

# Latitudinal pattern of the thermal sensitivity of running speed in the endemic lizard *Liolaemus multimaculatus*

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## Abstract

Physiological performance in lizards may be affected by climate across latitudinal or altitudinal gradients. In the coastal dune barriers in central-eastern Argentina, the annual maximum environmental temperature decreases up to 2°C from low to high latitudes, while the mean relative humidity of the air decreases from 50% to 25%. *Liolaemus multimaculatus*, a lizard in the family Liolaemidae, is restricted to these coastal dunes. We investigated the locomotor performance of the species at 6 different sites distributed throughout its range in these dune barriers. We inquired whether locomotor performance metrics were sensitive to the thermal regime attributable to latitude. The thermal performance breadth increased from 7% to 82% with latitude, due to a decrease in its critical thermal minimum of up to 5°C at higher latitudes. Lizards from high latitude sites showed a thermal optimum, that is, the body temperature at which maximum speed is achieved, up to 4°C lower than that of lizards from the low latitude. At relatively low temperatures, the maximum running speed of high-latitude individuals was faster than that of low-latitude ones. Thermal parameters of locomotor performance were labile, decreasing as a function of latitude. These results show populations of *L. multimaculatus* adjust thermal physiology to cope with local climatic variations. This suggests that thermal sensitivity responds to the magnitude of latitudinal fluctuations in environmental temperature.

**Key words:** latitude, *Liolaemus*, reptile, running speed, temperature, thermal sensitivity

## INTRODUCTION

Environmental temperature affects the body temperature of ectotherms, in turn influencing their performance,

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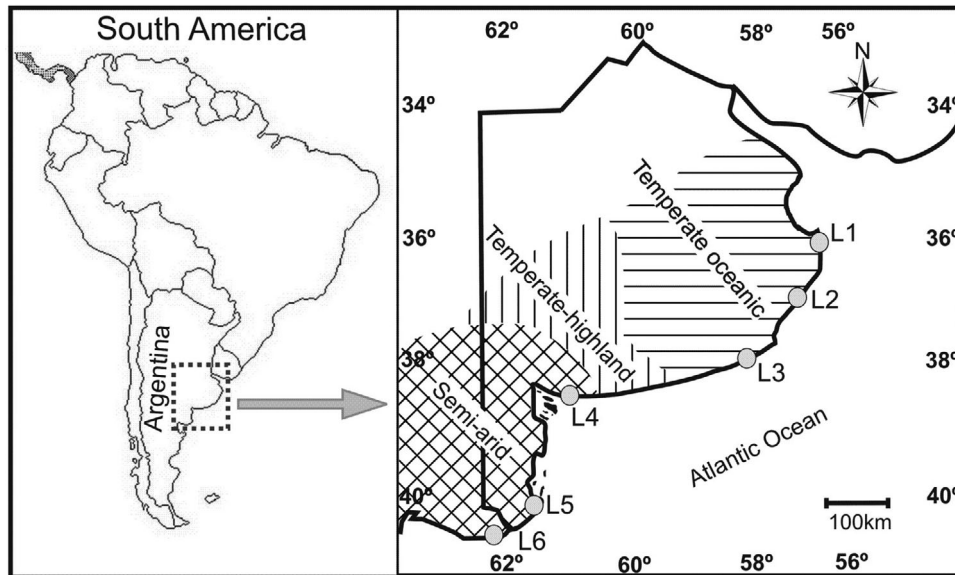
physiology, and fitness (Blouin-Demers & Weatherhead 2008; Rodríguez-Serrano *et al.* 2009; Bozinovic *et al.* 2011; Obregón *et al.* 2020). Environmental temperature varies across geographic gradients, generally decreasing with altitude and latitude (van Berkum 1988; Gvoždík 2002; Cruz *et al.* 2005; Sunday *et al.* 2014). In ectotherms such as lizards, regulatory behaviors and acclimatization may compensate for thermal variation within a habitat (Aubret & Shine 2010; Huey *et al.* 2012; Block *et al.* 2013). Hertz *et al.* (1983) described 2 major positions on the adaptation of lizard thermal physiology, the “static”

and “labile” views of thermal physiology. The static view considers that closely related species and populations display behavioral adjustments that buffer the variation in the thermal physiology along a geographic gradient, and therefore, physiological parameters are conserved (Bogert 1959; Huey *et al.* 2003). In contrast, the labile point of view contends that ectotherms respond to divergent thermal regimes by adapting their thermal physiology (Hertz *et al.* 1983).

The range of body temperatures within which an organism exhibits voluntary coordinated movement, called the thermal tolerance breadth, is strongly linked to environmental conditions (Crowley 1985; Carothers *et al.* 1997). In many lizards, the thermal tolerance breadth increases with latitude because the lower thermal limit (i.e. the minimum critical temperature,  $CT_{Min}$ ) declines with latitude at a greater rate than the upper thermal limit (maximum critical temperature,  $CT_{Max}$ ; Cruz *et al.* 2005; Sunday *et al.* 2011; Bonino *et al.* 2015). Thermal clines can also drive changes in thermal parameters, such as the degree to which physiological traits vary with temperature (van Berkum 1988; Huey & Kingsolver 1989). The climatic variability hypothesis (CVH—Gaston & Blackburn 2000) states that as the magnitude of climatic fluctuation experienced by terrestrial ectotherms increases with latitude and/or altitude, the thermal sensitivity decreases in relation to environmental fluctuations and, consequently, generalist forms are favored (Kontopoulos *et al.* 2020). In contrast, adaptation to stable environments leads to an increase in thermal sensitivity with a trend toward thermal specialist forms (Huey & Stevenson 1979; Angilletta *et al.* 2006). Individuals carry out vital activities within the thermal performance breadth, which encompasses high levels of physiological performance and includes a subset of temperatures within the thermal tolerance breadth (Huey & Stevenson 1979; Hertz *et al.* 1983). Thus, maintaining field body temperature within the thermal performance breadth favors the integration of performance and fitness (Angilletta 2009; Sinclair *et al.* 2016). As physiological systems are adapted to the environmental thermal regime, individuals that face a narrow array of temperatures in the field are expected to have narrow thermal performance breadth (van Berkum 1988). The boundaries of thermal performance breadth and the thermal optimum (the body temperature at which maximum performance is achieved) tend to shift toward lower temperatures in lizards from relatively cold environments with respect to those from warmer sites (Fernández *et al.* 2011; Pettersen 2020). In addition, lizards with relatively high thermal optima typically present both highest thermal preference and critical thermal limits,

supporting the thermal coadaptation hypothesis (TCH—Huey & Bennett 1987; Bennett & Huey 1990; Garland *et al.* 1991; Blouin-Demers *et al.* 2003; Patterson *et al.* 2017).

In reptiles, locomotion reflects the integration or coadaptation of behavioral, morphological, and physiological traits with direct implications for Darwinian fitness (Irschick & Garland 2001). The maximum running speed ( $V_{max}$ ) is a commonly studied indicator of lizard locomotor performance because such measure provides the most direct link between integrated physiological capacities and Darwinian fitness (Bennett & Huey 1990), and it may be applied to ecological tasks such as prey capture, predator avoidance, or reproductive success (Irschick & Losos 1998). The effects of temperature on locomotor performance may be described by thermal performance curves from which the thermal optimum, the thermal performance breadth, and the thermal tolerance breadth can be estimated (Hertz *et al.* 1983; Angilletta 2009). The significance of differential body temperature-performance relationships can be viewed as a reaction norm that may allow the identification of trade-offs between the breadth and the maximum level of specialization (Huey & Stevenson 1979; Bonino *et al.* 2015; Gilbert & Miles 2016). Variation in the thermal optimum or shape of the thermal performance curves may suggest different ecological or evolutionary trade-offs acting on the different traits, buffering a species against environmental restrictions (Huey & Kingsolver 1989; Angilletta 2001; Angilletta *et al.* 2002a, 2003). The association between thermal optimum and maximum performance relies on the relative importance of thermodynamic constraint versus biochemical adaptation (Angilletta *et al.* 2010). The thermodynamic constraint, the “hotter is better” hypothesis, argues that at relatively high temperatures warm-adapted organisms will outperform cold-adapted organisms because there is a positive relationship between the thermal optimum and maximum performance (Huey & Kingsolver 1989). This hypothesis stems from the observation that if hotter is better ectotherms need to have a system in which the thermodynamics of enzymes, cellular components and physiological environment have coevolved to that increased temperature (Phillips *et al.* 2014). In contrast, the biochemical adaptation hypothesis holds that biochemical processes can compensate for any thermodynamic advantages of hotter temperatures on physiological performance (Seebacher *et al.* 2003, 2009; Angilletta 2009; Angilletta *et al.* 2010). As a consequence, individuals from cold areas may attain the same level of performance as lizards adapted to warm climates (Hertz *et al.* 1983; Zamora-Camacho *et al.* 2015) or even



**Figure 1** Records of occurrence of the lizard *Liolaemus multimaculatus*, endemic to the Atlantic coastal dune Barriers of Central-Eastern Argentina. Grey circles indicate the 6 sampled localities along the latitudinal gradient. L1, San Clemente del Tuyú at 36°S; L2, Reserva de Biosfera Mar Chiquito at 37°S; L3, Mar del Sud at 38°S; L4, Pehuen-Co at 39°S; L5, Bahía San Blas at 40°S; L6, Balneario El Cóndor at 41°S. Marked areas on the map to the right represent the regionalization of climate in the area, taken from Aliaga *et al.* (2017) and modified from Stellatelli *et al.* (2020), the Temperate Oceanic Zone in horizontal black solid lines; the Temperate-Highland of Ventania Hills Zone in vertical black solid lines; and the Semi-arid Zone in grid black lines.

may have higher performances at relatively low temperatures (Hare *et al.* 2010; McElroy 2014).

