

Vulnerability to global warming of the critically endangered Añelo Sand Dunes Lizard (*Liolaemus cuyumhue*) from the Monte Desert, Patagonia Argentina

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Abstract: The body temperature of lizards is strongly influenced by the thermal quality of microhabitats, exploiting the favourable environmental temperatures, and avoiding exposure to extreme thermal conditions. For these reasons, reptile populations are considered to be especially vulnerable to changes in environmental temperatures produced by climate change. Here, we study the thermal physiology of the critically endangered Añelo Sand Dunes Lizard (*Liolaemus cuyumhue* Avila, Morando, Perez and Sites, 2009). We hypothesise that (i) there is a thermal coadaptation between optimal temperature for locomotor performance of *L. cuyumhue* and its thermal preference; (ii) *L. cuyumhue* lives in an environment with low thermal quality; and (iii) a rise in environmental temperatures due to global warming will impose a decrement in locomotor speed represented by lower warming tolerance and narrower thermal safety margins, increasing their already high vulnerability. We recorded field body temperatures (T_b), preferred body temperatures (T_{pref}), the operative temperature (T_e), and the thermal sensitivity of locomotion at different body temperatures. Our results indicate that this lizard is not currently under environmental stress or exceeding its thermal limits, but that it is thermoregulating below T_{pref} to avoid overheating, and that an increase in environmental temperature higher than 3.5 °C will strongly affect the use of microhabitats with direct sun exposure.

Key words: climate change, vulnerable, *Liolaemus cuyumhue*, Añelo Sand Dunes Lizard, thermal sensitivity, locomotion, optimal temperature.

Résumé : La température du corps des reptiles est fortement influencée par la qualité thermique des microhabitats, l'exploitation de températures ambiantes favorables et l'évitement de conditions thermiques extrêmes. Pour ces raisons, les populations de reptiles sont considérées être particulièrement vulnérables aux variations des températures ambiantes découlant des changements climatiques. Nous étudions la physiologie thermique d'une espèce de lézard en danger critique, *Liolaemus cuyumhue* Avila, Morando, Perez et Sites, 2009. Nous postulons que (i) il y a coadaptation thermique entre la température optimale pour la performance locomotrice de *L. cuyumhue* et sa température de prédilection, (ii) *L. cuyumhue* vit dans un milieu de mauvaise qualité thermique et (iii) une hausse des températures ambiantes causée par le réchauffement planétaire entraînera une baisse de la vitesse de locomotion représentée par une tolérance plus faible au réchauffement et des plages de sécurité thermiques plus étroites, rehaussant la vulnérabilité déjà élevée de l'espèce. Nous avons enregistré la température du corps sur le terrain (T_b), les températures du corps de prédilection (T_{pref}), la température opérative (T_e) et la sensibilité thermique de la locomotion à différentes températures du corps. Nos résultats indiquent que ce lézard n'est présentement pas assujéti à un stress environnemental et que ses limites thermiques ne sont pas dépassées, mais qu'il fait preuve de thermorégulation pour se maintenir à des températures inférieures à sa T_{pref} afin d'éviter la surchauffe, et qu'une hausse de plus de 3,5 °C des températures ambiantes aura une forte incidence sur l'utilisation de microhabitats caractérisés par une exposition directe au soleil. [Traduit par la Rédaction]

Mots-clés : changement climatique, vulnérable, *Liolaemus cuyumhue*, lézard, sensibilité thermique, locomotion, température optimale.

Introduction

Ectotherms are not capable of producing and using metabolic heat for thermoregulation, and thus regulate their body temperature by behaviourally exploiting thermal resources (Bogert 1959).

Through behavioural thermoregulation, ectotherms (and particularly reptiles) attempt to deal with the environmental conditions that can dramatically determine behavioural and physiological processes (Huey 1982; Van Damme et al. 1991; Angilletta et al.

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Fig. 1. Adult male (A) and habitat (B) of Añelo Sand Dunes Lizard (*Liolaemus cuyumhue*). Colour version online.



2002a). As a result, the body temperature of reptiles is strongly influenced by the thermal quality of microhabitats, exploiting the favourable environmental temperatures, and avoiding exposure to extreme thermal conditions (Hertz et al. 1993; Besson and Cree 2010). For these reasons, reptiles are considered to be especially vulnerable to changes in environmental temperatures produced by climate change (e.g., Deutsch et al. 2008; El-Gabbas et al. 2016; Winter et al. 2016).

Many lizard populations across the world may be at risk of extinction due to the rapidly warming climate. In these populations, environmental temperatures increasingly exceed the thermal tolerances of lizards, limiting the activity, which translates ecologically into a constraint on available foraging and reproduction times (Grant and Dunham 1988; Huey et al. 2009; Sinervo et al. 2010; Kubisch et al. 2016; Kirchhof et al. 2017). However, the susceptibility of lizards to altered thermal niches depends on the interaction of many factors (Kirchhof et al. 2017), including availability of microhabitats, daily activity patterns, and foraging behaviour (e.g., Tingley et al. 2013; Böhm et al. 2016). A standard way to estimate the ecological consequences of raising temperature involves measuring how body temperature affects organismal-level performance (such as locomotion, digestive efficiency, or foraging rate; Huey and Slatkin 1976; Sinclair et al. 2016). Locomotion is an important temperature-dependent whole-organism functional performance trait of reptiles used in many ecologically relevant activities such as foraging, courtship, and escape from predators (Jayne and Bennett 1990; Pinch and Claussen 2003). Several authors have suggested that the action of natural selection over many generations would ensure that thermoregulatory behaviour and locomotion's thermal physiology have coevolved (Huey and Bennett 1987; Angilletta et al. 2006). The relationship between temperature and locomotor performance is generally described by a thermal performance curve (TPC) that allows one to estimate the optimal temperature for maximum performance (T_o) and the thermal performance breadth (e.g., B_{80}) (Gómez Alés et al. 2018; Cabezas-Cartes et al. 2019).

In particular, deserts are among the most extreme habitats inhabited by lizards due to the challenges imposed by thermal and hydric constraints (Labra et al. 2001; Lara-Reséndiz et al. 2014; Kirchhof et al. 2017). Lizards can experience large temperature differences in these environments by simply moving from shade into open sunlight (Hertz 1992; Bauwens et al. 1996). Some diurnal desert lizards during the warmest seasons usually thermoregulate so that they maintain body temperatures below their preferred temperature (T_{pref}) values to avoid reaching their critical thermal maximum (CT_{max} ; risk-avoidance hypothesis; Martin and Huey 2008). This strategy reduces the risk of overheating

when there is low spatial thermal heterogeneity for behavioural thermoregulation (Labra et al. 2001; Lara-Reséndiz et al. 2015; Kirchhof et al. 2017).

The genus *Liolaemus* Wiegmann, 1834 is one of the most diverse genera of reptiles, represented by more than 262 recognised species of lizards (Olave et al. 2020), and its members can be found in a wide variety of environments (Medina et al. 2012). Species of the genus *Liolaemus* are known to present low variability in T_{pref} values, usually between 30 and 38 °C (Labra et al. 2009; Medina et al. 2012; Moreno Azócar et al. 2013; Cruz et al. 2014). However, thermoregulation or selection of different microenvironments seems to be flexible enough to deal with the environmental constraints in most species of the genus (Ibargüengoytia et al. 2010; Kirchhof et al. 2017; Stelatelli et al. 2020).

Within the subgenus *Eulaemus* Girard, 1858, morphological, behavioural, and molecular studies have resolved a clade of arenicolous lizards known as the *Liolaemus wiegmanni* group (Etheridge 2000; Olave et al. 2014; Villamil et al. 2019); it is also known as “the sand lizards’ clade” of *Liolaemus* because of its specialisations for diving under the sand. The *wiegmanni* group includes 12 species of oviparous lizards (Villamil et al. 2019); some of them with a very restricted geographic distribution. Herewithin, we study the thermal physiology and the thermal sensitivity of locomotor performance in the Añelo Sand Dunes Lizard (*Liolaemus cuyumhue* Avila, Morando, Perez and Sites, 2009), an insectivorous desert lizard, from the *wiegmanni* group (Fig. 1A). This species has been categorised as critically endangered by the International Union for the Conservation of Nature (IUCN) (Avila 2016). *Liolaemus cuyumhue* is endemic to an isolated Mediterranean aeolian sand dune system in the region known as Bajo de Añelo in the center-east of Neuquén province, Argentina (Avila et al. 2009). The known distribution of this species covers about 1000 km² (M.V. Brizio, unpublished data). Individuals of *L. cuyumhue* are observed only on bare or sparsely vegetated dunes with extensive areas of open sand (Fig. 1B). Besides its restricted distribution, the habitat of *L. cuyumhue* is constantly altered by intense grazing and oil and gas exploitation. This particular region is where oil companies conduct some of the more intensive operations in Argentina. New rigs, tracks, and roads are opened regularly, frequently modifying areas that are suitable for the species (Avila 2016).

