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Behavioral compensation buffers body temperatures of two *Liolaemus* lizards under contrasting environments from the temperate Pampas: a Bogert effect?

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Postural adjustments and microhabitat selection are two behavioral mechanisms that lizards extensively use to regulate their body temperatures. The Bogert effect occurs when behavioral thermoregulation buffers potential changes in body temperatures of congeneric organisms due to environmental variation, in turn precluding physiological evolution. We compared field body temperatures (Tb) and behavioral thermoregulation traits between two *Liolaemus* lizards: the saxicolous *Liolaemus tandiliensis* and the arenicolous *Liolaemus wiegmannii*. These species are spatially segregated in two thermally contrasting environments from the SE of the temperate Pampas of Argentina. During summer, the mean operative temperature (Te) of the coastal sand dunes occupied by *L. wiegmannii* was 9 °C higher than that of the Tandilia mountains inhabited by *L. tandiliensis*. Despite the contrasting thermal conditions of both habitats, the mean Tb of *L. tandiliensis* (34.72 °C) was similar to that of *L. wiegmannii* (35.01 °C). The behavioral thermoregulation mechanisms varied considerably between both species. *Liolaemus tandiliensis* combined static body posture with displacements towards sunlit areas. In contrast, *L. wiegmannii* combined elevated and prostrated body postures with movements towards full and filtered sun patches. Environmental gradients offer diverse challenges impelling lizards to find different behavioral thermoregulation adaptations in order to partially cope with environmental constraints. This occurs in many species of *Liolaemus* that are thermoregulatory efficient despite of the climatic adversities. In this study, two species of *Liolaemus* used different postural and microhabitat path-selection strategies

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according to climate, allowing them to buffer changes in *T*b, thus suggesting that the Bogert effect may be occurring in these two species.

KEY WORDS: behavior, *Liolaemus*, reptiles, temperate climate, thermoregulation.

INTRODUCTION

The body temperature of reptiles is dependent on the magnitude of the temperature variation in the environment and the organisms' ability to regulate heat exchange (Martín et al. 1995). The notion of thermoregulation implies that organisms actively use behavioral or physiological adjustments to control their body temperatures in two different ways: by the passive exchange of heat with the environment, and by the maintenance of their body temperature within a narrow range of temperatures (Stevenson 1985; Castilla et al. 1999). Under a variety of environmental conditions, most diurnal lizards are able to regulate their body temperature within relatively narrow temperature changes during the active periods (Avery 1982). Whether body temperature is affected by environmental changes will depend on the effectiveness of the lizard's thermoregulatory behavior, because a precise thermoregulation requires a flexible thermoregulatory strategy to cope with temporal or geographical variation in the thermal environment (McGinnis 1970; Adolph 1990).

Individuals are often capable of maintaining a relatively constant body temperature, even in temporally variable environments, through compensation by behavioral flexibility (Sunday et al. 2014). Behavioral mechanisms, such as shuttling, microsite selection, and postural adjustments, can overcome the variation of the thermal environment (Huey et al. 2003; Díaz & Cabezas-Díaz 2004; McConnachie et al. 2009). As environments become colder (e.g. as a function of altitude), congeneric lizards tend to occupy more open habitats, increase basking frequencies, and restrict times of activity to maintain their body temperature across geographical thermal gradients (Hertz & Huey 1981; Marquet et al. 1989). Bogert (1949, 1959) proposed that the lack of geographic variation in the body temperature of different lizard populations or congeneric species reflects the effectiveness of behavioral thermoregulation, which may enable lizards to maintain similar body temperatures in diverse thermal environments. He also recognised that this lack of variation in body temperatures along a geographic gradient would blunt selection for variation in the physiology of thermal sensitivity. Thus, he stated that behavior could constrain the evolution of other traits. Huey et al. (2003) revalidated the idea that behavior might play such a conservative role in the evolution of thermal physiology of many lizards' genera, calling this the Bogert effect.

