



Effect of temperature on the locomotor performance of species in a lizard assemblage in the Puna region of Argentina

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Abstract

Locomotion is relevant to the ecology of reptiles because of its presumed influence on an organism's Darwinian fitness. Moreover, in ectothermic species, physiological performance capacity is affected by body temperature. We analyzed two components of locomotor performance in three species of lizards, *Phymaturus extrilidus*, *Liolaemus parvus*, and *Liolaemus ruibali*, in the Puna environment of Argentina. First, we estimated the thermal sensitivity of locomotion by measuring sprint speed at four different body temperatures. We included two measures of sprint speed: initial velocity and long sprint for sustained runs. Based on these data, we calculated the optimal temperature for performance and the optimal performance breadth. We also estimated endurance capacity at a single temperature. Maximum sprint speed for *L. parvus* was greater than *L. ruibali* and *P. extrilidus* in both initial velocity and long sprint. In contrast, *L. parvus* exhibited lower levels of endurance than *L. ruibali* and *P. extrilidus*. However, endurance in *L. ruibali* exceeded that of *P. extrilidus*. The species differed in the optimal temperature for the initial velocity with the lowest for *L. ruibali* (31.8 °C) followed by *P. extrilidus* (33.25 °C) and then *L. parvus* (36.25 °C). The optimal temperature for long sprint varied between 32 and 36 °C for all species. We found that all species attained maximum performance at body temperatures commonly experienced during daily activity, which was higher than the thermal quality of the environment. We found evidence for thermal sensitivity in locomotor performance in these species. However, we also show that the broad thermal breadth of performance suggests that the lizards are capable of sustaining near optimal levels of locomotor performance at ambient temperatures that would appear to be suboptimal. Thus, this lizard assemblage is capable of coping with the highly variable climatic conditions in the Puna region of Argentina.

Keywords Sprint speed · Endurance · Thermal optimum · *Phymaturus extrilidus* · *Liolaemus parvus* · *Liolaemus ruibali*

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Introduction

Locomotion is a relevant trait in the ecology of reptiles, and of animals in general, as it is linked to numerous life history characteristics and has direct implications on the fitness of an organism (Le Galliard et al. 2004; Irschick and Meyers 2007; Strobbe et al. 2009; Vanhooydonck et al. 2015; Iburgüengoytía et al. 2016). Various locomotor performance traits have been linked to predator escape (Lima and Dill 1990; Calsbeek and Cox 2010), foraging mode (Huey et al. 1984; Miles et al. 2007a, b), reproductive success (Husak et al. 2006; Byers et al. 2010), territorial defense (Garland et al. 1990; Robson and Miles 2000), and survival (Miles 2004; Gilbert and Miles 2017). In general, the estimates of locomotor performance such as sprint speed (initial velocity and long sprint; van Berkum 1988; Angilletta et al. 2002; Huey et al. 2009) and endurance (Robson and Miles 2000)

have been estimated using a variety of methods. However, theory suggests that sprint speed and endurance are assumed to present conflicting demands on locomotor performance, and, consequently, cannot be simultaneously maximized (Vanhooydonck et al. 2001). For this reason, a trade-off between these performance parameters is predicted, with faster lizards exhibiting lower values for endurance and vice versa. Nevertheless, the expected trade-off between these traits has not been detected (Huey et al. 1984; Tsuji et al. 1989; Sorci et al. 1995; Vanhooydonck et al. 2001; Pinch and Claussen 2003).

In ectotherms, performance is intimately linked with temperature (Huey and Stevenson 1979; Marsh and Bennett 1986; Huey and Kingsolver 1989; Kingsolver 2009). The relationship between temperature and performance is described by a thermal performance curve (TPC). Estimation of the optimal temperature for maximum performance (T_o) can be determined using TPCs (Huey and Stevenson 1979; Huey and Kingsolver 1989). In addition, TPCs allow the estimation of the thermal performance breadth (the range of temperatures that results in an ectotherm performing at or above some level, e.g., 80%), and the thermal tolerance zone. The latter describes the range of temperatures at which an ectotherm can be active. The lower end of the tolerance zone is defined as the critical thermal minimum (CT_{min}), whereas the upper end is defined as the critical thermal maximum (CT_{max}). When ambient temperatures exceed these limits, the capacity for an organism's normal functioning ceases. Thermal performance curves typically have an asymmetrical shape, such that physiological capacity increases slowly below T_o ; above T_o performance decreases rapidly (Bonino et al. 2015). However, we recognize that ectotherms are often exposed to thermal conditions below or above the optimum temperature for physiological performance, which may have deleterious consequences for survival and reproduction.

The strength of selection acting on thermal performance breadth can differ between constant or fluctuating environments (Huey and Slatkin 1976; Huey and Stevenson 1979). Ectotherms within the tropics experience low fluctuations in daily temperatures and limited seasonal variation. Therefore, species in the tropics tend to have a narrower thermal tolerance than temperate-zone lizards (Janzen 1967; Huey et al. 2009). Nevertheless, this pattern is not consistent for thermal performance breadth. For example, in tropical lizard species such as *Anolis*, the performance breadth is not consistently narrower than temperate-zone lizards, such as *Sceloporus*. Rather, the pattern suggests that the thermal performance breadth correlates with variability in field-active body temperatures (T_b s) exhibited by individuals (Crowley 1985; van Berkum 1988; Angilletta et al. 2002). Thus, lizards with a broad geographical distribution or that inhabit sites with large environmental thermal amplitudes (that is high seasonality) tend to exhibit greater variability in their

T_b s, and, consequently, broader thermal performance breadth (van Berkum 1988; Huey and Kingsolver 1989; Gaston and Blackburn 2000; Cruz et al. 2005; Angilletta 2009).

On the other hand, reptiles may use behavioral thermoregulation to buffer the effects of ambient temperature on physiological performance (Huey et al. 2009). Therefore, large changes in ambient temperature have a limited effect on performance as a consequence of individual's selecting microhabitats that minimize variation in T_b . The previous studies have shown that optimal temperature for physiological performance is at or near the preferred temperatures (Huey and Bennett 1987; Martín and Huey 2008). The tight connection between behavioral thermoregulation and thermal physiology has been used as the evidence of coadaptation. An advantage of coadaptation is the potential increase in amplitude of temperatures that maximize individual performance (Huey and Bennett 1987; Angilletta et al. 2002). Yet, to date, there is scant evidence supporting the hypothesis of coadaptation; indeed, there is evidence to the contrary (Angilletta et al. 2002).

Lizard species occupying the habitats in the Andes Mountains of Argentina provide the opportunity to examine how environmental variation in ambient temperature affects locomotor performance in ectothermic vertebrates. In this study, we focus on two genera of lizards from the family Liolaemidae, *Phymaturus* and *Liolaemus*, that often coexist along broad latitudinal and elevational gradients along the Andes mountain range in Argentina and Chile (Díaz Gómez 2009). Individuals of species from these two genera inhabit environments characterized by substantial variation in ambient temperature. Research analyzing the thermal dependence of locomotor performance is scarce for these two genera of lizards (Bonino et al. 2011, 2015; Fernández et al. 2011; Fernández and Ibarquengoytía 2012; Kubisch et al. 2011, 2016). At the southern end of the arid, Puna region in Argentina, three endemic species of Liolaemidae coexist in sympatry: *P. extrilidus*, *L. parvus*, and *L. ruibali*. These species present an ideal system for determining the influence of ambient temperature on locomotor performance, and whether these species exhibit similar responses to seasonal variation in the thermal environment. Given that variation in ambient temperatures can be quite large in the Puna region (Márquez et al. 2014), we predict that these species should have large thermal tolerances (i.e., the difference between critical thermal minimum and maximum temperatures), optimal temperatures for performance (T_o) that coincide with field-active body temperatures, and broad thermal performance breadths (defined below).