In this paper, we aim to study the most relevant parameters of the thermal physiology of *L. cuyumhue* to estimate the thermal sensitivity of locomotor performance, the thermal quality of its habitat, and the effects of an increase in environmental temperature, due to climate change, predicted for the region where this lizard lives (based on IPCC 2014; Barros et al. 2015). We hypothesise that (i) there is a thermal coadaptation (Huey and Bennett

1987; Angilletta et al. 2006) between optimal temperature for locomotor performance of *L. cuyumhue* and its thermal preference; (ii) *L. cuyumhue* lives in an environment with low thermal quality; (iii) a rise in environmental temperatures due to global warming will impose a decrement in locomotor speed represented by lower warming tolerance and narrower thermal safety margins, increasing their already high vulnerability.

Materials and methods

Study site and fieldwork

The study was carried out in the Bajo de Añelo basin, located in the center-east of Neuquén province, Argentina (37.4°S to 38.5°S and 68.4°W to 69.8°W). The Bajo de Añelo basin comprises the lowest area of the province (230 m above sea level) and covers an area of 9000 km², placed within the Monte Desert region. The climate is temperate arid to semi-arid, with a mean annual temperature of 14.2 °C and a mean annual precipitation of 137.2 mm, occurring mainly in winter and spring (Busso and Bonvissuto 2009). The vegetation presents a marked physiognomic–floristic homogeneity, characterised by being a shrubby steppe with perennial foliage represented by Jarillas (genus *Larrea* Cav.) with little herbaceous cover (Fig. 1B) and scarcity of grasses and trees (Leon et al. 1998; Roig et al. 2009).

We captured 20 adult specimens of *L. cuyumhue* (8 females and 12 males) by lasso when they were active between the hours of 0800 and 2000 on 6 March 2020 (austral summer). Considering the critically endangered conservation status of the species, we worked with the minimum sample size needed for statistical significance. Our experimental design was planned to minimise the time spent in captivity and the stress suffered by the individuals.

Immediately after capture, T_b was measured (TES 1303 Electrical Electronic Corp., Taipei, Taiwan, China; ± 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 1 cm above the ground (T_a) of the microenvironment where each lizard was captured. Each capture site was georeferenced with a GPS (Garmin eTrex® Touch 35).

The day after capture, lizards were carried to the laboratory located at Centro Regional Universitario Bariloche (CRUB) in individual cloth bags. During experiments (5 days), lizards were kept individually at room temperature (20–22 °C) in a quiet site. After experiments, body mass (Pesola 10 g, ± 0.3 g) and snout–vent length (SVL; digital calliper Lee Tools, ± 0.02 mm) were measured and sex recorded (based on the presence of pre-cloacal pores in males). All the lizards were released in good condition at their exact capture sites.

Ethics approval

Lizards were cared for following the Canadian Council on Animal Care (CCAC) guidelines and the *Guide for the Care and Use of Laboratory Animals* (8th edition; National Academies Press, Washington, D.C., USA), as well as the regulations detailed in the Argentinean National Law N° 14346.

Preferred body temperatures

We measured preferred body temperatures (T_{pref}) the day after capture. Lizards were placed individually in an open-top terrarium (100 cm \times 20 cm \times 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. The body temperatures of lizards were measured every 10 s for 3 h with a temperature Data Acquisition Module (USB-TC08; OMEGA, Biel/Bienne, Switzerland) using miniature size insulated thermocouples (OMEGA® part No. SSC-TT-T-40-72, diameter 0.076 mm). This thermocouple was 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 body temperatures preferred in the laboratory.

Effects of body temperature on locomotor performance

We performed locomotor performance trials on a racetrack 7.5 cm wide and 1.20 m long, leading to a shelter. Photocells, positioned at 15 cm intervals along the track, signalled 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 photoreceptors (0.15 m), which is relevant for predator escape and prey capture, and (2) long runs (LR), defined as the speed between the first and the last photoreceptors (1.05 m), which indicated the locomotor capability of the lizard to perform activities such as foraging, territorial defence, and courtship (Cabezas-Cartes et al. 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. The lizards did not rest between the three consecutive trials, but they were always rested at least 4 h between the different temperature treatments.

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 temperatures following the methodology of Cabezas-Cartes et al. (2019). 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. Trials were conducted at five different T_b s (22 ± 1 , 28 ± 1 , 33 ± 1 , 36 ± 1 °C, and 39.5 ± 1 °C) during three consecutive days. The order of each trial's temperature was established randomly. The T_b s for the treatments were chosen based on the following criteria: the median T_b in the field (33 °C) and the mean T_{pref} obtained in the laboratory for *L. cuyumhue* (36 °C). The T_b at 22 and 28 °C were included to define the shape of the curve. Also, we estimated performance at 39.5 °C to evaluate the locomotor performance at the mean $T_{pref} + 3.5$ °C. This is the environmental temperature increase anticipated by the end of this century at our study site based on the climatic assessment from IPCC (2014) and Barros et al. (2015).

Thermal tolerance

To determine the critical thermal minimum (CT_{min}), we place individually a subsample of eight lizards in a transparent plastic box (15 cm \times 10 cm \times 5 cm) in a refrigerator at -10 °C. T_b was measured every 30 s using a mini-infrared thermometer (DT-810 CEM) at a distance within 5 mm (Chukwuka et al. 2019). Lizards were observed throughout the experiment and we recorded and considered CT_{min} to be the T_b at which an individual was no longer able to right itself when placed on its back (Lowe and Vance 1955; Van Damme et al. 1991).

The same subsample of eight lizards was also used to determine critical thermal maximum (CT_{max}), the day after the CT_{min} experiments. Each lizard was placed in an open terrarium (with a diameter of 25 cm and 35 cm high) with an infrared 150 W lamp placed 40 cm overhead. The T_b was monitored every 30 s following the same methodology used in the CT_{min} experiments. Each lizard was carefully observed throughout the experiment and we recorded and considered CT_{max} to be 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 source and cooled quickly to avoid overheating. None of the individuals died during the trials.

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

Operative temperatures (T_e) represent the null distribution of potential body temperatures expected in non-thermoregulating animals (Hertz et al. 1993). The T_e was measured using grey polyvinyl chloride (PVC) oval plastic models, 100 mm length and 20 mm diameter, to mimic an adult *L. cuyumhue*. The model was chosen to represent a living animal and was validated for the King's Tree Iguana (*Liolaemus kingii* (Bell, 1843)), a species of similar shape and size compared with *L. cuyumhue*, showing no differences between the model temperature and the live animal temperature (Wilcoxon's signed rank test: $Z = 0.558$, $P = 0.577$; simple linear regression: $R^2 = 0.992$, $F_{[1,47]} = 5440.99$, $P < 0.001$; F. Duran, unpublished data). Each model was connected to a thermistor connected to data loggers (HOBO Onset Computer Corporation, Bourne, Massachusetts, USA). The eight models were placed in areas where we usually find the species: sun models (two on the sand, one buried in the sand, and two buried under grass) and shadow models (two under dense and loose bush and one buried under shade). The data loggers were programmed to record temperatures every minute during the day of capture. In our analyses, we used the T_e s recorded for 28 days between the hours of 0830 and 2000, which is the daily period of activity according to our 4 years of personal observations while working with this population.

