Potential benefits from global warming to the thermal biology and locomotor performance of an endangered Patagonian lizard

Facundo Cabezas-Cartes*, Jimena B. Fernández*, Fernando Duran and Erika L. Kubisch

Laboratorio de Ecofisiología e Historia de vida de Reptiles, Instituto de Investigaciones en Biodiversidad y Medio Ambiente, Universidad Nacional del Comahue, CONICET, San Carlos de Bariloche, Río Negro, Argentina
* These authors contributed equally to this work.

ABSTRACT

Global warming can significantly affect many aspects of the biology of animal species, including their thermal physiology and physiological performance. Thermal performance curves provide a heuristic model to evaluate the impacts of temperature on the ecophysiology of ectotherms. When integrated with other thermal biology parameters, they can be used to predict the impacts of climate change on individual fitness and population viability. In this study, we combine holistic measures of thermal physiology and the thermal sensitivity of locomotor performance with environmental temperatures measured at fine scale to estimate the vulnerability to global warming of the endangered Patagonian lizard *Phymaturus tenebrosus*. Our results indicate that this lizard exhibits its preferred temperatures and maximum locomotor performance at higher temperatures than the mean temperature it currently experiences in its habitat. In addition, it exhibits a low effectiveness of thermoregulation, being a poor thermoregulator. In view of the results obtained, we suggest that the climatic conditions of Patagonia may be advantageous for *P. tenebrosus* to survive future global warming, since its thermal physiology and locomotor performance may improve under increasing in environmental temperatures in its habitat.

INTRODUCTION

In recent decades, global warming has emerged as one of the most serious threats to biodiversity. In particular, it has been shown that rising temperatures can significantly affect many aspects of animal species' biology, such as physiology (increased metabolic rates (*Dillon, Wang & Huey, 2010*)), morphology (shrinking body size (*Sheridan & Bickford, 2011*)), life cycle demography (*Daufresne, Lengfellner & Sommer, 2009*), life history (*Bestion et al., 2015*), phenology, and distribution (*Parmesan & Yohe, 2003*). As a consequence of these changes within species, community structure can also be affected

Corresponding author
Jimena B. Fernández,
jimenafernandez@comahue-conicet.gob.ar

(*Walther, 2010*). Understanding how climate change affects the physiology of different kinds of organisms is a critical challenge in modern ecology and evolutionary biology (*Pörtner & Farrell, 2008*). For example, the responses of endotherms are probably different from those of ectotherms (*Bozinovic & Pörtner, 2015*). Reptiles, as ectotherms, are particularly susceptible to changes in climate since most of their physiological functions, including locomotion, digestion, reproduction, and growth, are tightly correlated with environmental conditions, especially with temperature (*Adolph & Porter, 1993*; *Angilletta, 2009*). Moreover, in recent years several studies have reported current and predicted future potential extinctions of lizards' populations as consequence of rising temperatures (*Sinervo et al., 2010*; *Kubisch, Fernández & Ibargüengoytía, 2016*; *Vicenzi et al., 2017*). However, other authors suggest that the effects of rising temperatures may be less detrimental than previously postulated, especially in species with high dispersal ability (*Araújo, Thuiller & Pearson, 2006*) or in species occurring at high latitudes or altitudes like some liolaemids (*Bonino et al., 2015a*; *Gómez Alés et al., 2018*).

The effects of increasing environmental temperatures on lizards' populations will depend, at a fine scale, on the availability of microenvironmental temperatures that allow organisms to effectively thermoregulate and reach body temperatures (T_b) within a range which allows peak performance of the most relevant physiological processes (*Angilletta, Hill & Robson, 2002*; *Angilletta, 2009*). However, this will also depend upon the effectiveness of thermoregulation of the species (*E*), which determines the degree to which thermoregulatory activity by the animals compensate for the thermal shortcomings of a particular habitat (*Hertz, Huey & Stevenson, 1993*). If lizards are unable to reach and maintain T_b within a range that maximizes the performance of functions directly related to fitness (i.e., locomotion, digestion, growth rate, reproduction), they will be forced to disperse to more suitable environments in order to survive (*Vicenzi et al., 2017*). Species with a high degree of endemicity, or which live in isolated patches and exhibit low vagility, might be at high risk of extinction (*Chamaille-Jammes et al., 2006*; *Bonino et al., 2015b*; *Vicenzi et al., 2017*). Furthermore, other studies propose that terrestrial ectotherms may have limited capacity to migrate in order to avoid negative effects on fitness due to global warming (*Buckley, Tewksbury & Deutsch, 2013*; *Ofori et al., 2017*).

The influence of temperature on physiological performance is generally studied by "thermal performance curves" (TPCs; *Angilletta, 2009*), which describe how a given performance trait responds to T_b (*Huey & Stevenson, 1979*; *Huey & Bennett, 1987*). The information provided by these curves, such as optimal temperature (T_o), performance breadth, and critical temperatures, are essential to estimate the effects that changes in environmental temperature can induce in natural populations of ectotherms (*Sinclair et al., 2016*). In reptiles, one of the most used measurements of physiological performance is locomotor performance, because it reflects the interaction of several underlying physiological processes and is usually applied to ecological tasks relevant for natural and sexual selection, such as competition for food, predator avoidance, territory defense, and mate choice (*Garland & Losos, 1994*; *Irschick & Garland, 2001*; *Irschick et al., 2008*).

Here, we study the thermal physiology and the thermal sensitivity of locomotor performance in the endangered viviparous lizard *Phymaturus tenebrosus* (Fig. 1).

This species is a medium-sized lizard endemic to northwestern arid Patagonia (*Perez et al., 2011*). At present, *P. tenebrosus* is only known from a very restricted area in southwest Río Negro and Neuquén, Argentina (*Kubisch et al., 2017*). Recent climatic predictions for this region suggest an extreme increase in temperature of 3–3.5 °C and a decline in average daily precipitation of 0.75–1 mm by the end of this century, in comparison to current conditions ("representative concentration pathway" scenario 8.5, *IPCC, 2014*; *Barros et al., 2015*). Our focal species has been recently categorized by the IUCN as Endangered (*Abdala, 2017*), due to factors such as its limited and isolated distribution on rocky outcrops, specialization on a saxicolous and herbivorous lifestyle, viviparous reproductive mode, low annual reproductive output (*Ibargüengoytía, 2004*), and acquisition of sexual maturity at 7–9 years of age, with a maximum life span of 16 years (*Piantoni, Cussac & Ibargüengoytía, 2006*). In addition, *Sinervo et al. (2010)* predicts a high extinction risk for this lizard due to climate change. Other factors affecting its conservation are the high frequency of fires and sheep farming (*Abdala et al., 2012*), which intensify the natural fragmentation of its habitat.

