



# Range increment or range detriment? Predicting potential changes in distribution caused by climate change for the endemic high-Andean lizard *Phymaturus palluma*



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## ARTICLE INFO

### Article history:

Received 18 August 2016

Received in revised form 8 December 2016

Accepted 23 December 2016

Available online xxxx

### Keywords:

Andes

*Phymaturus*

Thermoregulatory efficiency

Range shift

Conservation

## ABSTRACT

An increase in temperatures and frequency of drought events are predicted in the High Andes due to climate change. Species could respond with changes in its range, abundance and phenology. Here, we used a species distribution model to assess and predict the vulnerability to climate change of the endemic lizard *Phymaturus palluma* of the Andes. The model is based on a study of the thermoregulatory behaviour of the species. We measured body temperature ( $T_b$ ) and assessed its relationship with micro-environmental temperatures to determine the main source of heat used by lizards. We also quantified the preferred temperature ( $T_p$ ) and maximum and minimum critical temperatures ( $CT_{max}$  and  $CT_{min}$ ), and collected operative temperature ( $T_e$ ). We used  $T_b$ ,  $T_p$  and  $T_e$  to calculate the effectiveness of thermoregulation. We linked these physiological variables with climatic variables obtained from a set of global climate layers. The model predicts a substantial reduction in the available habitat over the species current distributional range. However, the model also predicted new potential distribution areas towards the West Andes, at higher elevations. Nevertheless, because of the species specialized habits and low dispersal capability, we suggest the likelihood of expansion to these new sites is marginal. Thus, distribution shifts are unlikely to prevent extinction in *Phymaturus*. Conservation strategies should be focused in the protection of the current distribution areas that remain suitable in the different future climate projections. Additional data are needed to determine the potential for phenotypic plasticity to mitigate the probable population decline in this species.

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## 1. Introduction

Climate change is a pervasive anthropogenic disturbance whose effect is likely to restructure natural biological systems. Rising temperatures have already resulted in shifts in species range, abundance and phenology (Parmesan, 2006; Thomas et al., 2004; Thomas et al., 2006). Another consequence of climate change is the extirpation of populations and ultimately extinction of species, an outcome supported by the numerous local extirpations already registered in the past decade (Kubisch et al., 2016; Sinervo et al., 2010; Thomas et al., 2004). There is evidence that reveals a close relationship between physiological responses to climatic variables, like tolerance, capacity and plasticity, and the geographic range of species and populations (Bozinovic et al.,

2011a; Pörtner et al., 2006; Somero, 2011) For example, in terrestrial animals, there generally exists a broader range of physiological tolerance at higher latitudes, because the climatic variability experienced increases with latitude and this allows these species to be more extensively distributed (Bozinovic et al., 2011a). This close relationship indicates that physiological traits can be used to predict not only the current range of any species but also the potential range under different climate scenarios (Bozinovic et al., 2011a). On the other hand, one of the most critical topics in biology today is to understand how organisms could respond through thermal adaptation to climate change in a framework that encompasses an integration of range of mechanisms from molecular to ecological (Bozinovic et al., 2011a; Kingsolver and Woods, 2016; Pörtner et al., 2006; Somero, 2011).

Ectotherms are especially vulnerable to climate change (Deutsch et al., 2008), because ambient temperature exerts a strong influence on multiple physiological processes such as locomotion, digestion, energy assimilation, growth and reproduction (Adolph and Porter, 1993; Angilletta, 2001; Shine, 2004; Zug et al., 2001). In particular, terrestrial

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ectotherms like lizards, may be sensitive to climate change due to their limited vagility and dependence on basking behaviour to regulate their body temperature (Root and Schneider, 2002; Zug et al., 2001). According to Huey et al. (2010), extinction probability will be correlated with the magnitude of warming within a habitat during the reproductive season, since an increment in ambient temperatures will probably result in lizards spending longer periods in thermal refuges. A consequence of this scenario would be the reduction in foraging time, and therefore, the net energy gain would be insufficient to meet the costs of reproduction leading to demographic collapse and ultimately extinction (Adolph and Porter, 1993; Huey et al., 2010). Several studies predict that climate change will principally threaten tropical ectotherms, while temperate ectotherms should resist or even benefit from the warmer temperatures (Deutsch et al., 2008; Huey et al., 2009; Kearney et al., 2009; Piantoni et al., 2015). In lizards that inhabit mid-latitudes, an increase in mean temperature could have a positive influence, such as an increase in the length of the growing season and in the frequency in which species experience temperatures close to their optimal ones. But these advantages can be counteracted by the negative influence of increased magnitudes and durations of heat stress during summer, especially in adult individuals (Bestion et al., 2015; Kingsolver et al., 2013; Vasseur et al., 2014). In fact, not only the increase in mean temperature will have effect in ectotherms, the temporal pattern and duration of temperature exposure will influence their thermal tolerance and survival (Bozinovic et al., 2011b; Bozinovic et al., 2016; Kingsolver et al., 2013). Moreover, Kearney (2013) has showed that warming causes reductions in population growth rate even under increasing activity times as well as when food is abundant. An underappreciated aspect of rising temperatures is that viviparous species are especially vulnerable to climate change, as activity time influences maternal basking regimes, which in turn influences the gestation period and offspring viability (Shine and Harlow, 1993). Furthermore, viviparity appears as an adaptation to cold climates (Shine, 2005), and as this adaptation is predominantly viable in these environments, viviparous species in high latitudes–elevations are predicted to result in a higher risk of range contractions, fragmentations, and hence, extinctions, compared with oviparous species (Pincheira-Donoso et al., 2013; Sinervo et al., 2010). In addition, viviparous lizard species that inhabit arid montane regions are vulnerable because the effect of climate change is more rapidly apparent in populations which are isolated and in high elevations (Barrows et al., 2010; Chamaillé-Jammes et al., 2006; Sinervo et al., 2010).