To estimate thermoregulatory efficiency, we applied the methodology of Hertz et al. (1993), using the information on T_{pref} obtained in the thermal gradient and the availability of T_e in the natural environment. We calculate the d_b (thermoregulatory accuracy) as the absolute mean deviation of T_b from T_{set} for each individual. Then, we calculated the d_e as 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 and hourly variations in temperature that characterises the Monte Desert climate, the T_e is highly dynamic. Hence, we used the mean value of obtained T_e s considering all the models recorded from 1 h before each individual lizard was captured (sensu Cabezas-Cartes et al. 2019). Using the mean values of d_b and d_e , we calculated the effectiveness of thermoregulation (E) using the formula $E = 1 - (d_b/d_e)$ (Hertz et al. 1993), which integrates the mean degree to which *L. cuyumhue* 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 a thermoconformer, whereas when the E index approaches a value of one, the species can be considered a highly effective thermoregulator. If the E index is close to 0.5, then the species is considered a moderate thermoregulator (Hertz et al. 1993). Negative values of the E index are attributed to individuals that actively avoid thermally stable microhabitats (Huey and Slatkin 1976; Hertz et al. 1993). Finally, following Blouin-Demers and Weatherhead (2001), we measured the index of effectiveness of thermoregulation ($d_e - d_b$) to quantify the extent of departure from perfect thermoconformity.

In addition, we calculated two indices to estimate vulnerability to global warming. Firstly, we determined the warming tolerance (WT) index, which defines how much warming can be tolerated by an ectotherm before its performance is reduced to lethal levels, and is calculated as the difference between mean CT_{max} and mean T_e (sensu Deutsch et al. 2008; Logan et al. 2013). Secondly, we determined the thermal safety margin (TSM) for physiological performance as the difference between T_o and mean T_e , which gives an indication of how close the thermal optima of animals 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 2 D version 5.01.2 software to create locomotor performance curves (TPCs) as functions of temperature during SR

Table 1. Median \pm standard error (SE) and minimum and maximum temperature values of all models discriminated by microhabitat in which the model was located.

Microhabitats	Temperature ($^{\circ}\text{C}$)	
	Median \pm SE	Minimum and maximum values
On the sand (south–north)	37.0 \pm 0.15	17.3–64.3
On the sand (east–west)	34.5 \pm 0.16	14.5–62.2
Buried in the sun	37.4 \pm 0.14	15.6–55.2
Buried under grass	34.6 \pm 0.10	15.7–46.5
Under dense bush	29.4 \pm 0.10	12.7–45.3
Under loose bush	32.6 \pm 0.08	15.3–46.4
Buried under shade	27.5 \pm 0.08	15.0–48.2

and LR. The values of CT_{min} and CT_{max} were used as the extreme values of the curves. We chose the model according to the adjusted R^2 (following Angilletta 2006). The best candidate model for the overall sample was fitted to each individual 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_b s over which performance is greater than or equal to 80% of the V_{max} ; sensu Ben-Ezra et al. 2008) of each individual for LR and SR. We used the statistical software RStudio version 1.2.1335 (R Core Team 2020) and Sigma Plot version 11.0 for statistical analyses and to generate figures, respectively. Relationships between T_b , T_s , and T_a were analysed by simple linear regressions. To compare samples from the same lizard, we used paired t tests or the non-parametric alternative Wilcoxon's signed rank test when the assumptions of parametric statistics were not met. Means are reported with \pm standard errors (\pm SE). To analyse the effect of temperature on speed, we applied a linear mixed model (LMM) with a normal distribution; we performed post hoc pairwise comparisons (Tukey's test) between levels for the temperature effect.

Results

Body measurements and their relationship with locomotor performance

The mean SVL of *L. cuyumhue* ($N = 20$) was 49.3 ± 4.32 mm and the median body mass was 4.1 g (range 3.3–8.7 g). There was no relationship between maximum speeds during SR or LR and SVL (linear correlation: $R_{SR} = 0.13$, $R_{LR} = 0.09$, $P > 0.5$) or body mass (linear correlation: $R_{SR} = 0.11$, $R_{LR} = 0.06$, $P > 0.5$).

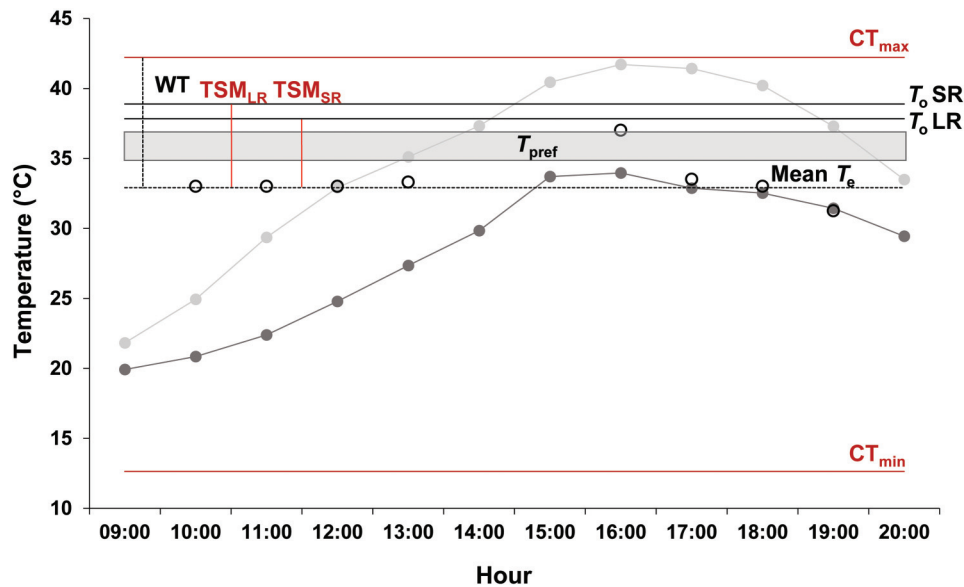
Field temperatures

The median T_b in the field was 33°C (range 31 – 37°C). Lizards were captured in microenvironments with a median T_a of 29°C (range 20 – 39°C) and a mean T_s of $38.2 \pm 6.58^{\circ}\text{C}$. There was a relationship between T_b and T_s (linear regression: $F_{[1,19]} = 8.02$, $R^2 = 0.27$, $P < 0.05$). The mean T_e was $32.9 \pm 0.09^{\circ}\text{C}$ (Table 1). The median T_e of sun models was $35.3 \pm 0.11^{\circ}\text{C}$ (range 15.7 – 51.1°C ; Fig. 2), whereas the median T_e of shadow models was $29.1 \pm 0.09^{\circ}\text{C}$ (range 15.0 – 45.9°C ; Fig. 2).

Thermal performance curves

The relationship between T_b and maximum speed for the overall sample was best described by an asymptotic logistic curve of the non-linear family for SR (adjusted $R^2 = 0.45$; Fig. 3, lower panel) and LR (adjusted $R^2 = 0.57$; Fig. 3, upper panel). Lizards ran faster during SR than LR (median $V_{max,SR} = 1.19$ m/s, $V_{max,LR} = 0.56$ m/s; Wilcoxon's signed rank test: $W = 1$, $P < 0.001$; Fig. 3). However, the T_o was similar between SR and LR (median $T_o,SR = 37.8^{\circ}\text{C}$, $T_o,LR = 38.9^{\circ}\text{C}$; Wilcoxon's signed rank test: $W = 115$, $P = 0.21$; Fig. 3). Considering the thermal performance breadth at which 80% of maximal speed could be reached (B_{80}), there was no difference between SR and LR ($B_{80,SR} = 32.3$ – 40.3°C , $B_{80,LR} = 33.3$ – 40.5°C ; Wilcoxon's signed rank test: $W = 85$, $P = 0.98$; Fig. 3). The

Fig. 2. Microenvironmental temperatures (T_e) of sun models (light grey line) and shadow models (dark grey line) during daily activity period of the Añelo Sand Dunes Lizard (*Liolaemus cuyumhue*). The critical thermal maximum (CT_{max}), critical thermal minimum (CT_{min}), optimal temperature during SR (T_{oSR}) and LR (T_{oLR}), and the mean T_e are indicated by horizontal lines. Additionally, the warming tolerance (WT; broken vertical line) and thermal safety margin (TSM; red vertical lines) indices are shown, as well as the set-point range of the preferred temperature (T_{pref} ; grey rectangle) and the mean body temperatures per hour of capture (T_b ; open circles). Colour version online.



median B_{80} for SR was 8.2 °C (range 3.0–9.8 °C), whereas the median B_{80} for LR was 7.4 °C (range 1.9–11.8 °C).