In this paper, we hypothesize that: (1) the preferred body temperature of *P. tenebrosus* (T_{pref}) is correlated with its T_o for locomotor performance, as postulated by the thermal coadaptation hypothesis (*Huey & Bennett, 1987*; *Angilletta et al., 2006*); (2) *P. tenebrosus* is capable of attaining high locomotor performance in the field by reaching and maintaining T_{pref} in the field, as has been observed in other species of the genus (*Corbalán, Debandi & Kubisch, 2013*; *Gómez Alés, Acosta & Laspiur, 2017*; *Vicenzi et al., 2017*; *Duran, Kubisch & Boretto, 2018*); (3) the potential increase in temperature due to global warming will affect locomotor performance of the species, considering the narrow thermal performance breadth observed in other *Phymaturus* (*Bonino et al., 2015a*; *Gómez Alés et al., 2018*; *Vicenzi et al., 2019*), increasing their vulnerability to extinction. Consequently, we predict that the T_o for locomotor performance will be included within the thermal preference range of the species, that *P. tenebrosus* is an efficient thermoregulator like other species of the genus, and that under a global warming scenario, locomotor performance will decrease, threatening the viability of the species.

MATERIALS AND METHODS

Study site and field work

The study site is located on a rocky outcrop near Villa Llanquín, Río Negro, Argentina (40°52′S, 70°57′W, 1,200 m above sea level). Field work was carried out during summer (late January) of two consecutive years (2018 and 2019). This area is included within the Sub-Andean district of the Patagonic Phytogeographic Province (*Cabrera, 1976*), and it is characterized by a cool (mean annual air temperature: 10.66 °C) and semi-humid climate (mean total annual precipitation: 343 mm). The dominant landscape is barren steppe, with shrubby, low herbaceous coverage and bare soil percentages above 50% (*Cabrera, 1978*).

We captured 34 adult specimens of *P. tenebrosus* (15 females and 19 males) by hand or noose when they were active, between 900 to 1900 h. Considering the endangered conservation status of the species (*Abdala, 2017*) we aimed to work with the minimum

Figure 1 Adult of *Phymaturus tenebrosus.* Photo by Erika Kubisch.

sample size needed for statistical significance. Also, we did not include pregnant females in our sample, determining the reproductive status of females by palpation as in other *Phymaturus* (*Boretto et al., 2014*; *Ibargüengoytía et al., 2016*). Moreover, we used only a subset of individuals ($N = 20$) for the thermal tolerance experiments. Finally, our experimental design was planned to minimize the time spent in captivity and the stress suffered by the individuals.

Adult status was determined according to the minimum size at sexual maturity (85 mm in females and 87 mm in males) reported by *Ibargüengoytía (2004)*. Immediately after capture, T_b was measured (TES 1,303, $\pm$ 0.03 °C digital thermometer) using a thermocouple (TES TP-K01, 1.62 mm diameter) inserted approximately 0.5 cm inside the cloaca. The temperature measurements were taken within 10 s of capture to prevent heat transfer from the operator's hands. We also recorded the substrate temperature (T_s) and the air temperature one cm above the ground (T_a) of the microenvironment where each lizard was captured.

Every capture site was georeferenced (three m resolution, GARMIN Map 60C Sx), and photographed (VC-03 Nikon camera, D3100) using a lizard model in the same position than the lizard was captured, allowing us to return each lizard to their exact capture site after experiments. A scientific collecting permit (Disposición No. 108/17) was obtained from the Secretaría de Ambiente y Desarrollo Sustentable of Rio Negro Province, Argentina. Lizards were cared for following the ASIH/HL/SSAR Guidelines for Use of Live Amphibians and Reptiles, as well as the regulations detailed in the Argentinean National Law N° 14346.

Lizards were carried to the laboratory in individual cloth bags. During experiments (4 days), lizards were kept in their respective individual bag at room temperature (20–22 °C)

in a quiet site, taking care of the asepsis and avoided contact between individual lizards to minimize stress. After experiments, body weight (Pesola 50 ± 0.3 g) and snout-vent length (SVL; digital caliper Lee Tools ± 0.02 mm) were measured and sex recorded (based on the presence of pre-cloacal pores in males).

Preferred body temperatures

Preferred body temperatures were measured the day after capture. Lizards were placed individually in an open-top terrarium (100 × 20 × 17 cm), with a thermal gradient (20–50 °C) produced by a 75 W incandescent light bulb in a lamp over one end of the terrarium. Lizard T_b were measured every 10 s for 2 h with a temperature Data Acquisition Module (USB-TC08; OMEGA, Biel/Bienne, Switzerland), using an ultra-thin (0.08 mm) catheter thermocouple, fastened to the belly and to the base of the lizard's tail with hypoallergenic tape, to keep the thermocouple in position during the experiment. For each individual, we estimated the mean T_{pref} and the minimum and maximum temperature set-points (T_{set}) as the central 50% of all T_b preferred in the laboratory.

Effects of body temperature on locomotor performance

Locomotor performance trials were performed on a racetrack 0.075 m wide and 1.20 m long, leading to a shelter. Photocells, positioned at 0.15-m intervals along the track, signaled passing lizards to a laptop that calculated speed over each 0.15-m section. Two types of runs were considered in the analyses: (1) sprint runs (SR), defined as the speed reached between the first and the second photoreceptor (0.15-m), which is relevant for predator escape and prey capture (*Cabezas-Cartes, Kubisch & Ibargüengoytía, 2014*), and (2) long runs (LR), defined as the speed between the first and the last photoreceptor (1.05 m), which indicated the locomotor capability of the lizard to perform activities such as foraging, territorial defense, and courtship (*Cabezas-Cartes, Kubisch & Ibargüengoytía, 2014*). Lizards ran three consecutive times at each experimental temperature, and only the maximum run speed (V_{max}) for SR and LR of the three repetitions was considered for the analyses. Between these three consecutive trials lizards did not rest, but they were always rested at least 4 h between the different treatments.

Before and after each run, the lizard's T_b was measured using a thermocouple inserted 0.5 cm inside the cloaca (catheter probe TES TP-K01) and connected to a digital thermometer (TES 1302; TES Electrical Electronic Corp., Taipei, Taiwan, China, ±0.01 °C). Trials were conducted at five T_b (20 ± 1 °C; 25 ± 1 °C; 30 ± 1 °C; 36 ± 1 °C; 39 ± 1 °C) during three consecutive days. The T_bs were chosen based on the following criteria: the minimum temperature at which we found lizards active in the field (19 °C), the median T_b in the field (26.3 °C), and the mean T_{pref} (35.4 °C) obtained in the laboratory for *P. tenebrosus* (this study). The T_b at 30 °C was included to define the shape of the curve. Also, we estimated performance at 39 °C, to evaluate the locomotor performance at the mean T_{pref} + 3.5 °C, simulating a potential shift in field active T_b (*Gilbert & Miles, 2017*) anticipated by the end of this century at our study site, given the climatic assessment from the *IPCC (2014*; *Barros et al., 2015)*. Locomotor performance trials were carried out in an environmental chamber equipped with an air conditioner, heat lamps, electric heaters, and

a thermostat to set the desired temperature. Lizards were placed at the specified temperature 1 h prior to the run, following the methods of *Angilletta, Hill & Robson (2002)*, *Fernández et al. (2011)*, *Kubisch, Fernández & Ibargüengoytía (2011)*, and *Kubisch et al. (2016)*.