There are numerous reports of populations or congeneric species of lizards that live under different thermal conditions and have variable thermophysiology (e.g. Scheers & Van Damme 2002; Vidal et al. 2008; Bouazza et al. 2016). Ecological constraints may cause some lizard populations to function at suboptimal levels, independently of the degree of conservatism in the thermal physiology of the genus (Andrews et al. 1999). The inability of lizards to thermoregulate near their preferred temperature range is presumably the result of reduced thermal opportunities related to geography and climate seasonality (Andrews 1998). Thermoregulatory behavior may be energetically expensive during periods of poor thermal quality or in poor quality habitats (Downes & Shine 1998; Row & Blouin-Demers 2006; Cadena & Tattersall 2009). As an alternative to overcome large environmental and climate changes, lizards must

accommodate to the local ambient temperature variation through a combination of behavioral and/or physiological adaptive evolution (Niewiarowski 2001; Basson & Clusella-Trullas 2015). Hence, plastic responses in the form of acclimatization of the body temperature are vital to cope with climate variation and favor performance, while minimizing behavioral costs in sub-optimal conditions (Hadamová & Gvoždík 2011; Basson 2013). Modifications of the thermal physiology together with behavioral compensation (i.e. Bogert effect) of thermal ecology can interact to define the thermal biology of many lizard taxa, such as the genus *Liolaemus* (Carothers et al. 2001; Vidal et al. 2008; Rodríguez-Serrano et al. 2009).

Liolaemus comprises more than 250 recognised species constituting the world's second most speciose lizard genus (Lobo et al. 2010; Abdala & Quinteros 2014). This group of South American reptiles has a wide distribution range that extends from the extremely warm Atacama Desert to the cold Patagonian steppe, and from sea level on the South Atlantic coast up to 5000 m asl in the Andes (Cei 1993; Cruz et al. 2014). A flexible thermal physiology combined with behavioral compensation of thermal ecology and microhabitat selection, allowed *Liolaemus* to colonise extreme habitats along its distribution range (Carothers et al. 2001; Rodríguez-Serrano et al. 2009). Some species of *Liolaemus* have similar body temperatures despite inhabiting contrasting thermal conditions (e.g. *L. nigromaculatus, L. nitidus, L. lutzae, L. multimaculatus*; Labra et al. 2008, 2009), independently of their phylogenetic relatedness, while coexisting in the same climatic zone (Valdecantos et al. 2013). At present, most studies of *Liolaemus'* thermal biology have primarily focused on thermoregulation parameters, such as field body temperature, preferred body temperature and critical tolerance temperatures among habitat variation (e.g. along altitudinal or latitudinal gradients; Carothers et al. 1997, 1998; Cruz et al. 2005; Villavicencio et al. 2007; Labra et al. 2008, 2009; Medina et al. 2009, 2012; Rodríguez-Serrano et al. 2009; Gutiérrez et al. 2010; Bonino et al. 2011; Maia-Carneiro et al. 2012; Moreno Azócar et al. 2013; Kubisch et al. 2016). In contrast, less attention has been given to comparative studies about behavioral processes that may shape the parameters of thermoregulation in *Liolaemidae* (e.g. Labra et al. 2001; Corbalán & Debandi 2013; Maia-Carneiro & Rocha 2013). In this sense, different studies suggested that microclimatic thermal changes induce shifts in behavioral strategies (Block et al. 2013) and in certain thermoregulation parameters of some *Liolaemus* species (Stellatelli et al. 2013).

The lizards *Liolaemus tandiliensis* and *Liolaemus wiegmannii* occur in two separate localities in the SE of the temperate Pampas from Argentina and belong to different clades in the radiation of this genus. However, these species have similar body size and shape and both are oviparous and insectivorous (Vega 2001; Vega et al. 2008). The endemic *L. tandiliensis* [snout-vent length (SVL) of adults: 49–58 mm] is included in the *L. alticolor-bibronii* group of the *L. chiliensis* clade, and inhabits the rocky grounds of the Tandilia mountain range at elevations up to 250 m (Vega et al. 2008; Quinteros 2012). The arenicolous *L. wiegmannii* (SVL of adults: 42–64 mm) belongs to the *L. wiegmannii* group of the *L. boulengeri* series (Etheridge 2000; Lobo et al. 2010), and it is widely distributed in Argentina, including the Atlantic coastal sand dunes of the Buenos Aires province, where it occurs on loose sandy substrates with a relatively sparse vegetation cover (Vega 2001; Stellatelli et al. 2014). Recent studies have shown that *L. tandiliensis* and *L. wiegmannii* have field body temperatures between 34 and 36 °C and preferred temperatures near 38 °C. Both species are moderately efficient thermoregulators despite that there is a difference of 7 ºC between the ambient temperature of coastal sand dunes and inland mountains of the SE Argentinean Pampas (Stellatelli et al. 2013; Villalba 2016).