Effects of temperature on running speed

Thermal performance curves showed an effect of temperature on the speed of *L. cuyumhue*. The sprint speed increased with temperature ranging from 22 to 39.5 °C (Figs. 3 and 4). Sprint speeds differed among trials (LMM: $F_{[4,76]} = 16.55$, $P < 0.001$) (Fig. 4). The speed of long runs increased with temperature ranging from 22 °C to its maximum speed at 36 °C (Figs. 3 and 4). There were differences (LMM: $F_{[4,72]} = 23.43$, $P < 0.001$) in speed among trials (Fig. 4).

Thermal physiology of *L. cuyumhue*, effectiveness of thermoregulation, and vulnerability to global warming

The mean T_{pref} of *L. cuyumhue* was 35.9 ± 1.43 °C with a set-point range of 34.8–36.8 °C (Fig. 2). For the interquartile range of T_{pref} , 80% of *L. cuyumhue* T_b s were below this range and 20% were within it. In the case of the T_e , 13.4% were within the T_{pref} interquartile range, 66.5% were below it, and 24% were above it (Fig. 2). The T_{pref} was similar to T_o for SR (SR — Wilcoxon's signed rank test: $W = 137$, $P = 0.09$); in contrast, T_o for LR was higher than T_{pref} (paired t test: $t = 4.86$, $P < 0.001$). The mean critical minimum and maximum temperatures were 12.6 ± 1.35 and 42.2 ± 1.24 °C, respectively. Our results may indicate that *L. cuyumhue* is a moderate thermoregulator during the end of the summer season ($E = 0.64$, $d_b = 2$, $d_e = 5.52$, $d_e - d_b = 3.52$). The result for TSM and WT indices are shown in Table 2.

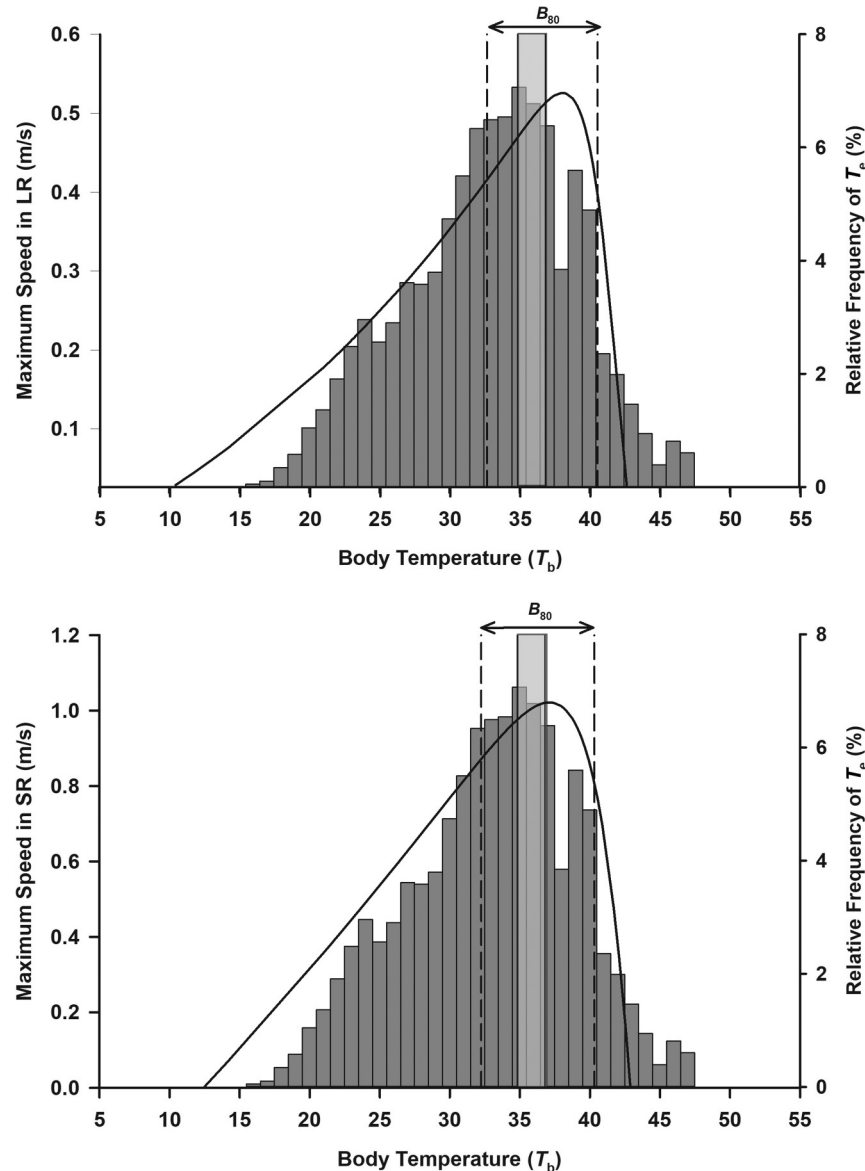
Discussion

This is the first study that describes locomotor performance and the possible effects of global warming in a species of the *wiegmannii* group, and particularly in the critically endangered *L. cuyumhue*. Our work suggests that *L. cuyumhue* is not currently under environmental stress or exceeding its thermal limits, but that it is thermoregulating below T_{pref} to avoid overheating, and that an increase in environmental temperature higher than 3.5 °C (predicted by the climate change models; Barros et al. 2015) will strongly affect the use of microhabitats with direct sun exposure.

The mean T_{pref} of *L. cuyumhue* (35.9 °C) is lower than the mean T_{pref} of other species of the *wiegmannii* group such as the Sand Dune Lizard (*Liolaemus multimaculatus* (Duméril and Bibron, 1837)) (37.2 °C; Stelletelli et al. 2020) and *Liolaemus wiegmannii* (Duméril and Bibron, 1837) (38.1 °C; Stelletelli et al. 2013), but is similar to the mean T_{pref} of *Liolaemus riojanus* Cei, 1979 (36.2 °C; Cruz et al. 2014). This result is in accordance with Rodríguez-Serrano et al. (2009), who suggested that thermal biology in the genus *Liolaemus* varies with an ecological gradient of ambient temperature. Thus, during summer, *L. cuyumhue* would likely reach a threshold beyond which the risks of overheating outweigh the benefits of thermoregulating to achieve their T_{pref} . Consequently, during the hottest period of the year, *L. cuyumhue* may prefer to stay in the shade, keeping body temperatures slightly below T_{pref} (like 80% of the individuals in this study) rather than expose itself to the direct sun, which could quickly increase T_b and reach lethal temperatures (Grant and Dunham 1988). This thermoregulatory behaviour has also been reported in the Husab Sand Lizard (*Pedioplanis husabensis* Berger-dell'mour and Mayer, 1989) of the Namib Desert (Kirchhof et al. 2017); it is opposite to the behaviour reported in the Sonoran Horned Lizard (*Phrynosoma goodii* Stejneger, 1893) of the Sonoran Desert, where T_b is never below T_{pref} (Lara-Resendiz et al. 2014). Furthermore, it is important to note that the T_{pref} is not an immutable variable, but it can vary temporally, spatially, and in different times of the life cycle of an organism (Andrews 1998; Stelletelli et al. 2013, 2020; Astudillo et al. 2019).

Regarding thermal sensitivity of locomotor performance, our results support the hypothesis that at least for sprint runs optimal temperature (36.9 °C) has coevolved with T_{pref} . This means that *L. cuyumhue* has an optimum adaptation for sprint runs, similar to the sympatric nocturnal gecko *Homonota darwini* Boulenger, 1885 (Ibargüengoytia et al. 2007; Aguilar and Cruz 2010). However, T_o for long runs (38.3 °C) was higher than T_{pref} . In this sense, Martin and Huey (2008) found that there is a tight relationship between T_{pref} and T_o , but that thermal preferences should not necessarily match temperatures optimal for fitness. Consequently, total fitness over time might be maximised by centring thermal preferences at a temperature below T_o , as we observed in our results

Fig. 3. Thermal performance curves for long runs (LR; upper panel) and sprints (SR; lower panel) of the Añelo Sand Dunes Lizard (*Liolaemus cuyumhue*). Vertical broken lines represent performance breadth (B_{80}) in SR and LR. Grey bars represent the percent frequency distribution of all operative temperatures (T_e) between activity hours. The light grey bar represents the set-point range of preferred body temperatures (T_{pref}) obtained in the laboratory.