Thermal tolerance

To determine the critical thermal minimum (CT_{min}), a subsample of 20 lizards were placed individually in a plastic transparent box ($15 \times 10 \times 5$ cm) in a refrigerator at -10 °C. T_b was measured every 15 s (with a temperature Data Acquisition Module, USB-TC08; OMEGA, Biel/Bienne, Switzerland) using an ultra-thin (0.08 mm) catheter thermocouple fastened to the belly and to the base of the lizard's tail. Lizards were observed throughout the experiment and we recorded and considered as CT_{min} the T_b at which an individual was no longer able to right itself when placed on its back.

The same subsample of 20 lizards were also used to determine critical thermal maximum (CT_{max}). Each lizard was placed in an open-top terrarium ($15 \times 20 \times 20$ cm) with an infrared 150-W lamp 40 cm overhead. The T_b was monitored every 15 s following the same methodology used to the CT_{min}. Each lizard was carefully observed throughout the experiment and we recorded and considered as CT_{max} the T_b at which an individual was unable to right itself when it was placed on its back. After reaching CT_{max}, each lizard was removed from heat and cooled quickly to avoid overheating.

Operative temperatures, effectiveness of thermoregulation, and vulnerability to global warming

The operative temperature (T_e) represents the "null" distribution of T_b that non-thermoregulating animals would achieve in their environment (*Hertz, Huey & Stevenson, 1993*). The T_e was measured using gray PVC oval plastic models 35×10 mm in cross-section and 120 mm long, to mimic an adult *P. tenebrosus*. The model was chosen to represent a living animal and was validated for a *Phymaturus* species of similar shape and size to *P. tenebrosus*, showing a strong association between the model temperature and the live animal temperature ($R = 0.98$; *Gómez Alés, Acosta & Laspiur, 2017*). Each model was connected to a thermistor and both ends were sealed with silicone (Fastix®, AKAPOL S.A., Buenos Aires, Argentina). The thermistor was connected to data loggers (HOBO Onset Computer Corporation, Bourne (MA), USA). The models were placed in the most extreme thermal situations present at our field site: three models inside crevices (shelters used by lizards) and three models exposed on the rock. *Phymaturus* lizards usually shift between sun patches and rock crevices to thermoregulate (*Duran, Kubisch & Boretto, 2018*). The data loggers were programed to record temperatures every 30 min during 2 months of the lizards' active season (from the end of January to the end of March). In our analyses, we used the T_es recorded between 900 and 1,900 h (daily period of activity; personal observation).

In order to estimate the thermoregulatory effectiveness of a subset of our sample of *P. tenebrosus* ($N = 11$), we applied the methodology of *Hertz, Huey & Stevenson (1993)*, using the information on T_{pref} obtained in the thermal gradient and the availability of T_e in

the natural environment. We defined the d_b (individual deviation) as an index based on the average extent to which each individual experienced T_b outside the set-point range of their T_{pref}. The d_b was estimated as the average of the absolute value of the deviations of T_b from T_{set} of each individual. Then, we calculated the d_e as an index of the mean thermal quality of the habitat from an organism's perspective. The d_e was estimated as the mean of the deviation of T_e from the T_{set} of each individual. Considering the high daily variation in temperature that characterizes the Patagonian climate, the T_e is highly dynamic. Hence, we used the mean value of T_e from the overall models recorded from one hour before each individual lizard was captured (*Duran, Kubisch & Boretto, 2018*). The effectiveness of thermoregulation (E) was defined as the degree of active selection of the thermal microhabitat and calculated using the formula $E = 1 - (d_b/d_e)$, which integrates the average degree to which *P. tenebrosus* experienced T_b outside the set-point range (d_b), and the corresponding d_e. When the E index approaches zero the species is considered to be a thermoconformer, whereas when the E index approaches a value of one the species can be considered a highly effective thermoregulator. Finally, if the E index is close to 0.5, the species is considered to be a moderate thermoregulator (*Hertz, Huey & Stevenson, 1993*).

In addition, we calculate two indices to estimate vulnerability to global warming: the warming tolerance (WT), which defines how much warming can be tolerated by an ectotherm before its performance is reduced to lethal levels, and is defined as the difference between mean CT_{max} and mean T_e (sensu *Deutsch et al. (2008)* and *Logan et al. (2013)*). Also, we determined the thermal safety margin (TSM) for physiological performance as the difference between the T_o and mean T_e, which gives an indication of how close animals' thermal optima are to the current climatic temperature in their environment (*Deutsch et al., 2008*; *Andrew et al., 2013*).

Statistical analyses

To quantify the thermal sensitivity for locomotor performance, we used Table Curve 2D v5.01.2 software to create locomotor performance curves (TPCs) as function of temperature during SR and LR. The values of CT_{min} and CT_{max} were used as the extreme values of the curves (speed equal to 0 m/s). We chose the model according to the adjusted R^2 and the lowest Akaike information criterion (AIC) (following *Angilletta (2006)*). Also, we estimated the differential AICc (Δi), which is the difference between a given model's AIC and the lowest AIC, and the Akaike weight (w_i), as a measure of the strength of the evidence for each model, indicating the probability that a given model is the best among a series of candidate models (*Burnham & Anderson, 2002*). The best candidate model for the overall sample was fitted to each individual in order to estimate the V_{max}, the T_o (the T_b at which performance is maximal) and the performance breadth (B_{80}, the range of T_bs over which performance is greater than or equal to 80% of the V_{max}; sensu *Ben-Ezra, Bulté & Blouin-Demers (2008)*) of each individual for LR and SR.

We used the statistical software programs Sigma Stat 3.5® and Sigma Plot 14.0® for statistical analyses and to generate figures. Relationships between variables were analyzed by simple linear regressions. To compare two related samples, we used paired *t*-tests or the non-parametric alternative Wilcoxon signed rank test when the assumptions of parametric statistics were not met. Means are reported ± standard error.

