Activity Patterns and Thermoregulatory Behavior of the Viviparous Lizard *Phymaturus palluma* in Aconcagua Provincial Park, Argentine Andes

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Abstract.—Temperature has a significant influence on physiology, ecology, and life history of ectotherms. Despite environmental fluctuations, lizards have developed behavioral mechanisms to maintain a relatively constant body temperature. These behaviors are particularly important for lizards living at high elevations like the high mountain lizard *Phymaturus palluma*, an endemic lizard to Central Andes. We studied how this species thermoregulates throughout the day and how abiotic and biophysical factors influence their activity. We recorded lizard activity and body postures and orientations at different times of the day during two seasons. Results indicate that *P. palluma* invest most of their time and energy in thermoregulation to maintain an optimal body temperature. Lizards activity raised with operative temperature of sun-exposed rocks up to an optimum and declined above that temperature. In addition, activity was negatively correlated with crevice temperature and positively correlated with mean operative temperature. Lizards changed their heat source along the day, using heliothermy most part of daytime and thigmothermy in the afternoon. Body postures were related to operative temperatures, so they may play an important role in thermoregulation. In contrast, body orientations were not related to operative temperatures. This study supports the idea that the benefit of thermoregulatory behaviors exceeds the energetic costs and the risk of predation involved in basking activities.

Key Words.—basking; harsh environments; heliothermy; Liolaemidae; thermoregulation; thigmothermy

Introduction

Temperature has a significant influence on reptile physiology, ecology, and life history (Cowles and Bogert 1944; Huey 1982; Adolph and Porter 1993), as well as affecting organisms in a variety of ways, such as their locomotion, growth, reproduction, activity time, population density, and ultimately, fitness and survival (Huey and Stevenson 1979; Angilletta et al. 2002; Pörtner et al. 2006; Angilletta 2009; Bozinovic et al. 2011). In ectotherms, environmental temperature is a critical factor because individuals depend on finding heat sources to achieve physiologically optimal temperatures (Pörtner et al. 2006). To cope with the heterogeneity of the thermal environment over space and time, ectotherms regulate their temperature to different ways, ranging from organisms that conform to environmental temperature (thermoconformers) to organisms that maintain a nearly constant body temperature independently of the environmental fluctuations (thermoregulators; Angilletta 2009).

In some terrestrial ectotherms, achieving and maintaining the body temperature (T_b) within an optimal range during part of the day results in a challenge due to the high daily temperature amplitude (Huey and Slatkin 1976; Angilletta et al. 2002). This is particularly true for lizards at high elevations and latitudes, where temperature fluctuations constraint thermoregulation. Thus, these individuals often exhibit a lower and more variable T_b than those at lower elevations and latitudes (Bauwens et al. 1990; Lemos-Espinal and Ballinger 1995; Zamora-Camacho et al. 2013). To deal with environmental fluctuations, organisms can make changes in behavior, physiology, or both, and thereby achieve and maintain an appropriate T_b (Cowles and Bogert 1944; Huey and Slatkin 1976; Angilletta et al. 2002). Skin reflectance can also play a role in thermoregulation (Clusella-Trullas et al. 2009). Among the behavioral mechanisms used by ectotherms to thermoregulate are modification of activity time, postural adjustments, and selection of thermally appropriate microhabitats (Huey 1974).

Lizards modify their daily and seasonal activity patterns according to the variation in the thermal regime

and ambient temperatures. In this way, lizards either retreat into refuges to avoid overheating during hot days (Sinervo et al. 2010) or remain inactive during cold months (Cei 1986). During activity periods, individuals warm up mainly by means of solar radiation (heliothermic behavior), substratum conduction (thigmothermic behavior), or both (Zug et al. 2001). To maximize heat gain, lizards can thermoregulate by changing their body postures (Martín et al. 1995) or by modifying their body orientation based on the incidence of solar radiation, which allows them to effectively adjust the amount of radiant heat gained from the sun (Muth 1977). Shuttling between sun and shade patches also allows lizards to increase or decrease heat gain (Huey 1974). These thermoregulatory behaviors allow lizards to cope with the thermal variation and to achieve a relatively constant T_b which favors the overall organism performance (Angilletta 2009).

In high elevation environments, thermoregulatory behaviors allow ectotherms to take advantage of the high solar radiation (Gates 1980) and reach high T_bs despite the low air temperature (Pearson 1954; Pearson and Bradford 1976; Hertz and Huey 1981; Adolph 1990). Actually, most high elevation mountain lizards are found to be efficient thermoregulators (Ibargüengoytía et al. 2008; Aguado and Braña 2014; Ortega et al. 2016; Vicenzi et al. 2017). Thus, in lizards living in mountain habitats, thermoregulatory behaviors comprise a large part of the time budget of a lizard and have a profound impact on their life histories (Adolph and Porter 1993) because time invested in thermoregulation cannot be used for other activities such as reproduction, feeding, social behaviors, and territory defense (Huey and Slatkin 1976; Huey 1982; Wilms et al. 2011; Aguado and Braña 2014).