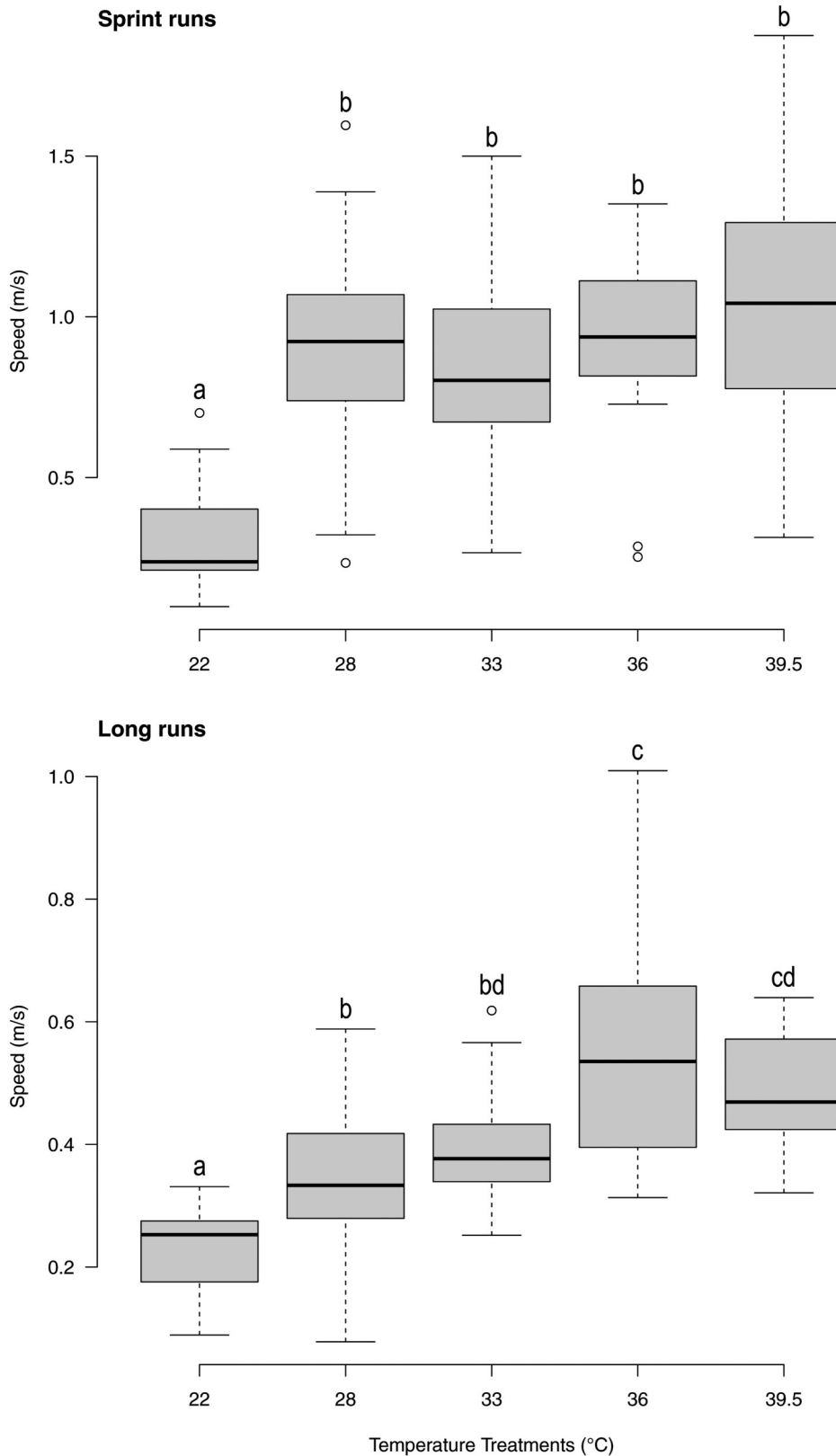
for long runs. Also, it is important to point out that optimal temperatures will probably be different for digestion, bite force, reproductive processes, and other essential physiological performances with narrower optimal temperature ranges (Angilletta et al. 2002a).

Speed for long runs increased with temperature in almost all of the temperature treatments (Fig. 4), which is in contrast with Angilletta et al. (2002b), who found in Eastern Fence Lizard (*Sceloporus undulatus* (Bosc and Daudin, 1801)) that speed was not affected by temperature over a broad range, between 27.5 and 38 °C. In the case of sprint runs, the only difference was found between the trial at 22 °C and all the other temperatures; thus, it seems to be a wide range of body temperatures over which locomotor performance for sprint runs is high and similar (28–39.5 °C). Hence, *L. cuyumhue* select body temperatures that optimise sprint runs in a broad thermal range, which could provide an enhanced ability to escape from predators and optimise food acquisition,

among other social activities (Fernández et al. 2011; Cabezas-Cartes et al. 2014; Gómez Alés et al. 2018). Miles et al. (2001) found similar results for Galápagos Lava Lizards (*Microlophus albemarlensis* (Baur, 1890)) that inhabit open areas with little shade (similar to our study site), where sprint speed is critical to avoid predators. Additionally, Kubisch et al. (2011) found that the sprint run is the type of run most often used and the most important for *Liolaemus pictus argentinus* Müller and Hellmich, 1939. Moreover, the speed for sprint runs was higher than the speed for long runs in other species of *Liolaemus* (Fernández et al. 2011; Kubisch et al. 2011; Gómez Alés et al. 2018). Preferences for sprints may respond not only to external environmental conditions, but also to physiological constraints, for example, the type of muscle fibre present in the hind-limb muscles, among others (Kingsolver and Huey 2003; Fernández et al. 2011; Fuller et al. 2011).

Regarding the effectiveness of thermoregulation ($E = 0.64$), *L. cuyumhue* may behave like a moderate thermoregulator during

Fig. 4. Box plots indicating median, 25th and 75th percentiles, and extremes of the maximum speeds of sprint (upper panel) and long runs (lower panel) of the Añelo Sand Dunes Lizard (*Liolaemus cuyumhue*) at the five temperature treatments (22, 28, 33, 36, and 39.5 °C). Letters (a, b, c, d) indicate differences among temperature treatments (Tukey's post hoc test, $P < 0.05$).



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Table 2. Thermal safety margins (TSM) of sprint (SR) and long runs (LR) and the warming tolerance (WT) indices of the Añelo Sand Dunes Lizard (*Liolaemus cuyumhue*) under different values of operative temperature (T_e ; mean values of all the models, mean values of shadow models, and mean values of sun models).

	TSM _{SR} (°C)	TSM _{LR} (°C)	WT (°C)
$T_{e,mean}$	5.0	5.4	9.3
$T_{e,shadow}$	8.9	9.3	13.2
$T_{e,sun}$	2.6	3.0	6.9

the late summer season. The value of the thermal quality index ($d_e = 5.52$) is similar to the one calculated by Stellatelli et al. (2020) in populations of *L. multimaculatus*, which also live in dune environments with anthropogenic disturbances. It is important to note that in our study the T_b s were observed only in one day of late summer, and that they may change during the year, as seasonality has been recorded to be an important factor affecting body temperatures of temperate species of lizards (Stellatelli et al. 2018). The values of T_e show that the cost of thermoregulation is high in some microhabitats, and this could restrict vital activities such as searching for food, mating, avoiding predators, or engaging in social interactions (Huey and Slatkin 1976; Downes and Shine 1998). Selective microhabitat use, namely midday sheltering in vegetated patches, may allow evasion of critical maximum temperatures while enhancing the previously mentioned vital activities (Rocha 1995; Liz et al. 2019). According to Sartorius et al. (2002), xeric shrublands in deserts are ideal for lizard thermoregulation because the spatial scale of thermal variation is often small and movements between macrohabitats are not required to change thermal status. Also, specifically sand lizards select partially shaded sites in the warmest periods of the day and adopted raised postures to promote heat loss via air movement, in contrast to other species that move from open to shady areas to avoid overheating in the warmer periods of the day (Bujes and Verrastro 2008; Block et al. 2013; Maia-Carneiro and Rocha 2013). In this sense, for *L. cuyumhue*, the thermoregulatory behaviour and the use of microhabitats, specifically shaded ones, are the only way they could buffer the stressful conditions of the low thermal quality environment that they inhabit.