The endemic lizard *Liolaemus multimaculatus* (snout-vent length up to 72 mm) belongs to the *L. wiegmannii* clade in the family Liolaemidae (Etheridge 2000; Verrastro *et al.* 2017). This species is observed exclusively on the sand barrier dunes of the Atlantic coast from Buenos Aires Province to the north of Rio Negro Province, Argentina (Cei 1993; Etheridge 2000; Vega 2001; see Fig. 1). The geographic range spans a latitudinal gradient of climatic conditions (Isla 2017; Aliaga *et al.* 2017; Fig. 1). Toward high latitude, the mean annual environmental temperature decreases by 2°C, while the thermal amplitude increases by 2°C with respect to low latitude, and the relative humidity decreases up to 25% (Stellatelli *et al.* 2020). Despite the latitudinal changes in climatic conditions, *L. multimaculatus* conserves its field body temperature in different sites (mean  $T_b = 34.07 \pm 3.02^\circ\text{C}$ ), while its preferred temperatures decrease up to 2°C toward higher latitudes (Stellatelli *et al.* 2020). Liolaemid lizards show a complex mixture of conservative thermal biology traits, such as field body temperature and  $CT_{\text{Max}}$ ; and labile ones, such as preferred temperatures (Labra *et al.* 2009; Rodríguez-Serrano *et al.* 2009; Medina *et al.* 2012; Moreno Azócar *et al.* 2013). Parameters

of the thermal physiology in liolaemids, such as  $CT_{\text{Min}}$  and thermal optimum, tend to lability when broad geographic and taxonomic scales are considered (Cruz *et al.* 2005; Labra *et al.* 2009; Rodríguez-Serrano *et al.* 2009; Medina *et al.* 2012; Moreno Azócar *et al.* 2013; Bonino *et al.* 2015) or when populations of the same species are compared between different localities (Artacho *et al.* 2017; Cecchetto *et al.* 2020). Discerning the physiological responses in the context of climatic variability due to latitude is an important task that contributes to an understanding of theoretical topics in biology, and it can be useful in establishing management strategies in view of future scenarios of environmental change.

Our main aim was to study the thermal sensitivity of locomotion of *L. multimaculatus* in a latitudinal gradient. We compared the locomotor performance of *L. multimaculatus* among 6 populations distributed throughout the entire geographic range to inquire if the locomotor performance metrics were sensitive to variation in the thermal regime attributable to latitude. In particular, we aimed to answer the following questions: (1) Does the thermal tolerance breadth vary along the latitudinal distribution range? (2) Are there significant relationships between locomotor performance parameters (thermal optimum, thermal performance breadth, maximum running speed) and

latitude? (3) Is there any relationship between the locomotor performance parameters and critical thermal limits? We made several predictions about the patterns that we expected to find. First, based on the climatic variability hypothesis (Gaston & Blackburn 2000; Cruz *et al.* 2005), lizards experiencing a broader range of climatic fluctuations would exhibit lower thermal sensitivity. We expected the individuals of *L. multimaculatus* from higher latitudes to have broader thermal tolerance breadth and thermal performance breadth than the individuals from lower latitudes. Second, we expected a locally adapted response in liolaemid lizards (Labra *et al.* 2009; Cecchetto *et al.* 2020); therefore, individuals of *L. multimaculatus* from higher latitudes were expected to show relatively lower thermal optimum and decreased limits of thermal performance breadth in comparison with those from lower latitudes. Third, lizards from low-temperature environments would have higher physiological performance at low temperatures than those from warm-temperature environments (Hare *et al.* 2010); therefore, at relatively low temperatures, the  $V_{\max}$  of *L. multimaculatus* individuals from higher latitudes would be higher than that of individuals inhabiting lower latitudes. If thermal traits of lizards are the result of coevolution (Garland *et al.* 1991; Bonino *et al.* 2011), positive relationships could be found between thermal optimum and critical thermal limits of *L. multimaculatus*.

## MATERIALS AND METHODS

### Study site and sampling design

The study was carried out along the Atlantic coastline, extending 700 km through the provinces of Buenos Aires and Rio Negro, Argentina, encompassing the entire geographic range of *L. multimaculatus* (Cei 1993; Block 2014; Kacoliris *et al.* 2016). This coastline includes 3 barrier dune formations that extend from low (36°S) to high latitudes (41°S): the Eastern Barrier Dune, the Austral Barrier Dune, and the Patagones Barrier Dune (Isla 2017; Cortizo & Isla 2012; Bértola *et al.* 2021). We sampled *L. multimaculatus* at 6 independent locations along this latitudinal gradient: San Clemente del Tuyú (Site 36°S: 36°20'S, 56°44'W), Reserva de Biosfera Mar Chiquito (Site 37°S: 37°44'S, 57°25'W), Mar del Sud (Site 38°S: 38°21'S, 58°00'W), Reserva Pehuen Comonte Hermoso (Site 39°S: 39°00'S, 61°31'W), Bahía San Blas (Site 40°S: 40°34'S, 62°12'W), and Balneario El Condor (Site 41°S: 41°01'S, 62°47'W; Fig. 1). Sites from 36°S to 38°S of the northeast coastline of the Buenos Aires province, have a temperate oceanic climate

characterized by humid weather and low-intensity, frequent droughts associated with the movement and proximity of the stationary cyclones of the South Atlantic (Isla 2017; Aliaga *et al.* 2017; Fig. 1). Sites in latitudes from 39°S to 41°S represent the southern portion of the geographic range of *L. multimaculatus*, with a semi-arid climate influenced by the arid southwest diagonal of the Pampas biome and characterized by low mean annual temperatures, few precipitation events, and windier conditions than in the low latitude area (Aliaga *et al.* 2017; Fig. 1). The geographic range of *L. multimaculatus* spans a latitudinal gradient of climatic conditions; in particular, the annual maximum air environmental temperature decreases up to 2°C while the mean relative humidity of the air decreases from 50% to 25% (Stelletti *et al.* 2020). In addition, precipitation varies from 1000 mm/year in low latitude to 369 mm/year in high latitude (Aliaga *et al.* 2017). The structure of the sampled habitat was relatively consistent throughout the geographic range. We purposefully selected sites with scarce to null anthropogenic impact, since *L. multimaculatus* is a sand-dwelling specialist species sensitive to disturbance (Vega *et al.* 2000).

### Lizard collection and husbandry

Lizards were captured on consecutive days, always under similar weather conditions (sunny days) at the end of the spring (December) during the daily period of activity of the species (from 0800 to 1800 hours; Vega 2001). A total of 101 adult lizards were captured by lassoing (36°S:  $n = 19$ , 37°S:  $n = 15$ , 38°S:  $n = 23$ , 39°S:  $n = 13$ , 40°S:  $n = 11$ , 41°S:  $n = 20$ ) (Fitzgerald 2012). Only adult males and non-pregnant adult females were considered, to avoid potential sources of variation associated with ontogenetic stage and reproductive condition (Moreno Azócar *et al.* 2020), individuals were sexed according to external sexually dimorphic characters (Cei 1993; Vega 1997). Lizards' geographical locations were recorded using a GPS device (eTrex Vista HCx, Garmin®, Taiwan, China). Captured lizards were marked temporally by writing a number on their belly using a non-toxic black pen for identification; next, they were placed individually in a cloth bag (Ferner & Plummer 2016) and transported to the laboratory at Instituto de Investigaciones Marinas y Costeras (Mar del Plata, Argentina). We measured the snout-vent length (SVL) of each lizard with a digital caliper (SC111001, Schwyz®, Argentina;  $\pm 0.01$  mm) and the body mass (BM) with a digital pocket scale (CH02, Diamond Premium®, China;  $\pm 0.1$  g). Groups of 4 to 6 lizards were kept in PVC terrariums (0.60 × 0.40 × 0.30 m, L × W × H) filled with sand to a depth of 40 mm; no agonistic

interactions were observed during the captivity. The individuals were kept under controlled air temperature (30°C), the photoperiod was set to resemble the natural daylight hours (L:D = 14:10), and water was provided ad libitum. Lizards were fed *Tenebrio molitor* larvae ad libitum after the experiments. Experiments were performed between 1 and 3 days after capture (Corbalán *et al.* 2013; Gómez Alés *et al.* 2017). The lizard sample was divided and randomly assigned to 2 different subsamples so that each subsample would start with one of the 2 experimental tests (either critical temperatures or locomotor performance) and then perform the other one. All of the lizards were released at the exact capture point after the experiments (none of the individuals died during the trials).

