

Does acclimation at higher temperatures affect the locomotor performance of one of the southernmost reptiles in the world?

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Abstract. When an animal in the laboratory experiences a change in temperature, physiological processes are affected but they stabilize under the new temperature condition over a few weeks by a process of phenotypic plasticity called acclimation, but whether an organism can acclimate or not depends on the trait and the taxon. *Liolaemus sarmientoi* is one of the southernmost reptiles in the world, inhabiting the extreme and arid environment of Patagonia, Argentina, characterised by great seasonal climatic variation and cold air temperatures throughout the year (mean air temperature of 8 °C; ranging from 1.2 to 14.1 °C). However, these lizards prefer body temperatures in the laboratory ranging from 26.3 to 37.8 °C (mean $T_{pref} = 34.4 \pm 0.28$ °C), temperatures that they rarely achieve in nature. Herein, we explore the effects of thermal acclimation on performance of *L. sarmientoi* at a temperature higher than their mean natural environmental temperature during their activity period (austral spring-summer). We analysed the speed in sprint and long runs at medium and high temperatures in the field and again after a period of acclimation of 20 days at 21 °C. Acclimation to higher and constant temperature resulted in a decrease in running speed in both long and sprint runs, suggesting potentially negative effects for natural populations if environmental temperature increases.

Keywords. Lizard, *Liolaemus sarmientoi*, acclimation, locomotor performance, high latitude.

INTRODUCTION

Ectotherms from temperate environments are subject to considerable daily fluctuations in environmental and body temperatures (Bennett and Dawson, 1976), but behavioural thermoregulation, particularly by reptiles, can modify the daily amplitude of body

temperature (Cowles and Bogert, 1944; Hertz et al., 1993). Moreover, the tolerance of organisms to low or high temperature extremes is not fixed, but is generally preconditioned by the thermal experience in their environment (Schmidt-Nielsen, 1997). When an animal is exposed to a change in temperature, physiological processes resulting in a form of phenotypic plasticity known as acclimation take place (Bennett, 1990; Schmidt-Nielsen, 1997). For example, an acclimation period of exposure to either hot or cold temperatures, results in a gradually greater physiological tolerance to the induced temperature (Angilletta, 2009).

Thermal acclimation in ectotherms can affect running or swimming performance (Elphick and Shine, 1998; Kingsolver and Huey, 1998; Glanville and Seebacher, 2006; Wilson et al., 2007), lethal temperatures (Kaufmann and Bennett, 1989), and metabolism (Jacobson and Whitford, 1970; Rogowitz, 1996), among others. In this regard, lizards are good biological models for testing effects of possible long-term climate variation on animals (Sinervo et al., 2010). Physiological responses to temperature in lizards have typically been measured by quantifying running velocity on a treadmill or race track (Bennett, 1980; Hertz et al., 1983; Van Damme et al., 1992; Bauwens et al., 1995; Angilletta et al., 2002; Ibarzüengoytía et al., 2007; Aguilar and Cruz, 2010; Fernández et al., 2011; Kubisch et al., 2011). Lizards of the genus *Liolaemus* from the cold temperate climate of Patagonia show reduced locomotor performance at the lower temperatures, typical of their environment. Yet, in most cases they have a thermal optimum for performance that is lower than their preferred temperature in laboratory (Bonino et al., 2011; Fernández et al., 2011; Kubisch et al., 2011).

In this study we assess the effects of thermal acclimation in *Liolaemus sarmientoi*, one of the southernmost reptiles in the world. We test running speed in long and sprint runs, two ecologically relevant parameters of the behavioural responses, used to capture prey, escape from predators, and potentially other social activities, such as territorial competition and mating (Bennett, 1980; Christian and Tracy, 1981; van Berkum, 1988; Huey et al., 2009). *Liolaemus sarmientoi* occurs between 49° and 53°S latitude in isolated outcrops of ancient volcanic craters in an extreme and arid area of the Patagonian steppe (Santa Cruz Province, Argentina; Roig, 1989; Oliva et al., 2001). Experiencing a mean annual environmental temperature of 12 °C, *L. sarmientoi* achieves a body temperature of about 26 °C by behavioural thermoregulation, but when placed in a laboratory thermal gradient they prefer higher temperatures (mean T_{pref} : 34.4 ± 0.28 °C; Ibarzüengoytía et al., 2010), which they rarely attain in their natural habitat. However, *L. sarmientoi* exhibits high running speeds in long and sprint runs in a wide range of temperatures, a range that exceeds temperatures they can achieve by thermoregulation in nature (Fernández et al., 2011).

The origin of *Liolaemus* in warm and humid climate conditions of the early Miocene of Patagonia (Gasparini et al., 1986; Schulte et al., 2000; Albino, 1994, 2011) could explain the consistent preference for high temperatures in the genus (Medina et al., 2012) exceeding field body temperatures up to 6 °C (Labra, 1998; Medina et al., 2009, 2012; Rodriguez-Serrano et al., 2009). The differences between field active and preferred body temperatures in the southernmost lizards, *Liolaemus magellanicus* and *L. sarmientoi* (Ibarzüengoytía et al., 2010) and their greater running performance at high temperatures (Fernández et al., 2011), together with recent glacial recessions occurring between 7600 and 2500 BP from areas now occupied by *L. sarmientoi* (Schobinger, 1973; Coronato et

al., 2007), suggests that while the Miocene ancestors of *L. sarmientoi* lived at warmer and lower latitudes, their descendants have recently colonized southern and colder latitudes (Cei, 1986; Etheridge, 1995).

Therefore, we hypothesize that although southern populations evolved adaptations to colder temperatures and shorter activity seasons (Fernández et al., 2010), they would retain some of their warm-climate adaptations, or lose them more slowly, resulting in greater phenotypic plasticity in thermal physiology compared to ancestral or northern populations. If selection against warm-climate traits was weak, then such plasticity would be broad in colonizing populations but would slowly narrow. Herein, we test the prediction that individuals from *L. sarmientoi* will exhibit greater locomotor performance when acclimated to temperatures well above their normal field temperatures.