Phymaturus extrilidus is an herbivorous species that is found in habitats at high elevations. It is dorsoventrally flattened, which is presumably an adaptation to occupy narrow cracks in rocks as a refuge from predators. The other two species, *L. parvus* and *L. ruibali*, are morphologically

similar, despite inhabiting different habitats. *Liolaemus parvus* is insectivorous and lives in sites with rocks and meadows, whereas *L. ruibali* is omnivorous and mainly inhabits flat areas characterized by open shrubland consisting of widely scattered, low growing shrubs (*Lycium charrar*, *Artemisia mendozana*, *Adesmia horrida*, among others; Márquez et al. 2014). This partitioning of trophic resources and microhabitats may facilitate coexistence among the species, lead to morphological differentiation; favor the evolution of differences in their thermal biology, or a combination of these. In addition to morphological and ecological differences between these genera, we expect that locomotor performance and thermal tolerance should be more similar between species in the genus *Liolaemus*, than between these and *P. extrilidus*. This is because the two *Liolaemus* species are more closely related to each other than to *Phymaturus* (Abdala and Quinteros 2014).

The objectives of this study were to (1) quantify variation in the initial velocity and long sprint at different temperatures, (2) measure endurance and test for a trade-off with running speed, (3) measure critical thermal limits (CT_{\min} and CT_{\max}), and (4) explore the relationship between optimal temperature for performance in relation to field activity body temperatures (T_b), preferred temperatures (T_{pref}), and environmental operative temperatures (T_e) for *P. extrilidus*, *L. parvus*, and *L. ruibali*.

Materials and methods

Fieldwork

Fieldwork was carried out at the “Don Carmelo” Reserve located in the western part of the Ullum Department (30°56.99'S, 69°04.83'W; 3166 m amsl), in the foothills of the Precordillera of the Andes Mountains in the province of San Juan, Argentina. The reserve is situated in the mountainous terrain east of the Andes. This area is within the Puna desert ecoregion and lies between 2700 and 3400 m above mean sea level (amsl) (Roig Juñent et al. 2003). The climate is cold and dry, with a median annual temperature below 8 °C. Daily temperatures exhibit large fluctuations from spring to fall (nocturnal temperatures below 0 °C and diurnal temperatures exceed 30 °C). The region also experiences substantial seasonal temperature fluctuations, with snow from June to October (Cabrera 1994; Martínez Carretero 1995; Roig and Martínez Carretero 1998; Roig Juñent et al. 2003) and hot and dry conditions during the austral summer.

We captured individuals of *P. extrilidus*, *L. parvus*, and *L. ruibali* using nooses or by hand between 10:00 h and 19:00 h during November 2014. This corresponds with the diurnal activity period for the species and within the breeding

season. For each individual, we recorded field body temperature using a digital thermometer with a K-type thermocouple (TES Electronic Corp., Taipei, Taiwan 1303 digital thermometer, accuracy ± 0.01 °C; TP-K01 thermocouples, 1.62 mm diameter). We also measured snout-vent length (SVL) using a Vernier caliper to the nearest 0.02 mm, and body mass (BM) with a Pesola® spring scale ± 0.05 g. We also determined sex by the presence of precloacal pores and the eversion of the hemipenis in males. Females were identified using coloration and presence of embryos and follicles (by palpation). The research was authorized by Secretaría de Medio Ambiente, Dirección de Conservación y Áreas Protegidas, Provincia de San Juan (exp. no. 13004047, J.C.A.).

Husbandry

After capture, the lizards were brought to the laboratory and held in 100 × 30 × 40 cm terraria. Each individual was held in a separate terrarium. We held lizards for a period of 5 days, which time required for estimating the performance traits. The terraria were kept in a room at an ambient temperature of 24 °C and lizards were provided with ad libitum water. We did not feed the lizards prior to the experiments.

Locomotor performance

Velocity

Sprint performance was measured between 10:00 and 19:00 h during the normal activity period of lizards. We used a linear track measuring 0.08 m wide and 1.2 m long to quantify sprint speed. A series of infrared sensors were placed along the walls of the track at intervals of 0.15 m to measure speed. The sensors were connected to a computer, which calculated the speed between each 0.15 m split. We used the difference in time between successive sensors to estimate velocity. Based on the data from the sensors, we calculate: the initial velocity (IV) determined by the difference time between the first and second sensors (0.15 m) and can be considered an estimate of acceleration; and long sprint (LS) that was calculated by the difference in time registered between the first and last sensors (1.05 m). We consider this estimate to best represent the locomotor capacity of lizards to carry out activities such as foraging, territorial defense, and courtship (*sensu* Cabezas Cartes et al. 2014).

We induced lizards (*P. extrilidus* $N=19$, *L. parvus* $N=16$, and *L. ruibali* $N=15$) to run at four temperatures within the range of thermal tolerance for each species (23, 38, 28, and 33 ± 1 °C, respectively) in random order. Prior to running a lizard, we kept it in a terrarium at the desired temperature for 1 h.

We ran a lizard three consecutive times at each temperature. The fastest run was used as estimate of maximum

performance for both IV and LS. Lizards were run at one temperature per day and rested for 24 h between temperature treatments. As a control, we repeated a run at the initial temperature to determine if individual performance had exhibited a decrease in speed over the course of the study (Huey et al. 1990; Angilletta et al. 2002).

We used the sprint trials to calculate the initial velocity and long sprint for each lizard ($V_{i\max}$) and the maximum speed for the species (V_{\max} ; Fernández et al. 2011; Kubisch et al. 2011). We also used the change in sprint performance among the temperatures to estimate the optimal sprint temperature (T_o) for each species. We used the average body temperatures of each lizard at which speed was the highest. We estimated the thermal performance breadth (B_{80}) by calculating the range of body temperatures where performance was equal to or higher than 80% of V_{\max} (see Hertz et al. 1983).

Endurance capacity

Endurance measurements were taken following the methodology used by Miles et al. (2000), Robson and Miles (2000), Vanhooydonck et al. (2001), and Angilletta et al. (2002). Lizards were placed on a motorized treadmill and a mild stimulus was applied to their hind legs to make them run. Endurance was measured as the time (in seconds) the lizard ran before becoming exhausted at a constant speed of 0.5 km/h (following Miles 1994). The lizards were considered to be fatigued when they did not demonstrate a righting response when placed on their backs (Huey et al. 1990; Robson and Miles 2000). Only one trial was carried out for each lizard, at 32 °C (*P. eximilis*) and 33 °C (*Liolaemus*). We selected these temperatures, because they correspond to the field-active body temperature for the species (Gómez Alés et al. 2017, Gómez Alés unpublished data).