### Determination of the thermal tolerance breadth

Minimum critical temperature ( $CT_{Min}$ ) and maximum critical temperature ( $CT_{Max}$ ) were recorded for all captured individuals.  $CT_{Max}$  and  $CT_{Min}$  are the upper and lower body temperatures, respectively, at which the righting response is lost after being set in the supine position (Adolph 1990; Carothers *et al.* 1997; Bonino *et al.* 2011). Each lizard was exposed to temperatures close to its critical temperature until it lost coordination and the trial was stopped (Bonino *et al.* 2015). To measure the lizards' body temperature, we inserted ultrathin thermocouples (1 mm) within the cloaca (10 mm), held in place by adhesive tape, connected to a digital thermometer (SC133, Schwyz®, Buenos Aires, Argentina;  $\pm 0.01^\circ\text{C}$ ). We followed the procedures of Cruz *et al.* (2005) to obtain measurements of  $CT_{Min}$  and  $CT_{Max}$ . To determine  $CT_{Max}$ , each individual lizard was placed in an aluminum cylindrical bucket (260 mm in diameter  $\times$  340 mm in depth), containing a 30 mm layer of sand. The individual was previously cooled to 18°C and then placed in the cylinder and heated by an incandescent 100 W light bulb (Phillips®, Germany) 70 mm above the bucket. Body temperature at the start of the trial was monitored every 20 s, and then, every 10 s following the onset of panting. Finally, we used the signs of muscular spasms as a cue for  $CT_{Max}$  (sensu Cruz *et al.* 2005). To determine  $CT_{Min}$ , each individual lizard (initial body temperature = 20°C) was introduced in a plastic container (lid had holes for temperature and air exchange), which was placed in a  $-20^\circ\text{C}$  freezer, and the lizard body temperature was monitored every 20 s (Cruz *et al.* 2005). In the trials of  $CT_{Max}$  and  $CT_{Min}$ , we used initial body temperatures of 18°C and 20°C, respectively, as baselines in which a lizard would heat up or cool down at a known rate (Cruz *et al.* 2005). Heating and cooling

rates in the laboratory were controlled to achieve a rate of  $\Delta 1^\circ\text{C}$  per minute; we chose these fast-changing rates for comparative purposes and to avoid rapid acclimation or "hardening" effects which can lead to an overestimation of critical thermal limits (Rezende *et al.* 2011; Herrando-Pérez *et al.* 2020). The thermal tolerance breadth (TTB) was calculated by subtracting the  $CT_{Min}$  from the  $CT_{Max}$  (Cruz *et al.* 2005).

### Locomotor performance trials

We used a horizontal racetrack, 1.5 m in length and 0.10 m in width, with the bottom surface covered with cork to provide traction (Bonino *et al.* 2015). The racetrack was equipped with 8 LED sensors spaced every 0.185 m, connected to an electronic circuit and attached to a laptop (Moreno Azócar *et al.* 2020). For each run, the lizard was placed at the beginning of the racetrack, then released and forced to run by slightly tapping them on the base of their tail and continuously chasing it across the track but taking care to not interfere with the running speed (Angilletta *et al.* 2002a; Bonino *et al.* 2011, 2015; Fernández *et al.* 2017). To measure the maximum running speed, we considered the long run that is defined as the fastest speed between any 2 sequential photoreceptors of the racetrack (Bonino *et al.* 2011; Fernández *et al.* 2011; Cabezas-Cartes *et al.* 2019). Each individual ran 3 times at each of the 5 different body temperatures (22°C, 26°C, 30°C, 34°C, and 38°C) on consecutive days with temperatures set randomly (Bonino *et al.* 2011; Moreno Azócar *et al.* 2020). These specific temperatures were chosen for the trials because they are within the thermal tolerance breadth of liolaemid lizards. Additionally, these temperatures are congruent with the body temperatures experienced by *L. multimaculatus* and other congeneric lizards in the field ( $T_b = 27\text{--}37^\circ\text{C}$ ; Cruz *et al.* 2005; Labra *et al.* 2009; Rodríguez-Serrano *et al.* 2009; Medina *et al.* 2012; Moreno Azócar *et al.* 2013). Temperatures of 34°C and 38 °C are near the range of preferred temperatures of *L. multimaculatus* and other liolaemid lizards, while 22°C, 26°C, and 30°C are expected to be physiologically suboptimal for most *Liolaemus* species (Medina *et al.* 2009; Bonino *et al.* 2011; Cruz *et al.* 2014; Cabezas-Cartes *et al.* 2019; Stelletti *et al.* 2020). For these reasons, this set of trial temperatures was used in previous studies of locomotor performance in liolaemid lizards (e.g. Bonino *et al.* 2011, 2015).

Before each trial, lizards were placed into an incubation chamber (Semedic IF290; Semedic, Buenos Aires, Argentina) for 1 h to achieve the desired body temperature. The body temperature was checked before and after

each trial using an ultra-fine thermocouple connected to a digital thermometer (SC133, Schwyz®, Buenos Aires, Argentina;  $\pm 0.01^\circ\text{C}$ ). Each lizard was given 2 h rest between trials. Each run was scored as “poor”, “good” or “excellent”. A run was classified as “poor” when a lizard took too long to run the given distance, made a U-turn, or stopped too many times; by contrast, a “good” run meant that the lizard ran correctly but made some stops. Finally, an “excellent” run meant that the lizard ran the entire race-track non-stop and at a rational speed (Tulli *et al.* 2012). For the analysis, we considered the best trial of each lizard at each temperature, which was defined as either the only trial in which the individual met “good” or “excellent” score or the trial with the highest running speed (Losos *et al.* 2002; Gómez Alés *et al.* 2018).

### Thermal performance curves and thermal sensitivity parameters

To distinguish the thermal sensitivity for locomotor performance, we used TableCurve 2D (version 55.01 Systat Software Inc.) software and created locomotor performance curves as a function of temperature (i.e. thermal performance curve, TPC). We plotted the maximum running speed (m/s) of each lizard at each of the 5 trial temperatures.  $CT_{\text{Min}}$  and  $CT_{\text{Max}}$  of each individual were used as the boundaries of the curves (speed of 0 m/s). We fitted 4 different curves according to Angilletta (2006), with the data of each individual and then calculated the Akaike information criterion. We chose the model according to the lowest AIC and the adjusted  $R^2$  (following Angilletta 2006; Cabezas-Cartes *et al.* 2019). Additionally, we visually inspected the biological significance of the selected model (Moreno Azócar *et al.* 2020). Finally, we used a modified exponent of the Gaussian model to fitting the thermal performance curve of each individual (Angilletta 2006, 2009). Four parameters were calculated for each individual, as follows: (1)  $V_{\text{max}}$ —the speed value at the top point of a TPC; (2) thermal optimum for  $V_{\text{max}}$  ( $T_o$ )—the temperature value at the top point of a TPC; (3) thermal performance breadth ( $B_{80}$ )—the temperature range over which a lizard ran at 80% of  $V_{\text{max}}$ ; and (4) boundaries of  $B_{80}$ —the lower and upper bounds of the performance breadth,  $LB_{80}$  and  $UB_{80}$ , respectively (Bonino *et al.* 2011; Wu *et al.* 2018).

### Data analysis

Normality and homoscedasticity of the data were evaluated by Kolmogorov–Smirnov and Shapiro–Wilks tests, respectively (Zar 1999). Latitude and all thermal vari-

ables were Ln-transformed to meet the assumption of linearity (Zar 1999). We used regression to identify trends in thermal sensitivity in respect to latitudinal gradients. Linear regressions with latitude as an explanatory variable and thermal metrics ( $CT_{\text{Min}}$ ,  $CT_{\text{Max}}$ , TTB,  $B_{80}$ ,  $LB_{80}$ ,  $UB_{80}$ ,  $T_o$ , and  $V_{\text{max}}$ ) as response variables were performed (Angilletta *et al.* 2010). Linear regressions were also used to check for potential relationships between  $V_{\text{max}}$  and body size (SVL, BM) and between  $V_{\text{max}}$  and  $T_o$  (Zar 1999; Savage *et al.* 2004). To test for thermodynamic constraints (hotter is better hypothesis), we regressed the natural logarithm of performance  $\max[\ln(V_{\text{max}})]$  against the inverse of the Boltzmann’s Constant (K) and  $T_o$  [ $1/(K \times T_o)$ ] following Savage *et al.* (2004) and Angilletta *et al.* (2010). Pearson’s correlations were performed to check for potential associations between  $T_o$ ,  $LB_{80}$ ,  $UB_{80}$ ,  $B_{80}$ ,  $CT_{\text{Min}}$ ,  $CT_{\text{Max}}$ , and TTB (Garland *et al.* 1991; Zar 1999). Generalized linear mixed models (GLMM) with Gamma error structure and inverse function were built to test the effects of temperature trial and latitude on maximum running speed (Crawley 2007). The models were constructed with latitude ( $36^\circ\text{S}$ ,  $37^\circ\text{S}$ ,  $38^\circ\text{S}$ ,  $39^\circ\text{S}$ ,  $40^\circ\text{S}$ ,  $41^\circ\text{S}$ ) and temperature trial ( $22^\circ\text{C}$ ,  $26^\circ\text{C}$ ,  $30^\circ\text{C}$ ,  $34^\circ\text{C}$ ,  $38^\circ\text{C}$ ) as explanatory variables (fixed factors), and the maximum running speed of lizards as the response variable. In every model, the individuals’ identity was included as a random effect. All statistical analyses were carried out using R software, version 4.0.1 (R Core Team 2020).