MATERIALS AND METHODS

Study sites and captures

Field work was carried out in Santa Cruz province, Argentina (50°S, 72°W and 51°S, 70°W; 133 m a.s.l.). The climate that prevails in this region is cold temperate, semiarid (Soto and Vázquez, 2001), dominated by sub-polar cold and humid air masses with winds increasing toward the south which contribute to aridity, a distinctive feature of the Patagonian climate (Camilloni, 2007). The mean annual air temperature is 8.04 °C (ranging from 1.2 to 14.1 °C), but the mean air temperature during the lizard's activity period from October to March is 12.1 °C (according to the closest Meteorological Station in Río Gallegos, Santa Cruz; Fig. 1).

We captured 36 individuals of *Liolaemus sarmientoi* by hand or noose during February 2009, when lizards were at the end of the reproductive season (Fernández, pers. comm.). Capture permission was obtained from the Wildlife Delegation of Santa Cruz province, according to disposition 09/09.

Experiments

Lizards were prompted to run in nature at low, high, and medium temperatures without acclimation (published in Fernández et al., 2011). They were then brought to the laboratory where we measured their preferred body temperature (see Ibarzüengoytía et al., 2010). Subsequently, the same individuals were acclimated for the present study for 20 days at a mean temperature of 21 ± 0.02 °C (from 18.3 to 23.6 °C). The 21 °C was selected because it is the mean micro-environmental air temperature recorded 1 cm above the ground of each lizard capture site during the day when they were showing activity outside the burrows (Ibarzüengoytía and Cussac, 2002; Ibarzüengoytía et al., 2010), and it is expected to mimic a more constant and higher temperature than they would experience naturally.

During the acclimation period, lizards were placed in an open-top terrarium (15 × 20 × 20 cm) with a sand floor, and were provided with water, mealworm larvae (*Tenebrio molitor*), and house crickets (*Achetus domestica*) *ad libitum*. Considering that loss of body condition is extremely relevant, because lizards in losing reserves will tend to select for lower preferred temperatures (Brown and Griffin, 2003), we omitted data generated by seven of the original 36 animals captured because they had lost more than 20% of their body mass during captivity; this caution follows the protocol of Hertz et al. (1983), Huey et al. (1989), and Kaufmann and Bennett (1989). In addition, we analysed the relationship between the proportions of body mass lost and running speed to indicate whether

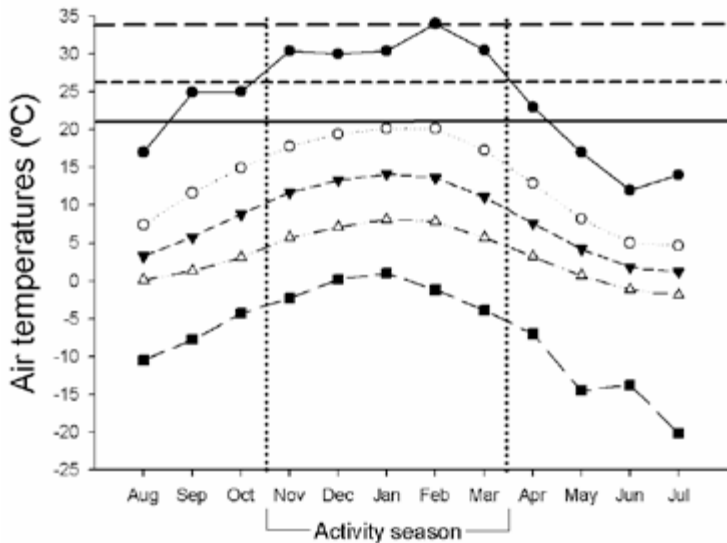


Fig. 1. Air temperatures according to the Meteorological Station of Río Gallegos, Santa Cruz: maximum and minimum extremes (black dots and squares), maximum and minimum means (white dots and triangles), and mean (black triangle) temperatures throughout the year. There are also indicated the lizards' activity season (dotted lines), mean field body temperature (short dashed line), mean preferred body temperature (long dashed line) and mean air temperature of microhabitats (solid line; which corresponds to acclimation temperature) from Ibarquengoytía et al. (2010).

whole-animal physical condition was correlated with performance (following Kaufmann and Bennett, 1989). For that reason, we worked with 29 individuals (nine males, 11 females, and nine juveniles) of *L. sarmientoi*. The sex and reproductive condition were achieved by presence of pre-cloacal pores in males and morphology, respectively. There were not pregnant females in the sample.

Lizards were prompted to run along a plastic track (0.1 m wide and 1.5 m long), waiting 24 h after captures, at two body temperatures: medium (21 °C) and high (30 °C). These temperatures were controlled outdoors in appropriate microenvironments, where lizards achieved a body temperature approximately equal to 21 or 30 °C. The body temperature of each lizard (T_b) was measured before each run using a thermocouple inserted 1 cm inside the cloaca (Catheter probe TES TP-K01, 1.62 mm diameter), and connected to a TES 1302 digital thermometer (TES Electrical Electronic Corp., Taipei, Taiwan, ± 0.01 °C).

We used two types of runs following the methods of Ibarquengoytía et al. (2007), Fernández et al. (2011), and Kubisch et al. (2011): 1) long runs (LR) of 1 m, each animal running three consecutive times while being stimulated by gently touching their tail or the back of their legs and taking care not to interfere with the running speed, and 2) sprint runs (SR) of 0.2 m, each animal running five consecutive times with a single initial stimulus. The SR represents the first burst or escape response from a predator, and the 0.2 m length is appropriate because the top velocity is reached usually in the first milliseconds of the response (Bonino et al., 2011). After long runs, lizards were left in the shade for a minimum rest period of 4 h before undertaking the sprint runs.

The runs were performed outdoors after 24 h of capture (Fernández et al., 2011) and after the acclimation period. The runs were filmed using a Sony DCR-SR 45 video camera recorded in NTSC

with error of ± 0.03 frame per second. Videos were processed using Microsoft Windows Movie Maker version 2.1.4026.0 (error ± 0.06 s) in order to register the time and determine the running speed (total error ± 0.0045 s).

In our analysis of running speeds, only the speed of the fastest non-stop LR and SR was used for each lizard during each of the two temperature trials. We calculated the maximum speed achieved by each lizard ($V_{\max i}$); the maximum $V_{\max i}$ which correspond to the speed of the fastest lizard for both LR ($V_{\max LR}$) and SR ($V_{\max SR}$); the thermal optimum (T_o ; as the T_b at $V_{\max LR}$ and $V_{\max SR}$); and the performance breadth (B_{80} ; calculated as the range of T_b at which performance is greater than or equal to 80% of the V_{\max} for all individuals), following the methods of Huey and Stevenson (1979) and Angilletta et al. (2002). The body temperature recorded for each individual before trials was used to calculate the B_{80} and analyse it in relation to the percentage of maximal performance in long and sprint runs.