In South America, liolaemids offer an opportunity to analyse how climate change can affect the lizard species diversity. The family Liolaemidae is composed of three genera, the monospecific genus *Ctenoblepharys*, the wide-distributed genus *Liolaemus* and the specialized genus *Phymaturus*. In particular, the genus *Phymaturus* is comprised of species that are characterized by a narrow ecological range. All species are viviparous, saxicolous and herbivorous (Cei, 1986). Several studies have proposed that those species with highly specialized habitat requirements, particular life histories (such as delayed maturation, low clutch frequency, small clutch size; Chevin et al., 2010; Kearney, 2013), and low dispersal rates are the most vulnerable to climate change (Penman et al., 2010). The genus *Phymaturus* meets all these criteria. Most species of *Phymaturus* are restricted to isolated rock promontories (Cei, 1986, 1993). Therefore, the availability of rocky habitats with crevices limits the range of possible environments to be inhabited by this genus (Debandi et al., 2012). The specialized habitat requirements and the limited vagility of *Phymaturus* suggest low dispersal rates for this species. In addition, generation times are particularly long; most individuals within a species require between seven and nine years to reach sexual maturity (Boretto et al., 2015; Piantoni et al., 2006). Moreover, the reproductive output of *Phymaturus* species is low; females have biennial reproductive cycles and small clutch sizes ( $N = 2$ ) (Boretto et al., 2007, 2014; Cabezas Cartes et al., 2010; Habit and Ortiz, 1996). As all species of the genus, the focal species for

this study, *Phymaturus palluma* (Molina, 1782), is considered as a vulnerable species (Abdala et al., 2012). *Phymaturus palluma* is an endemic species which inhabits valleys surrounded by the highest peaks of the Andes, from the southwest of San Juan to the northwest of Mendoza province in Argentina, between 2400 and 3600 masl. This is one of the regions considered to be particularly vulnerable to current or future climate impacts (De Sherbinin, 2014; IPCC, 2013). Recent projections predict that the biodiversity of high Andes habitats are currently classified as severely threatened because of the reduction in water availability due to receding glaciers, land degradation and desertification (Barros et al., 2014b; IPCC, 2013). According to the RCP (Representative Concentration Pathway) 8.5 scenario (IPCC, 2013), by the end of this century, the projected warming for this area will be from 3 °C to 4 °C relative to current climate conditions, and this warming will be more intense during summer months (Barros et al., 2014b). The rising temperature combined with an increase in the frequency and duration of drought events will lead to glaciers receding, some of which will even disappear, causing a reduction in river flow above 50% and consequently an increase in water deficits in downstream locations (Barros et al., 2014b; Boninsegna and Villalba, 2006; Nuñez et al., 2009; IPCC, 2013). These projected climate changes for the Andes zone is an example of what has been predicted for various countries (IPCC, 2013) and reported as a threat, in particular, for viviparous lizards inhabiting high altitudes (Barrows et al., 2010; Ortega et al., 2016; Sinervo et al., 2010). In order to assess the vulnerability of *Phymaturus palluma* and to support the design of conservation strategies we evaluated the exposure, sensitivity and adaptive capacity of the species sensu Dawson et al. (2011). To achieve our goal, we use physiological and ecological data to estimate the shifts in the current climatically suitable habitat and identify potential habitats that could be exploited given projected future climates. We predicted that, as a result of the increase in air temperature and the reduction of precipitation due to climate change, the populations of *Phymaturus palluma* would be threatened by a loss in their current range of distribution. Based on these predictions, we determined the risk of future extirpations and identified those sites that should be considered for conservation priorities.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the Punta de Vacas gorge within the Aconcagua Provincial Park (32.8453°S, 69.7619°W, WGS84, 2500 masl), Mendoza, Argentina. The site is characterized by cold semi-arid climate (BSk) of Köppen classification (based in the combination of temperature and precipitation with distribution of native vegetation), with maximum temperatures of 28 °C and minimum temperatures of −4 °C (Soria, 2003). The mean annual precipitation is 150 mm (Soria, 2003). In this harsh environment, lizards remain inactive during the cold months (Cei, 1986; Videla, 1982). The area belongs to the Altoandina phytogeographic province. The vegetation is predominated by the shrub species *Adesmia* (Fabaceae), *Tetraglochin alatum* (Rosaceae) and *Berberis empetrifolia* (Berberidaceae) as well as the grasses *Poa* and *Stipa* (Poaceae). Other vegetation patches consist of *Tropaeolum polyphyllum* (Tropaeolaceae), *Convolvulus arvensis* (Convolvulaceae), *Elymus erianthus* (Poaceae) and *Melica chilensis* (Poaceae) (Méndez et al., 2006).

### 2.2. Capture methods and thermal characteristics

A total of 207 individuals of *Phymaturus palluma* of the same population were captured by hand or noose in rocky outcrops between November 2013 and March 2014. The body temperature ( $T_b$ , sensu Pough and Gans, 1982) of lizards was recorded within 15 s of capture by inserting a TES TP-K01 thermocouple 10 mm into the cloaca of the lizard. Micro-environmental temperatures were also recorded at the

capture site in order to identify the main heat sources used by lizards. Substrate temperature ( $T_s$ ) was measured by placing the thermocouple (TES TP-K01) onto the rock surface. We measured air temperature ( $T_a$ ) 2 cm above the ground using a TES TP-K06 gas probe. Both thermocouples were connected to a TES 1312A digital thermometer (range:  $-50$  to  $1300$  °C, resolution:  $0.1/1$  °C). Between November 2013 and March 2014 we also registered social and feeding behaviour, newborn recruitment, months and hours of activity and microhabitat use.

We measured operative temperatures ( $T_e$ , sensu Bakken, 1992) in the field using physical models (Bakken and Angilletta, 2014; Hertz et al., 1993) constructed of 3-layered propylene tubes filled with cryogel (according to Corbalán et al., 2013). Both ends were sealed with cork. A temperature probe connected to a 4-channel Onset HOBO logger passed through the cork into the tube. Models were calibrated by comparing different sizes and colours simultaneously with the temperature of live *Phymaturus* exposed to sunshine and shade prior to deployment. The best model was selected according to the highest correlation between the model and  $T_b$  of *P. palluma* ( $r = 0.87$ ,  $P < 0.001$ ;  $N = 3979$ ). We recorded  $T_e$  during two consecutive activity periods of the lizards (October 2013 to April 2014 and October 2014 to April 2015). During each period, we placed eight models in each representative microsite used by the species (exposed rocks, shaded rocks, inside crevices, and crevices exposed partially to the sun). We used two models per microsite and each model was moved to different microsites during field work. We programmed the data loggers to record temperatures every 15 min. We only used the temperature data recorded during the animal's daily period of activity (between 9:00 and 18:00) for the analyses.

### 2.3. Laboratory experiments

#### 2.3.1. Estimation of preferred body temperatures

In December 2013, 66 individuals were captured by hand or noose and transported to the laboratory to perform thermal experiments. We georeferenced each capture location using a handheld GPS (Garmin eTrex 20) to return all individuals to their capture site after the completion of the experiments. The laboratory was located in the National Gendarmerie Headquarters, a few metres from the sampling site. Two wooden terraria of  $1 \times 1$  m with six separated lanes were used for estimating the preferred body temperature of the lizards ( $T_p$ , Hertz et al., 1993; Pough and Gans, 1982). A 75 W halogen lamp (equivalent to 100 W incandescent lamp) was placed at the end of each lane and a sheet of aluminium foil was used in this end to cover 2/3 of the roof and walls of the terrarium to generate a temperature gradient (from  $20$  °C to  $45$  °C, following the methodology of Paranjpe et al., 2012). We placed one individual in each lane. We affixed an ultrafine (44 ga) Type T thermocouple to the belly of each lizard using surgical tape. The thermocouples were connected to an 8-channel datalogger (OMEGA TC-08, range:  $-270$  a  $1820$  °C accuracy:  $\pm 202$  0.2% rdg +  $0.5$  °C). The sampling rate for body temperature was set at 1 s for an overall duration of 120 min. We allowed lizards to acclimate to the gradient for 15 min before starting to record the lizards' temperatures.