Thermal tolerance: CT_{\min} and CT_{\max}

Minimum critical temperature (CT_{\min}) and maximum critical temperature (CT_{\max}) were recorded for each individual (*P. eximilis* $N=20$, *L. parvus* $N=15$, and *L. ruibali* $N=15$). In both cases, the critical temperature was determined when the individual lost its righting response after being placed on its back. In addition, we used the signs of muscular spasms as a cue for CT_{\max} (Jacobson and Whitford 1970; Pough and Gans 1982; Cruz et al. 2005).

To determine CT_{\min} , individuals were placed separately in a plastic terrarium within a refrigerator set at a constant temperature (−15 °C). Body temperature was measured every 20 s as we tested the righting response of the individual. We recorded the temperature when a lizard failed to right itself. To determine CT_{\max} , individuals were placed in cylindrical vessel (25 cm diameter and 35 cm height),

with sterile sand as substrate. A 150-W incandescent light bulb was placed above the cylinder at a distance of 50 cm from the surface of the sand. As with CT_{\min} , we checked T_b every 10 s until the lizard lost its righting ability. We immediately removed the lizard from the cylinder and allowed it to recover. We inserted ultrathin thermocouples (1 mm) within the cloaca (10 mm) held in place by hypoallergenic adhesive tape to record CT_{\min} and CT_{\max} . The thermocouples were connected to a data acquisition module (OMEGA®, USB TC-08), which allowed us to monitor the T_b of lizards. This method prevents manipulating the lizard every time that cloacal temperature is taken. None of the individuals died during the trials.

Thermal tolerance for each species was calculated as the difference between the critical thermal limits, $\overline{CT}_{\max} - \overline{CT}_{\min}$ (Cruz et al. 2005). We also computed the thermal safety margin, which is estimated as the difference between T_o and CT_{\max} , and following Deutsch et al. (2008) as the difference between T_o and mean T_c . Critical thermal limits were used to compute the thermal sensitivity curves for the initial velocity and long sprint (Angilletta et al. 2002).

Statistical analyses

The relationship among variables was assessed using ordinary and multiple regression analyses. For comparisons between means, we used paired and unpaired *t tests* and one-way repeated-measures analysis of variance (R-ANOVA). We also conducted post hoc tests to compare means among different groups. Sprint speed and endurance were compared among species with an ANCOVA, using SVL as a covariate. To test for correlations among the performance traits (long sprint vs. endurance, and initial velocity vs. endurance), we log-transformed the data and calculated Pearson product–moment correlation coefficients. Prior to conducting any statistical procedure, we evaluated whether the data followed a normal distribution and homogeneity of variance among groups using Kolmogorov–Smirnov and Shapiro–Wilk tests, respectively. In cases where data did not comply with the assumptions for parametric statistics, we used the equivalent non-parametric test (e.g., Mann–Whitney *U test*, Wilcoxon and Friedman; Sokal and Rohlf 1969). Tests were performed in Sigma Stat 3.5® and Statistica version 7.0 (Statsoft Inc., Tulsa, OK). Descriptive statistics are represented as mean \pm standard error or median. Significance level was fixed at $\alpha=0.05$. For multiple tests, significance levels were corrected using a sequential Bonferroni adjustment (Rice 1989; Chandler 1995). We estimated the thermal performance curves using a Kumaraswamy equation based on a custom R script (Sheth and Angert 2014, MW Sears unpublished). In addition, we compared the shape of the thermal performance curve between species using a

generalized additive mixed model (GAMM; Zajitschek et al. 2012). The latter two analyses used the computing environment R and the nlsLM function from the minpack.lm package (Kumaraswamy fitting) and function gamm in the mgcv package (Wood 2017).

Results

Relationship between maximum individual speed ($V_{i\max}$) and snout–vent length and body mass

The average values of snout–vent length and body mass for each species and sex are given in Table 1. The snout–vent length and body mass of *P. extrilidus* and *L. parvus*, did not differ between the sexes (*t* test, SVL: *P. extrilidus* $P=0.98$, *L. parvus* $P=0.56$, BM: *P. extrilidus* $P=0.94$, *L. parvus* $P=0.83$). However, SVL in *L. ruibali* males was significantly greater than females (Mann–Whitney, $U=37.5$, $P=0.03$), but there was no significant difference in body mass (Mann–Whitney, $P=0.70$).

In all species, long sprint was uncorrelated with SVL or body mass (multiple regression: *P. extrilidus* $F_{2,17}=0.89$; *L. parvus* $F_{2,14}=1.62$; *L. ruibali* $F_{2,13}=0.453$; all $P>0.05$). Similarly, the initial velocity was not significantly correlated with SVL or body mass (Multiple regression: *P. extrilidus* $F_{2,17}=0.36$; *L. parvus* $F_{2,14}=0.84$; *L. ruibali* $F_{2,13}=0.55$; all $P>0.05$).

Effect of temperature on running speed (initial velocity and long sprint)

Thermal performance curves showed a significant effect of temperature on speed for all species in the initial and long sprint (GAMM: $F_{P. extrilidus}=2.62$; $F_{L. parvus}=2.2$; $F_{L. ruibali}=0.93$; $P<0.001$; Fig. 1). The long sprint of *P.*

extrilidus increased with temperature, with its minimum speed at 23 °C, maximum speed at 33 °C, and a decreased speed at 38 °C. However, we found significant differences between trials at 23–33 °C and 33–38 °C (repeated-measures ANOVA on ranks: $F_{3,71}=5.46$; Bonferroni corrected $P_{33^{\circ}-23^{\circ}}=0.002$; $P_{33^{\circ}-38^{\circ}}=0.044$). For *L. parvus*, there were no differences between trials (repeated-measures ANOVA on ranks: $F_{3,60}=1.53$; $P=0.20$), suggesting a broad thermal performance breadth. However, its maximum speed was also attained at 33 °C. Finally, long sprint of *L. ruibali* increased with temperature, with the highest value occurring at 38 °C, though significant differences were only found between trials at 23–33 and 23–38 °C (Friedman repeated-measures ANOVA on ranks: $\chi^2_{3,56}=10.10$; $P=0.018$; Dunn's method: $Q_{33^{\circ}-23^{\circ}}=2.73$, $Q_{38^{\circ}-23^{\circ}}=2.73$; $P<0.05$).

The initial velocity in *P. extrilidus* increased with temperature, with minimum initial speed occurring at 23 °C and maximum value at 33 °C, which subsequently decreased at warmer temperatures (i.e., 38 °C). Significant differences were only found between 23 and 33 °C (repeated-measures ANOVA on ranks: $F_{3,71}=3.99$; Bonferroni corrected $P_{33^{\circ}-23^{\circ}}=0.007$). For *L. parvus*, there were no differences between trials (Friedman repeated-measures ANOVA on ranks: $\chi^2_{3,60}=6.37$; $P=0.09$). The initial velocity of *L. ruibali* increased with temperature, reaching its maximum at 33 °C, though significant differences were only found between trials at 23 and 33 °C (Friedman repeated-measures ANOVA on ranks: $\chi^2_{3,52}=9.64$; $P=0.022$; Dunn's method: $Q_{33^{\circ}-23^{\circ}}=2.88$; $P<0.05$).