RESULTS

Body measurements and their relationship with locomotor performance

The mean SVL of *P. tenebrosus* (N = 34) at Villa Llanquín was 92.19 (± 0.85 mm) and the median body mass was 27.65 (range 14.12–35.00 g). There was no relationship between maximum speeds during SR or LR and SVL (linear regression: $F_{SR\ 1,29} = 0.40$; $F_{LR\ 1,31} = 0.005$; $P > 0.5$) or body mass (linear regression: $F_{SR\ 1,\ 28} = 1.41$; $F_{LR\ 1,\ 30} = 0.18$; $P > 0.5$).

Field temperatures

The median T_b in the field was 26.3 °C (range 16.50–33.00 °C). Lizards were captured in microenvironments with a mean T_a of 23.08 ± 0.67 °C, and a mean T_s of 23.85 ± 0.88 °C. The mean T_e for all physical models was 19.59 ± 0.09 °C (range = 1.15–53.74 °C; Figs. 2 and 3). The mean T_e of exposed models was 22.10 ± 0.21 °C, while the mean T_e of models placed inside crevices was 17.07 ± 0.14 °C.

Thermal performance curves

The relationship between T_b and maximum speed for the overall sample was best described by a curve of the Pearson family for both SR (Adj $R^2 = 0.57$; Fig. 2A) and LR (Adj $R^2 = 0.85$; Fig. 2B) according to the lowest AIC. Lizards ran faster during SR than LR (Median V_{max} SR = 1.65 m/s, V_{max} LR = 1.38 m/s; Wilcoxon signed rank test: $W = -357.000$; $P < 0.001$; Fig. 2). However, the T_o was similar between SR and LR (Median T_o SR = 35.18 °C, T_o LR = 36.09 °C; Wilcoxon signed rank test: $W = 182.000$; $P = 0.08$; Fig. 2). Considering the thermal performance breadth at which 80% of maximal speed could be reached (B_{80}) there was no difference between SR and LR ($B_{80\ SR} = 28.36$–39.07, $B_{80\ LR} = 29.57$–39.46; Paired *t*-test: $t_{30} = -1.29$, $P = 0.21$, Fig. 2). The mean B_{80} for SR was 8.95 ± 0.71 °C, while the mean B_{80} for LR was 9.93 ± 0.41 °C.

Thermal physiology of *P. tenebrosus*, effectiveness of thermoregulation, and vulnerability to global warming

The mean T_{pref} of *P. tenebrosus* in the laboratory was 35.36 ± 0.38 °C with a set-point of T_{pref} of 34.09–36.59 °C (Figs. 2 and 3). The T_{pref} was similar to the mean T_o for both SR and LR (SR: Wilcoxon signed rank test: $W = 36.000$; $P = 0.70$, Fig. 2A; LR: Paired *t*-test: $t_{30} = 0.90$; $P = 0.37$, Fig. 2B). The mean critical minimum and maximum temperatures were $CT_{min} = 7.62 ± 0.20$ °C and $CT_{max} = 42.90 ± 0.21$ °C, respectively.

Our results indicate that *P. tenebrosus* has a very low effectiveness of thermoregulation ($E = 0.19$), primarily because it exhibits a low accuracy of thermoregulation ($d_b = 9.28$), and inhabits a low-quality thermal environment ($d_e = 11.48$). The indices to estimate its vulnerability to global warming were: WT = 23.30 °C and TSM for SR = 15.58 °C and for LR = 16.30 °C (Fig. 3).

DISCUSSION

The interplay between environmental temperature and thermal physiology in ectotherms can be analyzed by several physiological parameters (such as T_{pref}, TPCs, CT_{max}, CT_{min},
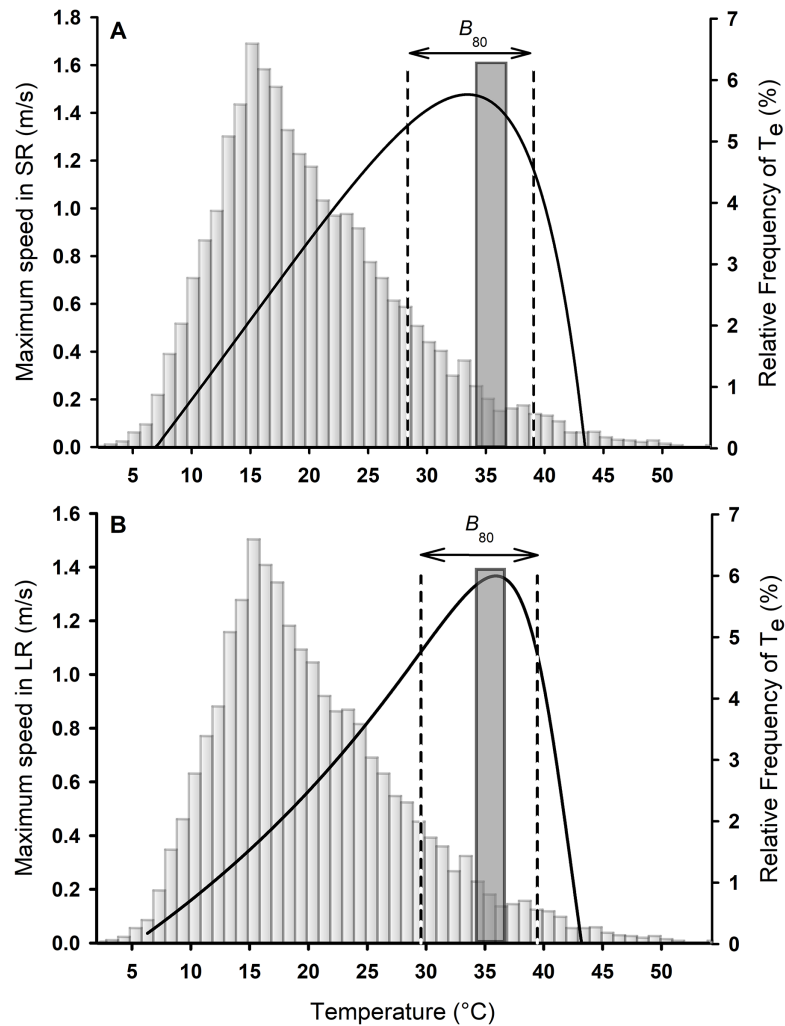
Figure 2 Thermal performance curves for sprints (A) and long runs (B) for *Phymaturus tenebrosus*.
Vertical dashed black lines represent performance breadth during SR and LR (B_{80}). Gray bars represent the percentage frequency distribution of all operative temperatures between activity hours, from January to March 2019. The dark gray bar and striped bar represent the set point range of T_{pref} obtained in the laboratory.