High Mountain Lizards (*Phymaturus palluma*) are saxicolous, viviparous, and herbivorous lizards, which exhibit sexual dimorphism in size and color (Cei 1986). These lizards are endemic to the highlands of the Central Andes of Argentina (Cei 1996). In the Central Andes, where the climate is continental with high seasonality (Corte and Espizua 1981), *P. palluma* remain dormant during autumn, winter, and part of spring (from March to October), and start activity in the middle of spring (October and November). During activity, this species is an efficient thermoregulator and in the Aconcagua Province Park of Argentina they exhibit T_bs higher than the microenvironmental and operative temperatures (Vicenzi et al. 2017). Despite this thermoregulation efficiency, most *P. palluma* showed lower values for field T_bs than their set point of preferred body temperatures (Vicenzi et al. 2017). The aim of this study was to understand which factors influence the activity pattern of *P. palluma* and how they adopt different behavioral mechanisms to deal with the

variation of thermal sources. Consequently, we have evaluated the relationship between activity patterns and biophysical and abiotic factors, and the use of different microhabitats and the acquisition of different body postures and orientations in relation with the operative temperatures.

MATERIALS AND METHODS

Study site.—We conducted fieldwork in the Punta de Vacas Valley in Aconcagua Provincial Park (32.8453°S, 69.7619°W, WGS84, 2,500 m above sea level), Mendoza, Argentina. The area belongs to the Altoandina phytogeographic province and is dominated by the shrub species *Adesmia* (Fabaceae), *Tetraglochin* (Rosaceae), and *Berberis* (Berberidaceae), as well as the grasses *Poa* and *Stipa* (Poaceae; Méndez et al. 2006). The climate at the site is cold semiarid (BSk) according to the Köppen classification, where temperatures fluctuate between -4° to 28° C and the mean annual precipitation is 150 mm (Soria 2003).

Fieldwork.—We delimited a grid (200 × 60 m) over a relatively flat area with typical vegetation and numerous rocky outcrops suitable for *P. palluma*. The site provided a fine-grained mosaic of microhabitats and sun-shade patches in which lizards could readily move. Within the grid, we captured by noose adult *P. palluma,* for which we determined sex, and we marked them permanently with jewelry beads sutured through the tail (Fisher and Muth 1989). Color-coded combinations of beads allowed us to identify individuals. We determined reproductive state of females (gravid or non-gravid) by abdominal palpation according to Lancaster et al. (2008), and we released all individuals at the capture site. We carried out visual surveys per day in four time-intervals (0900, 1100, 1400, 1600) to estimate the activity and thermoregulatory behavior of lizards. Each survey was conducted along three parallel transect lines that were 200 m long and crossed the entire study area. We walked the transects during the activity period of these lizards for at least three consecutive days during each sampling session. We separated the transects by 20 m each and walked them in opposite directions without following a consecutive order (e.g., 3, 1, 2) to avoid disturbing lizards in adjacent transects. It took an average of 35–40 min to walk along each transect. We sampled for 52 d in the austral spring and summer, from November 2013 to March 2014, and from October 2014 to March 2015. We observed each lizard by using binoculars from a maximum distance of approximately 10 m. For each observation, we recorded the time, cloudiness, and identity of the lizard. We also recorded if the lizard was exclusively basking (the lizard remained motionless during a prolonged stop [> 15 s] on a perch;

Figure 1. Body postures and orientations for High Mountain Lizard (*Phymaturus palluma*). (a) posture 1 (head on the substrate or raised, chest and abdomen pressed against the substrate); (b) posture 2 (head and chest raised, abdomen pressed against the substrate); (c) posture 3 (head, chest, and abdomen raised above the substrate); (d) orientation facing away from the sun; (e) orientation facing towards the sun; and (f) orientation parallel to sun rays. (Photographed by Nadia Vicenzi).

Diego-Rasilla and Pérez-Mellado 2000) or whether another behavior was involved, such as foraging or moving. We recorded the postures, body orientations, and sun exposure when basking of lizards. We identified three types of basking postures based on the degree of contact between the body of the lizard and the substrate (Sartorius et al., 2002). We classified postures as: (1) posture 1, the head is in contact with the substrate or raised, and the chest and abdomen are pressed against the substrate; (2) posture 2, the head and chest are raised and the abdomen is pressed against the substrate; and (3) posture 3, the head, chest, and abdomen are raised above the substrate (Fig. 1). Postures with more contact with the substrate, such as posture 1, are usually associated with thigmothermic behavior, and more elevated postures, postures 2 and 3, are associated with heliothermic behavior (McConnachie et al. 2009).

Based on the saxicolous habits of the lizards, we defined three types of body orientations: (1) facing towards the sun (in a horizontal position, head directed to the sun), (2) facing away from the sun (in a horizontal position, head directed away from the sun), and (3) parallel to the sun (in a vertical position, leaning against a rock; Fig. 1). We also identified three types of sun exposure: full sun, sun filtered through vegetation, and full shade. We recorded the first behavior seen and when possible, the presence of lizards inside refuges.