After completion of the measurement of thermal preference, we recorded the sex of each individual, measured their mass (with a Pesola micro-line spring scale,  $100 \text{ g} \times 1 \text{ g}$ ), snout-vent length and tail length (with a digital calliper,  $0.01$  mm accuracy). Adult males are identified by their prominent ventral pores and colour pattern, which differs between the sexes after sexual maturity (Boretto et al., 2007; Cabezas Cartes et al., 2010; Habit and Ortiz, 1996). We classified any individuals without ventral pores smaller than a pregnant female as juvenile females, whereas individuals with scarce development of vent pores and faint coloration were juvenile males.

#### 2.3.2. Estimation of critical thermal temperatures

After the preferred body temperature trial, lizards were allowed to rest for 24 h before performing the critical temperature limit experiments. Only adult males ( $N = 28$ ) were used to estimate the critical thermal

temperatures in order to avoid stress in pregnant females. We defined the lower and upper critical thermal limits ( $CT_{min}$  and  $CT_{max}$ , respectively) as the temperatures at which the animal cannot right itself when placed on its back, i.e., it loses the righting reflex (Clusella-Trullas et al., 2011; McConnachie et al., 2007; Spellerberg, 1972).

In order to obtain the critical thermal minimum, each lizard was placed individually into a transparent plastic box (length  $\times$  width  $\times$  height =  $30 \text{ cm} \times 18 \text{ cm} \times 15 \text{ cm}$ ) within a portable fridge, which was maintained at around  $3$  °C using water with ice and salt. Body temperature of lizards was measured every second with a 44 ga thermocouple taped to the belly of the lizard and connected to a 2-channel TES 1307 datalogger. Individuals were kept in the plastic box until they reached their critical thermal minimum. Then, lizards were removed to a warmer place and allowed to recover their mobility.

Twenty-four hours later, we determined critical thermal maximum. Males were placed in a cylindrical terrarium (20 cm diameter, 23 cm height) with soil and rocks substrate, under a heating infrared lamp (100 W). The procedure was similar to that performed for critical thermal minimum. As soon as the righting reflex was lost, the individual was immediately cooled with room-temperature water (Huang et al., 2006). All lizards recovered within 5 min and none of them died after the experiments. After that, each lizard was release at the site of capture.

### 2.4. Statistic analyses to determine the main heat sources used by lizards and effectiveness of thermoregulation

The main heat sources used by the lizards was determined by comparing the  $T_b$  with micro environmental temperatures recorded in each lizard's capture site using Friedman repeated measures analysis of variance on ranks and the Tukey test as a posteriori test, and linear regressions to analyse the dependence between the  $T_b$  and the micro environmental variables.

In order to determine the efficiency of thermoregulation and the preferred body temperature we used the methodology proposed by Hertz et al. (1993). We calculated the mean preferred body temperature ( $T_p$ ) from the preferred temperatures obtained from each lizard ( $N = 7200$  measurements per individual) and  $T_{set}$  (the interquartile range of  $T_p$ ) for each individual ( $N = 66$ ). The accuracy of  $T_b$  was calculated as the average of the absolute value of the deviations of  $T_b$  from upper or lower bound of  $T_{set}$  (individual deviation,  $d_b$ ). Operative temperature,  $T_e$ , was obtained from the average of the temperatures registered by all the models during the study period. To calculate the thermal quality of habitat ( $d_e$ ) we obtained the average of the absolute value of the deviations of  $T_e$  from the upper or lower bound of  $T_{set}$  (Hertz et al., 1993). Finally, we calculated two indexes of effectiveness of thermoregulation. One of them (E index), proposed by Hertz et al. (1993), defined as  $E = 1 - (\text{Mean } d_b / \text{Mean } d_e)$ , which approaches zero when animals do not thermoregulate and approaches one when lizards are efficient thermoregulators. The other index, proposed by Blouin-Demers and Weatherhead (2001, 2002), calculated as the difference between  $d_e$  and  $d_b$ , is indicative of how much an animal departs from thermoconformity (Blouin-Demers and Weatherhead, 2001; Wilms et al., 2011).

Finally, for the critical thermal data, we analysed the relationship between critical temperatures with body mass and snout-vent length using regression analyses. The  $CT_{min}$  and  $CT_{max}$  for the population were estimated as the average of the values obtained from each individual.

The assumptions of normality and homogeneity of variance for parametric procedures were checked using Shapiro-Wilk's and Levene's tests, respectively. All statistical analyses were carried out using R (R Core Team, 2016) and Sigma Plot 10.0®. All results are presented as mean  $\pm$  standard error.

### 2.5. Species distribution model

We performed Species Distribution Modelling (SDM) to predict *Phymaturus palluma* range given an increase in ambient temperature