In this study, we evaluated whether different thermal environments affect the field body temperature and the thermoregulatory behavior of the lizards *Liolaemus tandiliensis* and *L. wiegmannii* that exploit two contrasting habitats from the SE temperate Pampas in Buenos Aires province, Argentina. We also analysed the thermal behavior of these species in terms of body posture and exposure to the sun, and its relationship to environmental variables (hour of the day, environmental temperatures), body temperature and individual intrinsic factors (age, sex and body size). Particularly, we aimed to answer the following questions: (1) What is the magnitude of the difference between the field body temperature of *L. tandiliensis* and *L. wiegmannii*? (2) Are there interspecific differences in the frequencies of body postures and sun exposure between *L. tandiliensis* and *L. wiegmannii*? (3) What type of microhabitat temperature (substrate or air) constitutes the most important heat source for body temperature regulation? (4) What is the relationship between thermoregulatory behavior traits, environmental variables (hour of day, temperature), body temperature and intrinsic factors (sex, age, body size)? We hypothesised that the field body temperature of lizards is buffered by thermoregulatory behavioral strategies that compensate the variability of the thermal environment. Therefore, we predict that during daily activity, the mountain lizard *L. tandiliensis* will behave to favor heat absorption whereas the sand dune lizard *L. wiegmannii* will behave to induce heat dissipation. Because of these behavioral compensations, the body temperatures of *L. tandiliensis* and *L. wiegmannii* will not differ.

MATERIALS AND METHODS

Study areas

Fieldwork was carried out during summer (February and March of 2014, 2015) in two different areas representative of the typical habitats of each species in the temperate Pampas, SE of the Buenos Aires province, Argentina. The data for *L. tandiliensis* were recorded in a plot of 35 ha at Sierra de Los Padres (37°53′S; 57°50′W) located in the Tandilia mountain range. The landscape consists of patches of quartzitic rocks within a mosaic of mountains that rise up to 50–250 m asl, sparsely covered with several species of small grasses of the genera *Stipa, Poa, Briza* and *Paspalum*, and shrubs of *Baccharis, Colletia* and *Discaria* (Cabrera 1976; Burkart et al. 1999). Data for *L. wiegmannii* were collected in a plot of 35 ha at the Faro Querandí Natural Reserve (37° 22′S; 57°04′W) located in the Atlantic coastal dunes from Buenos Aires province, about 130 km away from the Tandilia mountains. This study plot is a well-preserved dune field sparsely covered with less than 50% of vegetation, composed mainly of grasslands of the genera *Poa, Panicum* and *Androtrichum*, scrublands of *Cortaderia*, and shrublands and mixed steppes of *Senecio, Achyrocline, Tessaria, Baccharis* and *Discaria* (Stellatelli et al. 2016). The SE Pampas is located in a mid-latitude climate, with average maximum temperatures of 33 °C in summer and 9 °C in winter, and the mean annual precipitation ranges from 800 to 1000 mm. During the summer months (January to March), the mean air temperature in the Tandilia mountain is approximately 24 °C, while in the coastal sand dunes the mean summer temperature is 26 °C (Burgos & Vidal 1995; NASA 2000–2016).