In reference to our last hypothesis, about the effect that global warming could have on *L. cuyumhue*, our results suggest that this species would be affected by this phenomenon. Despite the high warming tolerance index ($WT = 9.31$), the thermal safety margins show that if the latest IPCC predictions are correct (an increase of 3.5 °C between the years 2016 and 2035 for our study site), then *L. cuyumhue* will be forced to avoid microhabitats exposed to the sun to maintain its performance within optimal values. To survive, *L. cuyumhue* must rely on access to shelters during seasonal and daily extreme temperatures (Sunday et al. 2014); as a consequence, the time and space available for lizards to perform vital activities are expected to decrease (Sinervo et al. 2010; Logan et al. 2013). Recent studies suggest that ectothermic organisms from desert environments have a high extinction probability under current rates of global warming because it is unlikely that they will have a sufficiently rapid adaptive change in T_b to buffer from those changes in ambient temperature (Deutsch et al. 2008; Sinervo et al. 2010). In addition, Li et al. (2017) suggests that this risk differs among desert species, with higher risk for those having narrower thermal safety margins, as is the case of *L. cuyumhue* compared with the Mongolia Racerunner (*Eremias argus* Peters, 1869), the Multi-ocellated Racerunner (*Eremias multiocellata* Günther, 1872), and Przewalski's Toadhead Agama (*Phrynocephalus przewalskii* Strauch, 1876) from the Chinese Hobq Desert. Also, according to several authors, species from arid middle latitudes (20°S–40°S) may be more vulnerable to climate warming than tropical species

because of the higher thermal variability in temperate zones, which increases the incidence of lethal temperatures (Clusella-Trullas et al. 2011; Vasseur et al. 2014; Kubisch et al. 2016), but this was not observed in our results. In this sense, the warming tolerance was lower and the thermal safety margin was similar in four tropical species of the genus *Anolis* Daudin, 1802 ($WT = 3.1$ – 7.8 °C, $TSM = 1.5$ – 5.5 °C; Logan et al. 2013) with those of *L. cuyumhue*.

Unfortunately, *L. cuyumhue* is already avoiding exposure to direct sun during the extreme temperatures of the day; therefore, given the future climate change scenario, the availability of suitable microhabitats for thermoregulation could be compromised, increasing its vulnerability. Currently, most distributions of *L. cuyumhue* suffer from high anthropogenic impact and from lack of any kind of protection for this essential environment, making our findings of its ability to cope with temperature threats particularly important. Therefore, accounting for its strict endemism, as well as the WT and TSM values in shade, we can point out the importance of microhabitats for the persistence of this species and consequently the importance of implementing urgent measures to protect the current suitable habitats that support populations of *L. cuyumhue*. In conclusion, similar to other studies, we show that the quality of the microhabitats is essential for the persistence of desert lizards (Flesch et al. 2017; Huey and Pianka 2018). Future research activities should be focused on studying basic aspects of the biology such as feeding, reproduction, and use of time space for the implementation of an appropriate management plan for this species. Also, studies of the physiological plasticity of this species as a short-term response to overcome global warming are necessary.

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References

- Aguilar, R., and Cruz, F.B. 2010. Refuge use in a Patagonian nocturnal lizard, *Homonota darwini*: the role of temperature. *J. Herpetol.* **44**(2): 236–241. doi:10.1670/08-270.1.
- Andrew, N.R., Hart, R.A., Jung, M.P., Hemmings, Z., and Terblanche, J.S. 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. *J. Insect Physiol.* **59**(9): 870–880. doi:10.1016/j.jinsphys.2013.06.003. PMID:23806604.
- Andrews, R.M. 1998. Geographic variation in field body temperature of *Sceloporus* lizards. *J. Therm. Biol.* **23**(6): 329–334. doi:10.1016/S0306-4565(98)00018-7.
- Angilletta, M.J., Niewiarowski, P.H., and Navas, A.C. 2002a. The evolution of thermal physiology in endotherms. *J. Therm. Biol.* **27**: 249–268. doi:10.2741/e148. PMID:20515760.