We recorded operative temperatures (T_e, *sensu* Bakken 1992) in the field using eight biophysical models. The models were previously calibrated in the laboratory by comparing different sizes and colors simultaneously with the body temperature of live *Phymaturus* exposed to sun and shade. Following the methods in Corbalán et al. (2013), we constructed models using three-layered propylene pipes. Pipes were 15 cm long, filled with cryogel, and sealed with corks at both ends. We inserted temperature probes through the corks and connected them to a four-channel HOBO datalogger (Onset Computer Corporation, Bourne, Massachusetts, USA; operating range: -20° to 70° C, accuracy: ± 0.21° C from 0° to 50° C). These models have a good fit for T_b of *P. palluma* ($r = 0.87$, $F_{1,3977} = 12,788.1$, $P < 0.001$, n = 3,978; Vicenzi et al. 2017). Operative temperature represents the product of interactions between biophysical and morphological factors that influence the T_b of an ectotherm and the null distribution of T_b that non-regulating animals would achieve (Bakken and Gates 1975; Hertz et al. 1993). To obtain the T_e in the field during each sampling period, we placed two models in each representative microhabitat

used by the lizards: sun-exposed rocks, shaded rocks, rock crevices used as shelter by the lizards, and wide rock crevices that receive direct sun radiation (sun-exposed crevices). We programmed the data loggers to record temperatures every 15 min. Giving that microhabitats were randomly chosen at each field trip, we were able to capture a representative sample of the environmental heterogeneity of the site. We obtained T_e for a total of 52 d including spring and summer over two consecutive years. In all statistical analyses, we used each the average T_e per hour of each microhabitat and then the total average of T_e, which is the average hourly temperature registered in all microhabitats. We used only T_e during daily period of activity (0900–1700) of a lizard. In addition to T_e, we also registered air temperature (T_a), rock temperature (T_{rock}), crevice temperature (T_{crev}), soil temperature (T_{soil}), and air humidity every 5 min using an Onset HOBO weather micro-station. For these variables, we used average hourly values for all statistical analyses.

Analyses.—We defined emergence as the number of lizards observed in the first time interval (0900–1100), and activity as the total number of lizards observed during each time interval. We used a Multiple Regression model to estimate the relationship between emergence and both abiotic and biophysical variables. The model selection was done according to the adjusted r^2. We used a Generalized Linear Mixed Model (GLMM) to evaluate which variables (abiotic and biophysical) affected the activity of lizards throughout the day, with the variable survey entered as the random factor. We selected the predictive best GLMM according to the Akaike Information Criterion (AIC; Legendre and Legendre 1998; Burnham and Anderson 2002). The independent abiotic and biophysical variables used in each statistical analysis were air temperature (T_a), rock temperature (T_{rock}), soil temperature (T_{soil}), crevice temperature (T_{crev}), air humidity, cloudiness, total average of operative temperature (T_e) and average of T_e on sun-exposed rocks, T_e on shaded rocks, T_e inside crevices, and T_e on sun-exposed crevices. We determined the degree of multicollinearity among independent variables by examining the correlation matrix of independent variables and variance inflation factors (VIFs) in the statistical models. We removed those variables exhibiting large correlation coefficients ($r > 0.80$) and VIFs > 10 (Sokal and Rolf 1995; Chatterjee et al. 2000).

To explore the daily activity pattern, we used a Chi-square test. We compared the observed number of active individuals per time interval with the proportion expected, taking into account the expected proportion of active individuals in a unimodal and bimodal pattern. We calculated expected values manually. We made a Chi-square Test of Independence to determine if

there were differences among the frequencies of non-gravid females, gravid females, and males among time intervals. We made a cell-by-cell comparison of observed and estimated expected frequencies and calculated the standardized residuals as post hoc test. The standardized residuals having absolute values that exceeds about 2 indicated lack of fit of null hypothesis in that cell (Agresti 2007). In addition, we explored if non-gravid females, gravid females, and males showed differences in activity and if they were related with the T_e of sun-exposed rocks using a Kruskal-Wallis test, because the assumptions of normality and homogeneity of variance were not met. We tested the relationship between operative temperature of sun-exposed rocks and thermoregulatory behavior (body posture and orientation) using Chi-squared test of Independence. Results were related to the preferred temperature of the species obtained in the laboratory in previous studies (mean $T_p = 35.15°$ C; T_p range, 33.35–37.29° C; Vicenzi et al. 2017). We carried out all statistical analyses in R (R Core Team 2018) and using Sigma Stats 10.0®. We checked the assumptions of normality and homogeneity of variance using Shapiro-Wilk's and Bartlett's tests, respectively. We give means with ± one standard error (SE). Alpha was set to 0.05 for statistical significance.