Field survey

Measurements of air and body temperatures and behavioral observations were conducted throughout the lizard's daily activity period (0900–1700 hr; Vega 2001; Vega et al. 2008). We walked randomly through each plot, retracing our steps until a lizard was sighted, whereupon we stopped at 3–6 m from the lizard to record hour of the day (hr), body posture, and exposure to

the sun. Body postures and positions were categorised according to Muth (1977) and McConnachie et al. (2009) as follows: (a) prostrated (body flat on the substrate surface with the head raised or flat on the ground), (b) raised (front of body and head raised, forelegs partially or fully extended, abdomen and tail flat on the ground), and (c) other (any other body posture or position assumed). Exposure to the sun was classified following Adolph (1990) and Block et al. (2013): (a) full sun (when the lizard was resting fully exposed to the sun), (b) filtered sun (when the lizard was still, under filtered sun by vegetation), and (c) shade (when the lizard was fully in shade). To avoid confounding effects that might affect lizard behavior, the same person performed all the sampling by walking at the same speed (40 m/min) and wearing the same clothing, while another person recorded subject behavior and hour of the day (Burger & Gochfeld 1993; Stellatelli et al. 2015). Following the initial observation, we proceeded to capture the lizard using a noose to measure body temperature (Tb) at 1 cm inside the vent (sensu Pough & Gans 1982) with an ultra-thin thermocouple (TP-K01, TES Electrical Electronic Corp., Taipei, Taiwan; 1.62 mm diameter) connected to a digital thermometer (TES-1300, TES Electrical Electronic Corp., Taipei, Taiwan; – 50–1300 °C). To avoid heat transfer, we handled the individuals by the head. We recorded the Tb within 20 sec after capture and then measured the snout-vent length (SVL) with a digital caliper (SC111001, Schwyz Co ®, Buenos Aires, Argentina; ± 0.01 mm) (Stellatelli et al. 2013). We determined the age of the lizards based on SVL [for *L. wiegmannii*: adult ≥ 42 mm > juvenile (Martori & Aun 1997), for *L. tandiliensis*: adult > 49 mm ≥ juvenile (Vega et al. 2008)]. We sexed the adults, based on secondary sexually dimorphic characters, such as the presence of precloacal glands and body coloration (Cei 1993; Vega et al. 2008). Merging the data of sex and age we determined three sex-age groups (Gr); juvenile, male and female. We applied temporary color marks in the individuals' belly with a black non-toxic pen marker to avoid recaptures (sensu Plummer & Ferner 2012). At the moment of capture of the individual we also recorded the substratum temperature (Ts), directly on the ground surface, and the air temperature (Ta) at 1 cm above the ground, using a thermocouple connected to a digital thermometer (TES-1300, TES Electrical Electronic Corp., Taipei, Taiwan; – 50–1300 °C). We measured operative temperatures (Te) in the field (sensu Hertz et al. 1993) using five regular data loggers (DS1921G, iButton Sunnyvale ®, CA, USA) that registered temperatures every 10 min between 09:00 and 17:00 hr during all the sampling days. The measuring devices were placed randomly in different kind of microsites (e.g., in the sun, shade, in bare soil, on rocks, under vegetation, in crevices; sensu Vitt & Sartorius 1999). Thus, we covered the spatial and temporal availabilities of microenvironmental temperatures for thermoregulation (sensu Duran et al. 2017). We obtained a specific Te value for each lizard by averaging the temperatures that were registered by the five data loggers at the hour of capture of the individual, or within the 10-min interval that included the capture time.

Data analysis

Normality and homoscedasticity were evaluated with Kolmogorov-Smirnov and Levene´s tests, respectively. We used data transformations ($Log_{10}(x)$) to fit both assumptions (Zar 1984). To compare Tb between sex-age group (juveniles, males, females) and species type (*L. tandiliensis, L. wiegmannii*) we used a two-way ANCOVA and Tukey's post hoc comparison test (α = 0.05), with SVL as the covariate (Zar 1984). We performed a two-way ANOVA and Tukey's post hoc comparison test (α = 0.05) to contrast environmental temperatures (Te, Ts, Ta) between species and sex-age groups (Zar 1984). We used a two-way ANOVA and Tukey's post hoc comparison test (α = 0.05) to compare body and environmental temperatures within each lizard species (Zar 1984). To explore how Tb is related to Te, Ts, Ta and SVL, we used generalised linear models (GLM) with the Gamma error structure and inverse function. We constructed four models (two for each species of lizard) because of the collinearity between the predictors Ts and Ta (Crawley 2007). We constructed six GLMs with binomial error structure and logit function to evaluate which factor explains the behavior of each species of lizard. We used presence/absence of individuals in each category of body posture (prostrated, raised, other), exposure to the sun (full sun, filtered sun, shade) as the response variables and Hr, Gr, Tb, Te and SVL as explanatory variables (Crawley 2007). In certain