Because we compared the same animals before and after acclimation, data from Fernández et al. (2011; $V_{\max LR}$, $V_{\max SR}$, B_{80} , and T_o) and Iburgüengoytia et al. (2010; the set-point range as the central 50% of the preferred body temperatures, T_{pref}) from unacclimated lizards were recalculated including only the individuals used in the acclimation experiment for the present study.

Statistical analyses

For statistical analyses, speeds were standardized as the residuals of the regressions between the maximum speed of each lizard ($V_{\max i}$) and their body temperature (T_b), with the purpose to isolate the effect of the acclimation period on performance when running at medium and high temperatures trials. By using residuals we removed the differences we found in the individual's body temperatures before and after acclimation at medium temperatures (Wilcoxon signed rank test, long runs: $W = -304.00$, $N = 27$; sprint runs: $W = -435.00$, $N = 29$, $P < 0.001$) and high temperatures (Paired t-test, sprint runs: $t_{28} = -2.99$, $P = 0.01$) and in long and sprint runs at medium temperatures (Paired t-test, unacclimated: $t_{27} = -6.78$, $P < 0.001$) and high temperatures (Paired t-test, acclimated: $t_{26} = -2.24$, $P = 0.03$).

Analyses were conducted using the statistical programs Sigma Stat 3.5^{*}, SPSS 15.0^{*}, and Sigma Plot 10.0^{*}. The dependence between variables was analysed by linear regression. Paired *t*-tests were used to test differences between two related samples and Two-way repeated measures analysis of variance (Two-Way RMANOVA) for repeated samples, the Holm-Sidak test was used as a *posteriori* test. The assumptions of normality and homogeneity of variance for parametric procedures were checked using the Kolmogorov-Smirnov and Levene's tests, respectively. When either of these assumptions was not met, we used an equivalent nonparametric test such as Wilcoxon Signed Rank for the comparison of medians of two related samples. The significance level used for all statistical tests was $P < 0.05$ (Sokal and Rohlf, 1969; Norusis, 1986). Best-fit regressions were chosen according the highest R-squared value.

RESULTS

Relationship between running speed and body mass lost

Lizards showed a mean mass loss of 13.13% during acclimation, except in one individual that gained 4.17%. There was no relationship between percentage of mass lost during acclimation and the maximum speed achieved by each lizard ($V_{\max i}$) in either LRs (Linear Regression, $F_{1,27} = 2.08$; $R^2 = 0.074$; slope = -0.0151 ; $P = 0.16$) or SRs (Linear Regression, $F_{1,28} = 3.56$; $R^2 = 0.117$; slope = 0.0096 ; $P = 0.07$).

Maximum running speed (V_{\max}) for unacclimated and acclimated lizards

In long and sprint runs no lizard was able to run as fast as before acclimation. In long runs, the maximum speed achieved by each lizard ($V_{\max i}$; Table 1) was higher in unacclimated than in acclimated individuals (Paired t-test, $t_{27} = 2.62$, $P = 0.014$; Fig. 2) and also in sprint runs (Wilcoxon, $W = -184.00$, $n = 29$, $P = 0.037$; Fig. 2). The V_{\max} (maximum $V_{\max i}$, which is the speed of the fastest lizard) for unacclimated lizards in long runs was 1.56 m/s ($V_{\max LR}$) at thermal optimum (T_o) = 31 °C and in sprint runs was 1.54 m/s ($V_{\max SR}$) at $T_o = 27$ °C.

The relationship between unacclimated and acclimated lizards in long runs did not show a linear ($R^2 = 0.10$; $F_{1,27} = 2.93$; $P = 0.10$) or quadratic regression ($R^2 = 0.10$; $F_{1,27} = 1.43$; $P = 0.24$), but in sprint runs the best fit corresponded to quadratic regression ($R^2 = 0.63$; $F_{2,28} = 22.50$; $P < 0.01$; Fig. 2).

Comparisons between the speed of long and sprint runs in unacclimated and acclimated individuals.

In unacclimated lizards the temperature trial (21 or 30 °C) did not affect their speed (Two-Way RMANOVA, $F_{1,27} < 0.001$; $P = 1.000$; Fig. 3), although speed was affected by the type of run only at 30 °C (Two-Way RMANOVA, $F_{1,27} = 10.41$; $P = 0.003$; Holm-Sidak, $t_{27} = 3.44$, $P = 0.001$; Fig. 3, white dots). There was no interaction between the temperature trial and the type of run (Two-Way RMANOVA, $F_{1,27} = 2.33$, $P = 0.138$).

In acclimated lizards the speed also was not affected by the temperature trial (21 or 30 °C; Two-Way RMANOVA, $F_{1,26} < 0.001$; $P = 1.000$; Fig. 3), although the speed was affected by the type of run (Two-Way RMANOVA, $F_{1,26} = 3.57$; $P = 0.070$; Fig. 3). There also was no interaction between the temperature trial and the type of run (Two-Way RMANOVA, $F_{1,26} = 0.52$, $P = 0.821$).

Table 1. Running speeds (m/s) by temperature trial (°C) for each unacclimated and acclimated lizards running long (LR) and sprint (SR) runs. It is shown the number of individuals (n), minimum, maximum, mean, standard error (\pm SE), and variance for the maximum speed achieved by each lizard in each trial ($V_{\max i}$).