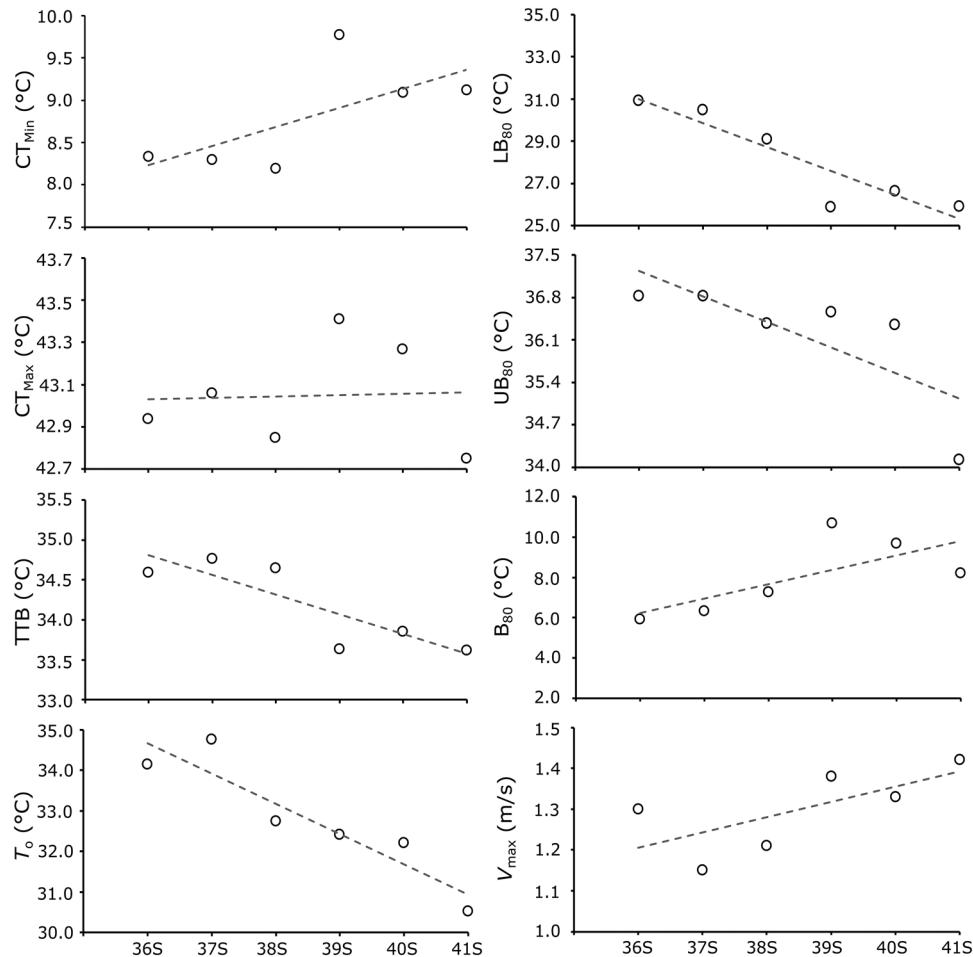
### Ethical statement

Field work was carried out with approval of the Wildlife Service of Buenos Aires Province (permit # 003–18; Organismo Provincial para el Desarrollo Sostenible, OPDS). This study also counted with the approval from the Animal Ethics Committee of Facultad de Ciencias Exactas y Naturales from Universidad Nacional de Mar del Plata, Argentina (CICUAL RD 255). We followed international standards for the Care and Use of Live Amphibians and Reptiles (CCAC/ASIH/HL/SSAR) as well as the regulations detailed in Argentinian National Law #14,346.

## RESULTS

### Thermal tolerance breadth

The  $CT_{\text{Min}}$  and the TTB were significantly affected by latitude (Linear Regression,  $CT_{\text{Min}}$ :  $R^2 = 0.536$ , intercept = 21.39, slope = 1.24,  $F_{1,99} = 6.67$ ,  $P = 0.011$ ; TTB:  $R^2 = 0.628$ , intercept =  $-2.28$ , slope = 0.374,



**Figure 2** Relationships between thermal performance parameters and latitude. References: open circles, mean values of the thermal parameters at each latitude;  $CT_{Min}$ , minimum critical temperature;  $CT_{Max}$ , maximum critical temperature; TTB, thermal tolerance breadth;  $T_o$ , thermal optimum for running speed;  $LB_{80}$ , lower bound of the thermal performance breadth;  $UB_{80}$  upper bound of the thermal performance breadth;  $B_{80}$ , thermal performance breadth;  $V_{max}$ , maximum running speed.

$F_{1,99} = 7.70$ ,  $P = 0.007$ ; Fig. 2). The absolute value of the  $CT_{Min}$  increased while the wide of the TTB decreased in function of the latitude (Table 1; Figs 2 and 3). There was no significant relationship between  $CT_{Max}$  and latitude ( $R^2 = 0.000$ , intercept = 3.20, slope = 0.03,  $F_{1,99} = 0.53$ ,  $P = 0.466$ ; Table 1; Figs 2 and 3).

### Thermal performance curves and thermal sensitivity parameters

There were variations in both the position and the shape of the TPC when the latitudes of the distribution range of *L. multimaculatus* were contrasted (Fig. 3), since

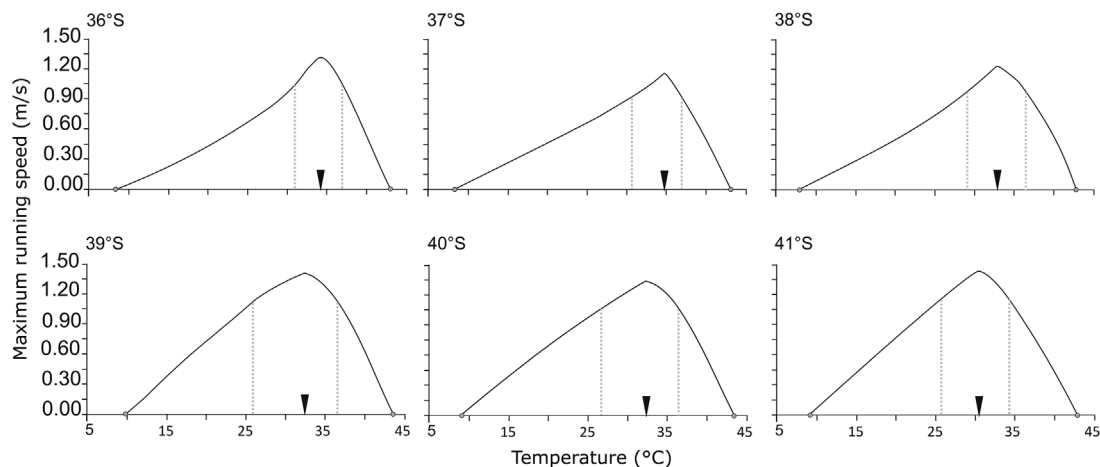
the TPCs of the high latitudes tending to be wider and having a less pronounced peaks than those in low latitudes. The  $B_{80}$  was significantly related with latitude ( $R^2 = 0.31$ , intercept = 85.39, slope = 5.36,  $F_{1,99} = 10.33$ ,  $P = 0.002$ ), the thermal performance breadth increased from 7% to 82% with latitude (Table 1; Figs 2 and 3). The  $LB_{80}$  was significantly related with latitude ( $R^2 = 0.37$ , intercept = -31.96, slope = 2.27,  $F_{1,99} = 16.33$ ,  $P < 0.001$ ; Figs 2 and 3). The mean value of  $LB_{80}$  decreased up to 5°C with latitude (Table 1; Figs 2 and 3). The  $UB_{80}$  was significantly related with latitude ( $R^2 = 0.04$ , intercept = -8.37, slope = 0.77,  $F_{1,99} = 5.28$ ,  $P = 0.024$ ; Table 1; Figs 2 and 3). The  $UB_{80}$  showed the lowest mean value at the highest latitude (Table 1;