cases, some predictor variables or categories were removed to improve the model fit (Nicholls 1989). For the analysis of "other" body postures or "shade" categories, only males and females were considered since no juveniles were observed in either case. We evaluated each model with all the possible combinations of predictor variables, and we based the model selection on Akaike's information criterion (AIC; Burnham & Anderson 2002). We used two additional parameters to model selection: the difference in AIC between the best approximating model and all the other models (ΔAIC, values between 0 and 2 indicate substantial support for the models); and model weights (w), which indicate the probability that the model is the best among the whole set of candidate models (Burnham & Anderson 2002). The parameter estimates were calculated by the model averaging technique (multimodel inference) from the w of all the candidate models (Burnham & Anderson 2002). We also assessed the degree to which 95% confidence intervals of parameter estimates overlapped zero. All statistical analyses were carried out using R software version 3.1.3 (R Development Core Team 2015). Multicollinearity was analyzed before model analysis. We considered two predictors to be collinear when the Spearman rank correlation coefficient (R) was > 0.6. When variables were strongly correlated, we retained those with the clearest ecological meaning for the species (Lennon 1999; Austin 2007). We used a z-test (α = 0.05) with Yates' correction for continuity to compare the frequency of each type of body position and exposure to the sun between *L. tandiliensis* and *L. wiegmannii* (Zar 1984).

RESULTS

Body, operative and environmental temperatures

We recorded data from 68 individuals of *L. tandiliensis* (23 males, 14 females and 31 juveniles) and 70 *L. wiegmannii* (33 males, 29 females and 8 juveniles). The field body temperature did not vary significantly between species (two-way ANCOVA: $F_{1,131} = 2.37$, $P = 0.135$; Fig. 1), or sex-age group ($F_{2,131} = 0.61$, $P = 0.544$), and there was no significant interaction between these factors ($F_{2,131} = 0.10$, $P = 0.902$). The mean Tb of *L. tandiliensis* was 34.72 °C (SD = 3.79 °C; $n = 68$), ranging from 22.30 °C to 43.00 °C, whereas the mean Tb of *L. wiegmannii* was 35.01 °C (SD = 4.43 °C; $n = 70$), ranging from 20.20 °C to 40.80 °C (Fig. 1). The Te was significantly different between habitats (two-way ANOVA: $F_{1,132} = 104.87$, $P < 0.001$; Fig. 1), but no effect of sex-age group was observed ($F_{2,132} = 1.42$, $P = 0.244$), and there was no significant interaction between these factors ($F_{2,132} = 2.96$, $P = 0.055$). The mean Te was 9.31 °C lower in the Tandilia mountains ($\bar{X} \pm$ SD: 30.49 ± 3.28 °C, $n = 68$) than in the Atlantic coastal sand dunes (39.80 ± 4.53 °C, $n = 70$; Fig. 1). The Ts at the lizards capture site did not vary between species ($F_{1,132} = 276$, $P = 0.09$; Fig. 1), nor among sex-age groups ($F_{2,132} = 2.45$, $P = 0.09$), and there was no significant interaction between these factors ($F_{2,132} = 0.05$, $P = 0.946$). The Ta did not differ between both species ($F_{1,132} = 0.03$, $P = 0.863$; Fig. 1) or among sex-age groups ($F_{2,132} = 2.51$, $P = 0.08$) and there was no significant interaction between these factors ($F_{2,132} = 0.22$, $P = 0.804$). Body temperature of *L. tandiliensis* differed significantly from operative and environmental temperatures (one-way ANOVA: $F_{3,268} = 14.69$, $P < 0.001$; Fig. 1). The Tb of *L. tandiliensis* was 4.52 °C higher than Te and 2.38 °C higher than Ta, whereas there was no difference between Tb and Ts (Fig. 1). The mean Te of the Tandilia mountains was approximately 2–3 °C lower than the microhabitat temperatures (Ts and Ta), whereas there was no difference between Ts and Ta (Fig. 1). *Liolaemus wiegmannii* showed differences between body and environmental temperatures (one-way ANOVA: $F_{3,276} = 18.22$, $P < 0.001$; Fig. 1). The mean Tb was about 5 °C lower than the mean Te, while Tb was not significantly different to Ts or
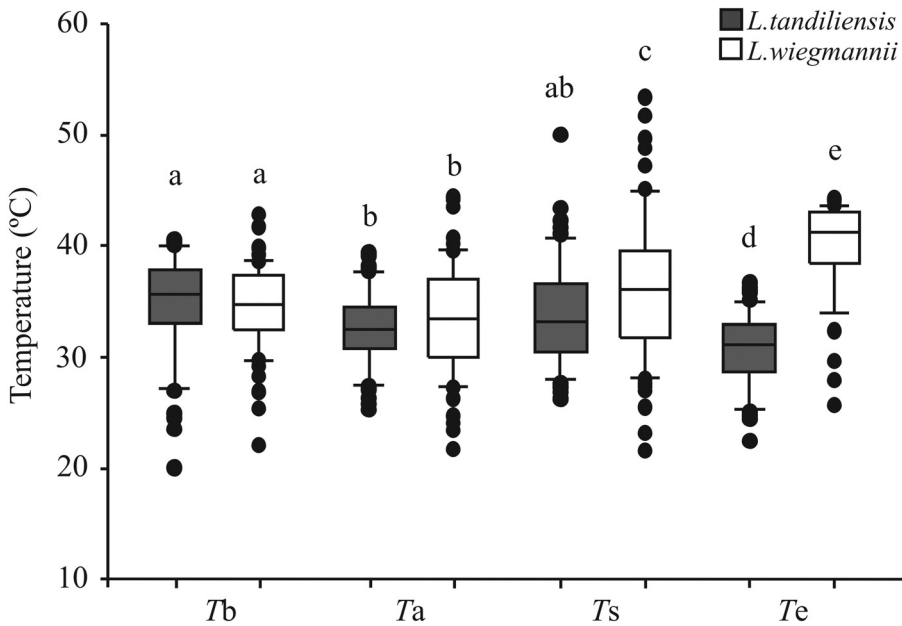
Fig. 1. — Inter and intraspecific comparisons of field body temperature (*T*b), operative temperature (*T*e), environmental temperature of substrate (*T*s) and air (*T*a) in *L. tandiliensis* (n = 68) and *L. wiegmannii* (n = 70). Horizontal bar denotes median; vertical bar denotes range; and upper–lower boundary of boxes denotes quartile. Different letters over the bars indicate statistically significant differences according to Tukey post hoc tests ($P < 0.05$).