Variable	Temperature trial (°C)	n	Minimum (m/s)	Maximum (m/s)	Mean (m/s)	(\pm) SE	Variance (m/s)
<i>Unacclimated</i>							
LR $V_{\max i}$	21	28	0.313	1.149	0.766	0.039	0.044
	30	28	0.238	1.563	1.063	0.078	0.170
SR $V_{\max i}$	21	29	0.426	1.000	0.735	0.030	0.026
	30	29	0.083	1.538	0.884	0.060	0.104
<i>Acclimated</i>							
LR $V_{\max i}$	21	27	0.314	0.935	0.630	0.037	0.037
	30	27	0.258	1.449	0.858	0.056	0.084
SR $V_{\max i}$	21	29	0.278	1.053	0.688	0.034	0.034
	30	29	0.230	1.000	0.902	0.033	0.032

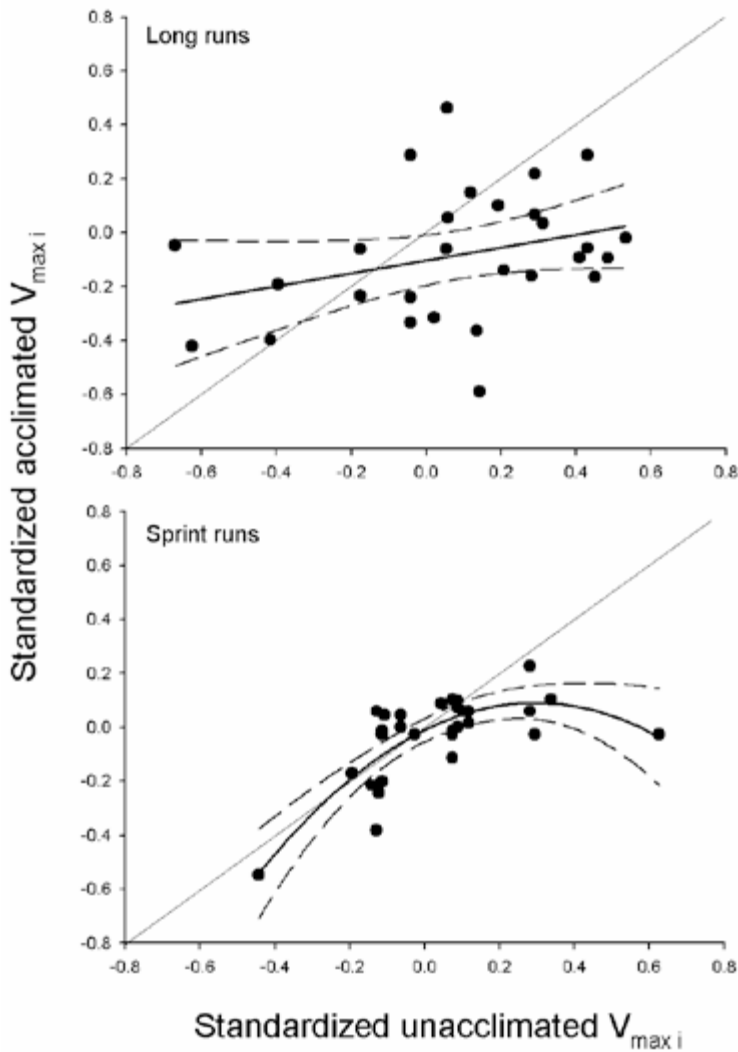


Fig. 2. Regressions (black solid lines) and 95% confidence intervals (dashed lines) of standardized maximum speed ($V_{max i}$) for each unacclimated versus acclimated lizard in long runs ($y = -0.10 + 0.24x$) and sprint runs ($y = -0.01 + 0.69x - 1.16x^2$) of *Liolaemus sarmientoi*. Line of equality intersects the origin.

In unacclimated lizards the relationship between long and sprint runs did not show a linear regression at 21 °C ($R^2 = 0.13$; $F_{1,27} = 4.00$; $P = 0.06$), but it did at 30 °C ($R^2 = 0.66$; $F_{1,27} = 50.02$; $P < 0.01$; Fig. 3), this also happen in acclimated lizards at 21 °C ($R^2 = 0.19$; $F_{1,26} = 5.77$; $P = 0.02$; Fig. 3) and at 30 °C ($R^2 = 0.20$; $F_{1,26} = 6.31$; $P = 0.02$; Fig. 3).

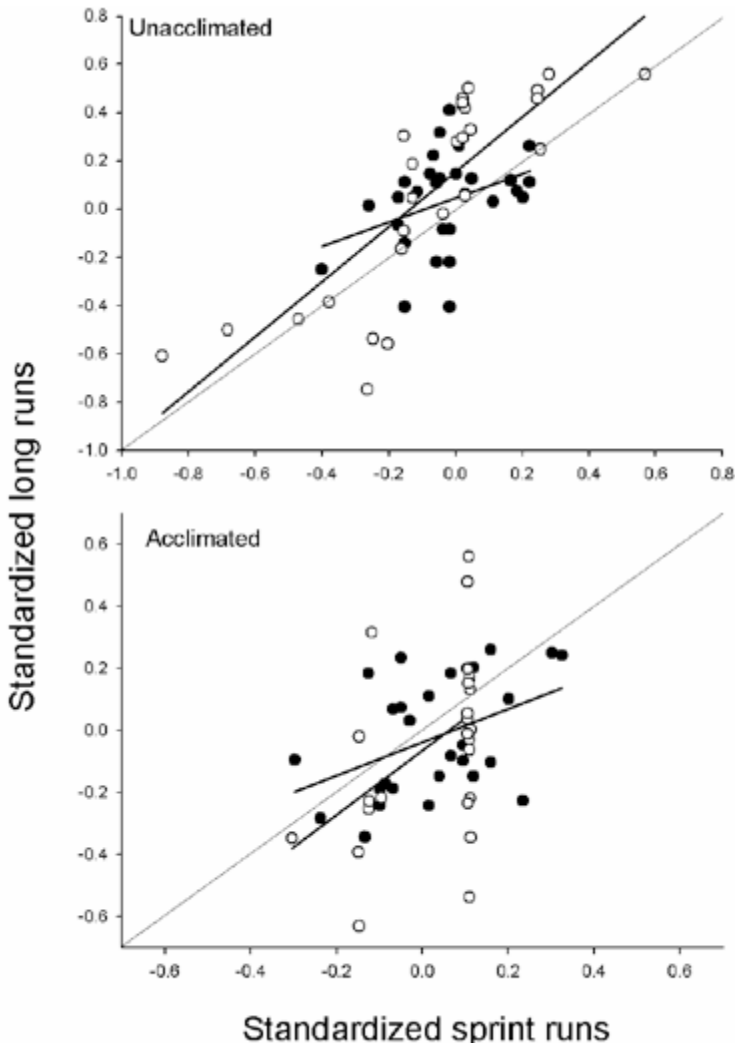


Fig. 3. Linear regressions (black solid lines) of standardized speed for long versus sprint runs at medium (21 °C, black dots) and high temperatures (30 °C, white dots) for unacclimated and acclimated *Liolaemus sarmientoi*. Line of equality intersects the origin.