Results

Activity patterns.—We captured and marked 95 adults (54 females and 41 males). Because we did not find differences in the number of lizards observed in the two years ($F_{1,120} = 2.80$, $P = 0.090$), we pooled the data for emergence and activity. We removed the variables T_e inside crevices and on sun-exposed crevices, crevice humidity, and rock temperature from the analyses because they exhibited high indices of correlation (> 0.80). Emergence was positively related to the T_e on sun-exposed crevices, T_{rock} and T_{soil} and was negatively correlated to cloudiness ($F_{4,25} = 17.02$, $P < 0.001$, n = 30, Adjusted $r^2 = 0.69$; Table 1). The VIF values of

Table 1. Relationship between abiotic factors (soil temperature: T_{soil}; rock temperature: T_{rock}; cloudiness) and biophysical factors (operative temperature, T_e, of sun-exposed crevice) with emergence of High Mountain Lizard (*Phymaturus palluma*). Coefficient values, confidence intervals (2.5–97.5%), and *P*-values from a Multiple Regression analysis are shown.

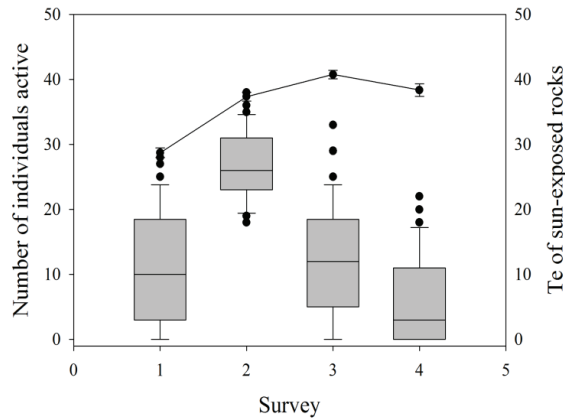| Variable	Coefficient	Confidence Intervals	*P*-values
Intercept	-35.64	-51.3, -19.9	< 0.001
T_e sun-exposed crevice	1.33	0.8–1.9	< 0.001
T_{soil}	0.37	-0.1–0.83	0.105
T_{rock}	0.62	-0.11–1.36	0.093
Cloudiness	-6.59	-12.8, -0.39	0.038

Figure 2. Box plot of number of active High Mountain Lizard (*Phymaturus palluma*) per survey. The solid line shows variation in operative temperature of lizards on sun-exposed rocks.
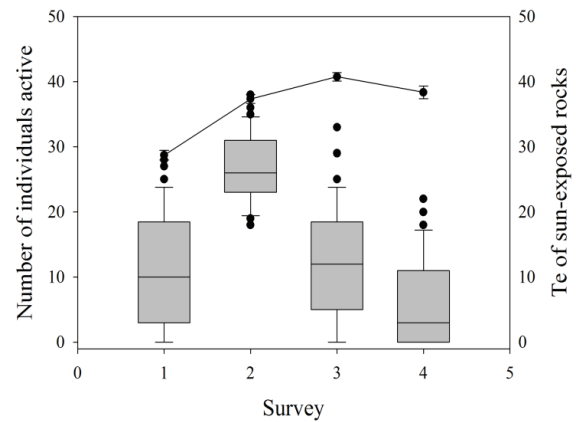

Figure 3. Number of High Mountain Lizard (*Phymaturus palluma*) in refuges in relation to the operative temperature in sun-exposed rocks.

the variables included in the multiple regressions were lower than 10 (VIF_{Tair} = 1.78, VIF_{Tcrev} = 1.53, $VIF_{Air\ humidity}$ = 1.49, VIF_{Tsoil} = 2.27, VIF_{Trock} = 2.06, $VIF_{Te\ on\ sun-exposed\ crevices}$ = 2.92, $VIF_{Te\ on\ sun-exposed\ rocks}$ = 3.90, and $VIF_{cloudiness}$ = 1.57). Activity started between 0900 and 1000 (GMT-3 time zone) from October to February, and around 1030 in March. The minimum T_a value recorded at which any individual started activity was 16.3° C, which corresponds to a T_e around 10.8° C in the sun-exposed crevices. The activity (number of active lizards per survey time interval) was positively related the total average of T_e, negatively correlated with T_{crev}, and had a parabolic with a single peak relationship with T_e on sun-exposed rocks (Table 2 and 3). The VIF values of the variables that were included in the full GLMM were lower than 10 (VIF_{Tair} = 2.55, VIF_{Tcrev} = 3.07, VIF_{Tair} = 2.58, VIF_{Tsoil} = 2.40, VIF_{Trock} = 2.84, VIF_{Air} humidity = 1.49, T_e on sun-exposed rocks = 4.03, T_e^2 on sun-exposed rocks = 2.04, T_e average = 3.33, T_e^2 average = 2.12, and cloudiness = 1.27).