WT, and TSM), which are useful to predict the ecological consequences of climate warming for individual fitness and, therefore, to assess the vulnerability of ectotherms to climate change (*Deutsch et al., 2008*; *Sinclair et al., 2016*; *Gilbert & Miles, 2017*). As we predicted, *P. tenebrosus* reached their T_o in both types of runs at temperatures within the thermal preference range (during LR) or near the lower T_{set} of T_{pref} (during SR). The T_o was similar to what was previously reported for a small sample of this species (T_o = 35.4 °C, N = 3; *Bonino et al., 2015a*). There are only two other species in the genus *Phymaturus* for which TPCs have been published. In the case of *P. extrilidus* the T_o (LR = 32.5, SR = 33.25) was lower than their T_{pref} (35.74), but they attained their maximum locomotor performance at temperatures they generally experienced during daily activity (*Gómez Alés et al., 2018*). In contrast, *P. palluma*, similarly to *P. tenebrosus*, exhibited T_{pref} that optimized
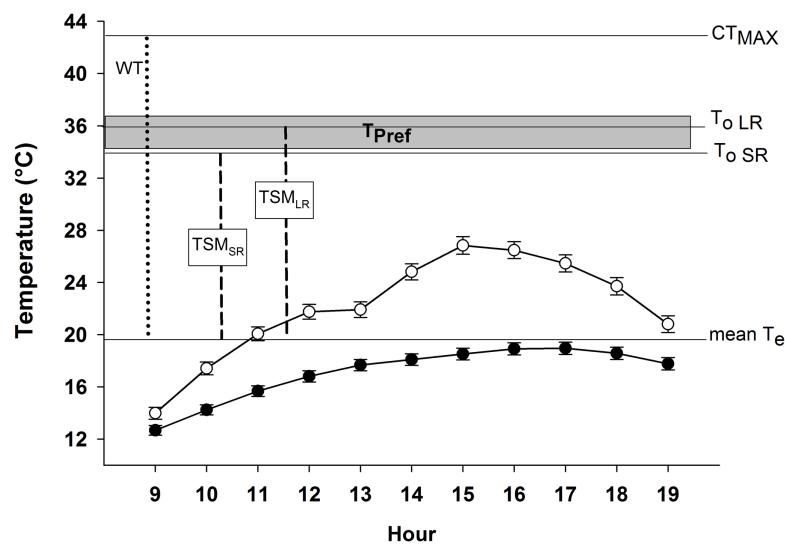
Figure 3 Microenvironmental temperatures (T_e) of exposed models (empty circles) and models inside crevices (filled circles) during activity period of *Phymaturus tenebrosus* in Villa Llanquín. The critical thermal maximum (CT_{Max}), optimal temperature during SR ($T_{o\ SR}$), and LR ($T_{o\ LR}$), are indicated with horizontal lines, as well as the mean T_e. In addition, the warming tolerance (WT, dotted line) and thermal safety margin (TSM, dashed lines) indexes are shown, as well as the set point range of the preferred temperature (T_{pref}, gray rectangle).

their performance ($T_{o\ LR} = 35.9$, $T_{o\ SR} = 35.18$, $T_{pref} = 35.36$; *Vicenzi et al., 2019*). These results reinforce the hypothesis of coadaptation of thermoregulatory behavior and thermal physiology, which states that individuals select T_b that optimize their physiological functions and, hence, fitness (*Huey & Stevenson, 1979*; *Huey & Bennett, 1987*; *Angilletta, Hill & Robson, 2002*; *Bonino et al., 2011*).

The T_e and field T_b for *P. tenebrosus* are below its T_{pref} and also below the temperatures at which these lizards reach maximum locomotor performance (T_o and B_{80}, for SR and LR). In addition, the indices of efficiency of thermoregulation showed that *P. tenebrosus* has the lowest E index reported for the genus (*Corbalán, Debandi & Kubisch, 2013*; *Gómez Alés, Acosta & Laspiur, 2017*; *Vicenzi et al., 2017*; *Duran, Kubisch & Boretto, 2018*), with limited ability to achieve T_{pref} in their natural environment. This lizard can thus be considered a poor thermoregulator, similar to *Liolaemus sarmientoi* from southern Patagonia (50°S; $E = 0.30$, mean $T_b = 26.18$ °C; *Ibargüengoytía et al., 2010*). Despite of living in cold-temperate climates, *P. tenebrosus* as several other Liolaemidae lizards, presents a conservative high value of T_{pref}, generally higher than the mean T_e and mean T_b (*Cruz et al., 2009*; *Labra, Pienaar & Hansen, 2009*; *Rodríguez-Serrano, Navas & Bozinovic, 2009*; *Ibargüengoytía et al., 2010*; *Kubisch, Fernández & Ibargüengoytía, 2011*; *Medina et al., 2012*; *Moreno Azócar et al., 2013*; *Corbalán, Debandi & Kubisch, 2013*). This could be partially explained by the fact that thermoregulation is an expensive behavior that increases energy expenditures and risk of predation (*Sears & Angilletta, 2015*) and also by the low availability of T_{pref} in the microenvironments that most of Patagonian lizards inhabit.

Phymaturus tenebrosus lives under harsher conditions than other *Phymaturus* from Patagonia, because it lives at high latitudes and also next to the Andes, which produces a colder and more humid climate (*Kubisch et al., 2017*), than the steppe habitats where other congeners occur (*Cabezas-Cartes, 2016*). For example, the Patagonian *P. querque* ($E = 0.44$) and *P. zapalensis* ($E = 0.47$) from Zapala, Neuquén (39°S, 70°W) experience higher T_e than their mean T_b and T_{pref} (*Duran, Kubisch & Boretto, 2018*), which allow them to thermoregulate more effectively than *P. tenebrosus*. Whereas northern species of the genus like *P. payuniae* ($E = 0.64$; *Corbalán, Debandi & Kubisch, 2013*), *P. palluma* ($E = 0.79$; *Vicenzi et al., 2017*), and *P. extrilidus* ($E = 0.65$; *Gómez Alés, Acosta & Laspiur, 2017*) are also more efficient thermoregulators than *P. tenebrosus*, despite of inhabiting low thermal quality environments.

Most recent studies in lepidosaurians have found negative effects of climate change, highlighting these animals' vulnerability to temperature variation (*Diele-Viegas & Rocha, 2018*). However, it was also suggested that thermal tolerance breadths of ectotherms generally increase with latitude, and also that these ectotherms live at cooler temperatures than their physiological optima, so warming may enhance fitness in high-latitude species (*Deutsch et al., 2008*; *Fernández et al., 2011*; *Sunday et al., 2014*; *Bonino et al., 2015a*). In the case of *P. palluma* from the highlands of the Central Andes (*Vicenzi et al., 2019*) the T_{pref} and T_o are very similar to those found for *P. tenebrosus* in this study, but the indices to estimate vulnerability to global warming are substantially different. *P. palluma* experiences T_e that included the B_{80} and the set point range of T_{pref}, but has very low values of WT and TSM. Thus, the authors estimated that with an increase in temperatures due to global warming, this Andean species will become vulnerable to extinction. In the case of *P. tenebrosus*, in contrast to our predictions, the indices to estimate vulnerability to global warming are very high, indicating that lizards of this species cannot reach temperatures near their T_o for locomotor performance or their T_{pref}. So, as was also suggested for the congener *P. extrilidus* (*Gómez Alés et al., 2018*), the southernmost reptiles of the world (*L. sarmientoi* and *L. magellanicus*, *Fernández et al., 2011*), and other liolaemids (*Bonino et al., 2015a*), our study species has a wide safety margin until fitness would decline, and may actually benefit from predicted climate warming for at least the next few decades.