Comparisons between the speed of unacclimated and acclimated lizards in long and sprint run

In long runs the speed of lizards was not affected by the temperature trial (Two-Way RMANOVA, $F_{1,26} < 0.001$, $P = 1.000$; Fig. 4), however speed was affected by the acclimation only when lizards ran at 30 °C (Two-Way RMANOVA, $F_{1,26} = 8.22$; $P = 0.008$; Holm-Sidak, $t_{26} = 4.22$, $P < 0.001$; Fig. 4, white dots). There was interaction between the temperature trial and acclimation (Two-Way RMANOVA, $F_{1,26} = 9.74$, $P = 0.004$).

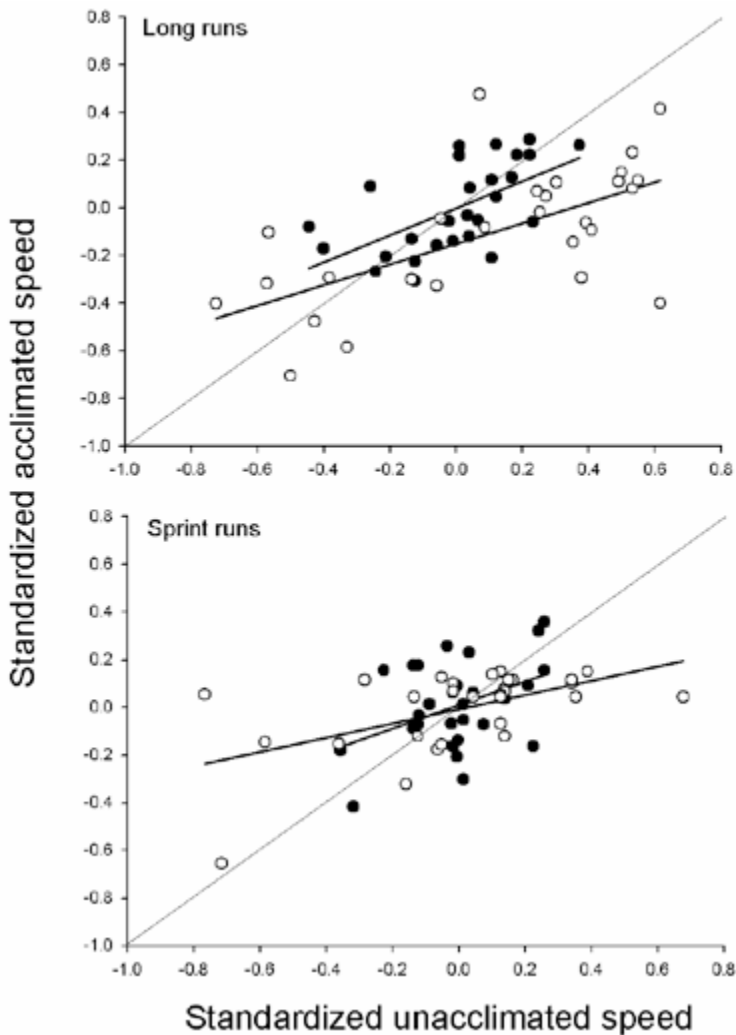


Fig. 4. Linear regressions (black solid lines) of standardized speed for unacclimated versus acclimated individuals of *Liolaemus sarmientoi* at medium (21 °C, black dots) and high temperatures (30 °C, white dots) trials for long and sprint runs. Line of equality intersects the origin.

In sprint runs the speed of lizards also was not affected by the temperature trial (Two-Way RMANOVA, $F_{1,28} < 0.001$; $P = 1.000$; Fig. 4), although the speed was affected by the acclimation (Two-Way RMANOVA, $F_{1,28} < 0.001$; $P = 0.957$; Fig. 4). There was no interaction between the temperature trial and acclimation (Two-Way RMANOVA, $F_{1,28} = 0.14$, $P = 0.716$).

In long runs the relationship between unacclimated and acclimated lizards showed a linear regression at 21 °C ($R^2 = 0.36$; $F_{1,26} = 14.13$; $P < 0.01$; Fig. 4) and at 30 °C ($R^2 = 0.40$; $F_{1,26} = 16.73$; $P < 0.01$; Fig. 4), this also happen in sprint runs at 21 °C ($R^2 = 0.17$; $F_{1,28} = 5.73$; $P = 0.02$; Fig. 4) and at 30 °C ($R^2 = 0.30$; $F_{1,28} = 11.76$; $P < 0.01$; Fig. 4).

Percentage of maximal performance in long and sprint runs and the set-point range of preferred body temperatures (T_{pref})

In long runs, 65% of adults before acclimation and 10 % of them after acclimation ran at the same speed or faster than 80% of the adult $V_{max LR}$ (1.56 m/s, $n = 20$) in a range of T_b from 25 to 34 °C and 28 to 30 °C (B_{80}), respectively (Fig. 5, upper panels). In sprint runs before acclimation, 25 % of the lizards ran at the same speed or faster than 80% of the $V_{max SR}$ in a range of T_b from 27 to 31 °C, and after acclimation no lizard ran at an equal or greater speed than 80% of the $V_{max SR}$ (Fig. 5, lower panels). The range from 60 to 68% of the maximal speed for sprint runs was achieved by 55% of unacclimated lizards at temperatures ranging from 25 to 35 °C, and after acclimation it was achieved by 85% of them at temperatures ranging from 20 to 35 °C (Fig. 5, lower panels). The set-point (the central 50%) of the preferred body temperatures (T_{pref}) for adults analysed in the present study ranged between 27.3 and 39.7 °C (Fig. 5).