and a diminution in precipitations due to climate change using the R package “biomod2” (Hijmans and Elith, 2014; Thuiller et al., 2014). For this, we 1) compiled locations of occurrence of the species, 2) extracted the environmental predictor variables from spatial databases, 3) fitted a model to estimate sites of occurrence, and 4) used this model to predict the distribution across the region of interest in the future (Hijmans and Elith, 2014). In order to perform the model, we obtained 18 georeferenced points of species occurrence data from the Herpetological collection of IADIZA, bibliography and field trips. We obtained monthly environmental variables (precipitation, maximum temperature) and altitude from the global meteorological database Worldclim (<http://www.worldclim.org/>) at a 30 s resolution. We used current climatic data (from 1950 to 2000) and projections of future data (for 2050 and 2070). According to the 5th Intergovernmental Panel on Climate Change (IPCC, 2013), we considered two different scenarios of CO<sub>2</sub> emissions (Representative Concentration Pathways (RCPs) of 4.5 and 8.5) for future data, generated by the Max Planck Institute for Meteorology (MPI-ESM\_LR). All layers were cropped to the study area comprising the area between 30° to 36°S and 66° to 76°W. In addition, to increase the accuracy of the model, we incorporated physiological variables of the species. To achieve this, we linked the physiological variables with the physical ones. The physiological variables used were the upper bound of preferred temperature (Kubisch et al., 2016) and the T<sub>e</sub> registered over spring and summer of 2013–2014 and 2014–2015, during the activity season. From these temperatures, we calculated potential hours of activity (H<sub>a</sub>) and potential hours of restriction (H<sub>r</sub>). According to Kubisch et al. (2016), we defined H<sub>a</sub> as the duration of time where T<sub>e</sub> exceeded 25 °C and is lower than the upper bound of T<sub>p</sub>, and H<sub>r</sub> as the duration of time where T<sub>e</sub> exceeded the upper bound T<sub>p</sub>. We assumed that upper T<sub>p</sub> represents the mean maximum voluntary temperature. Thus, above this temperature, lizards could not be active. Since we are working with only one species and our observations show that lizards could still be active between the lower and upper T<sub>set</sub>, we desired to use this more stringent threshold than the one used by Sinervo et al. (2010) methodology which considered H<sub>r</sub> as those where T<sub>e</sub> exceeded the average T<sub>p</sub>. We calculated a logistical function that linked behaviour (H<sub>a</sub> and H<sub>r</sub>) with physiology (Upper T<sub>p</sub>) and the daily maximum temperature from Punta de Vacas Valley (BDHI, 2015) from two activity seasons (Spring and Summer of 2013–2014 and 2014–2015). We used a nonlinear least squares (“nls”) function of the package “stats” (R Core Team, 2016) to obtain the sigmoid curves. We calculated the best curve to H<sub>a</sub> ( $H_a = (9.96719348 / (1 + 0.01417205 * \exp(-0.36770600 * (\text{Maximum Daily Temperature} - \text{Upper } T_p))))^{1/5.18508335}$ ) and the best curve to H<sub>r</sub> ( $H_r \sim 6.9475056 / (1 + \exp(-0.2956906 * ((\text{Maximum Temperature} - \text{Upper } T_p) - (-12.0012455)))$ ). The parameters obtained from the logistical equations allowed us to link the upper T<sub>p</sub> data with the monthly maximum temperature data obtained from Worldclim, and to calculate projections of Activity and Restriction Hours in current and different future scenarios. The General Linear Model (GLM) used to estimate the current sites of occurrence were constructed with these projections of Activity and Restriction Hours, precipitation and altitude as explanatory variables. To evaluate the performance of the model we used Receive Operating Characteristic (ROC). A ROC score of 1 indicates perfect spatial agreement between a prediction and test map, while ROC score of 0.5 represents agreement due to chance (Bodtker et al., 2009). We selected models that have a ROC score of at least 0.75 (Elith et al., 2006). The same GLM was used to predict the potential distribution in the future.

### 3. Results

#### 3.1. Field observations

In Punta de Vacas Valley we registered active individuals of *Phymaturus palluma* from mid-October to mid-March (austral spring

and summer). In the study site, lizards start activity between 9:00 h to 11:00 h, when the sun directly reaches the valley, and finalize about 18:00 h, when the valley enters in shadows. We observed heliothermic behaviour during most part of the day and thigmothermic behaviour in the last hours of the activity period. We registered individuals eating mostly the shrubby vegetation *Tetraglochin alatum*, *Berberis empetrifolia*, *Ephedra* sp., *Adesmia pinifolia* and *A. aegiceras* and during their flowering period, the exotics *Medicago sativa* and *Convolvulus arvensis*. Individuals were observed on the rocks and exceptionally on the ground that surrounds the rocks. We also registered the type of crevice used, which usually are >20 cm deep and <5 cm wide. *Phymaturus palluma* lives in groups of one male, one to three females, and juveniles. Males exhibited territorial behaviour. We observed presence of newborns the last weeks of February and the first weeks of March, in general accompanied by postpartum females and other juveniles.

#### 3.2. Thermal biology

##### 3.2.1. Relationship between micro-environmental and body temperatures

The average T<sub>b</sub> (median = 32.3 °C, N = 186) was higher than the T<sub>s</sub> and T<sub>a</sub> (Friedman Repeated Measures Analysis of Variance on Rank Test  $\chi^2_{2, 186} = 183.109$ ;  $P < 0.001$ , Tukey Test:  $q_{T_b, T_a} = 18.15$ ;  $q_{T_b, T_{sUS}} = 3.84$ ;  $P < 0.05$ ). T<sub>b</sub> depends significantly on T<sub>s</sub> and T<sub>a</sub> (Linear Regression  $F_{1, 184} = 48.86$ ,  $F_{1, 184} = 20.74$ ;  $P < 0.001$  in both cases; Fig. 1). There were no differences between pregnant and nonpregnant females in T<sub>b</sub> (ANOVA,  $F = 0.85$ ;  $df = 1/75$ ;  $P > 0.05$ ). But juveniles showed higher values than adults in T<sub>b</sub> (Kruskal Wallis Test:  $H = 13.534$ ;  $df = 2$ ;  $P = 0.001$ ; Dunn's Method:  $q_{j-m} = 3.446$ ;  $q_{j-f} = 2.993$ ;  $P < 0.05$ ,  $q_{f-m} = 0.708$ ;  $P > 0.05$ ).

##### 3.2.2. Determination of preferred body temperature and effectiveness of thermoregulation

The mean preferred temperature for *P. palluma* was  $35.15 \pm 0.09$ , whereas the lower and upper T<sub>p</sub> registered were  $31.31 \pm 0.18$  °C and  $38.38 \pm 0.1$  °C respectively. Preferred temperature (T<sub>p</sub>) was not different between sexes or between adults and juveniles (ANOVA,  $F = 0.71$ ;  $df = 2/63$ ;  $P > 0.05$ ). Field activity body temperatures were below the preferred temperature (Paired *t*-test,  $t = -8.45$ ,  $P < 0.001$ ). Based on the distribution of temperatures recorded in the field, 83.33% of the records of T<sub>b</sub> (N = 55) had values below the T<sub>set</sub>, and only 16.66% of T<sub>b</sub> (N = 9) were bracketed by T<sub>set</sub>. The mean d<sub>b</sub> was  $2.99 \pm 0.33$ .

The effectiveness of thermoregulation was high, with an E value of 0.79 and the difference between d<sub>e</sub> and d<sub>b</sub> was 11.18 (Table 1).