**Table 1** Thermal tolerance breadth and locomotor performance parameters of *Liolaemus multimaculatus* individuals at 6 latitudes (36°S, 37°S, 38°S, 39°S, 40°S, 41°S)

	LATITUDE					
	36°S (n = 19)	37°S (n = 15)	38°S (n = 23)	39°S (n = 13)	40°S (n = 11)	41°S (n = 20)
CT <sub>Min</sub> (°C)	8.33 (0.56)	8.29 (1.32)	8.19 (1.60)	9.77 (1.47)	9.09 (1.42)	9.12 (1.21)
CT <sub>Max</sub> (°C)	42.94 (0.69)	43.06 (0.63)	42.85 (0.72)	43.41 (0.56)	43.27 (0.39)	42.75 (0.55)
TTB (°C)	34.60 (0.85)	34.77 (1.59)	34.65 (1.67)	33.64 (1.60)	33.86 (1.61)	33.62 (1.38)
B <sub>80</sub> (°C)	5.90 (2.13)	6.32 (3.63)	7.28 (3.56)	10.69 (3.92)	9.69 (2.71)	8.21 (3.59)
LB <sub>80</sub> (°C)	30.93 (2.84)	30.50 (5.05)	29.10 (4.24)	25.88 (5.01)	26.65 (4.82)	25.92 (5.59)
UB <sub>80</sub> (°C)	36.83 (2.43)	36.83 (2.29)	36.38 (4.02)	36.57 (3.72)	36.35 (3.75)	34.13 (4.87)
T <sub>0</sub> (°C)	34.15 (2.66)	34.75 (2.90)	32.74 (4.33)	32.41 (5.06)	32.20 (5.03)	30.52 (5.80)
V <sub>max</sub> (m/s)	1.30 (0.44)	1.15 (0.54)	1.21 (0.44)	1.38 (0.39)	1.33 (0.31)	1.42 (0.53)
V <sub>22</sub> (m/s)	0.34 (0.12)	0.34 (0.26)	0.53 (0.34)	0.88 (0.24)	0.79 (0.30)	0.62 (0.35)
V <sub>26</sub> (m/s)	0.57 (0.20)	0.36 (0.39)	0.79 (0.40)	1.04 (0.49)	1.01 (0.41)	1.02 (0.62)
V <sub>30</sub> (m/s)	0.90 (0.55)	0.85 (0.77)	0.86 (0.46)	1.06 (0.36)	1.13 (0.38)	0.97 (0.29)
V <sub>34</sub> (m/s)	1.12 (0.22)	0.83 (0.43)	0.99 (0.52)	1.13 (0.44)	1.07 (0.39)	0.93 (0.39)
V <sub>38</sub> (m/s)	0.96 (0.48)	0.71 (0.36)	0.82 (0.27)	1.09 (0.30)	0.94 (0.37)	0.72 (0.37)

The values correspond to the mean with the standard deviation between parentheses and “n” indicates the sample size.

References: CT<sub>Min</sub>, critical thermal minimum; CT<sub>Max</sub>, critical thermal maximum; TTB, thermal tolerance breadth; T<sub>0</sub>, thermal optimum at running speed (i.e., temperature at which V<sub>max</sub> is achieved, °C); B<sub>80</sub>, performance breadth (i.e., the amplitude of the temperature range over which a lizard ran at 80% of V<sub>max</sub>); LB<sub>80</sub> and UB<sub>80</sub> correspond to lower and upper limits of B<sub>80</sub>, respectively); V<sub>max</sub>, maximum running speed (m/s) at T<sub>0</sub>; V<sub>22</sub>, maximum running speed (m/s) at 22°C; V<sub>26</sub>, maximum running speed (m/s) at 26°C; V<sub>30</sub>, maximum running speed (m/s) at 30°C; V<sub>34</sub>, maximum running speed (m/s) at 34°C; V<sub>38</sub>, maximum running speed (m/s) at 38°C.



**Figure 3** Thermal performance curves showing the relationship between body temperature (°C) and maximum running speed (V<sub>max</sub>, m/s) of *Liolaemus multimaculatus*. References: vertical grey dashed lines, boundaries of the performance breadth (B<sub>80</sub>)—the temperature range over which lizards ran at 80% of V<sub>max</sub>; black triangle, thermal optimum of performance—where the performance is maximized; grey circles, limits of the thermal tolerance breadth (CT<sub>Min</sub>, CT<sub>Max</sub>).



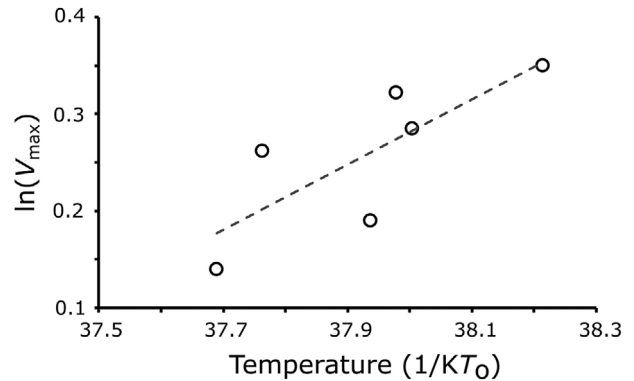
Figs 2 and 3). There was a significant relationship between  $T_o$  and latitude ( $R^2 = 0.79$ , intercept =  $-17.89$ , slope =  $1.37$ ,  $F_{1,99} = 9.58$ ,  $P = 0.003$ ). The mean value of  $T_o$  decreased in function of latitude, from  $2^\circ\text{C}$  to  $4^\circ\text{C}$  (Table 1; Figs 2 and 3). The  $V_{\max}$  was not affected by latitude ( $R^2 = 0.00$ , intercept =  $24.72$ , slope =  $1.57$ ,  $F_{1,99} = 1.95$ ,  $P = 0.166$ ; Table 1; Figs 2 and 3).

### Associations between thermal performance parameters and critical thermal limits

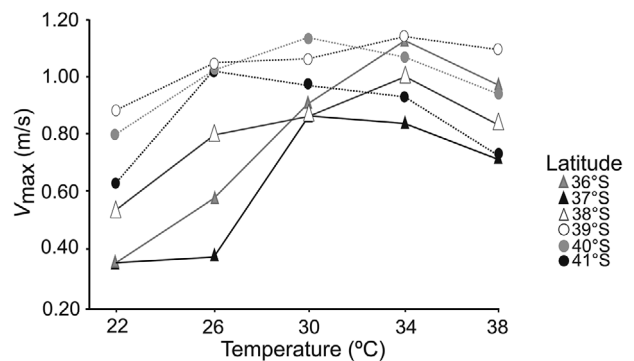
There were no significant relationships between  $T_o$  and critical thermal limits (Pearson's correlation,  $\text{CT}_{\text{Min}}$ :  $r = -0.085$ ,  $P = 0.397$ ,  $n = 101$ ;  $\text{CT}_{\text{Max}}$ :  $r = 0.051$ ,  $P = 0.610$ ,  $n = 101$ ) or between  $T_o$  and TTB ( $r = 0.102$ ,  $P = 0.311$ ,  $n = 101$ ). The  $\text{LB}_{80}$  was correlated with  $\text{CT}_{\text{Min}}$  ( $r = -0.188$ ,  $P = 0.048$ ,  $n = 101$ ) and TTB ( $r = 0.212$ ,  $P = 0.032$ ,  $n = 101$ ), but not with  $\text{CT}_{\text{Max}}$  ( $r = 0.087$ ,  $P = 0.384$ ,  $n = 101$ ). There were no significant relationships between  $\text{UB}_{80}$  and critical thermal limits ( $\text{CT}_{\text{Min}}$ :  $r = -0.021$ ,  $P = 0.833$ ,  $n = 101$ ;  $\text{CT}_{\text{Max}}$ :  $r = 0.020$ ,  $P = 0.838$ ,  $n = 101$ ) or between  $\text{UB}_{80}$  and TTB ( $r = 0.028$ ,  $P = 0.774$ ,  $n = 101$ ). There was a significant negative relationship between  $\text{B}_{80}$  and TTB ( $r = -0.262$ ,  $P = 0.008$ ,  $n = 101$ ).