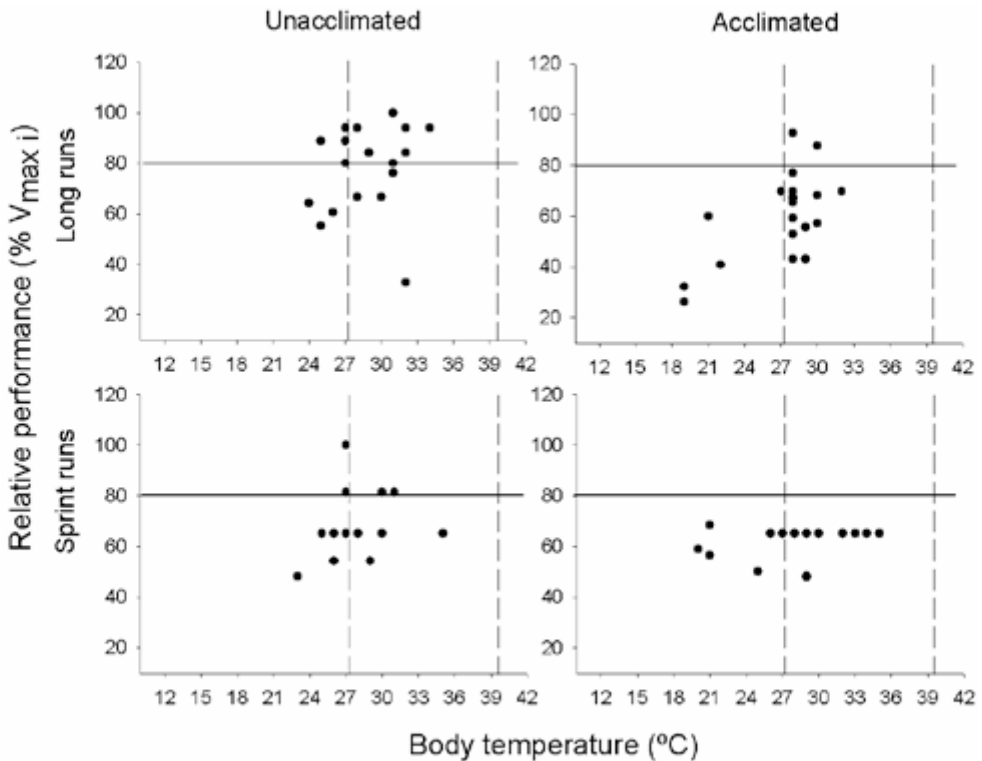


Fig. 5. Relationship between relative performance (% $V_{max i}$) with body temperature (°C) of adults of *Liolaemus sarmientoi* in unacclimated and acclimated long (upper panels) and sprint runs (lower panels). Horizontal solid line indicates the 80 % of performance breadth (B_{80}), and vertical dashed lines indicate the central 50% of the preferred body temperature (T_{pref}) of adults in laboratory

DISCUSSION

Liolaemus sarmientoi, in one of the southernmost environment of the world, achieves the highest speed in long runs when their body temperature ranges from 25 to 35 °C (Fernández et al., 2011). In contrast, the sympatric *Liolaemus magellanicus* shows no difference in speed between long and sprint runs, and reaches its maximal performance only over a narrow range of high temperatures (from 30 to 34 °C), which are included within the set-point range of T_{pref} unlikely to be found in nature (Fernández et al., 2011). *Liolaemus sarmientoi* performance is consistent with an evolutionary trend toward the ability to run fast over a broader range of temperatures, especially in long runs, including those low temperatures they often experience in their current environment (Fernández et al., 2011). In addition, contrary to our expectance, most of the lizards were not able to run as fast as before acclimation, that is, acclimation at higher temperatures in *L. sarmientoi*, rather than enhancing performance, resulted in a detrimental effect on running speed, more conspicuous in long runs. Moreover, even the differences observed prior to acclimation, higher speeds in long than in sprint runs, disappeared following acclimation.

Thermal sensitivity of locomotor performance can vary among ectotherms, and thermal acclimation enhances some physiological performance in some species depending on the temperatures at which are acclimated (Huey et al., 1999; Angilletta et al., 2009). In amphibians after metamorphosis, the general pattern shows no beneficial acclimation in their locomotor performance to different temperatures (Feder, 1986; Knowles and Weigl, 1990; Marvin, 2003). Thus, Wilson and Franklin (2000) predict that the locomotor performance of animals in terrestrial habitats should be more thermally insensitive than their performance in aquatic habitats. Therefore, amphibians that shift from a thermally buffered aquatic environment to a variable terrestrial environment lose their ability to acclimate their locomotor physiology. In this sense, ectotherms like *L. sarmientoi* that live in a thermally variable environment exposed to a daily and yearly high fluctuations of body temperature, characteristic of high latitudes, could evolve locomotor capabilities independent of temperature fluctuations, with a corresponding loss of the ability to acclimate, such as happens in amphibians. The same pattern was observed in the desert night lizard (*Xantusia vigilis*) that was incapable of acclimating locomotor performance to either 20 or 30 °C for 50 days (Kaufmann and Bennett, 1989). Present results show that *L. sarmientoi*, in a manner similar to that of high-altitude temperate-zone organisms (see Ghalambor et al., 2006), displays a broad thermal tolerance to cope with the large seasonal changes in temperature (Fig. 1), but also shows poor locomotor abilities after acclimation at higher temperatures.

The detrimental effect of high temperatures is also noticeable if we consider that speed was reduced in long runs only in lizards running at the high temperature trial but not in those running at medium temperatures (Fig. 4). The absence of a correlation between weight lost in captivity and running performance, provides support for the rejection of the hypothesis that a decrement in speed after acclimation results from a deterioration of physical condition during captivity, although we could consider other unnoticed factors, aside from mass lost (such as the lack of exercise or dehydration, among others) that may have been artefacts of captivity. Even so, the reduced locomotor performance found in *L. sarmientoi* at high temperatures may be affected by a lower aerobic capacity

during a long run at that temperature (Bennett and Licht, 1972), rather than an alteration in the contraction of muscles, which usually is not affected by high temperatures (Bennett, 1985; Else and Bennett, 1987; Kaufmann and Bennett, 1989). In addition, in sprint runs after a period of acclimation, *L. sarmientoi* showed a broader range of temperatures (from 20 to 35 °C) than before acclimation when its performance is between 60 to 68% of its maximal speed. The ability to achieve high speed even at low temperatures suggests that lizards under constant and higher environmental temperatures, such as during a “benign” austral summer, could switch their actual preferences from long to sprint runs. These results also suggest that differences in fitness within a population, relative to thermoregulatory behaviour, could result in a differential use of microhabitats (switch between open to vegetated areas) and locomotor preferences.