There was no significant relationship between maximum performance (initial velocity and long sprint) and body temperatures for any of the species (linear regression: initial velocity: $F_{P. extrilidus, 2,17}=0.15$; $F_{L. parvus, 2,14}=0.36$; $F_{L. ruibali, 2,13}=0.88$; all $P>0.05$; long sprint: $F_{P. extrilidus, 2,17}=1.48$; $F_{L. parvus, 2,14}=0.01$; $F_{L. ruibali, 2,13}=1.93$; all $P>0.05$).

Comparison between the initial velocity and long sprint for each temperature trial

The mean values of $V_{iv\max}$ and $V_{ls\max}$ for the three species are shown in Table 2. For *P. extrilidus*, the mean value for initial velocity was significantly greater than the mean value for long sprint (Wilcoxon test: $W=33$; $P=0.012$). However, when comparing among temperature trials, there were no significant differences between the two measures of velocity ($P>0.05$; Table 3). Mean initial velocity of *L. parvus* was significantly greater than long sprint (Wilcoxon Test: $W=29$; $P=0.043$). When we compared running speed for each temperature trial, the IV speed was greater than the LS speed at 23 °C and 28 °C ($P<0.05$; Table 3), whereas there were no significant differences for the remaining trials ($P>0.05$; Table 3). For *L. ruibali*, differences were only

Table 1 Snout–vent length (SVL) and body mass (BM) of the three species

Species	Sex	N	SVL (mm)	BM (g)
<i>Phymaturus extrilidus</i>	Overall	19	97.15 ± 3.25	33.93 ± 3.66
	Females	10	96.76 ± 2.56	33.95 ± 3.58
	Males	9	97.19 ± 3.51	33.86 ± 3.79
<i>Liolaemus parvus</i>	Overall	16	60.50 ± 3.30	6.09 ± 1.10
	Females	8	60.86 ± 3.07	6.17 ± 1.09
	Males	8	60.07 ± 3.52	5.87 ± 1.04
<i>Liolaemus ruibali</i>	Overall	15	59.20 ± 3.36	6.11 ± 1.32
	Females	7	58.92 ± 3.50	6.11 ± 1.48
	Males	8	59.14 ± 3.48	6.08 ± 1.37

Means are presented for the species (overall) and each sex. Values are means ± standard errors

N sample size

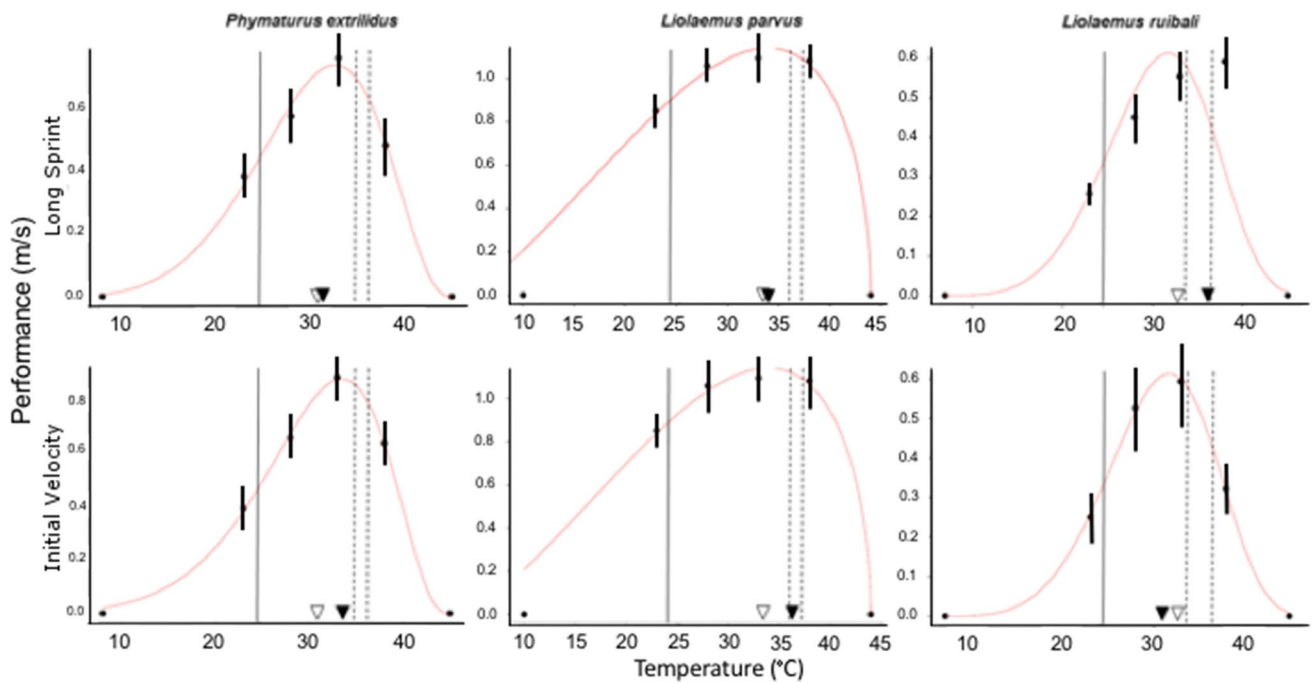


Fig. 1 Thermal performance curves showing the relationship between body temperature ($^{\circ}\text{C}$) and speed (m/s) of the initial velocity and long sprint for *Phymaturus extrilidus*, *Liolaemus parvus*, and *Liolaemus ruibali*. Black triangles designate the optimum temperature for performance (T_o) and white triangles shows the mean field-active body temperature (T_b). Broken vertical lines represent the set-point (inter-

quartile) range of selected temperatures in a laboratory thermal gradient. Continuous vertical lines are the average operative environmental temperature T_e , i.e., the distribution of potential T_b 's registered by a non-thermoregulating animals in a specific microhabitat (see Gómez Alés et al. 2017). The minimum and maximum critical temperatures were used as thermal limits to anchor the curves

Table 2 Individual maximum speed ($V_{i\text{max}}$) by sex and species (overall) for long sprint (LS) and initial velocity (IV)

Species	Run type	Velocity (m/s)		t test or Mann–Whitney	P value	Velocity (m/s) overall
		Males	Females			
<i>Phymaturus extrilidus</i>	LS	0.62 ± 0.09	0.97 ± 0.13	$t_{17} = -0.10$	0.97	0.81 ± 0.09
	IV	0.91 ± 0.17	1.22 ± 0.17	$t_{17} = 0.85$	0.40	1.07 ± 0.12
<i>Liolaemus parvus</i>	LS	1.66 ± 0.23	1.23 ± 0.09	$t_{14} = 1.67$	0.11	1.44 ± 0.13
	IV	2.08	1.26	$U = 92$	0.01	1.80 ± 0.18
<i>Liolaemus ruibali</i>	LS	0.70 ± 0.14	0.83 ± 0.11	$t_{13} = -1.67$	0.12	0.76 ± 0.09
	IV	0.87 ± 0.29	0.67 ± 0.18	$t_{13} = -0.56$	0.58	0.78 ± 0.17

Values are means \pm standard errors or median speed, and statistical analyses carried out and P values are indicated. Significant differences ($P < 0.05$) between sexes are indicated in bold

found on trials at 38°C (Table 3), with long sprint exceeding the value for the initial velocity.

