribución de dos especies de *Phymaturus* en la Payunia, Mendoza. XIII Congreso Argentino de Herpetología (AHA).
- Dunham A, Grant B, Overall K. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiol Zool.* 62:335–355.
- Díaz Gómez JM. 2009. Historical biogeography of *Phymaturus* (Iguania: Liolaemidae) from Andean and Patagonian South America. *Zool Scripta.* 38:1–7.
- Fisher M, Muth A. 1989. A technique for permanently marking lizards. *Herpetol Rev.* 20:45–46.
- Friendly M. 1994. Mosaic displays for multi-way contingency tables. *J. Am Statist Assoc.* 89:190–200.
- Hertz P, Huey R, Stevenson R. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am Nat.* 142:796–818.
- Huey RB. 1982. Biology of reptilia. In: Gans C, Pough FH, editors. *Temperature, physiology, and the ecology of reptiles*. New York: Academic Press. p. 25–91.
- Huey RB, Bennett AF. 1987. Phylogenetic studies of coadaptations: preferred temperatures versus optimal performance temperatures of lizards. *Evolution.* 41:1098–1115.
- Huey RB, Slatkin M. 1976. Cost and benefits of lizard thermoregulation. *Q Rev Biol.* 51:363–384.
- Ibargüengoytia 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.
- Ibargüengoytia NR, Medina SM, Fernandez JB, Gutierrez JA, Tappari F, Scolaro A. 2010. Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. *J Thermal Biol.* 35:21–27.
- InfoStat. 2009. InfoStat version 2009. Córdoba, Argentina: Grupo InfoStat, FCA, Universidad Nacional de Córdoba.
- Llambias EJ. 1966. Geología y petrología del volcán Payún Matrú. *Acta Geológica Ulloana.* 8:265–315.
- Llambias EJ. 2008. Sitios de interés geológico de la República Argentina. In: *El distrito volcánico de la Payunia: un paisaje lunar en nuestro planeta*. Buenos Aires: SEGEMAR. p. 263–280.
- Lobo F, Espinoza RE, Sanabria E, Quiroga L. 2012a. A new *Phymaturus* (Iguania: Liolaemidae) from the Southern extreme of the Argentine Puna. *Copeia.* 1:12–22.
- Lobo F, Nenda SJ, Slodki D. 2012b. A new lizard of *Phymaturus* (Iguania: Liolaemidae) from Argentina. *Herpetologica.* 68:121–133.
- Lobo F, Quinteros S. 2005. A morphology-based phylogeny of *Phymaturus* (Iguania: Liolaemidae) with the description of four new species from Argentina. *Pap Avulsos Zool.* 45:143–177.
- Martin-Vallejo J, Garcia-Fernandez J, Perez-Mellado V, Vicente-Vellardon JL. 1995. Habitat selection and thermal ecology of the sympatric lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain region of central Spain. *Herpetol J.* 5:181–188.
- McConnachie S, Alexander GJ, Whiting MJ. 2009. Selected body temperature and thermoregulatory behavior in the sit-and-wait foraging lizard *Pseudocordylus melanotus melanotus*. *Herpetol Monogr.* 23:108–122.

- Melville J, Schulte J. 2001. Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. *Aust Ecol.* 26:660–669.
- Meyer D, Zeileis A, Hornik K. 2006. The strucplot framework: visualizing multi-way contingency tables with vcd. *J Stat Softw.* 17:1–48.
- Pianka E, Vitt L. 2003. *Lizards: windows to the evolution of diversity*. Berkeley (CA): University California Press. Chapter 4, Escaping predators; p. 63–84.
- Porter W, Gates D. 1969. Thermodynamic equilibria of animals with environment. *Ecol Monog.* 39:245–270.
- R Development Core Team. 2010. *R: A language and environment for statistical computing*. Austria: R Foundation for Statistical Computing.
- Ribeiro LB, Gomides SC, Santos AO, Sousa BM. 2007. Thermoregulatory behavior of the saxicolous lizard, *Tropidurus torquatus* (Squamata, Tropiduridae), in a rocky outcrop in Minas Gerais, Brazil. *Herpetol Conserv Biol.* 3:63–70.
- Schwarzkopf L, Shine R. 1991. Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: why do gravid females bask more? *Oecologia.* 88:562–569.
- Scolaro JA, Ibarquengoytía NR, Pincheira-Donoso D. 2008. When starvation challenges the tradition of niche conservatism: on a new species of the saxicolous genus *Phymaturus* from Patagonia Argentina with pseudoarbooreal foraging behaviour (Iguania, Liolaeminae). *Zootaxa* 1786:48–60.
- Seebacher F, Shine R. 2004. Evaluating thermoregulation in reptiles: the fallacy of the inappropriately applied method. *Physiol Biochem Zool.* 77:688–695.
- Seebacher F, Franklin CE. 2005. Physiological mechanisms of thermoregulation in reptiles: a review. *J Comp Physiol.* 175:533–541.
- Sherwood L, Klandorf H, Yancey PH. 2005. *Animal physiology: from genes to organisms*. Belmont (Australia): Thomson/Brooks/Cole.
- Shine R. 1980. Costs of reproduction in reptiles. *Oecologia.* 46:92–100.
- Spellerberg IF. 1972. Temperature tolerances of south-east Australian reptiles examined in relation to reptile thermoregulatory behaviour and distribution. *Oecologia.* 9:23–46.
- Spellerberg IF. 1976. Adaptations of reptiles to cold. In: Bellairs Ad'A, Barry Cox, C, editors. *Morphology and biology of reptiles*. London: Academic Press. p. 261–285.
- Troncoso-Palacios J, Lobo F. 2012. A new species of *Phymaturus* (Iguania: Liolaemidae) of the *palluma* group from Central Chile. *Cuad Herpetol* 26:69–78.
- Vidal MA, Habit E, Victoriano P, Gonzalez-Gajardo A, Ortiz YJC. 2010. Thermoregulation and activity pattern of the high-mountain lizard *Phymaturus palluma* (Tropiduridae) in Chile. *Zoologia.* 27:13–18.
- Videla F. 1982. Observaciones etológicas preliminares sobre *Phymaturus palluma* (Reptilia-Iguanidae) del roquedal precordillerano mendocino. *Bol Mus Cs Nat y Antrop "C. Moyano"*. 3:57–62.
- Withers PC, O'Shea JE. 1993. Fauna of Australia. In: Glasby CG, Ross GJB, Beesley PL, editors. *Morphology and physiology of the Squamata*. Canberra: Australian Govt. Pub. Service. Chapter 24; p. 1–53.