Based on our results we propose that under a continued increase in environmental temperature this southern species of lizard, *L. sarmientoi*, assuming no adaptive or plastic behavioural compensation driven by rapid environmental change (Sinervo et al., 2010), may suffer a decrement in running speed that could directly affect their ability to escape from predators, capture prey, and perform several social activities. Climate-change scenarios predict increases in environmental temperature over a scale of decades (Sinervo et al., 2010), which would likely result in increased aridity, changes in community dynamics, such as increased competition and a southward shift in the geographical ranges of predators from northern latitudes, resulting in declines of prey populations (Lavilla, 2001). Under this scenario, we consider that a deeper knowledge of species reaction norms (sensu Stearns, 1989 and Via et al., 1995) of ecologically pertinent traits, like locomotor performance, would help in predicting the fitness consequences on reptiles caused by rising global temperature.

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REFERENCES

- Aguilar, R., Cruz, F.B. (2010): Refuge use in a Patagonian nocturnal lizard, *Homonota darwini*: the role of temperature. *J. Herpetol.* **44**: 236-241.
- Albino, A.M. (1994): Estado actual del registro de escamados extinguidos de América del Sur y sus implicancias paleoambientales. *Cuadernos de Herpetología* **8**: 146-154.

- Albino, A.M. (2011): Evolution of Squamata reptiles in Patagonia based on the fossil record. *Biol. J. Linn. Soc.* **103**: 441-457.
- Angilletta Jr., M.J. (2009): Thermal adaptation: a theoretical and empirical synthesis, pp. 289. Oxford University Press Inc., New York.
- Angilletta, M.J. Jr., Niewiarowski, P.H., Navas, C.A. (2002): The evolution of thermal physiology in ectotherms. *J. Thermal Biol.* **27**: 249-268.
- Bauwens, D., Garland Jr., T., Castilla, A.M., Van Damme, R. (1995): Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* **49**: 848-863.
- Bennett, A.F. (1980): The thermal dependence of lizard behaviour. *Anim. Behav.* **28**: 752-762.
- Bennett, A.F. (1985): Temperature and muscle. *J. Exp. Biol.* **115**: 333-344.
- Bennett, A.F. (1990): The thermal dependence of locomotor capacity. *Am. J. Physiol.* **259**: 253-258.
- Bennett, A.F., Dawson, W.R. (1976): Metabolism, pp. 127-223. In: Gans, C., Dawson, W.R., Eds, *Biology of the Reptilia*, Vol. 5. Academic Press, London and New York.
- Bennett, A.F., Licht, P. (1972): Anaerobic metabolism during activity in lizards. *J. Comp. Physiol.* **81**: 277-288.
- Bonino, M.F., Moreno Azócar, D.L., Tulli, M.J., Abdala, C.S., Perotti, M.G., Cruz, F.B. (2011): Running in cold weather: morphology, thermal biology, and performance in the southernmost lizard clade in the world (*Liolaemus lineomaculatus* section: *Liolaemini*: Iguania). *J. Exp. Zool. Part A* **315**: 495-503.
- Brown, R.P., Griffin, S. (2003): Lower selected body temperatures after food deprivation in the lizard *Anolis carolinensis*. *J. Therm. Biol.* **30**: 79-83.
- Camilloni, I. (2007): Atlas de sensibilidad ambiental de la costa y mar argentino: http://atlas.ambiente.gov.ar/tematicas/mt_01/pdfs/ME_01_Introduccion.pdf.
- Cei, J.M. (1986): Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas, pp. 527. Torino: Museo Regionale di Scienze Naturali, Monografía IV.
- Christian, K.A., Tracy, C.R. (1981): The effect of thermal environment on the ability of hatchling Galapagos Land iguanas to avoid predation during dispersal. *Oecologia* **49**: 218-223.
- Coronato, A., Borrromei, A.M., Rabassa, J. (2007): Paleoclimas y paleoesenarios en la Patagonia austral y en Tierra del Fuego durante el Cuaternario, pp. 18-48.
- Cowles, R.B., Bogert, C.M. (1944): A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* **83**: 265-296.
- Elphick, M.J., Shine, R. (1998): Long term effects of incubation temperatures on the morphology and locomotor performance of hatchling lizards (*Bassiana duperreyi*, Scincidae). *Biol. J. Linn. Soc.* **63**: 429-447.
- Else, P.L., Bennett, A.F. (1987): The thermal dependence of locomotor performance and muscle contractile function in the salamander *Ambystoma tigrinum nebulosum*. *J. Exp. Biol.* **128**: 219-233.
- Etheridge, R. (1995): Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the taxonomy of *Liolaeminae* (Reptilia: Squamata: Tropiduridae). *Am. Mus. Novit.* **3142**: 1-34.