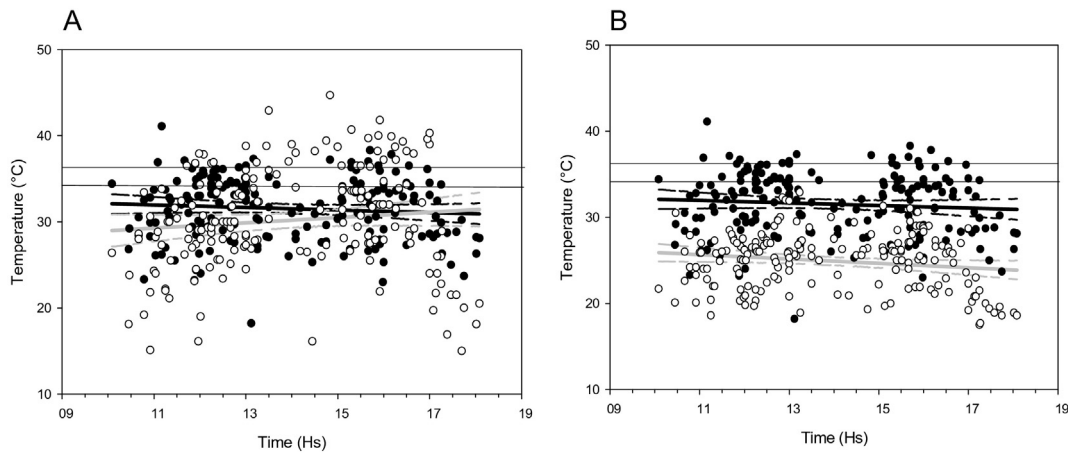
##### 3.2.3. Critical thermal temperatures

CT<sub>min</sub> was  $10.6 \pm 0.68$  °C and not related to body mass (Linear Regression,  $F_{1, 25} = 0.15$ ,  $R^2 = 0.006$ ,  $P = 0.69$ ) neither by snout-vent length (Linear Regression,  $F_{1, 25} = 0.97$ ,  $R^2 = 0.04$ ,  $P = 0.33$ ). CT<sub>max</sub> was  $41.18 \pm 0.22$  °C and increased with body mass (Linear Regression,  $F_{1, 25} = 7.2$ ,  $R^2 = 0.22$ ,  $P = 0.01$ ), but not with snout-vent length (Linear Regression,  $F_{1, 25} = 2.6$ ,  $R^2 = 0.09$ ,  $P = 0.11$ ).

#### 3.3. Species distribution model

The operative temperature data recorded from lizard models deployed in the field showed that during the two activity seasons estimated, the daily average of H<sub>a</sub> per month fluctuated from 6 to 9 h. Our data resulted in daily average H<sub>r</sub> varying from 2 to 6 h during the active season (Fig. 2).

Using the GLM selected to perform the SDM (Table 2), we produced a map of the current distribution of *P. palluma* (Fig. 3) and the predicted distributions for 2050 and 2070 for each of two scenarios based on different atmospheric CO<sub>2</sub> concentrations (Fig. 4). In each potential distribution maps, we added the georeferenced points of known populations. For 2050, with RCP 4.5 and 8.5 scenarios, our distributional modelling



**Fig. 1.** Linear regressions (solid lines) and 95% confidence intervals (dashed lines) of A) Body temperature (black lines and circles) and substrate temperature (grey lines and white circles) and B) Body temperature (black lines and circles) and air temperature (grey lines and white circles) along the day. Horizontal black lines represent set point of preferred temperature.

shows that only one known population would disappear. There would be a reduction in the potential distribution with respect to the current distribution, which would occur in the Eastern potential distribution range, and this would be accompanied by a diminishment of the habitat's thermal quality. In 2050, *P. palluma* would lose between 35 and 65% of its original range (Table 3). In contrast, in the Western part of the range, an expansion of a potentially suitable habitat would occur towards the North and South, increasing the current known area of thermally suitable habitats more than eight times. For 2070, with 4.5 and 8.5 RCP scenarios, our maps show a loss of suitable thermal habitat for five georeferenced localities in the Eastern part of the range, with a range loss between 73 and 85% with respect to the original distribution in the 4.5 and 8.5 scenarios. The current distribution of the Western populations would persist, but it would be accompanied by an increase between 8 (RCP 4.5) or 5 (RCP 8.5) times its area compared with the current distribution (Table 3).

**4. Discussion**

Environmental temperature is of paramount importance to reptilian physiology, ecology and behaviour (Huey, 1982). The ability of lizards to thermoregulate includes shuttling between sunny and shaded microenvironments, modifying the posture and regulating the time of activity to maintain their body temperatures within a relatively suitable range despite environmental fluctuations (Cowles and Bogert, 1944; Huey and Slatkin, 1976). Thermoregulatory efficiency is of vital importance to reduce the costs of thermoregulation beyond the physiological benefits, like the energy spent in locomotion or predation risk (DeWitt, 1967). *Phymaturus palluma* thermoregulates using rock crevices, shade and sun exposure to maintain a suitable range of body temperatures. Lizards attain higher temperatures than the substrate early in the morning

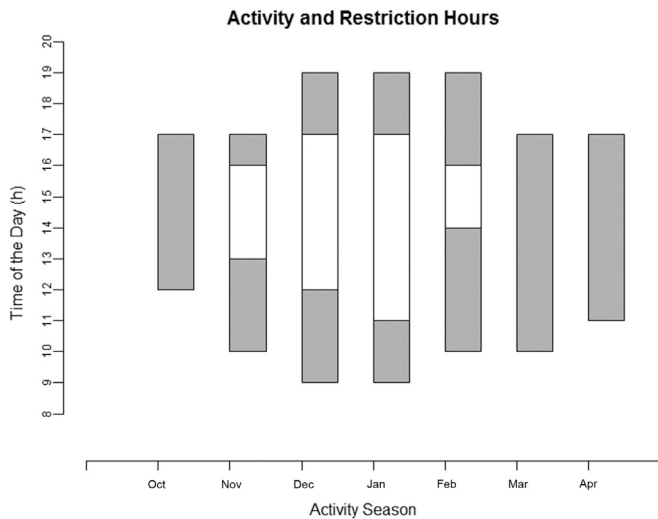
through heliothermy, and in the late afternoon, when the air temperature diminishes and the rocks remain warm, they shift to thigmothermy (Fig. 1). The flat body and mimetic colour pattern of *P. palluma* together with the prostrate body posture observed early in the morning can be envisioned as an optimized behaviour that counteracts their conspicuousness to potential predators. In addition, this behaviour allows them to avoid heat loss by convection in the belly and increase the dorsal surface area exposed to solar radiation. This shift between heliothermic and thigmothermic behaviours lets lizards regulate and maintain their  $T_b$  in a narrow range by effectively using solar radiation in the morning and heat conduction from the rock surface when solar radiation is lower in the afternoon (McConnachie et al., 2009). This behaviour has been also observed in other species like in the lizard *Callisaurus draconoides* (Muth, 1977) and in one of the southernmost species of the world, *Liolaemus sarmientoi* (Ibargüengoytía et al., 2010). Despite these thermoregulatory strategies, 83% of *P. palluma* lizards captured in the field had  $T_b$ 's lower than their  $T_{set}$  registered in the thermal gradient in laboratory.