- Angilletta, M.J., Hill, T., and Robson, M.A. 2002b. Is physiological performance optimized by thermoregulatory behavior?: A case study of the eastern fence lizard, *Sceloporus undulatus*. *J. Therm. Biol.* **27**(3): 199–204. doi:10.1016/S0306-4565(01)00084-5.
- Angilletta, M.J., Bennett, A.F., Guderley, H., Navas, C.A., Seebacher, F., and Wilson, R.S. 2006. Coadaptation: A unifying principle in evolutionary thermal biology. *Physiol. Biochem. Zool.* **79**(2): 282–294. doi:10.1086/499990. PMID:1655188.
- Astudillo, G., Córdoba, M., Alés, R.G., Acosta, J.C., and Villavicencio, H.J. 2019. Termorregulación de la lagartija *Liolaemus chacoensis* (Squamata: Liolaemidae) durante su ciclo reproductivo. *Rev. Biol. Trop.* **67**(6): 1505–1519. doi:10.15517/rbt.v67i6.35835.
- Avila, L.J. 2016. *Liolaemus cuyumhue*. The IUCN Red List of Threatened Species. 2016e.T56052426A56052434. International Union for the Conservation of Nature (IUCN) Global Species Programme Red List Unit, Cambridge, U.K. Available from <https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T56052426A56052434.en>.
- Avila, L.J., Morando, M., Perez, D.R., and Sites, J.W. 2009. A new species of *Liolaemus* from Añelo sand dunes, northern Patagonia, Neuquén, Argentina and molecular phylogenetic relationships of the *Liolaemus wiegmanni* species group (Squamata, Iguania, Liolaemini). *Zootaxa*, **2234**(1): 39–55. doi:10.11646/zootaxa.2234.1.3.
- Barros, V.R., Boninsegna, J.A., Camilloni, I.A., Chidiak, M., Magrín, G.O., and Rusticucci, M. 2015. Climate change in Argentina: Trends, projections, impacts and adaptation. *WIREs Clim. Change*, **6**(2): 151–169. doi:10.1002/wcc.316.
- Bauwens, D., Hertz, P.E., and Castilla, A.M. 1996. Thermoregulation in a lacertid lizard: The relative contributions of distinct behavioral mechanisms. *Ecology*, **77**(6): 1818–1830. doi:10.2307/2265786.
- Ben-Ezra, E., Bulté, G., and Blouin-Demers, G. 2008. Are locomotor performances coadapted to preferred basking temperature in the northern map turtle (*Graptemys geographica*)? *J. Herpetol.* **42**(2): 322–331. doi:10.1670/0718811.
- Besson, A.A., and Cree, A. 2010. A cold-adapted reptile becomes a more effective thermoregulator in a thermally challenging environment. *Oecologia*, **163**(3): 571–581. doi:10.1007/s00442-010-1571-y. PMID:20140685.
- Block, C., Stellatelli, O.A., García, G.O., Vega, L.E., and Isacch, J.P. 2013. Factors affecting the thermal behavior of the sand lizard *Liolaemus wiegmanni* in natural and modified grasslands of temperate coastal dunes from Argentina. *J. Therm. Biol.* **38**: 560–569. doi:10.1016/j.jtherbio.2013.09.009.
- Blouin-Demers, G., and Weatherhead, P.J. 2001. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology*, **82**(11): 3025–3043. doi:10.1890/0012-9658(2001)082[3025:TEOBRS]2.0.CO;2.
- Bogert, C.M. 1959. How reptiles regulate their body temperature. *Sci. Am.* **200**(4): 105–120. doi:10.1038/scientificamerican0459-105.
- Böhm, M., Williams, R., Bramhall, H.R., Mcmillan, K.M., Davidson, A.D., García, A., et al. 2016. Correlates of extinction risk in squamate reptiles: The relative importance of biology, geography, threat and range size. *Global Ecol. Biogeogr.* **25**(4): 391–405. doi:10.1111/geb.12419.
- Bujes, C.S., and Verrastro, L. 2008. Annual activity of the lizard *Liolaemus occipitalis* (Squamata, Liolaemidae) in the coastal sand dunes of southern Brazil. *Iheringia. Sér. Zool.* **98**(1): 156–160. doi:10.1590/S0073-47212008000100020.
- Busso, C.A., and Bonvisutto, G.L. 2009. Structure of vegetation patches in north-western Patagonia. *Biodivers. Conserv.* **18**(11): 3017–3041. doi:10.1007/s10531-009-9622-6.
- Cabezas-Cartes, F., Kubisch, E.L., and Iburgüengoytia, N.R. 2014. Consequences of volcanic ash deposition on the locomotor performance of the *Phymaturus spectabilis* lizard from Patagonia, Argentina. *J. Exp. Zool. Part A Ecol. Integr. Physiol.* **321**(3): 164–172. doi:10.1002/jez.1846.
- Cabezas-Cartes, F., Fernández, J.B., Duran, F., and Kubisch, E.L. 2019. Potential benefits from global warming to the thermal biology and locomotor performance of an endangered Patagonian lizard. *PeerJ*, **7**: e7437. doi:10.7717/peerj.7437. PMID:31413930.
- Chukwuka, C.O., Virens, J., and Cree, A. 2019. Accuracy of an inexpensive, compact infrared thermometer for measuring skin surface temperature of small lizards. *J. Therm. Biol.* **84**: 285–291. doi:10.1016/j.jtherbio.2019.07.016. PMID:31466766.
- Clusella-Trullas, S., Blackburn, T.M., and Chown, S.L. 2011. Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *Am. Nat.* **177**(6): 738–751. doi:10.1086/660021. PMID:21597251.
- Cruz, F.B., Moreno Azócar, D.L., Bonino, M.F., Schulte, J.A., II, Abdala, C.S., and Perotti, M.G. 2014. Clima, distribución geográfica y viviparismo en especies de *Liolaemus* (Reptilia: Squamata): cuando las hipótesis se ponen a prueba. *ECOS*, **23**(1): 37–45. doi:10.7818/ECOS.2014.23-1.06.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., and Martin, P.R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U.S.A.* **105**(18): 6668–6672. doi:10.1073/pnas.0709472105. PMID:18458348.
- Downes, S., and Shine, R. 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. *Anim. Behav.* **55**(5): 1387–1396. doi:10.1006/anbe.1997.0705. PMID:9632521.
- El-Gabbas, A., Baha El Din, S., Zalal, S., and Gilbert, F. 2016. Conserving Egypt's reptiles under climate change. *J. Arid Environ.* **127**: 211–221. doi:10.1016/j.jaridenv.2015.12.007.
- Etheridge, R. 2000. A review of lizards of the *Liolaemus wiegmanni* group (Squamata, Iguania, Tropiduridae), and a history of morphological change in the sand-dwelling species. *Herpetol. Monogr.* **14**: 293–352. doi:10.2307/1467049.
- Fernández, J.B., Smith, J., Sclaro, A., and Iburgüengoytia, N.R. 2011. Performance and thermal sensitivity of the southernmost lizards in the world, *Liolaemus sarmientoi* and *Liolaemus magellanicus*. *J. Therm. Biol.* **36**(1): 15–22. doi:10.1016/j.jtherbio.2010.09.006.
- Flesch, A.D., Rosen, P.C., and Holm, P. 2017. Long-term changes in abundances of Sonoran Desert lizards reveal complex responses to climatic variation. *Global Change Biol.* **23**(12): 5492–5508. doi:10.1111/gcb.13813.
- Fuller, P.O., Higham, T.E., and Clark, A.J. 2011. Posture, speed, and habitat structure: Three-dimensional hindlimb kinematics of two species of padless geckos. *Zoology*, **114**(2): 104–112. doi:10.1016/j.zool.2010.11.003. PMID:21392953.
- Gómez Alés, R., Acosta, J.C., Astudillo, V., Córdoba, M., Blanco, G.M., and Miles, D. 2018. Effect of temperature on the locomotor performance of species in a lizard assemblage in the Puna region of Argentina. *J. Comp. Physiol. B*, **188**(6): 977–990. doi:10.1007/s00360-018-1185-y. PMID:30288595.
- Grant, B.W., and Dunham, A.E. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, **69**(1): 167–176. doi:10.2307/1943171.
- Hertz, P.E. 1992. Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. *Oecologia*, **90**(1): 127–136. doi:10.1007/BF00317818. PMID:28312280.
- Hertz, P.E., Huey, R.B., and Stevenson, R.D. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* **142**(5): 796–818. doi:10.1086/285573. PMID:19425957.
- Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia*. Edited by C. Gans and F.H. Pough. Academic Press, New York. pp. 25–74.
- Huey, R.B., and Bennett, A.F. 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. PMID:28563407.
- Huey, R.B., and Pianka, E.R. 2018. Body temperature distributions of active diurnal lizards in three deserts: skewed up or skewed down? *Funct. Ecol.* **32**(2): 334–344. doi:10.1111/1365-2435.12966.
- Huey, R.B., and Slatkin, M. 1976. Cost and benefits of lizard thermoregulation. *Q. Rev. Biol.* **51**(3): 363–384. doi:10.1086/409470. doi:10.1086/409034. PMID:981504.
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Pérez, H.J.A., and Garland, A. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B Biol. Sci.* **276**(1664): 1939–1948. doi:10.1098/rspb.2008.1957. PMID:19324762.
- Iburgüengoytia, N., Blanco, G., Boretto, J., Marinero, J., Acosta, J.C., and Villavicencio, J. 2007. Reproductive biology and sexual dimorphism of a high-altitude population of the viviparous lizard *Phymaturus punae* from the Andes in Argentina. *Amphib.-Reptilia*, **28**(3): 427–432. doi:10.1163/156853807781374791.
- Iburgüengoytia, N.R., Medina, S.M., Fernández, J.B., Gutiérrez, J.A., Tappari, F., and Sclaro, A. 2010. Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. *J. Therm. Biol.* **35**(1): 21–27. doi:10.1016/j.jtherbio.2009.10.003.
- IPCC. 2014. Climate change 2014: Synthesis report. Cambridge University Press, Cambridge.
- Jayne, B.C., and Bennett, A.F. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution*, **44**(5): 1204–1229. doi:10.1111/j.1558-5646.1990.tb05226.x. PMID:28563892.
- Kingsolver, J.G., and Huey, R.B. 2003. Introduction: The evolution of morphology, performance, and fitness. *Integr. Comp. Biol.* **43**(3): 361–366. doi:10.1093/icb/43.3.361. PMID:21680444.
- Kirchhof, S., Hetem, R.S., Lease, H.M., Miles, D.B., Mitchell, D., McUller, J., et al. 2017. Thermoregulatory behavior and high thermal preference buffer impact of climate change in a Namib Desert lizard. *Ecosphere*, **8**(12): e20233. doi:10.1002/ecs2.2033.
- Kubisch, E.L., Fernández, J.B., and Iburgüengoytia, N.R. 2011. Is locomotor performance optimized at preferred body temperature? A study of *Liolaemus pictus argentinus* from northern Patagonia, Argentina. *J. Therm. Biol.* **36**(6): 328–333. doi:10.1016/j.jtherbio.2011.06.006.
- Kubisch, E.L., Fernández, J.B., and Iburgüengoytia, N.R. 2016. Vulnerability to climate warming of *Liolaemus pictus* (Squamata, Liolaemidae), a lizard from the cold temperate climate in Patagonia. *J. Comp. Physiol. B*, **186**(2): 243–253. doi:10.1007/s00360-015-0952-2. PMID:26679700.
- Labra, A., Pienaer, J., and Hansen, T.F. 2009. Evolution of thermal physiology in liolaemus lizards: Adaptation, phylogenetic inertia, and niche tracking. *Am. Nat.* **174**(2): 204–220. doi:10.1086/600088. PMID:19538089.
- Labra, A., Soto-Gamboa, M., and Bozinovic, F. 2001. Behavioral and physiological thermoregulation of Atacaman desert-dwelling *Liolaemus* lizards. *Ecoscience*, **8**(4): 413–420. doi:10.1080/11956860.2001.11682669.
- Lara-Resendiz, R.A., Jezkova, T., Rosen, P.C., and Méndez-de-la-Cruz, F.R. 2014. Thermoregulation during the summer season in the Goode's horned lizard *Phrynosoma goodei* (Iguania: Phrynosomatidae) in Sonoran Desert. *Amphib.-Reptilia*, **35**(1): 161–172. doi:10.1163/15685381-00002938.
- Lara-Resendiz, R.A., Gadsden, H., Rosen, P.C., Sivero, B., and Méndez-de-la-Cruz, F.R. 2015. Thermoregulation of two sympatric species of horned lizards in the Chihuahuan Desert and their local extinction risk. *J. Therm. Biol.* **48**: 1–10. doi:10.1016/j.jtherbio.2014.11.010. PMID:25660624.