The number of active lizards observed per survey followed an unimodal pattern, being the observed proportion of active individuals equal to 0.20 (0900–1100), 0.48 (1100–1300), 0.22 (1400– 1600), and 0.10 (1600–1800; χ^2 = 6.74, df = 3, P = 0.080; Fig. 2). Moreover, the number of lizards active per sex and reproductive state varied significantly among time intervals (χ^2 = 39.96, df = 6, n = 3,235, P < 0.001; see Post-Hoc Test in Table 4). Non-gravid females were more active from 0900 to 1300 (first and second time intervals), whereas males were more active from 1400 to 1800 (third and fourth time intervals; Table 4). In addition, gravid females were active at higher T_e (median T_e of exposed rocks = 39° C), than non-gravid females (median of T_e of exposed rocks = 36° C) and males (median of T_e of exposed rocks = 37° C). Refuge usage increased when T_e on sun-exposed rocks was higher than 40° C (Fig. 3).

Thermoregulatory behavior.—We found that basking represented more than 80% of the behavioral observations in all months. Postures and body orientations differed according to T_e on sun-exposed rocks (χ^2 = 2032.8, df = 140, n = 4,549, P < 0.001; Table 5, Fig. 4), with posture 1 being adopted at lower temperatures than posture 2 and 3, and posture 3 being adopted at the highest temperatures. Lizards were in posture 1 when the T_e on sun-exposed rocks (33.01 ± 0.15° C) was lower than T_p (T_p = 35.15° C). The posture 2 was used when mean T_e on sun-exposed rocks (36.07

Table 2. Relationship between abiotic factors (soil temperature: T_{soil}; rock temperature: T_{rock}; cloudiness) and biophysical factors (operative temperature, T_e, of sun-exposed crevice) with emergence of High Mountain Lizard (*Phymaturus palluma*). Coefficient values, confidence intervals (2.5–97.5%), and *P*-values from a Multiple Regression analysis are shown.

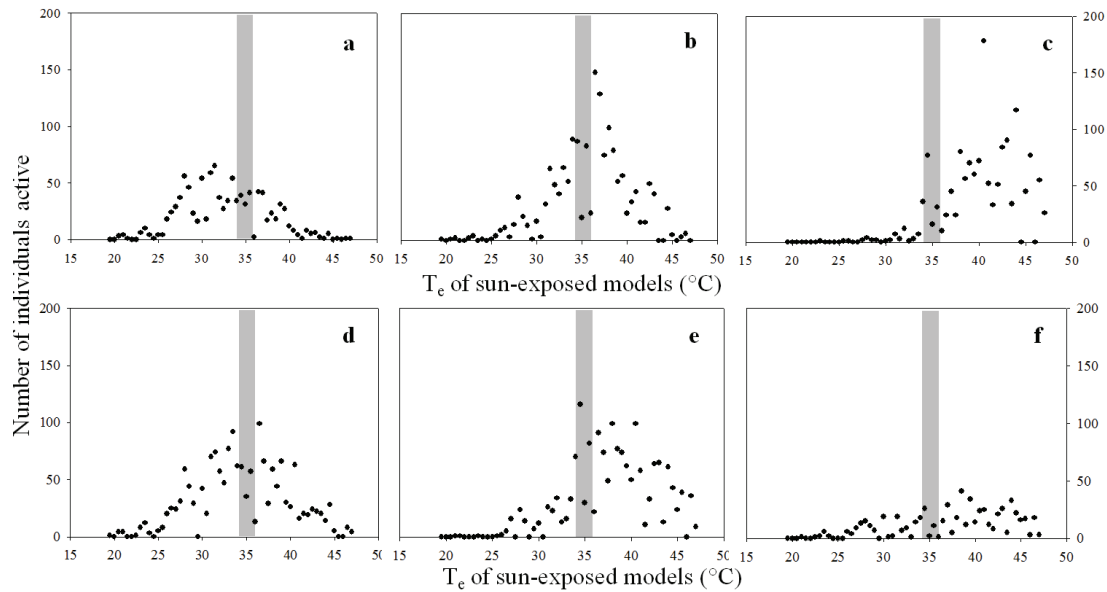| Intercept	T_e on sun	T_e^2 on sun	T_e	T_{air}	T_{crev}	T_{soil}	df	AICc	ΔAICc
20.73	-0.07	-0.06	0.39	0.43	-0.68		8	811.6	0
29.39	0.10	-0.06	0.40		-0.52		7	811.9	0.3
17.2	-0.12	-0.06	0.38				6	812.3	0.7
34.33	0.02	-0.06	0.50		-0.74	0.20	8	812.8	1.2
25.4	-0.13	-0.06	0.48	0.40	-0.85	0.17	9	812.8	1.2

Figure 4. Body posture (a) Posture 1, (b) Posture 2, (c) Posture 3, and body orientation (d) facing away from the sun, (e) facing towards the sun, and (f) parallel to sun rays of active High Mountain Lizard (*Phymaturus palluma*) in relation to operative temperature in sun-exposed rocks and rock temperature. Vertical gray band represents the set point of preferred temperature (34.2–36.1° C).

± 0.12° C) was near T_p, and the posture 3 when mean T_e on sun-exposed rocks (40.70 ± 0.12° C) was higher than T_p (Table 5, Fig. 4). Orientation varied according to mean T_e on sun-exposed rocks: facing-away orientation was observed at 35.60 ± 0.11° C, parallel orientation at 36.55 ± 0.18° C, and facing-towards orientation at 37.64 ± 0.1° C. During the daily activity period, 97.03% of lizards were seen in direct sun, 1.11% in filtered sun, and 1.86% in full shade.