In the highlands of the Andes as in Patagonia, the thermal environments show low quality for thermoregulation (high  $d_e$  values) (Corbalán et al., 2013; Ibargüengoytía et al., 2008; Medina et al., 2009, 2011; Moreno Azócar et al., 2013; Valdecantos et al., 2013). In these types of habitats, most ectotherms are efficient thermoregulators (Wilms et al., 2011). Accordingly, *P. palluma* actively behaves as an efficient thermoregulator as do other species which live in habitats with low thermal quality. Examples include *P. punae* in the Andes, *P. tenebrosus* in the Patagonian steppe (Ibargüengoytía et al., 2008), and *P. roigorum* and *P. payunia* in the Payunia region (Corbalán et al., 2013) of Argentina. Additional examples include *Zootoca vivipara* in the subalpine meadows of Czech Republic (Gvoždík, 2002), and *Iberocerta cyreni* (Aguado and Braña, 2014), and *I. galani* (Ortega et al., 2016) in the

**Table 1**

Snout-vent length (SVL), body mass (BM), field active body temperatures ( $T_b$ ), preferred body temperatures ( $T_p$ ), range of preferred temperature, individual deviation of  $T_b$  from  $T_{set}$  ( $d_b$ ), the index of the average thermal quality of a habitat from an organism's perspective ( $d_e$ ) and effectiveness of temperature regulation ( $E$ ), for *Phymaturus palluma*. Values in the table are mean  $\pm$  standard error and sample size (N).

Sex and reproductive condition	SVL + SE (mm)	BM (g)	$T_b$	$T_p$	Range $T_p$	$d_b$	$d_e$	E	$d_e - d_b$
Juvenile	71.45 $\pm$ 1.24 (58)	16.09 $\pm$ 0.8 (58)	33.16 $\pm$ 0.37 (58)	35.34 $\pm$ 0.28 (12)	34.01–36.8	3.17 $\pm$ 0.77 (12)		0.78 (12)	11 (12)
Non-pregnant females	91.44 $\pm$ 0.74 (73)	30.73 $\pm$ 0.81 (73)	31.57 $\pm$ 0.44 (73)	35.16 $\pm$ 0.13 (34)	33.35–37.29	3.11 $\pm$ 0.51 (34)		0.78 (34)	11.06 (34)
Pregnant females	93.6 $\pm$ 1.45 (15)	37.97 $\pm$ 1.47 (15)	30.51 $\pm$ 0.96 (15)						
Male	96.89 $\pm$ 1.54 (61)	44.71 $\pm$ 0.82 (61)	30.67 $\pm$ 0.52 (61)	35.01 $\pm$ 0.12 (20)	34.31–36.24	2.67 $\pm$ 0.49 (20)		0.81 (20)	11.5 (20)
Overall	87.60 $\pm$ 0.96 (207)	31.27 $\pm$ 0.89 (207)	31.67 $\pm$ 0.25 (207)	35.15 $\pm$ 0.09 (66)	33.35–37.29	2.99 $\pm$ 0.33 (66)	14.17 $\pm$ 0.1 (66)	0.79 (66)	11.18 (66)



**Fig. 2.** Potential hours of activity ( $H_a$ ) and potential hours of restriction ( $H_r$ ) during two years of the activity season 2013–2015 of *P. palluma*. Grey bars represent  $H_a$  and white bars represent  $H_r$ .

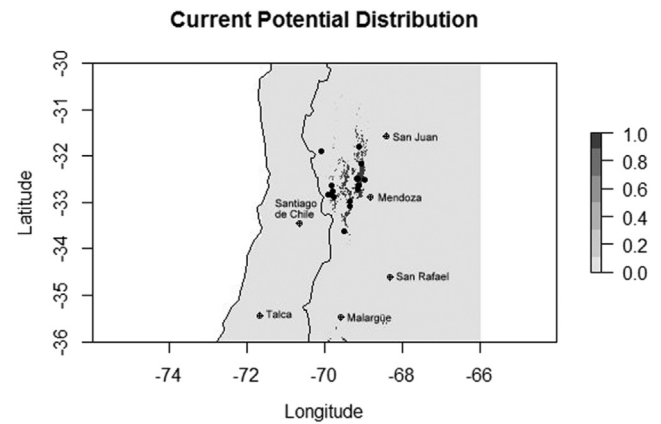
mountains of Central and Northwestern Spain. The habitat thermal quality is deducted from the  $d_e$  index (i.e., the average deviation of the operative temperatures with respect to the  $T_{set}$ ), and operative temperatures including all available microhabitats (Hertz et al., 1993). While crevice temperatures could remain relatively cold and constant, external temperatures could reach very high values. Andes valleys show extreme temperatures, too warm when it is sunny (principally during December and January) and too cold when the sun hides in the valley (Fig. 5). Taking into account that the upper bound of  $T_p$  (38.38 °C) of *P. palluma* is close to the  $CT_{max}$  (41.18 °C), and  $CT_{max}$  is lower than the highest operative temperature registered in the sun, lizards must keep away from sun exposure during part of the day to avoid overheating (Fig. 2, Table 4). As a consequence, their body temperatures at the moment of capture were below their preferred temperatures, since several times they were inside the crevices. To avoid the overheating risk, some lizards could respond to increasing temperatures evolving higher thermal tolerance (Gunderson and Stillman, 2015). However, recent studies suggest that the ability of terrestrial ectotherms to evolve higher heat resistance is limited (Araújo et al., 2013; Gunderson and Stillman, 2015; Kellermann et al., 2012). This would be particularly true for lizards of the genus *Phymaturus*, which are very conservative in their thermal physiology across their wide geographic range and are considered evolutionarily or ecologically constrained to modify their thermal niche (Cruz et al., 2009). However, future studies of phenotypic plasticity in thermal tolerance in species are needed.

When physiological adaptations (such as acclimatization) are unlikely in response to the rise in environmental temperatures caused by

**Table 2**

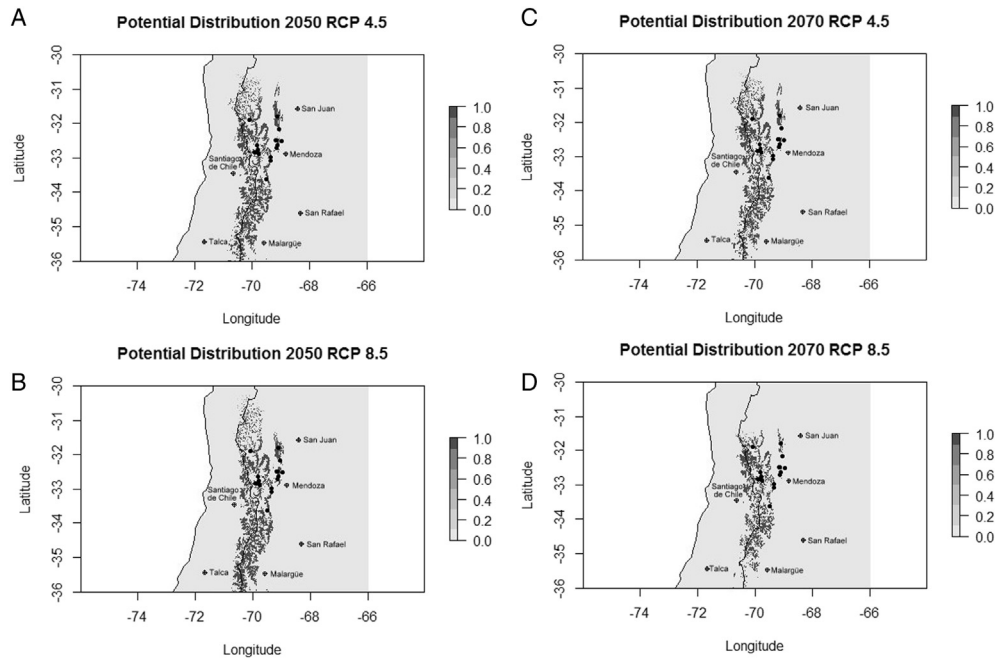
Coefficients of the General Linear Model used to estimate the current sites of occurrence and the potential distribution in the future. Interaction between variables are shown with an asterisk (\*).