Differences in the thermal sensitivity of speed between sexes for each species

For *P. extrilidus*, no significant differences between males and females were found for any of the temperature trials, both for IV and LS ($P > 0.05$; Tables 2, 3). For *L. parvus*, the IV was greater for males (Table 2); likewise, the IV speed for trials at 38°C was also greater for males (Table 3) and

there were no significant differences for the remaining trials ($P > 0.05$; Table 3). Male and female *L. ruibali* did not differ in speed at any temperature for IV and LS ($P > 0.05$; Tables 2, 3).

Comparison of running speed between species

Snout–vent length was significantly different between *P. extrilidus* and the two *Liolaemus* species, but not between *L. parvus* and *L. ruibali* (Kruskal–Wallis: $H_{2,48} = 35.43$; $P = 0.0005$; Dunn's Method: $Q_{L. parvus-L. ruibali} = 4.26$;

Table 3 Speeds for long sprint (LS) and initial velocity (IV) for each temperature treatment for each species (overall) and sex within each species

Species	Temperature °C	Run type	Speed (m/s)		Repeated-measures ANOVA or Friedman	P values	Speed (m/s) overall	Paired <i>t</i> test or Wilcoxon between runs	P values
			Males	Females					
<i>Phymaturus extrilidus</i>	23	LS	0.31±0.08	0.43±0.08	$F_{3,35} = 1.18$	0.33	0.38±0.06	$t_{34} = -0.110$	0.91
		IV	0.33±0.10	0.44±0.09					
	28	LS	0.48±0.09	0.66±0.11	$F_{3,35} = 0.59$	0.62	0.58±0.07	$t_{36} = -0.725$	0.47
		IV	0.60±0.12	0.71±0.12					
	33	LS	0.58±0.08	0.93±0.14	$F_{3,35} = 1.48$	0.24	0.76±0.09	$t_{36} = -0.724$	0.47
		IV	0.70±0.18	1.04±0.20					
	38	LS	0.35±0.05	0.60±0.13	$F_{3,35} = 0.16$	0.16	0.42	W=64	0.21
		IV	0.53±0.15	0.74±0.15					
<i>Liolaemus parvus</i>	23	LS	0.94±0.11	0.75±0.13	$F_{3,31} = 3.71$	0.07	0.84	W=10	0.01
		IV	1.79±0.35	1.05±0.16					
	28	LS	0.85	1.22	$X^2_{3,31} = 7.8$	0.06	1.05±0.08	$t_{30} = -2.438$	0.02
		IV	1.99	1.26					
	33	LS	1.19±0.21	0.99±0.14	$F_{3,31} = 1.41$	0.27	1.09±0.12	$t_{30} = 0.717$	0.47
		IV	1.18±0.20	0.73±0.18					
	38	LS	1.22±0.13	0.94±0.11	$q = 1.69$	0.63	1.08±0.09	$t_{30} = -1.235$	0.22
		IV	1.65±0.24	0.96±0.08					
<i>Liolaemus ruibali</i>	23	LS	0.08	0.15	$X^2_{3,31} = 6.25$	0.10	0.13	W=29	0.14
		IV	0.06	0.22					
	28	LS	0.37±0.12	0.51±0.18	$F_{3,23} = 0.37$	0.94	0.35	W=36	0.50
		IV	0.60±0.40	0.46±0.19					
	33	LS	0.52	0.59	$X^2_{3,31} = 1.80$	0.61	0.34	W=31	0.09
		IV	0.44	0.29					
	38	LS	0.65±0.14	0.53±0.05	$F_{3,27} = 2.62$	0.08	0.56	W=39	0.003
		IV	0.37±0.17	0.26±0.07					

Values are means ± standard errors or median speed, statistical analyses carried out and *P* values are indicated. Significant differences ($P < 0.05$) between sexes and between long sprint and initial velocity by treatment for each species are indicated in bold

$P > 0.05$; $Q_{P. extrilidus-L. parvus} = 4.63$; $Q_{P. extrilidus-L. ruibali} = 5.4$; $P < 0.05$; Table 1). Thus, we used ANCOVA with SVL as a covariate to evaluate differences in performance between species. The $V_{i\max}$ for LS and IV for *L. parvus* was higher than that of *L. ruibali* and *P. extrilidus* (ANCOVAs: $F_{LS(2,48)} = 11.2$; Bonferroni corrected $P_{L. parvus-L. ruibali} < 0.001$; $P_{L. parvus-P. extrilidus} < 0.001$; $F_{IV(2,48)} = 11.54$; Bonferroni corrected $P_{L. parvus-L. ruibali} < 0.001$; $P_{L. parvus-P. extrilidus} = 0.004$; Fig. 2). The three species also differed in the shape of the thermal performance curves (GAMM: $t_{P. extrilidus} = -2.95$; $t_{L. parvus} = 0.20$; $t_{L. ruibali} = -7.43$; $P < 0.01$; Fig. 1).