DISCUSSION

Lizards inhabiting mountain environments display different thermoregulatory behaviors to maintain appropriate body temperatures in spite of the thermal amplitude and the highly variable and unpredictable climate (Grbac and Bauwens 2001; Ibargüengoytía et al. 2008; Zamora-Camacho et al. 2013; Aguado and Braña 2014; Corbalán and Debandi 2014). During activity period, they come out of their refuges and move to sun-exposed crevices when their T_e rises above 10.76° C (near the minimum critical temperature for the species; Vicenzi et al. 2017). Similar to the saxicolous lizard *Tropidurus torquatus* (Ribeiro et al. 2007), *Phymaturus* lizards expose their heads to the sun in the morning until their body temperature is high enough to start their activities. These sun-exposed crevices allow them to heat

Table 3. Relationship between abiotic factors (crevice temperature, T_{crev}, and air temperature, T_{air}), and biophysical factors (average operative temperature, T_e, and on sun-exposed rocks, T_e on sun) with High Mountain Lizard (*Phymaturus palluma*) activity. Coefficient values, confidence intervals (2.5–97.5%), and *P*-values of the Generalized Linear Mixed Model (GLMM) with the lower Akaike Information Criterion value are shown.

Variable	Coefficient	Confidence Interval	*P*-Values
Intercept	20.73	1.01–40.1	0.044
T_{crev}	-0.68	-1.33, -0.03	0.045
T_{air}	0.43	-0.12–0.99	0.137
T_e average	0.39	0.01–0.77	0.047
T_e sun-exposed rocks	-0.07	-0.58–0.42	0.767
T_e^2 sun-exposed rocks	-0.06	-0.09, -0.03	< 0.001

Table 4. Comparison among the total number of active High Mountain Lizard (*Phymaturus palluma*) per sex and reproductive state among time intervals. Standardized residuals (in parentheses) as Post-hoc test results are shown. Standardized residual with absolute values > 2 indicated lack of fit with null hypothesis. Positive values of residuals indicate that were a higher number of individuals than the null hypothesis predicts, negative values indicate that were fewer active individuals than the null hypothesis predicts.

Time interval (h)	Non-gravid females	Gravid females	Males
First (0900–1100)	199 (5.42)	55 (-0.49)	327 (-4.63)
Second (1100–1300)	395 (-1.47)	184 (2.45)	1049 (-0.20)
Third (1400–1600)	151 (-2.71)	57 (-1.92)	496 (3.67)
Fourth (1600–1800)	76 (-0.77)	28 (-0.83)	218 (1.22)

Table 5. Post hoc test of the relationship between body posture and orientation of High Mountain Lizard (*Phymaturus palluma*) with operative temperature of sun-exposed rocks. Standardized residual with absolute values > 2 indicated lack of fit with null hypothesis. Positive and negative values of residuals indicate that there were more or fewer numbers of individuals, respectively, with a particular body posture (1, 2, or 3) or a body orientation (facing away, facing toward, or parallel) than the null hypothesis predicts.

Temperature (°C)	Posture 1	Posture 2	Postures 3	Facing away	Facing toward	Parallel
19	-0.54	1.04	-0.67	1.04	-0.72	-0.40
20	2.10	-0.56	-1.34	2.08	-1.44	-0.81
21	2.58	-0.57	-1.78	0.76	-0.58	-0.05
22	-0.77	1.47	-0.95	0.23	-1.02	1.33
23	4.09	-2.19	-3.00	3.46	-3.25	2.29
24	3.25	-0.93	-1.58	0.57	-1.69	1.34
25	2.51	-0.34	-2.03	3.43	-2.22	-1.51
26	7.03	-1.24	-5.12	4.37	-4.16	0.21
27	9.83	-3.64	-6.02	3.53	-3.85	2.48
28	9.94	-1.28	-8.00	4.85	-4.22	0.20
29	8.07	-1.52	-4.21	2.28	-3.29	-0.14
30	10.56	-3.40	-6.04	4.29	-4.88	1.62
31	9.88	0.54	-9.03	6.52	-5.06	-2.27
32	3.58	3.01	-7.00	4.99	-2.97	-1.92
33	4.51	2.98	9.08	9.42	-5.14	-3.43
34	-2.15	2.90	-1.89	-2.20	3.83	-1.44
35	2.22	1.64	-4.27	0.34	2.70	-3.71
36	-2.61	8.28	-6.78	1.38	1.43	-3.69
37	-2.16	8.96	-4.31	-2.28	0.31	-1.63
38	-5.42	4.04	1.25	-3.41	1.80	1.30
39	-2.00	-0.91	2.69	-2.27	1.94	0.47
40	-7.24	-6.86	15.1	-3.58	2.64	-1.18
41	-5.75	-0.07	4.83	-3.45	1.38	3.43
42	-5.63	-1.59	8.70	-4.55	2.40	0.05
43	-5.67	-3.54	9.41	-3.38	1.63	1.44
44	-6.36	-5.94	7.33	-4.02	4.30	5.91
45	-5.67	-6.95	13.8	-6.93	2.67	4.02
46	-4.13	-3.85	7.08	-4.06	2.05	3.77
47	-2.06	-3.33	7.13	-1.81	0.07	-0.13