Studies on thermal physiology in lizards generally reveal that climate change will allow them fewer hours of activity, with few opportunities to reproduce and forage, and will reduce performance capacity (*Sinervo et al., 2010*; *Buckley, Tewksbury & Deutsch, 2013*; *Gilbert & Miles, 2017*). For example, the Patagonian congeners *P. querque* and *P. zapalensis*, as well as the Andean *P. palluma*, are forced to retreat to cool refuges to avoid overheating during their active period because of high T_es (*Vicenzi et al., 2017*; *Duran, Kubisch & Boretto, 2018*). *P. tenebrosus* is an endangered species with ecological conditions that increase their vulnerability to global warming. However, the ability to withstand the impact of habitat warming might be important for this species to survive future global change. The present study together with some other studies on thermal physiology and locomotor performance of Andean and Patagonian lizards (*Bonino et al., 2011*, *2015a*; *Fernández et al., 2011*; *Gómez Alés et al., 2018*), suggest these animals are not likely to be threatened by the higher temperatures predicted as a result of global warming.

CONCLUSIONS

Phymaturus tenebrosus exhibit its maximum locomotor performance at temperatures similar to its T_{pref}. These temperatures are substantially higher than the mean temperature it currently experiences in its habitat. In addition, it exhibits a low effectiveness of thermoregulation, being a poor thermoregulator. Further research should analyze if current T_e (similar to the mean T_b) experienced by *P. tenebrosus* are optimal temperatures for other biological processes such as bite force, stamina, feeding rate, growth rate, or behavioral traits (territorial defense, courtship). However, in view of the results obtained, specifically based on the high TSMs estimated, we suggest that considering the higher temperatures predicted as a result of global warming, *P. tenebrosus* is likely to experience climatic conditions in Patagonia that may enhance its thermal physiology and locomotor performance, favoring the survival of this species to future global climate change.

ACKNOWLEDGEMENTS

We would like to thank Nora Ibargüengoytía for her valuable methodological and logistic support and Sonia Fontenla for kindly lending us the environmental chamber where we carried out the locomotor performance trials. Also, we would like to thank Donato D'Arielli, Fausto Valentino Cabezas, and Enrique Stigliano for their important help in the field. Besides, we are very grateful to Elizabeth Bastiaans who reviewed the English language of the manuscript. Félix Cruz and an anonymous reviewer made insightful comments to the manuscript that improved it significantly. We also thank Universidad Nacional del Comahue (CRUB).

Funding

The authors received no funding for this work.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Facundo Cabezas-Cartes conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Jimena B. Fernández conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Fernando Duran performed the experiments, analyzed the data, approved the final draft.
- Erika L. Kubisch conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

Lizards were cared for following the ASIH/HL/SSAR Guidelines for Use of Live Amphibians and Reptiles, as well as the regulations detailed in the Argentinean National Law N° 14346.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

A scientific collecting permit (Disposición No. 108/17) was obtained from the Secretaría de Ambiente y Desarrollo Sustentable of Rio Negro Province, Argentina.

Data Availability

The raw data are available in the Supplemental Files. The raw data shows all maximum speed achieved in sprint and long runs in each temperature trial by each lizard.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.7437#supplemental-information.

REFERENCES

Abdala S. 2017. *Phymaturus tenebrosus. The IUCN Red List of Threatened Species* **2017**:e.T5625180 DOI 10.2305/IUCN.UK.2017-2.RLTS.T56251804A56251807.en.

Abdala CS, Acosta JL, Acosta JC, Álvarez BB, Arias F, Avila LJ, Blanco MG, Bonino M, Boretto JM, Brancatelli G, Breitman MF, Cabrera MR, Cairo S, Corbalán V, Hernando A, Ibargüengoytía NR, Kacoliris F, Laspiur A, Montero R, Morando M, Pelegrin N, Pérez CHF, Quinteros AS, Semhan RV, Tedesco ME, Vega L, Zalba SM. 2012. Categorización del estado de conservación de las lagartijas y anfisbenas de la República Argentina. *Cuadernos de Herpetologia* **26**:1–31.

Adolph SC, Porter WP. 1993. Temperature, activity, and lizard life histories. *American Naturalist* **142(2)**:273–295 DOI 10.1086/285538.

Andrew NR, Hart RA, Jung M-P, Hemmings Z, Terblanche JS. 2013. Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. *Journal of Insect Physiology* **59(9)**:870–880 DOI 10.1016/j.jinsphys.2013.06.003.

Angilletta MJ Jr. 2006. Estimating and comparing thermal performance curves. *Journal of Thermal Biology* **31(7)**:541–545 DOI 10.1016/j.jtherbio.2006.06.002.

Angilletta MJ Jr. 2009. *Thermal adaptation: a theorerical and empirical synthesis.* Oxford: Oxford University Press.

Angilletta MJ Jr, Bennett AF, Guderley H, Navas CA, Seebacher F, Wilson RS. 2006. Coadaptation: a unifying principle in evolutionary thermal biology. *Physiological and Biochemical Zoology* **79(2)**:282–294 DOI 10.1086/499990.

Angilletta MJ Jr, Hill T, Robson MA. 2002. Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard, *Sceloporus undulatus*. *Journal of Thermal Biology* **27(3)**:199–204 DOI 10.1016/S0306-4565(01)00084-5.

Araújo MB, Thuiller W, Pearson RG. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* **33(10)**:1712–1728 DOI 10.1111/j.1365-2699.2006.01482.x.

Barros VR, Boninsegna JA, Camilloni IA, Chidiak M, Magrín GO, Rusticucci M. 2015. Climate change in Argentina: trends, projections, impacts and adaptation. *Wiley Interdisciplinary Reviews: Climate Change* **6(2)**:151–169 DOI 10.1002/wcc.316.

Ben-Ezra E, Bulté G, Blouin-Demers G. 2008. Are locomotor performances coadapted to preferred basking temperature in the northern map turtle (*Graptemys geographica*)? *Journal of Herpetology* **42(2)**:322–331 DOI 10.1670/07-1881.1.

Bestion E, Teyssier A, Richard M, Clobert J, Cote J. 2015. Live fast, die young: experimental evidence of population extinction risk due to climate change. *PLOS Biology* **13(10)**:e1002281 DOI 10.1371/journal.pbio.1002281.