*T*a ([Fig. 1](#)). *T*e was 3.38 °C higher than *T*s and 6.25 °C higher than *T*a ([Fig. 1](#)). Substrate temperature was 2.81 °C higher than *T*a ([Fig. 1](#)).

GLMs indicated that the *T*b of *L. tandiliensis* was explained in a similar way by two models, one including SVL and *T*s, and the other including SVL and *T*a as predictors. In both cases, a positive relationship among variables was found ([Tables 1–2](#)). In *L. wiegmannii*, *T*b was better explained by one model that included SVL and *T*s as predictors, with a positive relationship among the variables ([Tables 1–2](#)).

Thermoregulatory behavior

The proportion of individuals in prostrated body posture did not differ between *L. tandiliensis* and *L. wiegmannii* (z-test: $Z = 1.918$, df = 1, $P = 0.055$). However, there were interspecific differences between the proportion of lizards in a raised posture ($Z = 2.033$, df = 1, $P < 0.05$) and other types of postures ($Z = 4.73$, df = 1, $P < 0.001$; [Fig. 2](#)). There were interspecific differences in the proportion of individuals in full sun ($Z = 3.076$, df = 1, $P < 0.001$; [Fig. 2](#)) and in filtered sunlight ($Z = 3.195$, df = 1, $P < 0.001$), and there were no differences between the proportion of individuals in shade ($Z = -0.055$, df = 1, $P = 0.956$; [Fig. 2](#)).

Considering the variables Hr, *T*e, *T*b, SVL and Gr as potential predictors of different types of body postures and degrees of exposure to the sun, GLMs indicated

Table 1.