up and at the same time to be protected from potential predators. In terrestrial ectotherms, activity times are influenced by a combination of ambient conditions such as wind speed, humidity, and air temperature, as well as biophysical variables, such as operative temperature (Logan et al. 2015). In the high-elevation mountain lizard *P. palluma,* biophysical variables, such as the total average of T_e and the T_e on sun-exposed rocks, and abiotic variables, such as crevice temperature, were good predictors of activity.

In general, reptiles that are active throughout the year have a unimodal activity pattern during cool periods, and a bimodal pattern in the summer (Van Sluys 1992; Firth and Belan 1998; McConnachie et al.

2009); however, studies of species of the *Phymaturus* genus showed that the activity pattern could be similar in spring and summer. While *Phymaturus vociferator* had a bimodal pattern (Vidal et al. 2010), *P. palluma,* as well as *P. roigorum* and *P. payuniae* (Corbalán and Debandi 2014), showed a unimodal pattern in both seasons. The unimodal pattern registered, however, may change to bimodal in the hottest days of the summer. Apart from the fluctuations in activity, the *P. palluma* population had the highest number of active lizards at midday, as reported for other lizards from cold environments at high latitudes or elevations (Grbac and Bauwens 2001; Vidal et al. 2010; Aguado and Braña 2014). In Aconcagua Park at midday, the T_e of sun-

exposed rocks showed values that included the T_p of *P. palluma*, which suggests that the thermal quality of the habitat is better for this species at this time, allowing lizards to thermoregulate more easily (Gunderson and Leal 2015, 2016). The high temperatures registered in the afternoon, however, prevent lizards from having activities outside the shelters. There was a noticeable drop in the number of active lizards when the T_e on sun-exposed rocks was close to the critical thermal maximum ($CT_{max} = 41.18°$ C; Vicenzi et al. 2017). At or above the CT_{max}, movements are uncoordinated and disorganized, which reduces the ability of a lizard to escape from potentially fatal situations (Cowles and Bogert 1944). Thus, near CT_{max}, lizards need to retreat into cool refuges to avoid overheating (Sinervo et al. 2010). Following this expectation, the number of *P. palluma* in shelters increased when T_e on sun-exposed rocks was higher than 40° C. The activity restriction imposed by thermal constraint has been proposed by Sinervo et al. (2010) and Kubisch et al. (2016) as one of the main causes of population extirpations by climate warming in Liolaemids and other genera. To a lesser extent, we recorded lizards inside the shelters when temperatures were lower than 40° C, which was probably due to an adaptive strategy to conserve energy or water (Martín and López 2000), or to avoid predators (Webb and Whiting 2005), increasing the chance of survival and future reproduction (Rose 1981).

Additionally, we found a difference in the time of activity among males, non-gravid and gravid females of *P. palluma*. In general, females were more active in the morning and midday, while males were more active at midday and in the afternoon. Differences in the activity pattern within a population could be related to thermoregulation requirements or to social status (Martin and Lopez 2000). Because males and females of *P. palluma* showed similar field T_b (Vicenzi et al. 2017), probably males, which are larger than females, need to be active at warmer times of the day to achieve appropriate T_bs. Social status could have an important role in the different activity pattern observed between sexes, as was reported for *P. vociferator*, in which females emerge earlier to diminish the pressure of males on microhabitat selection (Vidal et al. 2010). This not the case, however, with *P. palluma* in which males and females share microhabitats used for basking and refuge (Vicenzi, 2018). Additionally, we recorded that more than the 55% of *P. palluma* gravid females were active at midday, when the T_e on sun-exposed rocks was 39° C, higher than those chosen by non-gravid females (36° C) and males (37° C). This could be related to the fact that gravid females had higher values of optimal temperatures for locomotor performance than males and non-gravid females (Vicenzi et al. 2018). In addition, because gravid and non-gravid females did not show

differences in their field T_b (Vicenzi et al. 2017), and gravid females were less active than non-gravid females at early morning and late afternoon, the activity in the warmest periods of the day probably allows gravid females to reduce basking periods and exposure to predators. Conversely, the broader activity period in males than females could be related to the higher energetic cost that they have to face as a result of their territorial behavior (Videla 1982). Territorial behavior includes patrolling and defense of the home range, which implies that males are more conspicuous than conspecifics increasing their vulnerability to predators (Waldschmidt and Tracy 1983; Magnhagen 1990; Martín and López 2000).