- Leon, R.J.C., Bran, D., Collantes, M., Paruelo, J.M., and Soriano, A. 1998. *Grandes umidades de vegetación de la Patagonia extra andina*. Ecol. Austral. **8**: 125–144.
- Li, S.R., Wang, Y., Ma, L., Zeng, Z.G., Bi, J.H., and Du, W.G. 2017. Thermal ecology of three coexistent desert lizards: Implications for habitat divergence and thermal vulnerability. J. Comp. Physiol. B, **187**(7): 1009–1018. doi:10.1007/s00360-017-1087-4. PMID:28324161.
- Liz, A.V., Santos, V., Ribeiro, T., Guimarães, M., and Verrastro, L. 2019. Are lizards sensitive to anomalous seasonal temperatures? Long-term thermobiological variability in a subtropical species. PLoS ONE, **14**(12): 1–16. doi:10.1371/journal.pone.0226399. PMID:31856183.
- Logan, M.L., Huynh, R.K., Precious, R.A., and Calsbeek, R.G. 2013. The impact of climate change measured at relevant spatial scales : new hope for tropical lizards. Global Change Biol. **19**(10): 1–10. doi:10.1111/gcb.12101. PMID:23504716.
- Lowe, C.H., and Vance, J.H. 1955. Acclimation of the critical thermal maximum of the reptile *Urosaurus ornatus*. Science, **122**(3158): 73–74. doi:10.1126/science.122.3158.73. PMID:17748800.
- Maia-Carneiro, T., and Rocha, C.F.D. 2013. Seasonal variations in behaviour of thermoregulation in juveniles and adults *Liolaemus lutzae* (Squamata, Liolaemidae) in a remnant of Brazilian restinga. Behav. Processes, **100**: 48–53. doi:10.1016/j.beproc.2013.08.001. PMID:23941976.
- Martin, T.L., and Huey, R.B. 2008. Why “suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. Am. Nat. **171**(3): 102–118. doi:10.1086/527502.
- Medina, M., Scolari, A., Méndez-de-la-Cruz, F., Sinervo, B., Miles, D.B., and Ibarguengoytia, N. 2012. Thermal biology of genus *Liolaemus*: A phylogenetic approach reveals advantages of the genus to survive climate change. J. Therm. Biol. **37**(8): 579–586. doi:10.1016/j.jtherbio.2012.06.006.
- Miles, D.B., Snell, H.L., and Snell, H.M. 2001. Intrapopulation variation in endurance of Galapagos lava lizards (*Microlophus albemarlensis*): Evidence for an interaction between natural and sexual selection. Evol. Ecol. Res. **3**(7): 795–804.
- Moreno Azócar, D.L., Vanhooydonck, B., Bonino, M.F., Perotti, M.G., Abdala, C.S., Schulte, J.A., and Cruz, F.B. 2013. Chasing the Patagonian sun: comparative thermal biology of *Liolaemus* lizards. Oecologia, **171**(4): 773–788. doi:10.1007/s00442-012-2447-0. PMID:23011849.
- Olave, M., Avila, L.J., Sites, J.W., and Morando, M. 2014. Multilocus phylogeny of the widely distributed South American lizard clade *Eulaemus* (Liolaemini, *Liolaemus*). Zool. Scr. **43**(4): 323–337. doi:10.1111/zsc.12053.
- Olave, M., Avila, L.J., Sites, J.W., and Morando, M. 2020. How important is it to consider lineage diversification heterogeneity in macroevolutionary studies? Lessons from the lizard family Liolaemidae. J. Biogeogr. **47**(6): 1–12. doi:10.1111/jbi.13807.
- Pinch, F.C., and Claussen, D.L. 2003. Effects of temperature and slope on the sprint speed and stamina of the Eastern Fence Lizard, *Sceloporus undulatus*. J. Herpetol. **37**(4): 671–679. doi:10.1670/183-02.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.r-project.org/>.
- Rocha, C.F.D. 1995. Ecologia termal de *Liolaemus lutzae* (Sauria: Tropiduridae) em uma área de restinga do sudeste do Brasil. Rev. Bras. Biol. **55**: 481–489.
- Rodríguez-Serrano, E., Navas, C.A., and Bozinovic, F. 2009. The comparative field body temperature among *Liolaemus* lizards: testing the static and the labile hypotheses. J. Therm. Biol. **34**(6): 306–309. doi:10.1016/j.jtherbio.2009.04.002.
- Roig, F.A., Roig-Juñent, S., and Corbalán, V. 2009. Biogeography of the Monte Desert. J. Arid Environ. **73**(2): 164–172. doi:10.1016/j.jaridenv.2008.07.016.
- Sartorius, S.S., Do Amaral, J.P.S., Durtsche, R.D., Deen, C.M., and Lutterschmidt, W.I. 2002. Thermoregulatory accuracy, precision, and effectiveness in two sand-dwelling lizards under mild environmental conditions. Can. J. Zool. **80**(11): 1966–1976. doi:10.1139/z02-191.
- Sinclair, B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slotsbo, S., et al. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecol. Lett. **19**(11): 1372–1385. doi:10.1111/ele.12686. PMID:27667778.
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Cruz, M.V.S., et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science, **328**(5980): 894–899. doi:10.1126/science.1184695. PMID:20466932.
- Stellatelli, O.A., Vega, L.E., Block, C., and Cruz, F.B. 2013. Effects on the thermoregulatory efficiency of two native lizards as a consequence of the habitat modification by the introduction of the exotic tree *Acacia longifolia*. J. Therm. Biol. **38**(3): 135–142. doi:10.1016/j.jtherbio.2012.12.005.
- Stellatelli, O.A., Villalba, A., Block, C., Vega, L.E., Dajil, J.E., and Cruz, F.B. 2018. Seasonal shifts in the thermal biology of the lizard *Liolaemus tandiliensis* (Squamata, Liolaemidae). J. Therm. Biol. **73**: 61–70. doi:10.1016/j.jtherbio.2018.02.009. PMID:29549992.
- Stellatelli, O.A., Vega, L.E., Block, C., Rocca, C., Bellagamba, P.J., and Cruz, F.B. 2020. Latitudinal comparison of the thermal biology in the endemic lizard *Liolaemus multimaculatus*. J. Therm. Biol. **88**: 102485. doi:10.1016/j.jtherbio.2019.102485. PMID:32125975.
- Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., and Huey, R.B. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc. Natl. Acad. Sci. U.S.A. **111**(15): 5610–5615. doi:10.1073/pnas.1316145111. PMID:24616528.
- Tingley, R., Hitchmough, R.A., and Chapple, D.G. 2013. Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol. Conserv. **165**: 62–68. doi:10.1016/j.biocon.2013.05.028.
- Van Damme, R., Bauwens, D., and Verheyen, R.F. 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. Funct. Ecol. **5**: 507–517. doi:10.2307/2389633.
- Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D.G., McCann, K.S., et al. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proc. R Soc. B Biol. Sci. **281**(1779): 20132612. doi:10.1098/rspb.2013.2612. PMID:24478296.
- Villamil, J., Avila, L.J., Morando, M., Sites, J.W., Leaché, A.D., Maneyro, R., and Camargo, A. 2019. Coalescent-based species delimitation in the sand lizards of the *Liolaemus wiegmanni* complex (Squamata : Liolaemidae). Mol. Phylogenet. Evol. **138**: 89–101. doi:10.1016/j.ympev.2019.05.024. PMID:31128241.
- Winter, M., Fiedler, W., Hochachka, W.M., Koehncke, A., Meiri, S., and De La Riva, I. 2016. Patterns and biases in climate change research on amphibians and reptiles: A systematic review. R Soc. Open Sci. **3**(9): 160158. doi:10.1098/rsos.160158. PMID:27703684.