Endurance capacity

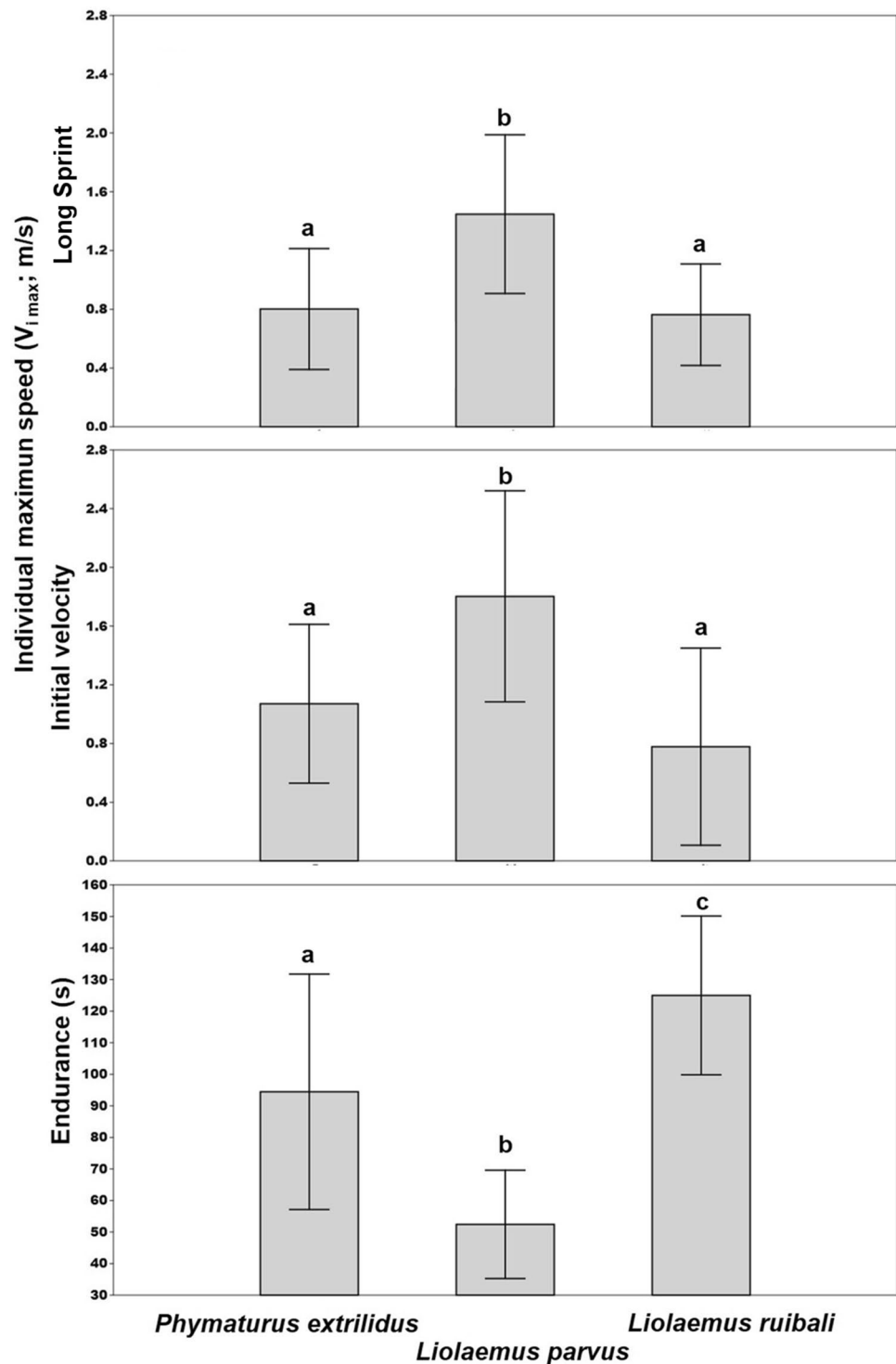
P. extrilidus exhibits a wide range of endurance capacity from 45 to 161 s (94.44 ± 9.32) at 32 °C. However, endurance was not associated with either SVL or BM (multiple regression: $F_{SVL 2,14} = 1.08$; $F_{BM 2,14} = 3.21$; $P > 0.05$). The range of endurance for *L. parvus* varied from 38 to 104 s (52.44 ± 4.29) at 33 °C, and was not associated with SVL, but did exhibit a positive and significant relation to

body mass (multiple regression: $F_{SVL 2,14} = 1.79$; $P > 0.05$; $F_{BM 2,14} = 4.93$; $P = 0.044$). For *L. ruibali*, endurance capacity varied from 89 to 178 s (125.0 ± 6.97) at 33 °C, and was not correlated with either SVL or BM (multiple regression: $F_{SVL 2,11} = 2.22$; $F_{BM 2,11} = 3.73$; $P > 0.05$). None of the species showed differences in endurance between males and females (*t* test: $t_{P. extrilidus, 14} = -0.22$; $t_{L. ruibali, 11} = -0.14$; $P > 0.05$; Mann–Whitney: $U_{L. parvus} = 31.5$; $P = 0.885$).

Correlation analyses between long sprint vs. endurance and initial velocity vs. endurance, at the same temperature, were not significant for any of the species (LS: Pearson: $r_{P. extrilidus} = -0.01$; $r_{L. parvus} = -0.39$; $r_{L. ruibali} = -0.12$; $P > 0.05$; IV: Pearson: $r_{P. extrilidus} = 0.22$; $r_{L. parvus} = -0.29$; $r_{L. ruibali} = -0.02$; $P > 0.05$).

Liolaemus parvus had lower endurance than *L. ruibali* and *P. extrilidus*. At the same time, differences were found between these two species, with endurance being greater for *L. ruibali* (ANCOVA: $F_{(2,46)} = 23.77$; Bonferroni corrected $P_{L. ruibali-L. parvus} < 0.0001$; $P_{L. ruibali-P. extrilidus} = 0.018$; $P_{P. extrilidus-L. parvus} < 0.001$; Fig. 2).

Fig. 2 Comparison of average locomotor performance for sprint speed (initial velocity and long sprint; m/s) and endurance (s) between the three species. Letters (a, b, c) indicate significant differences (Tukey's HSD test; $P < 0.05$)



Thermal tolerance: CT_{\min} and CT_{\max}

The critical thermal minimum (CT_{\min}) was higher for *L. parvus* than the other two species in the assemblage (ANCOVA: $F_{(2,46)} = 11.03$; Bonferroni corrected $P_{L. parvus-L. ruibali} < 0.001$; $P_{L. parvus-P. extrilidus} = 0.017$; Table 4). In contrast, the critical thermal maximum was similar

among the species (ANCOVA: $F_{(2,46)} = 2.98$; $P = 0.104$, Table 4). *Phymaturus extrilidus*, *Liolaemus parvus*, and *L. ruibali* showed a wide thermal tolerance (above 30 °C), and wide thermal safety margins (7–12 °C) for both types of runs. Thermal tolerance and thermal safety margins for long sprint and initial velocity of the three species are shown in Table 4.

Table 4 Field body temperature (T_b), preferred body temperature (T_{pref}) as estimated in the laboratory and set-point range of preferred temperature (T_{pref}) as estimated in the laboratory and set-point range of preferred temperature (T_{pref}), minimum and maximum critical temperatures (CT_{min} , CT_{max}), thermal tolerance (TT), and optimal temperature (T_o), and thermal safety margin (TSM)

Species	T_b	T_{pref}	Set-point range	CT_{min}	CT_{max}	TT	Run type	T_o	TSM	TSM _b
<i>Phymaturus extrilidus</i>	32.32 ± 3.13	35.74 ± 1.80	34.92 (± 2.03)–36.78 (± 1.65)	7.45 ± 1.89	44.45 ± 1.13	37.00 ± 2.16	LS	32.50 ± 2.28	12.00	7.95
							IV	33.25 ± 3.17	11.25	8.70
<i>Liolaemus parvus</i>	33.74 ± 2.46	36.66 ± 1.34	36.03 (± 1.60)–37.70 (± 1.26)	9.47 ± 1.43	43.20 ± 2.54	33.73 ± 2.95	LS	33.95 ± 4.81	9.05	9.40
							IV	36.25 ± 5.78	6.75	11.70
<i>Liolaemus ruibali</i>	33.47 ± 2.53	35.06 ± 1.97	33.92 (± 2.47)–36.28 (± 1.84)	6.62 ± 1.52	44.65 ± 0.98	38.03 ± 1.16	LS	36.25 ± 4.81	8.25	11.70
							IV	31.8 ± 3.53	12.70	7.25

Temperatures values (°C); values are means ± standard errors

The thermal safety margin as estimated following Deutsch et al. (2008) for long sprint (LS) and initial velocity (IV) of the three species is given in the column TSM_b

The minimum and maximum critical temperatures showed no relationship with SVL and body mass for any of the species (multiple regression: *P. extrilidus*: $F_{CTmin(2,19)} = 1.24$; $F_{CTmax(2,19)} = 0.28$; *L. parvus*: $F_{CTmin(2,13)} = 2.57$; $F_{CTmax(2,13)} = 0.98$; *L. ruibali*: $F_{CTmin(2,13)} = 0.81$; $F_{CTmax(2,13)} = 0.35$; $P > 0.05$).