Bonino MF, Azócar DLM, Tulli MJ, Abdala CS, Perotti MG, Cruz FB. 2011. Running in cold weather: morphology, thermal biology, and performance in the southernmost lizard clade in the world (*Liolaemus lineomaculatus* section: Liolaemini: Iguania). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* **315A(8)**:495–503 DOI 10.1002/jez.697.

Bonino MF, Moreno Azócar DL, Schulte JA, Abdala CS, Cruz FB. 2015a. Thermal sensitivity of cold climate lizards and the importance of distributional ranges. *Zoology* **118(4)**:281–290 DOI 10.1016/j.zool.2015.03.001.

Bonino MF, Moreno Azócar DL, Schulte JA, Cruz FB. 2015b. Climate change and lizards: changing species' geographic ranges in Patagonia. *Regional Environmental Change* **15(6)**:1121–1132 DOI 10.1007/s10113-014-0693-x.

Boretto JM, Cabezas-Cartes F, Tappari F, Méndez-De La Cruz F, Sinervo B, Scolaro AJ, Ibargüengoytía NR. 2014. Reproductive biology of *Phymaturus spectabilis* (Liolaemidae): females skip reproduction in cold and harsh environments of Patagonia, Argentina. *Herpetological Conservation and Biology* **9**:170–180.

Bozinovic F, Pörtner HO. 2015. Physiological ecology meets climate change. *Ecology and Evolution* **5(5)**:1025–1030 DOI 10.1002/ece3.1403.

Buckley LB, Tewksbury JJ, Deutsch CA. 2013. Can terrestrial ectotherms escape the heat of climate change by moving? *Proceedings of the Royal Society B: Biological Sciences* **280(1765)**:20131149 DOI 10.1098/rspb.2013.1149.

Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer.

Cabezas-Cartes F. 2016. *Análisis Comparado del Crecimiento, Longevidad e Inversión Reproductiva en el Género Phymaturus en un Gradiente Latitudinal y Altitudinal*. San Carlos de Bariloche: Universidad Nacional del Comahue.

Cabezas-Cartes F, Kubisch EL, Ibargüengoytía NR. 2014. Consequences of volcanic ash deposition on the locomotor performance of the *Phymaturus spectabilis* lizard from Patagonia, Argentina. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* **321(3)**:164–172 DOI 10.1002/jez.1846.

Cabrera AL. 1976. *Enciclopedia Argentina de agricultura y jardinería: regiones fitogeográficas Argentinas*. Buenos Aires: ACME S.A.C.I.

Cabrera AL. 1978. La vegetación de Patagonia y sus relaciones con la vegetación altoandina y puneña. In: Tholl C, Laver W, eds. *Geological Relations Between the Southern Temperate Zone and the Tropical Mountains*. Wiesbaden: Franz Steiner Verlag, 329–343.

Chamaille-Jammes S, Massot M, Aragon P, Clobert J. 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* **12(2)**:392–402 DOI 10.1111/j.1365-2486.2005.01088.x.

Corbalán V, Debandi G, Kubisch E. 2013. Thermal ecology of two sympatric saxicolous lizards of the genus *Phymaturus* from the Payunia region (Argentina). *Journal of Thermal Biology* **38(7)**:384–389 DOI 10.1016/j.jtherbio.2013.05.006.

Cruz FB, Belver L, Acosta JC, Villavicencio HJ, Blanco G, Cánovas MG. 2009. Thermal biology of *Phymaturus* lizards: evolutionary constraints or lack of environmental variation? *Zoology* **112(6)**:425–432 DOI 10.1016/j.zool.2009.03.004.

Daufresne M, Lengfellner K, Sommer U. 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **106(31)**:12788–12793 DOI 10.1073/pnas.0902080106.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* **105(18)**:6668–6672 DOI 10.1073/pnas.0709472105.

Diele-Viegas LM, Rocha CFD. 2018. Unraveling the influences of climate change in Lepidosauria (Reptilia). *Journal of Thermal Biology* **78**:401–414 DOI 10.1016/j.jtherbio.2018.11.005.

Dillon ME, Wang G, Huey RB. 2010. Global metabolic impacts of recent climate warming. *Nature* **467(7316)**:704–706 DOI 10.1038/nature09407.

Duran F, Kubisch EL, Boretto JM. 2018. Thermal physiology of three sympatric and syntopic Liolaemidae lizards in cold and arid environments of Patagonia (Argentina). *Journal of Comparative Physiology B* **188(1)**:141–152 DOI 10.1007/s00360-017-1116-3.

Fernández JB, Smith J Jr, Scolaro A, Ibargüengoytía NR. 2011. Performance and thermal sensitivity of the southernmost lizards in the world, *Liolaemus sarmientoi* and *Liolaemus magellanicus*. *Journal of Thermal Biology* **36(1)**:15–22 DOI 10.1016/j.jtherbio.2010.09.006.

Garland TJ, Losos JB. 1994. Ecological morphology of locomotor in squamate reptiles. In: Wainwright PC, Reilly SM, eds. *Ecological Morphology: Integrative Organismal Biology*. Chicago: University of Chicago Press, 240–302.

Gilbert AL, Miles DB. 2017. Natural selection on thermal preference, critical thermal maxima and locomotor performance. *Proceedings of the Royal Society B: Biological Sciences* **284(1860)**:20170536 DOI 10.1098/rspb.2017.0536.

Gómez Alés R, Acosta JC, Astudillo V, Córdoba M, Blanco GM, Miles D. 2018. Effect of temperature on the locomotor performance of species in a lizard assemblage in the Puna region of Argentina. *Journal of Comparative Physiology B* **188(6)**:977–990 DOI 10.1007/s00360-018-1185-y.

Gómez Alés R, Acosta JC, Laspiur A. 2017. Thermal biology in two syntopic lizards, *Phymaturus extrilidus* and *Liolaemus parvus*, in the Puna region of Argentina. *Journal of Thermal Biology* **68**:73–82 DOI 10.1016/j.jtherbio.2017.02.001.

Hertz PE, Huey RB, Stevenson RD. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *American Naturalist* **142(5)**:796–818 DOI 10.1086/285573.

Huey RB, Bennett AF. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* **41(5)**:1098–1115 DOI 10.1111/j.1558-5646.1987.tb05879.x.

Huey RB, Stevenson RD. 1979. Intergrating thermal physiology and ecology of ecotherms: a discussion of approaches. *American Zoologist* **19(1)**:357–366 DOI 10.1093/icb/19.1.357.

Ibargüengoytía NR. 2004. Prolonged cycles as a common reproductive pattern in viviparous lizards from Patagonia, Argentina: reproductive cycle of *Phymaturus patagonicus*. *Journal of Herpetology* 38(1):73–79 DOI 10.1670/47-02A.