### Effect of temperature on maximum running speed

The  $V_{\max}$  was not affected by body size since there was no relationship between maximum running speed and SVL (Linear regression:  $R^2 = 0.001$ , intercept =  $0.19$ , slope =  $0.06$ ,  $F_{1,99} = 0.10$ ,  $P = 0.747$ ) or body mass ( $R^2 = 0.006$ , intercept =  $0.11$ , slope =  $0.05$ ,  $F_{1,99} = 0.62$ ,  $P = 0.431$ ). There was no significant relationship between  $V_{\max}$  and the inverse of the Boltzmann's Constant and  $T_o$  ( $R^2 = 0.786$ , intercept =  $-12.50$ , slope =  $0.336$ ,  $F_{1,4} = 6.45$ ,  $P = 0.064$ , Fig. 4). The  $V_{\max}$  of *L. multimaculatus* was significantly affected by the temperatures used in the trials, differing between latitudes (Table 1; Fig. 5; Appendix 1). When we compared  $V_{\max}$  among latitudes, we observed that at temperature trials of  $22^\circ\text{C}$  and  $26^\circ\text{C}$ , the individuals from high latitude ( $39^\circ\text{S}$ ,  $40^\circ\text{S}$ , and  $41^\circ\text{S}$ ) ran faster than those from low latitudes ( $36^\circ\text{S}$  and  $37^\circ\text{S}$ ), while the  $V_{\max}$  at  $30^\circ\text{C}$ ,  $34^\circ\text{C}$ , and  $38^\circ\text{C}$  did not differ among latitudes (Table 1; Fig. 5; Appendix 1). Within-site comparisons showed that the individuals in the latitudes of  $36^\circ\text{S}$ ,  $37^\circ\text{S}$ , and  $38^\circ\text{S}$  reached similar and higher absolute mean values of  $V_{\max}$  at temperature trials of  $30^\circ\text{C}$ ,



**Figure 4** Relationship between the thermal optimum of performance ( $T_o$ ) and the maximum running speed ( $V_{\max}$ ). The data were analyzed considering the Arrhenius scale, in which the thermodynamic effect on maximal performance appear as a linear relationship between the inverse of the optimal temperature and the natural logarithm of performance (Savage *et al.* 2004, Angilletta *et al.* 2010).



**Figure 5** Results from general linear mixed models examining the effects of latitude ( $36^\circ\text{S}$ ,  $37^\circ\text{S}$ ,  $38^\circ\text{S}$ ,  $39^\circ\text{S}$ ,  $40^\circ\text{S}$  and  $41^\circ\text{S}$ ) and temperature trial ( $22^\circ\text{C}$ ,  $25^\circ\text{C}$ ,  $30^\circ\text{C}$ ,  $34^\circ\text{C}$ , and  $38^\circ\text{C}$ ) on mean maximum running speed ( $V_{\max}$ ) of *L. multimaculatus*. Grey triangles indicate the mean  $V_{\max}$  in the latitude  $36^\circ\text{S}$ , black triangles indicate the mean  $V_{\max}$  in the latitude  $37^\circ\text{S}$ , open triangles indicate the mean  $V_{\max}$  in the latitude  $38^\circ\text{S}$ , open circle denote means of  $V_{\max}$  in the latitude  $39^\circ\text{S}$ , grey circle denotes means of  $V_{\max}$  in the latitude  $40^\circ\text{S}$ , and black circle denote means of  $V_{\max}$  in the latitude  $41^\circ\text{S}$ .

$34^\circ\text{C}$ , and  $38^\circ\text{C}$  than at  $22^\circ\text{C}$  (Table 1; Fig. 5; Appendix 1). In the latitudes of  $39^\circ\text{S}$  and  $40^\circ\text{S}$ , the mean values of  $V_{\max}$  reached similar absolute mean values at all temperature trials. In the latitude of  $41^\circ\text{S}$ , the  $V_{\max}$  was higher at temperature trials of  $26^\circ\text{C}$ ,  $30^\circ\text{C}$ , and  $34^\circ\text{C}$  than at  $22^\circ\text{C}$  and  $38^\circ\text{C}$  (Table 1; Fig. 5; Appendix 1).

## DISCUSSION

The locomotor performance of *L. multimaculatus* was sensitive to latitude, which may be attributable to the different climatic conditions throughout the geographic range of the species. The thermal tolerance breadth (TTB) of *L. multimaculatus* was within the critical thermal limits registered for the genus (5°C to 48°C; Cruz *et al.* 2005; Bonino *et al.* 2015; Gómez Alés *et al.* 2018). We observed that a narrower TTB was associated with an increase in latitude, mostly because the lower thermal limit of TTB ( $CT_{Min}$ ) of individuals increased up to 1.6°C toward higher latitudes. The TTB of liolaemid lizards is associated with environmental variability, since it is a physiological trait that allows ectothermic species to cope with climatic variability (Moreno Azócar *et al.* 2013; Cruz *et al.* 2014). The  $CT_{Min}$  of reptiles is relatively labile across geographic regions and latitudes because it is affected by the thermal regime (Hoffman *et al.* 2011). In contrast, the upper thermal limit of TTB ( $CT_{Max}$ ) of *L. multimaculatus* did not vary since the  $CT_{Max}$  of lizards tends to be conservative because it approaches the lethal temperatures more than does  $CT_{Min}$  (Cruz *et al.* 2005; Grigg & Buckley 2013). These results contradict our first prediction and are not consistent with the climatic variability hypothesis (Gaston & Blackburn 2000). The decreased  $CT_{Min}$  of *L. multimaculatus* at low latitude sites is initially a counter-intuitive pattern, but it might also be explained as a response to relatively warm and thermally heterogeneous environments (Grigg & Buckley 2013). Lizards from warm environments may adjust their physiology to relatively colder temperatures by the active selection of microhabitats with low temperatures and avoidance of warm thermal patches (Senior *et al.* 2019). Llewelyn *et al.* (2017) found a negative association between critical temperatures and environmental temperature; skinks from warmer environments remain in relatively cold microenvironments and can tolerate lower temperatures than conspecifics from colder zones. The mismatch between  $CT_{Min}$  and environmental temperatures may be explained by behavioral adjustments to the environment that may lead some physiological traits to vary in the opposite direction with respect to geographical gradients (Pettersen 2020). The major challenge faced by *L. multimaculatus* at low latitude is to avoid overheating, operative temperatures in these sites reach 41°C, while individuals from higher latitudes need to use warmer microenvironments to increase their body temperature above low operative temperatures ( $T_c = 31.5^\circ\text{C}$ ; Stelletti *et al.* 2020). These results suggest that *L. multimaculatus* may adjust some physiological traits to the temperatures it fre-

quently experiences in the field. The documented pattern of preferred temperatures in this species indicates local physiological adaptations throughout its geographic range (Stelletti *et al.* 2020).

We observed the increase in latitude was associated with a broader thermal performance breadth (the range of temperatures over which lizards perform well) of *L. multimaculatus*, implying that the lower boundary of the thermal performance breadth of the lizards from the high latitude shifted towards lower temperatures. This pattern was evident in the asymmetry of the thermal performance curves, which in individuals from high latitude tended to be broader and exhibited a less pronounced peak than that in individuals from low latitude (see Fig. 3). The pattern of variation in the thermal performance breadth of *L. multimaculatus* followed the latitudinal gradient of environmental temperature, supporting our first prediction aligned with the climatic variability hypothesis (Gaston & Blackburn 2000). *Liolaemus* species from the *L. lineomaculatus* clade show broader thermal tolerance in relation to a more variable climate due to high latitude and/or latitude, since these lizard species are typical of cold and harsh Patagonian habitats (Bonino *et al.* 2011; Cecchetto *et al.* 2020). The magnitude of the variation in the thermal performance breadth is directly related to the capacity of a species to cope with climate variability due to geography, thus playing a role in the species success in expanding its range limits (Buckley 2010). Additionally, we observed that the thermal performance breadth of *L. multimaculatus* was close to the lowest values recorded for the genus, in agreement with Bonino *et al.* (2015), who reported that *Liolaemus* species with restricted distribution (like the endemic *L. multimaculatus*) show relatively narrower performance amplitude (thermal performance breadth  $\approx 8^\circ\text{C}$ ) than generalist species occupying broader geographic ranges for which thermal performance breadth is nearly 14°C (Bonino *et al.* 2015).