Optimum temperature at running speed (T_o), performance range (B_{80}) and its relation to field body temperatures (T_b), preferred body temperatures (T_{pref}), and operative body temperatures (T_e)

Field-active body temperature, preferred body temperature, and set-point range of the three species, are given in Table 4. For *P. extrilidus*, the thermal performance breadth (B_{80}) was not reached in any of the temperature trials for both runs (LS and IV). T_o was similar to field body temperature, but below the set-point range (Fig. 1; Table 4). The thermal performance breadth (B_{80}) for *L. parvus* was between 28 and 38 °C for long sprint and between 23 and 38 °C for the initial velocity. T_o for LS was similar to T_b and not within the set-point range, while T_o for IV was greater to T_b and was included in the set-point range (Fig. 1; Table 4). For *L. ruibali*, the B_{80} range was only reached at 33 °C for LS and 28 °C for IV. T_o for IV was less to T_b and was not included in the set-point range of T_{pref} , while T_o for LS was greater to T_b and was included in the set-point range (Fig. 1; Table 4). Finally, T_o of the three species of the assemblage were markedly greater than the operative environmental temperature (T_e ; 24.55 ± 5.41 °C; Gómez Alés et al. 2017; Fig. 1).

Discussion

Morphological differences between lizard species are often associated with different performance capacities, such as running speed and endurance, and may generate variation in the locomotor capacity of individuals in different ecological contexts (Arnold 1983; Miles 1994; Macrini and Irschick 1998; Calsbeek and Irschick 2007). Running speed was not related to body length or body mass in any of the species. In contrast, we found that body mass was positively related to endurance in *L. parvus*. The absence of a significant relationship between SVL, body mass, and speed has been reported for other *Liolaemus* species such as *L. sarmientoi*, *L. magellanicus*, and *L. pictus* (Fernández et al. 2011; Kubisch et al. 2011) and for some species of the group *L. lineomaculatus* (Bonino et al. 2011). The absence of an association between body size (either SVL or mass) and speed (mainly used for the evasion of predators) can be interpreted as an advantage for these species. For example, they could reduce a trade-off between gaining energy and capacity to

escape (Pérez Tris et al. 2004; Zamora Camacho et al. 2014), as observed in *Psammotromus algirus*, where mass losses induced by evasion of predation did not improve the escape performance during predator attacks, and fat lizards did not show variation in escape performance (Martín 1996; Pérez Tris et al. 2004).

In general, performance increased with temperature up to the thermal optimum, and then decreased beyond this value (Fig. 1). This pattern has been reported for *Liolaemini* lizards (Bonino et al. 2011; Fernández et al. 2011; Kubisch et al. 2011, 2016) and for lizards in general (Hertz et al. 1983; Bennett 1990; Ibarguengoytía et al. 2007; Gaby et al. 2011; Beal et al. 2014; McElroy 2014; among others), indicating that locomotor performance is sensitive to temperature. Nevertheless, the thermal performance breadth of running speeds (IV and LS) was wide for the three species of the assemblage. This pattern is similar to the world's southernmost species, *L. magellanicus* and *L. sarmientoi*, which attain high speeds at a wide range of temperatures. The pattern of locomotor efficiency at low temperatures may be interpreted as an adaptation to cold and variable environments (Fernández et al. 2011). The climate in the Puna region is cold, dry, and characterized by large thermal amplitudes and strong winds (Roig Juárez et al. 2003). Consequently, the ability to achieve high speeds across a wide range of temperatures provides an enhanced ability of these lizards to escape from predators, optimize food acquisition, and affect social interactions with conspecifics (e.g., territorial defense and reproduction), relative to lizards that have a narrow performance breadth (B_{80}), as in some tropical forest lizards (Hertz et al. 1983; van Berkum 1988; Huey et al. 2009).

Our measurement of long sprint over a longer distance has implications for foraging, territorial defense, and courtship, whereas the initial velocity may have a greater impact on the ability to flee from predators (Huey et al. 2009; Cabezas Cartes et al. 2014). Given the differences in the functional consequences of IV and LS, we expected to observe a trade-off in performance. We note that, in *P. extrilidus* and *L. parvus*, the initial velocity is higher than long sprint over 1 m, which has been observed in the other species of *Liolaemus* (Fernández et al. 2011). In *L. ruibali*, although there are no differences between LS and IV, we found higher values of long sprint at 38 °C, which coincides with T_o .

The observed differences in performance could be related to the type of habitat utilized; *P. extrilidus* and *L. parvus* inhabit primarily rocky areas and meadows with vegetation nearby, making it unnecessary to travel great distances to obtain food, but optimizing flight speeds (IV) should be favored by selection as these species are more exposed to predators in rocky areas (Corbalán and Debandí 2013; Gómez Alés et al. 2017; Acosta et al. 2018). On the other hand, *L. ruibali* inhabits flat areas with low vegetation cover

and open shrubland (Villavicencio et al. 2005; Acosta et al. 2018), so higher performance capacities in both estimates of speed would be beneficial for both foraging and fleeing from predators (Pietrek et al. 2009; Fuller et al. 2011).

No correlation was found between speed and endurance, which suggests a decoupling between these two measures of locomotor performance (Tsuji et al. 1989; Sorci et al. 1995). Other differences observed between the species include running speeds and endurance, where a trade-off is evident as was found by Vanhooydonck et al. (2001). *Liolaemus parvus* has greater running speed and lower endurance, while *L. ruibali* has lower running speeds and greater endurance than of the other species (Fig. 2), which could be due to differences in foraging behavior between species (Miles et al. 2007a, b). Huey et al. (1984) proposed that differences in locomotor capacity coevolve with feeding behavior. These authors found that widely-foraging lizards of the genus *Eremias* have greater endurance, whereas “sit-and-wait” species have greater running speeds. In this sense, the higher endurance of *L. ruibali* could be related to its feeding habits, as it is an omnivorous species characterized by a mixed foraging strategy (Villavicencio et al. 2005; Pérez unpublished data). Similarly, *P. extrilidus* is herbivorous, as are other species in the genus, and moves frequently among edible plants, which would explain its intermediate endurance. On the other hand, given that *L. parvus* feeds mainly on insects using a mixed foraging strategy (Acosta et al. 2018; Pérez unpublished data), maximizing its running speeds could also be advantageous.

In addition, the type of microhabitat could influence locomotion. Greater endurance could be linked to lizards that inhabit open areas with a little vegetation coverage and must, therefore, travel greater distances to find shelter (Jayne and Bennett 1990; Miles et al. 2001), which could explain greater endurance for *L. ruibali*. The saxicolous *P. extrilidus* and *L. parvus* reached greater speeds than *L. ruibali*, which is found in flat substrates. This differs from the pattern reported by Tulli et al. (2012), who found that saxicolous species were the slowest of the *Liolaemus* group studied. Moreover, many authors have established that differences in the utilization of microhabitats could lead to morphological differences (Arnold 1983; Lauder and Reilly 1991; Vanhooydonck and Van Damme 1999; Schulte et al. 2004; Goodman et al. 2008; Tulli et al. 2009) and that differences in body shape and limbs could have implications on locomotor capacity (Tulli et al. 2012). Although we did not find a link between SVL and performance, we did not include other morphological variables, such as forelimb and hind-limb length, in our analyses. These traits are known to positively influence locomotor performance (Miles 1994; Bonino and Garland Jr. 1999; Vanhooydonck and Van Damme 1999; Gifford et al. 2008; Kohlsdorf and Navas 2012). Therefore, we hypothesize that different lengths of the limbs among

the species (longer limbs in *P. extrilidus* and shorter in *L. ruibali*; Castro and Castillo unpublished data), could explain, in part, the interspecific differences in locomotor performance.