Ibargüengoytía NR, Cabezas-Cartes F, Boretto JM, Piantoni C, Kubisch EL, Fernández MS, Lara-Resendiz RA, Méndez-De La Cruz FR, Scolaro A, Sinervo B. 2016. Volcanic ash from Puyehue-Cordón Caulle eruptions affects running performance and body condition of *Phymaturus* lizards in Patagonia, Argentina. *Biological Journal of the Linnean Society* 118(4):842–851 DOI 10.1111/bij.12778.

Ibargüengoytía NR, Marlin Medina S, Fernández JB, Gutiérrez JA, Tappari F, Scolaro A. 2010. Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. *Journal of Thermal Biology* 35(1):21–27 DOI 10.1016/j.jtherbio.2009.10.003.

IPCC. 2014. *Climate change 2014. Synthesis report*. Cambridge: Cambridge University Press DOI 10.1017/CBO9781107415324.

Irschick DJ, Garland T Jr. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annual Review of Ecology and Systematics* 32(1):367–396 DOI 10.1146/annurev.ecolsys.32.081501.114048.

Irschick DJ, Meyers JJ, Husak JF, Le Galliard JF. 2008. How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research* 10:177–196.

Kubisch EL, Corbalán V, Ibargüengoytía NR, Sinervo B. 2016. Local extinction risk of three species of lizard from Patagonia as a result of global warming. *Canadian Journal of Zoology* 94(1):49–59 DOI 10.1139/cjz-2015-0024.

Kubisch EL, Fernández JB, Ibargüengoytía NR. 2011. Is locomotor performance optimised at preferred body temperature? A study of *Liolaemus pictus argentinus* from northern Patagonia, Argentina. *Journal of Thermal Biology* 36(6):328–333 DOI 10.1016/j.jtherbio.2011.06.006.

Kubisch EL, Fernández JB, Ibargüengoytía NR. 2016. Vulnerability to climate warming of *Liolaemus pictus* (Squamata, Liolaemidae), a lizard from the cold temperate climate in Patagonia, Argentina. *Journal of Comparative Physiology B* 186(2):243–253 DOI 10.1007/s00360-015-0952-2.

Kubisch E, Ippi S, Karlanian J, Ojeda V. 2017. Distribution extension of a rare *Phymaturus* lizard (Squamata: Liolaemidae) reaching Nahuel Huapi National Park (Argentina). *Herpetology Notes* 10:59–62.

Labra A, Pienaar J, Hansen TF. 2009. Evolution of thermal physiology in *Liolaemus* lizards: adaptation, phylogenetic inertia, and niche tracking. *American Naturalist* 174(2):204–220 DOI 10.1086/600088.

Logan ML, Huynh RK, Precious RA, Calsbeek RG. 2013. The impact of climate change measured at relevant spatial scales: new hope for tropical lizards. *Global Change Biology* 19(10):3093–3102 DOI 10.1111/gcb.12253.

Medina M, Scolaro A, Méndez-De La Cruz F, Sinervo B, Miles DB, Ibargüengoytía NR. 2012. Thermal biology of genus *Liolaemus*: a phylogenetic approach reveals advantages of the genus to survive climate change. *Journal of Thermal Biology* 37(8):579–586 DOI 10.1016/j.jtherbio.2012.06.006.

Moreno Azócar DL, Vanhooydonck B, Bonino MF, Perotti MG, Abdala CS, Schulte JA, Cruz FB. 2013. Chasing the Patagonian sun: comparative thermal biology of *Liolaemus* lizards. *Oecologia* 171(4):773–788 DOI 10.1007/s00442-012-2447-0.

Ofori BY, Stow AJ, Baumgartner JB, Beaumont LJ. 2017. Combining dispersal, landscape connectivity and habitat suitability to assess climate-induced changes in the distribution of Cunningham's skink, *Egernia cunninghami*. *PLOS ONE* **12(9)**:e0184193 DOI 10.1371/journal.pone.0184193.

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421(6918)**:37–42 DOI 10.1038/nature01286.

Perez CHF, Frutos N, Kozykariski M, Morando M, Perez DR, Avila LJ. 2011. Lizards of Rio Negro province, northern Patagonia, Argentina. *Check List* **7(3)**:202–219 DOI 10.15560/7.3.202.

Piantoni C, Cussac V, Ibargüengoytía N. 2006. Age and growth of the Patagonian lizard *Phymaturus patagonicus*. *Amphibia-Reptilia* **27(3)**:385–392 DOI 10.1163/156853806778189981.

Pörtner HO, Farrell AP. 2008. Physiology and climate change. *Science* **322(5902)**:690–692 DOI 10.1126/science.1163156.

Rodríguez-Serrano E, Navas CA, Bozinovic F. 2009. The comparative field body temperature among Liolaemus lizards: testing the static and the labile hypotheses. *Journal of Thermal Biology* **34(6)**:306–309 DOI 10.1016/j.jtherbio.2009.04.002.

Sears MW, Angilletta MJ Jr. 2015. Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. *American Naturalist* **185(4)**:E94–E102 DOI 10.1086/680008.

Sheridan JA, Bickford D. 2011. Shrinking body size as an ecological response to climate change. *Nature Climate Change* **1(8)**:401–406 DOI 10.1038/nclimate1259.

Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS, Slotsbo S, Dong Y, Harley CDG, Marshall DJ, Helmuth BS, Huey RB. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters* **19(11)**:1372–1385 DOI 10.1111/ele.12686.

Sinervo B, Méndez-De-La-Cruz F, Miles DB, Heulin B, Bastiaans E, Cruz MVS, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, Gadsden H, Avila LJ, Morando M, De La Riva IJ, Sepúlveda PV, Rocha CFD, Ibargüengoytía N, Puntriano CA, Massot M, Lepetz V, Oksanen TA, Chappie DG, Bauer AM, Branch WR, Clobert J, Sites JW. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328(5980)**:894–899 DOI 10.1126/science.1184695.

Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America* **111(15)**:5610–5615 DOI 10.1073/pnas.1316145111.

Vicenzi N, Corbalán V, Miles D, Sinervo B, Ibargüengoytía N. 2017. Range increment or range detriment? Predicting potential changes in distribution caused by climate change for the endemic high-Andean lizard *Phymaturus palluma*. *Biological Conservation* **206**:151–160 DOI 10.1016/j.biocon.2016.12.030.

Vicenzi N, Kubisch E, Ibargüengoytía N, Corbalán V. 2019. Thermal sensitivity of performance of *Phymaturus palluma* (Liolaemidae) in the highlands of Aconcagua: vulnerability to global warming in the Andes. *Amphibia-Reptilia* **40(2)**:207–218 DOI 10.1163/15685381-20181072.

Walther G-R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365(1549)**:2019–2024 DOI 10.1098/rstb.2010.0021.