Variable	Coefficient
Intercept	−4700
Precipitation <sup>2</sup>	−0.003591
Restriction hours	415.9
Restriction hours <sup>2</sup>	−176.8
Activity hours	912
Activity hours <sup>2</sup>	−274.1
Altitude	1.788
Altitude <sup>2</sup>	−0.0002837
Restriction hours*activity hours	1158
Restriction hours*altitude	−0.782
Activity hours*altitude	0.1440



**Fig. 3.** Current potential distribution map of *P. palluma*, black points represent current georeferenced locations. Grey scale from potential occurrence of *P. palluma*: from light grey (absence) to dark grey (presence).

climate change, organisms can respond in two principal ways: 1) adapt to new conditions by modifying their activity pattern (Kearney et al., 2009; Logan et al., 2013) or 2) modifying their distribution range (Thomas et al., 2006; Thomas, 2010). In the first case, to avoid overheating, one of the primary mechanisms by which lizards can thermoregulate is modifying its time of activity (Adolph and Porter, 1993; Huey et al., 1977). Therefore, in response to warming, it can be expected that lizards become more active earlier in the morning and/or later in the afternoon when temperatures are lower (Logan et al., 2013). However, this assumption could not be satisfied by some high mountain lizards. In *Phymaturus palluma*, the daily time of activity ( $H_a$ ) is constrained by the characteristics of the valleys that it inhabits. This species would not have the opportunity to modify their activity pattern since the hours of direct sunlight in the Andes Valleys are limited compared to the ones in the lowlands, due to the shade produced by mountain peaks to the west. Currently, *P. palluma* shows high values of  $H_r$  during midsummer (Fig. 2) when reproduction probably starts (Boretto et al., 2007, 2010, 2014). Therefore, a rise in temperature increases the hours of restriction ( $H_r$ ) and decreases the time available to perform vital activities such as foraging, growth, dispersal, territory defence and reproduction as has been reported for the genus *Phymaturus* and >1300 other species of lizards (Sinervo et al., 2010). High environmental temperatures can be even more deleterious for this species, since viviparous lizards have limited ability to adjust their body temperatures during gestation, not only due to their restrained mobility, but also due to the need to carefully thermoregulate to avoid high body temperatures that could be lethal to the developing embryos (Paranjpe et al., 2013). As a consequence, facing an increase of environmental temperature, lizards can be in risk of local extirpation (Kubisch et al., 2016). In the second case, organisms could respond to climate change by modifying their distributional range to areas with suitable climatic conditions. Our predictions show a loss of suitable climatic conditions in the Eastern portion of the current distribution, reducing the area by 2050 and almost disappearing in 2070. This loss will result in the extirpation of one third of current populations. On the other hand, our predictions also show an expansion in the potential distribution range towards the West region in the Northern and Southern portions of the species range for 2050 and 2070 in both scenarios (RCP 4.5 and 8.5). If individuals were able to disperse to these new sites, an increase in the range size would result in approximately five to eight times the size of the current geographic range (Table 3). However, the climatic conditions are not enough for an area to be colonized by a species. The genus *Phymaturus* exhibits a limited variation in several key niche and life history characteristics, such as microhabitat use, diet, and reproductive mode (Debandi et al., 2012). Most populations of *P. palluma* are isolated because high mountains act as biogeographic barriers; if we



**Fig. 4.** Future potential distribution maps of *P. palluma*. A) Potential distribution for 2050 with an RCP 4.5; B) Potential distribution for 2050 with an RCP 8.5; C) Potential distribution for 2070 with an RCP 4.5 and D) Potential distribution for 2070 with an RCP 8.5. Black points represent current georeferenced locations. Grey scale from potential occurrence of *P. palluma*: from light grey (absence) to dark grey (presence).

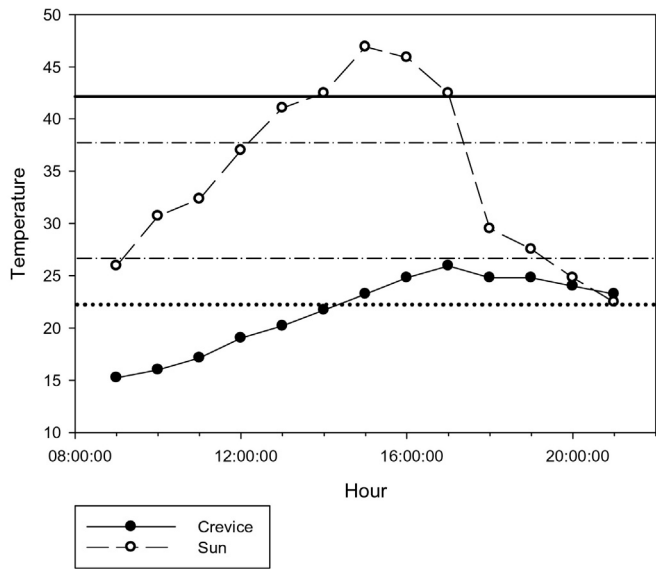
evaluated the future potential distribution areas, most of them are far from the current occupancy areas. In addition, the observation of marked individuals of *P. palluma* at the same site over a period of four years suggests a low dispersal capacity (Vicenzi, pers. obs.). The herbivorous diet and the strong dependence for substratum type (rocky outcrops) of *Phymaturus*, combined with their low dispersal capacity, could prevent the colonization of new areas. Currently, the shrubby vegetation in the area reaches up to 3800 masl (Méndez et al., 2006), just the limit of altitudinal distribution recently known for *P. palluma* (Vicenzi, pers. obs.). Consequently, to be colonized, the shrubby vegetation must also disperse and colonize these suitable areas before lizards arrive. Moreover, lizards would need suitable routes to shift their ranges, for example a rocky corridor to facilitate their movement into the new habitats. The capability to colonize new locations will depend on the individual's ability to use random movement or directed movement to disperse. In random movement individuals are unable to track environmental conditions, whereas in directed movement individuals disperse to new locations with better environmental conditions (Armsworth and Roughgarden, 2005). Individuals which disperse to suboptimal localities increase the vulnerability of the population extirpation but individuals which disperse to optimal localities will increase the probability of survivorship of the population. Moreover, recent studies suggest that the ability of migration in terrestrial ectotherms to mitigate fitness detriment in response to climate change will be modest (Buckley et al., 2013).