In the high-elevation Andes, lizards compensate for the variation in air temperatures using postures that take advantage of the high solar radiation (Pearson 1954). As was recorded in Side-blotched Lizards (*Uta stansburiana*) and Sand-dune Lizards (*Sceloporus arenicolous;* Sartorius et al. 2002), we found a relationship between body postures, T_p, and T_e. When the T_e on sun-exposed rocks was lower than T_p, *P. palluma* adopted a flattening posture (posture 1). This posture has been usually interpreted as thigmothermic behavior (McConnachie, et al. 2009); however, according to our data, the adoption of posture 1 in the morning, when rock temperature was below body temperature (Vicenzi et al. 2017), does not imply a thigmothermic behavior. Instead, this posture may be adopted to increase the dorsal surface area exposed to solar radiation. The relationship between the prostrated posture and heliothermy was also reported for Zebra-tailed Lizards (*Callisaurus draconoides)* and for Iberian Mountain Lizards (*Iberolacerta cyreni*; Muth 1977; Martín et al. 1995). Moreover, this posture observed in the mornings, in addition to the flat body and mimetic color pattern of *P. palluma*, can be seen as an optimized behavior that counteracts their conspicuousness to potential predators while warming up. Lizards adopted posture 2 when T_e on the sun was near their T_p, probably because this posture offers a balance between heat gain and loss by convection; however, when T_e on the sun was higher than T_p, lizards had to reduce surface area exposed to solar radiation to avoid overheating, and they adopted posture 3. Raising their bodies above the rock reduces contact with hot rocks, prevents heat gain by conduction and facilitates heat loss by convection (Muth 1977). During the afternoon, when rock temperature was still high and exceeded the air temperature (Vicenzi et al. 2017), lizards adopted posture 1 again, although in this case it could be interpreted as thigmothermic because the principal heat source was the substrate. Then, like other saxicolous lizards, such as Amazon Lava Lizards (*Tropidurus torquatus*; Ribeiro et al. 2007), Common Crag Lizard (*Pseudocordylus melanotus*; McConnachie

et al. 2009), *Phymaturus roigorum*, Payunia´s Lizard (*P. payuniae*; Corbalán and Debandi 2013) and *Phymaturus extrilidus* (Gómez Alés et al. 2017), *Phymaturus palluma* showed a thermoregulatory strategy that included shifts between heliothermic and thigmothermic behaviors, which means that the lizards used solar radiation most of the time and heat conduction from the rock surface in the late afternoon. *Phymaturus palluma* adopted facing-away orientation to the sun when T_e was included in the T_p range, but a facing-towards and parallel orientations when T_e was higher than the T_p range. The role of body orientation in thermoregulation is not entirely clear. It is possible that other factors such as camouflage, UV protection, or social interactions (as vigilance or visual signaling) may be better predictors of body orientation and posture (Brandt 2003; Van Dyk and Evans 2008; Penacchio et al. 2015).

Due to the low thermal quality of its environment (de index = 14.17; Vicenzi et al. 2017), *P. palluma* invest a high proportion of time in thermoregulatory activities and behave like efficient thermoregulators (thermoregulation index E = 0.75; Vicenzi et al. 2017). A higher thermoregulatory efficiency in ectotherms from habitats with low thermal quality was reported for other mountain lizards such as *Phymaturus extrilidus* (Gómez Alés et al. 2017), Payunia's Lizards (*Phymaturus payuniae*; Corbalán et al. 2013), Hispaniolan Stout Anoles (*Anolis cybotes*; Hertz and Huey 1981*)*, Western Fence Lizards *(Sceloporus occidentalis*; Adolph 1990), Sagebrush Lizards (*S. graciosus)*, European Common Lizards (*Zootoca vivipara*; Gvoždík 2002), and Cyren's Rock Lizards (*Iberolacerta cyreni*; Aguado and Braña 2014) among others. *Phymaturus palluma* uses thermoregulatory strategies such as changes in activity patterns and different body postures and orientations for basking. Lizards allocate more time to basking than to other activities, even though this increases the risk of predation. They avoid overheating during the hottest hours of the day by taking refuge in cold rock crevices, even to the detriment of other activities.

Although, the behavioral adjustments may be important to predict how lizards might cope with the increase in environmental temperatures due to climate change (Aguado and Braña 2014; Muñoz et al. 2014), the behavioral plasticity can be beneficial just in the short term, limiting the physiological adaptation required to endure a warming climate (Buckley et al. 2015). The Central Andes is one of the regions of the world considered to be vulnerable to climate impacts (Intergovernmental Panel on Climate Change 2013; de Sherbinin 2014), with a projected warming between 3–4° C by the end of the century (Barros et al. 2014). Under this scenario, one-third of *P. palluma* populations will probably be extirpated by 2070, because of the increase in ambient temperatures will decrease the time available

of lizards to perform vital activities (Vicenzi et al. 2017). Our study supports the idea that active thermoregulation based on behavioral adjustments such as changes in body postures, microhabitats and modifications of activity patterns in *P. palluma* is important to face the current cold environments; however, this kind of thermoregulation does not guarantee the success to face the global warming.

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