The thermal optimum for running speed, i.e. the body temperature at which maximum speed is achieved, of *L. multimaculatus* was within the range registered for liolaemid lizards ( $T_o$ : 27–36.25°C; Fernández *et al.* 2011; Bonino *et al.* 2011, 2015; Kubisch *et al.* 2016; Gómez Alés *et al.* 2018). The mean thermal optimum of *L. multimaculatus* individuals decreased up to 4°C towards high latitude, supporting our second prediction. The thermal optimum of lizards decreases in colder environments (Pettersen 2020), because climate drives local adaptation in thermal traits across populations (Sears & Angilletta 2003; Labra *et al.* 2009; Garcia-Porta *et al.* 2019). Liolaemid lizards living in the temperate cold climate of Patagonia show a remarkable capacity to endure low

temperatures, since their locomotor performance capacities and thermal sensitivities are adjusted at temperatures that are suboptimal for lizards from lower latitude (Cecchetto *et al.* 2020). The thermal optimum and the thermal performance breadth of *L. multimaculatus* showed weak to null associations with thermal tolerance breadth. In addition, the mean thermal optimum of *L. multimaculatus* was lower than its range of thermal preference (34.05–39.14°C; Stellatelli *et al.* 2013, 2020). This finding agrees with that of Garland *et al.* (1991) who found no evidence of significant coadaptation between thermal preference and measures of thermal sensitivity ( $T_o$ ,  $CT_{Min}$ , and  $CT_{Max}$ ) or between locomotor performance variables and the parameters of the thermal tolerance breadth of scincid lizards. Although the mismatch between mean thermal optimum and the range of thermal preference did not adjust to the thermal coadaptation hypothesis, the thermal performance breadth of *L. multimaculatus* overlapped between 25% and 31% of its range of thermal preference in low and high latitudes, respectively. The preferred temperatures of *L. multimaculatus* would cover a range of temperatures that may correspond to multiple vital functions beyond running performance. This is aligned with the model of multiple thermal optima that suggests that the mismatch between multiple functions (running, digestion) are maximized within the range of body temperatures, but not all at the same mean (Angilletta *et al.* 2002b).

The mean maximum running speed ( $V_{max}$ ) of *L. multimaculatus* was within the range of 2 sympatric species (*Liolaemus wiegmannii* and *L. gracilis*: 1.01 to 1.33 m/s; Block & Vega 2008; Dematteis 2019) and that of 20 other *Liolaemus* species ( $V_{max} = 0.76$ – $2.50$  m/s; Tulli *et al.* 2012; Bonino *et al.* 2011, 2015; Gómez Alés *et al.* 2018). In agreement with our third prediction, the individuals of *L. multimaculatus* from the high latitude performed better at relatively low temperatures, running 14%–38% faster than those from the low latitude at the experimental temperature trials between 22°C and 26°C, while  $V_{max}$  was not different between runs at 30°C and 38°C. Lizards from low-temperature environments have higher physiological performance at relatively low temperatures than those from warm-temperature environments (Senior *et al.* 2019). The high performance of cold-adapted lizards is explained by a low minimum cost of locomotion enabling them to maximize their aerobic speed at these low temperatures (Hare *et al.* 2010). Hence, physiological plasticity in the form of acclimatization or adaptation allows ectotherms to support changes in thermal environment and maximize performance, while reducing the costs of behavioral thermoregulation in sub-optimal

thermal conditions (Hadamová & Gvoždík 2011; Basson & Clusella-Trullas 2015). Many lizards run faster at cold temperatures because of physiological processes at cellular and subcellular levels related to the running (McElroy 2014). The biochemical adaptation hypothesis holds that biochemical changes can compensate the effect of temperature on performance (Angilletta *et al.* 2010; Sørensen *et al.* 2018). Bonino *et al.* (2015) suggested that biochemical adaptation compensates for effects on thermodynamic performance among liolaemid lizards inhabiting different thermal environments, as shown by the different populations of *L. multimaculatus* studied here. Structural changes of enzymes can cause orthologous allozymes that may enhance performance at specific temperatures, while gene duplications could lead to paralogous isozymes that allow performance at wider temperature ranges (Angilletta *et al.* 2003; Lockwood & Somero 2012). Furthermore, performance may be influenced by changes in concentrations of enzymes and/or the number and size of cells designated for specific functions (Seebacher *et al.* 2003, 2009; Czarnoleski *et al.* 2017).

The shape and position of thermal performance curves may change in response to local thermal conditions, implying local adaptation (Clusella-Trullas *et al.* 2011; Cecchetto *et al.* 2020). The *L. multimaculatus* individuals from the high latitude exhibited flatter and higher curves than those of their conspecifics from the low latitude. This was accompanied by an inverse pattern between the amplitudes of the thermal performance breadth ( $B_{80}$ : lowest latitude  $\approx 6^\circ\text{C}$ , highest latitude  $\approx 8^\circ\text{C}$ ) and of the range of preferred temperature (mean amplitude of  $T_{set\ point}$  range: lowest latitude =  $2.5^\circ\text{C}$ , highest latitude =  $1.3^\circ\text{C}$ ; Stellatelli *et al.* 2020). According to Bauwens *et al.* (1995), higher levels of performance are attained by lizard populations that combine a narrow and accurate range of preferred temperature with a broad and flat thermal performance curve, as we observed in *L. multimaculatus*. The trend we found in *L. multimaculatus* partially fits the “jack-of-all-temperatures” hypothesis (Huey & Hertz 1984), which postulates that there is a broadening of the thermal performance breadth, so that near-maximal sprinting is allowed at a broader range of temperatures. Increasing performance at one temperature does not always imply a decrease in performance at different temperatures (McElroy 2014). Therefore, “a jack-of-all-temperatures” can also be a “master of all temperatures” (Angilletta 2009). The relationship between performance level (i.e.  $V_{max}$ ) and thermal optimum was weak and with a positive slope, rejecting the “hotter is better” hypothesis (i.e. locomotor performance depends on the thermal optimum;

Huey & Kingsolver 1989). Angilletta *et al.* (2010) mentioned that the hotter-is-better hypothesis tends to be supported when comparing species, but often finds less support within species.

To conclude, the thermal sensitivity of running speed in *L. multimaculatus* locally varied by decreasing velocity as a function of the latitude. Our findings suggest that thermal sensitivity responded to the magnitude of fluctuations in environmental temperature in relation to latitude. Interpreting the shape of thermal performance curves allowed us to distinguish between lizards that presented high performance within a narrow range of temperatures (specialists) from those that performed well across a wide range of temperatures (generalists; Huey & Stevenson 1979), even within the same species (Gilbert & Miles 2016). Lizards for which the thermal performance curve displays the shape of a thermal specialist (such as the populations of *L. multimaculatus* from low latitudes) may have greater difficulty in adjusting to and performing in variable temperature regimes than thermal generalists, as shown by the populations of *L. multimaculatus* from higher latitudes (Huey & Slatkin 1976; Huey & Hertz 1984; Pontes-da-Silva *et al.* 2018). Polymorphism tends to increase the niche amplitude of species in such a way that thermal traits with greater variability may be favored in the presence of selective pressure, such as climate change (Logan *et al.* 2014; Obregón *et al.* 2020). The pattern of variation in the thermal sensitivity of *L. multimaculatus* may be due to adjustments mediated by flexibility of biochemical processes that maximize performance. Physiological compensatory adjustments along a spatial environmental gradient may favor the performance of populations in suboptimal thermal conditions, while minimizing costs and optimizing timing of activity (Basson & Clusella-Trullas 2015). Phenotypic plasticity or acclimatization provides possibilities for local populations of species to compensate for novel stressful conditions or to take advantage of opportunities for thermal niche expansion rising from climate change (Sinervo *et al.* 2010; Hoffmann & Sgro 2011; Llewelyn *et al.* 2018). The implications of our results may differ depending on whether they are due to phenotypic plasticity or to evolutionary adaptation. Future studies could focus on differentiating between evolution and acclimatization. Studies designed to identify physiological flexibility in populations will help identify the capacity of ectotherms for persisting in areas where climate change places them in settings where they must function near their species' physiological limits. Our findings along with emerging patterns from similar types of studies are important for making predictions about species' responses to future scenarios of climate

change in order to develop management programs to minimize biodiversity loss.

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### Appendix 1: Comparison of lizards running speed

Parameter	Estimate	SE	<i>t</i> -value	<i>P</i>
Intercept	1.50	0.16	9.11	<0.001*
<b>Latitude</b>				
36°S				
22°C vs 26°C	-1.15	0.33	-3.49	<0.001*
22°C vs 30°C	-1.78	0.30	-5.86	<0.001*
22°C vs 34°C	-1.98	0.30	-6.68	<0.001*
22°C vs 38°C	-1.84	0.30	-6.14	<0.001*
26°C vs 30°C	-0.65	0.20	-3.23	0.001*
26°C vs 34°C	-0.85	0.19	-4.46	<0.001*
26°C vs 38°C	-0.72	0.20	-3.63	<0.001*
30°C vs 34°C	-0.21	0.13	-1.53	0.126
30°C vs 38°C	-0.07	0.14	-0.49	0.624
34°C vs 38°C	0.14	0.13	1.05	0.294
37°S				
22°C vs 26°C	-0.13	0.43	-0.31	0.754
22°C vs 30°C	-1.60	0.34	-4.79	<0.001*
22°C vs 34°C	-1.59	0.34	-4.72	<0.001*
22°C vs 38°C	-1.40	0.35	-4.05	<0.001*
26°C vs 30°C	-1.47	0.32	-4.58	<0.001*
26°C vs 34°C	-1.45	0.32	-4.51	<0.001*
26°C vs 38°C	-1.26	0.33	-3.80	<0.001*
30°C vs 34°C	0.04	0.17	0.23	0.819
30°C vs 38°C	0.23	0.19	1.20	0.229
34°C vs 38°C	0.21	0.19	1.12	0.263