Thermal sensitivity in performance among ectotherms can be represented by an asymmetrical, nonlinear curve, thermal performance curve (TPC) that describes the effect of temperature on fitness (Huey and Stevenson 1979; Angilletta et al. 2002). Thermal tolerance ($CT_{\max} - CT_{\min}$) describes the range of temperatures where performance is greater than 0 and can be quite broad. However, the thermal performance breadth, defined as the range of temperatures at which performance is at 80% of maximum, is often narrower. If the thermal performance breadth is broad, then thermal limits will probably not play an important role in defining locomotor efficiency. However, if the thermal performance breadth is narrow, any change in the critical temperatures for acclimation will affect a lizard's locomotor capacity, at least at extreme temperatures (Kaufmann and Bennett 1989). In the context of global climate change, the studied species could cope with an increase in ambient temperatures, at least in locomotor performance, as the difference in temperatures between the performance extremes evaluated and the thermal limits obtained is wide (Fig. 1). Puna lizards are thermal generalists and have a wide thermal tolerance zone as was evident in the broad thermal safety margin (TSM; Table 4) for all three species, compared to the low TSM of *Liolaemus pictus* (0.43–0.64 °C) a lizard from the cold temperate climate (Kubisch et al. 2016) or tropical species of *Anolis* (*A. lemurinus* 1.5 °C, *A. bicaorum* 2.5 °C, *A. roatanensis* 3.4 °C, *A. allisoni* 4–5.5 °C; Logan et al. 2013). The thermal safety margins of Puna lizards suggest that, in the event of an increase in temperature, these species may not be as affected by impact of global warming on performance. Nevertheless, to test this hypothesis, it would be important to assess the flexibility of thermal parameters and performance for these species by conducting studies on acclimation to different temperatures.

We have shown how adjustments in thermal physiology are favorable for lizards living in cold and variable environments. In particular, a low thermal sensitivity is advantageous, because it allows the ability to achieve near maximal levels of locomotor performance (broader thermal performance breadth) at low T_b 's as in *Liolaemus pictus* from the Patagonian region of Argentina (Kubisch et al. 2016) and high elevation populations of *Phrynocephalus vlangalii* from Qinghai-Tibetan Plateau (Wu et al. 2018). Similarly, according to our predictions, *L. parvus* and *L. ruibali*, and to a lesser extent *P. extrilidus*, show a broad thermal performance breadth; this may be related to pronounced variation of environment temperature in the Puna region and to high variability on T_b 's that these species experience in the field (25–38 °C; Gómez Alés et al. 2017). Apparently, *L. parvus*

has the lowest thermal sensitivity in running speed. Several studies have shown that the physiological traits of species are related to its geographical distribution range (Buckley 2010; Kearney and Porter 2009; Bonino et al. 2015; Artacho et al. 2017). Thus, the narrow thermal performance breadth in *P. extrilidus* with respect to *L. parvus*, could be linked to the endemic character of *P. extrilidus*, whose distribution is restricted to our study site, whereas *L. parvus* and *L. ruibali* exhibit a broad latitudinal and altitudinal distribution (Lobo et al. 2012; Acosta et al. 2018). These two latter species may be thermal generalists. Similar results were found by Bonino et al. (2015), who observed in a group of Liolaemini species broader thermal performance breadth in species of wide distribution, suggesting a higher physiological plasticity in comparison with *Phymaturus tenebrosus*, a species with a highly restricted geographic distribution. Alternatively, differences in thermal performance breadth between syntopic species could reflect adaptations to divergent selective agents, e.g., variation in antipredator behavior, prey selection, or thermoregulation (Tepler et al. 2011; Yuan et al. 2016; Gómez Alés et al. 2017). Likewise, spatial differences in microclimates within a habitat type may confer greater tolerance to environmental variability in a species (Yuan et al. 2016). In this sense, *L. parvus* is an efficient thermoregulator and generalist in use of trophic and spatial resources, exploiting a wide range of thermally different microhabitats (Gómez Alés et al. 2017; Acosta et al. 2018), which would favor a broader thermal performance breadth with respect to *L. ruibali* and *P. extrilidus*.

The optimal temperature for locomotor performance has been evaluated for a limited number of species in the genus *Phymaturus*. Bonino et al. (2015) reported a T_o of 35.4 °C for *P. tenebrosus* in Patagonia, which is higher than the T_o that we found for *P. extrilidus*. However, our T_o results for the three species are within the range of temperatures reported for Liolaemini lizards (30.4–36.1 °C; Bonino et al. 2011, 2015; Fernández et al. 2011). One exception is the T_o for *L. pictus*, which has one of the lowest T_o values of the group (26 °C; Kubisch et al. 2011). Some authors have found a close correspondence between thermal optimum and preferred temperatures, and that maximum speeds often fall within the set-point range (Martín and Huey 2008; Bonino et al. 2011; Gaby et al. 2011). Such a pattern suggests coadaptation between preferred temperature and thermal optimum (Huey and Bennett 1987). We observed an overlap between T_o and T_{pref} for only *Liolaemus parvus* in IV and *L. ruibali* in LS. In contrast, T_{pref} for *P. extrilidus* was higher than the T_o (Fig. 1). We hypothesize that T_{pref} is selected to optimize other physiological functions such as digestion or endurance capacity (Angilletta 2009). Although we did not measure locomotor performance at each species T_{pref} (Table 4), we endeavored to select temperatures that bracketed the observed field body temperatures and potentially

warmer ambient temperatures expected with climate change. Lizard species occupying environments at high altitude and latitude, e.g., the Puna region, have limited availability of thermally suitable microhabitats and must engage in daily activities at low temperatures. Our results demonstrate the three species in our sample which achieved maximum performance at body temperatures commonly experienced during daily activity. Moreover, the field-active body temperatures are even higher than operative environmental temperatures (Fig. 1). Contrary to expectations, *L. parvus* and *L. ruibali* exhibited clear differences in running speeds and endurance, and, at the same time, differed from *P. extrilidus*. Consequently, despite their phylogenetic relatedness, and living in similar environmental conditions, differences in microhabitats use and trophic habits may explain the differences observed in speed and endurance.

We conclude that locomotor performance is sensitive to temperature in the studied species; nevertheless, there is a wide range of temperatures, mainly in *L. parvus*, in which the performance of species attain 80% or greater of the maximum speed, which allows them to face the highly variable climatic conditions of the Puna region.

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Compliance with ethical standards

Conflict of interest The authors confirm there are no known conflicts of interest associated with this publication.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This article does not contain any studies with human participants performed by any of the authors.

Informed consent Informed consent was not required.

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