The model applied in this study has been focused on the direct impacts of climate change on *P. palluma* thermal physiology and predicts the location of climatically suitable habitats, as an example of a saxicolous species from high altitude in the mountains. In order to avoid underestimating the spatial complexities of the area and intrinsic characteristics of the species, the integration of these effects into a framework that includes reproduction, activity patterns and dispersion capabilities is needed. An increase in  $H_r$  would force individuals of *P. palluma* to spend longer periods in refuges, and therefore, the net energy gain would become insufficient for growth, survival or reproduction. A rise in  $H_r$  has the ultimate outcome of threatening population growth rates (Huey et al., 2010). In this scenario, we could conclude that *P. palluma* is vulnerable to climate change despite the species high thermoregulatory efficiency and the current low thermal quality of its environment. This work represents a model of the impacts of climate change on species with “nowhere to go” and “no activity time to alter”. According to our model for 2050, between 35 and 65% of the current suitable area could be lost, and between 73 and 85% could disappear by 2070, leaving at least one-third of the known populations without a suitable habitat. Most of the areas predicted to remain climatically suitable are within legally protected areas. Nonetheless, some of these areas have high anthropogenic impact or low level of protection. For example, in Aconcagua Provincial Park, which comprises the majority of localities predicted to remain thermally suitable, the current levels of habitat protection may be insufficient (Barros et al., 2014a). In particular, informal

**Table 3**

Change in future potential range respect current potential range. Percentage of potential range loss, potential range gain, potential future range size without dispersal <sup>(1)</sup> and potential future range size with dispersal <sup>(2)</sup>.

	Range loss	Range gain	Future range size <sup>(1)</sup>	Future range size <sup>(2)</sup>
Current–Future 2050 RCP 4.5	65.4%	827.69%	34.6%	862.29%
Current–Future 2050 RCP 8.5	35.47%	813.65%	64.53%	878.18%
Current–Future 2070 RCP 4.5	73.64%	794.82%	26.36%	821.18%
Current–Future 2070 RCP 8.5	85.96%	542.42%	14.04%	556.46%



**Fig. 5.** Daily operative temperature variation. Dashed lines represent variation in temperature of model exposed to the sun and Solid line represent variation of temperature inside a crevice. Solid horizontal line represent  $CT_{max}$ , dashed horizontal line represent upper and lower  $T_p$  and dotted line represent average  $T_e$ .

trails made by visitors or pack animals (mostly mules) impact on soil and vegetation, fragmenting the landscape (Barros et al., 2013). Specifically shrubby vegetation, which comprises the majority of *Phymaturus palluma*'s diet, is intolerant to trampling (Cole, 2004). As most part of these trails extend along outcrops where populations of *P. palluma* inhabit (Vicenzi, pers. obs.), high priority should be given to current lizard's habitat through a more effective protection, excluding trails or pack animals from the outcrops. Then, conservation strategies should be focused on the protection of current suitable habitats that support populations of *Phymaturus*. On the other hand, our model shows an increase of at least 500% of potential range distribution, but most of these areas are inaccessible to current populations (natural physical barriers and their low capacity to migrate). Because climate change represents a significant threat to population viability in some species, especially for those with fragmented distributions and little capacity to migrate (Hoegh-Guldberg et al., 2008), we recommend that the protection of current suitable habitats as potential sites for assisted re-introduction efforts. Such caution could counteract the effects of climate change in *P. palluma*. In addition, our analysis showed the need to reinforce the idea of dynamic protected areas (Dawson et al., 2011). As climate change generates new suitable habitats, animals must have available usable corridors and buffer zones that will allow geographic re-distribution, primarily through natal dispersal. If conservation biologists and others flexible in the identification and use of corridors, buffer zones,

**Table 4**

Average operative temperature ( $T_e$ ) registered by lizard models exposed to sun during the activity season. Grey boxes represent the hours when  $T_e$  exceed the upper bound of preferred temperature. Means are presented for each hour of potential activity.

Hour	October	November	December	January	February	March	April
09:00	16.32	21.39	27.40	27.25	20.20	15.20	11.30
10:00	21.21	26.39	32.25	32.62	24.86	24.43	22.84
11:00	25.96	31.11	36.22	36.88	28.97	29.09	25.84
12:00	29.67	34.65	38.94	39.94	32.48	32.06	25.95
13:00	31.41	36.67	40.88	41.36	33.95	32.84	28.25
14:00	31.84	36.73	41.51	42.09	38.20	32.43	30.45
15:00	30.98	35.49	40.84	41.46	33.78	31.64	29.09
16:00	28.72	33.26	39.75	39.91	32.24	30.40	27.32
17:00	23.85	27.56	34.74	36.01	29.61	25.51	21.51
18:00	19.45	21.46	27.62	28.11	23.55	18.92	17.15

and habitats as they become modified by climate change, then the likelihood of avoiding local extinctions will be enhanced. We need to develop further studies which will allow us to interpret the driving forces, the trade-offs and constraints in thermal adaptation (Pörtner et al., 2006; Somero, 2011; Bozinovic et al., 2011a, 2011b; Kingsolver et al., 2013) to assess more accurately the vulnerability of the species to climate change. This knowledge, combined with different management strategies (such as monitoring populations in the long term, contingency plans, periodic re-evaluation of planned protected areas, and assisted colonization (see Dawson et al., 2011)), will allow the design and implementation of effective measures to protect biodiversity.

## Acknowledgements

We thank Rubén Massarelli, Carla Piantoni, Nicolás Pelegrin and Marisol Arellano for field assistance, Dr. John D. Krenz for English revision and anonymous reviewers for constructive comments on the manuscript. Thanks to Dirección de Recursos Naturales Renovables of Mendoza government, park rangers of Aconcagua Provincial Park and IADIZA for their support in conducting this research. Funding was provided in part through the Project "A Network of Institutes for Biotic and Economic Effects of Climate (IBEEC) in the Americas", the Project "Quantifying Climate-forced Extinction Risks for Lizards, Amphibians, and Plants" of NSF (EF-1241848), the project "Procesos fisiológicos que permiten la vida de lagartos en climas fríos de la patagonia" PIP 11220120100676, PICT 2013-1139, PICT2014-3100 and CONICET.

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