Continued

Parameter	Estimate	SE	<i>t</i> -value	<i>P</i>
38°S				
22°C vs 26°C	-0.61	0.20	-3.08	0.002*
22°C vs 30°C	-0.69	0.19	-3.59	<0.001*
22°C vs 34°C	-0.84	0.19	-4.53	<0.001*
22°C vs 38°C	-0.65	0.19	-3.35	<0.001*
26°C vs 30°C	-0.08	0.15	-0.58	0.564
26°C vs 34°C	-0.23	0.14	-1.72	0.085
26°C vs 38°C	-0.04	0.15	-0.30	0.764
30°C vs 34°C	-0.15	0.13	-1.14	0.255
30°C vs 38°C	0.04	0.14	0.29	0.772
34°C vs 38°C	0.19	0.13	1.46	0.144
39°S				
22°C vs 26°C	-0.17	0.17	-1.01	0.314
22°C vs 30°C	-0.19	0.17	-1.11	0.266
22°C vs 34°C	-0.25	0.17	-1.49	0.136
22°C vs 38°C	-0.21	0.17	-1.27	0.205
26°C vs 30°C	-0.02	0.15	-0.13	0.897
26°C vs 34°C	-0.08	0.15	-0.52	0.606
26°C vs 38°C	-0.04	0.15	-0.29	0.772
30°C vs 34°C	-0.06	0.15	-0.40	0.686
30°C vs 38°C	-0.03	0.15	-0.18	0.860
34°C vs 38°C	0.03	0.14	0.22	0.826
40°S				
22°C vs 26°C	-0.28	0.20	-1.37	0.171
22°C vs 30°C	-0.37	0.19	-1.90	0.057
22°C vs 34°C	-0.32	0.20	-1.62	0.104
22°C vs 38°C	-0.20	0.21	-0.95	0.342
26°C vs 30°C	-0.10	0.16	-0.62	0.533
26°C vs 34°C	-0.05	0.17	-0.32	0.748
26°C vs 38°C	0.07	0.18	0.38	0.701
30°C vs 34°C	0.05	0.16	0.28	0.777
30°C vs 38°C	0.17	0.17	0.97	0.330
34°C vs 38°C	0.12	0.18	0.65	0.512
41°S				
22°C vs 26°C	-0.61	0.18	-3.46	<0.001*
22°C vs 30°C	-0.57	0.18	-3.17	0.001*
22°C vs 34°C	-0.52	0.18	-2.89	0.004*
22°C vs 38°C	-0.23	0.20	-1.16	0.247

Continued

Parameter	Estimate	SE	<i>t</i> -value	<i>P</i>
26°C vs 30°C	0.04	0.13	0.33	0.741
26°C vs 34°C	0.08	0.13	0.63	0.528
26°C vs 38°C	0.38	0.16	2.40	0.016*
30°C vs 34°C	0.04	0.14	0.27	0.785
30°C vs 38°C	0.33	0.16	2.07	0.038*
34°C vs 38°C	0.29	0.16	1.79	0.073
<b>Temperature</b>				
22°C				
36°S vs 37°S	0.03	0.45	0.07	0.946
36°S vs 38°S	-0.99	0.36	-2.78	0.005*
36°S vs 39°S	-1.75	0.35	-4.95	<0.001*
36°S vs 40°S	-1.65	0.37	-4.49	<0.001*
36°S vs 41°S	-1.29	0.35	-3.67	<0.001*
37°S vs 38°S	-1.01	0.38	-2.66	0.008*
37°S vs 39°S	-1.77	0.38	-4.68	<0.001*
37°S vs 40°S	-1.67	0.39	-4.27	<0.001*
37°S vs 41°S	-1.31	0.38	-3.49	<0.001*
38°S vs 39°S	-0.77	0.26	-2.92	0.003*
38°S vs 40°S	-0.67	0.28	-2.38	0.017*
38°S vs 41°S	-0.31	0.26	-1.19	0.233
39°S vs 40°S	0.27	0.20	1.37	0.170
39°S vs 41°S	0.32	0.27	1.21	0.224
40°S vs 41°S	0.33	0.28	1.18	0.239
26°C				
36°S vs 37°S	1.01	0.37	2.70	0.007*
36°S vs 38°S	0.40	0.19	2.07	0.040*
36°S vs 39°S	-0.79	0.26	-3.03	0.003*
36°S vs 40°S	-0.78	0.27	-2.88	0.004*
36°S vs 41°S	-0.77	0.24	-3.19	0.005*
37°S vs 38°S	-1.47	0.35	-4.24	<0.001*
37°S vs 39°S	-1.80	0.36	-5.02	<0.001*
37°S vs 40°S	-1.79	0.37	-4.88	<0.001*
37°S vs 41°S	-1.77	0.34	-5.17	<0.001*
38°S vs 39°S	-0.32	0.22	-1.47	0.142
38°S vs 40°S	-0.32	0.23	-1.36	0.174
38°S vs 41°S	-0.30	0.20	-1.53	0.125
39°S vs 40°S	0.00	0.25	0.00	0.999
39°S vs 41°S	0.02	0.22	0.08	0.934

Continued

Parameter	Estimate	SE	<i>t</i> -value	<i>P</i>
40°S vs 41°S	-0.00	0.23	-0.01	0.988
30°C				
36°S vs 37°S	0.19	0.22	0.87	0.382
36°S vs 38°S	0.10	0.20	0.51	0.609
36°S vs 39°S	-0.15	0.22	-0.68	0.494
36°S vs 40°S	-0.23	0.23	-0.99	0.320
36°S vs 41°S	-0.07	0.20	-0.33	0.741
37°S vs 38°S	-0.07	0.21	-0.32	0.751
37°S vs 39°S	-0.32	0.24	-1.33	0.183
37°S vs 40°S	-0.38	0.24	-1.57	0.115
37°S vs 41°S	-0.24	0.22	-1.11	0.269
38°S vs 39°S	-0.25	0.22	-1.16	0.245
38°S vs 40°S	-0.32	0.22	-1.44	0.149
38°S vs 41°S	-0.17	0.19	-0.86	0.390
39°S vs 40°S	-0.07	0.24	-0.30	0.760
39°S vs 41°S	0.08	0.22	0.38	0.702
40°S vs 41°S	0.14	0.22	0.64	0.520
34°C				
36°S vs 37°S	0.42	0.21	1.97	0.051
36°S vs 38°S	0.16	0.18	0.90	0.365
36°S vs 39°S	-0.00	0.21	-0.01	0.993
36°S vs 40°S	0.03	0.22	0.14	0.889
36°S vs 41°S	0.18	0.19	0.95	0.343
37°S vs 38°S	-0.22	0.21	-1.06	0.288
37°S vs 39°S	-0.37	0.23	-1.59	0.111
37°S vs 40°S	-0.35	0.25	-1.40	0.160
37°S vs 41°S	-0.20	0.22	-0.92	0.357
38°S vs 39°S	-0.16	0.21	-0.78	0.437
38°S vs 40°S	-0.12	0.22	-0.57	0.571
38°S vs 41°S	0.03	0.19	0.16	0.873
39°S vs 40°S	0.03	0.24	0.13	0.896
39°S vs 41°S	0.18	0.22	0.85	0.397
40°S vs 41°S	0.13	0.23	0.58	0.563
38°C				
36°S vs 37°S	0.47	0.23	2.02	0.050
36°S vs 38°S	0.21	0.20	1.07	0.286
36°S vs 39°S	-0.11	0.22	-0.52	0.605
36°S vs 40°S	0.01	0.24	0.04	0.964

Continued

Parameter	Estimate	SE	<i>t</i> -value	<i>P</i>
36°S vs 41°S	0.34	0.22	1.56	0.119
37°S vs 38°S	−0.24	0.23	−1.04	0.300
37°S vs 39°S	−0.56	0.25	−2.26	0.024
37°S vs 40°S	−0.43	0.27	−1.63	0.103
37°S vs 41°S	−0.12	0.25	−0.48	0.633
38°S vs 39°S	−0.32	0.22	−1.47	0.142
38°S vs 40°S	−0.19	0.24	−0.80	0.422
38°S vs 41°S	0.13	0.21	0.61	0.543
39°S vs 40°S	0.12	0.25	0.48	0.632

Continued

Parameter	Estimate	SE	<i>t</i> -value	<i>P</i>
39°S vs 41°S	0.44	0.23	1.90	0.056
40°S vs 41°S	0.31	0.25	1.22	0.224

Fixed-factor contrasts from generalized linear mixed models (GLMMs) testing the effect of the interactions between experimental temperatures (22°C, 26°C, 30°C, 34°C, 38°C) and latitude (36°S, 37°S, 38°S, 39°S, 40°S, 41°S) on the maximum running speed ( $V_{\max}$ ) of *Liolaemus multimaculatus*. SE, standard error; *P*, probability value ( $\alpha = 0.05$ ); asterisks (\*), statistically significant differences.

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