Generalised linear models performed on factors influencing the body temperature in *L. tandiliensis* and *L. wiegnannii* in the Southeastern temperate Pampas of Argentina. Only models with strong support (i.e. ΔAIC < 2) are shown. References: SVL = snout-vent length; Te = operative temperature; Tb = field body temperature, Ts = substrate temperature; Ta = air temperature; w: model weight.

| | *L. tandiliensis* | | | | | *L. wiegnannii* | | | |
Model	Variables	R^2	ΔAIC	w	Model	Variables	R^2	ΔAIC	w
Best	+ SVL; + Ts	0.39	0.000	0.701	Best	+ SVL; + Ts	0.39	0.00	0.662
Global	+ SVL; + Te; + Ts	0.39	1.940	0.265	Global	+ SVL; + Te; + Ts	0.39	1.376	0.332
Null	—	0.00	42.240	0.000	Null	—	0.00	40.540	0.000
Best	+ SVL; + Ta	0.28	0.000	0.673	Best	+ SVL; + Ta	0.19	0.000	0.461
Global	+ SVL; − Te; + Ts	0.28	1.870	0.264	Global	+ SVL; + Te; + Ts	0.21	0.234	0.410
Null	—	0.00	108.700	0.000	Null	—	0.00	13.750	0.000

Table 2.

Coefficient estimates (± SE) from generalised linear models influencing the field body temperature in *L. tandiliensis* and *L. wiegmannii* in the Southeastern temperate Pampas of Argentina. References: CI: confidence interval (95%); SVL = snout-vent length; Te = operative temperature; Tb = field body temperature, Ts = substrate temperature; Ta = air temperature. Parameters likelihoods are model weight summed across all models that contained that parameter and are indicative of the importance of the variable. Explanatory variables with CI excluding zero are in bold.

Variable	*L. tandiliensis*			*L. wiegmannii*		
	Coefficient ± SE	CI	Parameter likelihood	Coefficient ± SE	CI	Parameter likelihood
Intercept	2.870 ± 0.111	2.650; 3.09		2.97 ± 0.009	2.780; 3.160	
SVL	**0.003 ± 0.001**	**0.001; 0.006**	**1.00**	**0.004 ± 0.001**	**0.001; 0.006**	**1.00**
Te	− 0.000 ± 0.001	− 0.002; 0.002	0.27	0.000 ± 0.001	− 0.002; 0.003	0.33
Ts	**0.016 ± 0.002**	**0.010; 0.021**	**1.00**	**0.009 ± 0.001**	**0.006; 0.012**	**1.00**
Intercept	2.840 ± 0.143	2.560; 3.120		3.060 ± 0.129	2.810; 3.310	
SVL	**0.003 ± 0.001**	**0.001; 0.006**	**1.00**	**0.004 ± 0.001**	**0.001; 0.006**	**1.00**
Te	− 0.000 ± 0.001	− 0.004; 0.002	0.28	0.002 ± 0.002	− 0.003; 0.007	0.51
Ta	**0.017 ± 0.004**	**0.009; 0.026**	**1.00**	**0.006 ± 0.002**	**0.000; 0.011**	**0.92**
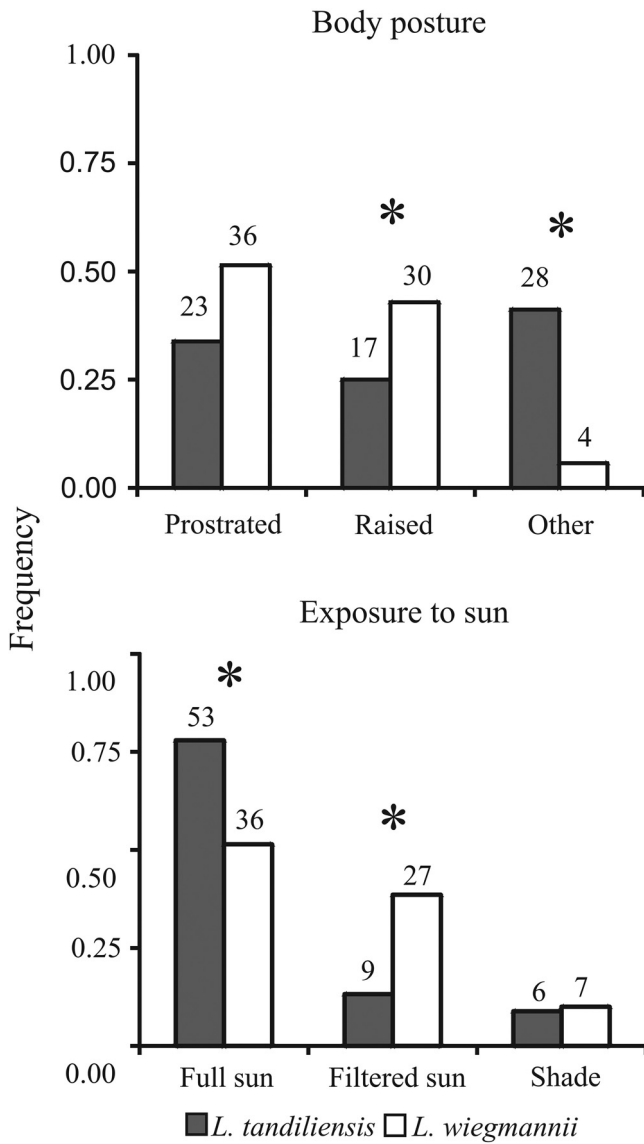
Fig. 2. — Proportion of individuals of *L. tandiliensis* (*n* = 68) and *L. wiegmannii* (*n* = 70) in each type of body posture and in different exposure to sun. The numbers on the bars indicate the number of individuals. Asterisks (*) over the bars indicate statistically significant interspecific differences ($P < 0.05$) found using z-test with Yates' correction.