- Feder, M.E. (1986): Effect of thermal acclimation on locomotor energetic and locomotor performance in a lungless salamander, *Desmognathus ochrophaeus*. *J. Exp. Biol.* **121**: 271-283.
- Fernández, J.B., Smith Jr., J., Sclaro, A., Iburgüengoytía, N.R. (2011): Performance and thermal sensitivity of the southernmost lizards in the world, *Liolaemus sarmientoi* and *Liolaemus magellanicus*. *J. Thermal Biol.* **36**: 15-22.
- Gasparini, Z., De la Fuente, M.S., Donadío, O. (1986): Los reptiles Cenozoicos de la Argentina: implicancias paleoambientales y evolución biogeográfica, pp. 119-130. IV Congreso Argentino de Paleontología y Bioestratigrafía (Mendoza), Acta 2.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J., Wang, G. (2006): Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Int. Comp. Biol.* **46**: 5-17.
- Glanville, E.J., Seebacher, F. (2006): Compensation for environmental change by complementary shifts of thermal sensitivity and thermoregulatory behavior in an ectotherm. *J. Exp. Biol.* **209**: 4869-4877.
- Hertz, P.E., Huey, R., Nevo, E. (1983): Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* **37**: 1075-1084.
- Huey, R.B., Berrigan, D., Gilchrist, G.W., Herron, J.C. (1999): Testing the adaptive significance of acclimation: a strong inference approach. *Amer. Zool.* **39**: 323-336.
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Alvarez-Pérez, H.J., Garland, T. Jr. (2009): Why tropical forest lizards are vulnerable to climate warming? *Proc. R. Soc.* **276**: 1939-1948.
- Huey, R.B., Niewiarowski, P.H., Kaufmann, J.S., Herron, J.C. (1989): Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? *Physiol. Zool.* **62**: 488-504.
- Huey, R.B., Stevenson, R.D. (1979): Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* **19**: 357-366.
- Iburgüengoytía, N.R., Cussac, V.E. (2002): Body temperatures of two viviparous *Liolaemus* lizard species, in Patagonian rain forest and steppe. *Herpetol. J.* **12**: 131-134.
- Iburgüengoytía, N.R., Medina, S.M., Fernández, J.B., Gutiérrez, J.A., Tappari, F., Sclaro, A. (2010): Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. *J. Thermal Biol.* **35**: 21-27.
- Iburgüengoytía, N. R., Renner, M., Boretto, J.M. Piantoni C., Cussac, V. (2007): Thermal effect on locomotion in the nocturnal gecko *Homonota darwini* (Gekkonidae). *Amphibia-Reptilia* **28**: 235-246.
- Jacobson, E.R., Whitford, W.G. (1970): The effect of acclimation on physiological responses to temperature in the snakes, *Thamnophis proximus* and *Natrix rhombifera*. *Comp. Biochem. Phys.* **35**: 439-449.
- Kaufmann, J.S, Bennett, A.F. (1989): The effect of temperature and thermal acclimation on locomotor performance in *Xantusia vigilis*, the desert night lizard. *Physiol. Zool.* **62**: 1047-1058.
- Kingsolver, J.G., Huey, R.H. (1998): Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. *Am. Zool.* **38**: 545-560.
- Knowles, T.W., Weigl, P.D. (1990): Thermal dependence of anuran burst locomotor performance. *Copeia* **1990**: 796-802.

- Kubisch, E.L., Fernández, J.B., Ibagüengoytía, N.R. (2011): Is locomotor performance optimised at preferred body temperature? A study of *Liolaemus pictus argentinus* from northern Patagonia, Argentina. *J. Thermal Biol.* **36**: 328-333.
- Labra, A. (1998): Selective body temperature of seven species of Chilean *Liolaemus* lizards. *Rev. Chil. Hist. Nat.* **71**: 349-358.
- Lavilla, E.O. (2001): Amenazas, declinaciones poblacionales y extinciones en anfibios argentinos. *Cuad. Herpetol.* **15**: 59-82.
- Marvin, G.A. (2003): Aquatic and terrestrial locomotor performance in a semiaquatic plethodontid salamander (*Pseudotriton ruber*): Influence of acute temperature, thermal acclimation, and body size. *Copeia* **2003**: 704-713.
- Medina, S.M., Gutiérrez J., Scolaro, A., Ibagüengoytía, N. (2009): Thermal responses to environmental constraints in two population of the oviparous lizard *Liolaemus bibronii* in Patagonia Argentina. *J. Therm. Biol.* **34**: 32-40.
- Medina, M., Scolaro, A., Méndez-De la Cruz, F.R., Sinervo, B.R., Miles, D.B., Ibagüengoytía, N.R. (2012): Thermal biology of genus *Liolaemus*: a phylogenetic approach reveals advantages of the genus to survive climate change. *J. Thermal Biol.* **37**: 579-586.
- Norusis, M. J. (1986): Advanced statistics SPSS/PC + for the IBM PC/XT/AT. Chicago: SPSS inc.
- Oliva, G., González, L., Rial, P., Livraghi, E. (2001): Áreas ecológicas de Santa Cruz y Tierra del Fuego, in: Borelli, P., Oliva, G. (Eds), Ganadería ovina sustentable en la Patagonia Austral: tecnología de Manejo Extensivo, pp. 41-82. INTA, EEA Santa Cruz.
- Rodríguez-Serrano, E., Navas, C.A., Bozinovic, F. (2009): The comparative field body temperature among *Liolaemus* lizards: Testing the static and the labile hypotheses. *J. Therm. Biol.* **34**: 306-309.
- Rogowitz, G.L. (1996): Evaluation of thermal acclimation and altitudinal variation of metabolism in a neotropical lizard, *Anolis gundlachi*. *Copeia* **3**: 535-542.
- Roig, F.A. (1989): La vegetación de la Patagonia, in: Correa, M.N., Flora Patagónica, Parte 1, pp. 40-166. Colección Científica del INTA, Tomo VIII. Santa Cruz.
- Schmidt-Nielsen, K. (1997): Chapter 6: Temperature effects, pp. 232-233, In: *Animal Physiology: Adaptation and environment*. Cambridge University Press.
- Schobinger, J. (1973): Prehistoria de Suramérica. Ed. Labor, S. A. pp: 27-47.
- Schulte, J.A., Macey, J.R., Espinoza, R.E., Larson, A. (2000): Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biol. J. Linn. Soc.* **69**: 75-102.
- Sinervo, B.R., Méndez-De la cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Victoriano-Sepulveda, P., Duarte-Rocha, C.F., Ibagüengoytía, N., Aguilar-Puntriano, C., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., Sites, J.W. Jr. (2010): Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**: 894-899.
- Sokal, R.R., Rohlf, F.J. (1969): *Biometry. The principles and practice of statistics in biological research*. USA: W.H. Freeman and Co.

- Soto, J., Vazquez, M. (2001): El gran libro de la provincia de Santa Cruz. Ed. Oriente- Alfa Centro literario.
- Stearns, S.C. (1989): The evolutionary significance of phenotypic plasticity. *BioScience* **39**: 436-445.
- van Berkum, F.H. (1988): Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am. Nat.* **132**: 327-343.
- Van Damme, R., Bauwens, D., Braña, F., Verheyen, R.F. (1992): Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizards *Podarcis muralis*. *Herpetologica* **48**: 220-228.
- Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S.M., Schlichting, C.D., Van Tienderen, P.H. (1995): Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.* **10**: 212-217.
- Wilson, R.S., Condon, C.H.L., Johnston, I.A. (2007): Consequences of thermal acclimation for the mating behaviour and swimming performance of female mosquito fish. *Phil. Trans. R. Soc. B* **362**: 2131-2139.
- Wilson, R.S., Franklin, C.E. (2000): Inability of adult *Limnodynastes peronii* (Amphibia: Anura) to thermally acclimate locomotor performance. *Comp. Biochem. Physiol. A* **127**: 21-28.