that the prostrated posture was negatively associated with the *T*b of *L. tandiliensis*; whereas in the case of *L. wiegmannii*, the prostrated posture was negatively associated with *T*e and positively with Hr (Tables 3–4). Raised posture was not explained by any variable in *L. tandiliensis*, since SVL and *T*b were included in the models but had

confidence intervals that included zero (Tables 3–4). The raised body posture of *L. wiegmannii* was positively related to *T*e (Tables 3–4). In both species, other body postures were not explained by any of the variables because the predictors selected by the models had confidence intervals that included zero (Tables 3–4). Exposure to full sun was positively associated with Hr, whereas it was negatively associated with *T*e for both species of lizards (Tables 3–4). The exposure to filtered sunlight was not explained by any of the variables in *L. tandiliensis*, whereas in *L. wiegmannii* it was positively related to *T*e (Tables 3–4). The permanence in the shade of individuals of *L. tandiliensis* and of *L. wiegmannii* was not explained by any of the variables included in the models, since all of them had confidence intervals that included zero (Tables 3–4).

DISCUSSION

The saxicolous lizard *Liolaemus tandiliensis* and the arenicolous *L. wiegmannii* are spatially segregated in two thermal contrasting environments from the SE of the Argentinean temperate Pampas. During the summer, the average environmental temperature (*T*e) of the Tandilia mountains was about 9 ºC lower than the *T*e of the Atlantic sand dunes. This suggests that without a thermoregulatory strategy *L. tandiliensis* and *L. wiegmannii* should have different field body temperatures (*T*b). However, the mean *T*b of *L. tandiliensis* (34.72 °C) was similar to the *T*b of *L. wiegmannii* (35.01 °C). Additionally, these temperature values were similar to those of other lizards from the SE of the Argentinean temperate Pampas, such as *L. multimaculatus* and *L. gracilis* (Vega 1999, 2001; Stellatelli et al. 2013). Therefore, the thermoregulatory behavior of liolaemid lizards, by the selection of different micro-environments, seems to be flexible enough to cope with climatic environmental constraints (Medina et al. 2009; Gutiérrez et al. 2010), except for those species that live in extremely harsh environments, such as southernmost Patagonian species (*L. magellanicus* and *L. sarmientoi*; see Ibargüengoytía et al. 2010). This suggests that interspecific similarities in *T*b are not only limited to the phylogenetically closest species, i.e. *T*bs are not nested within clades (Rodríguez-Serrano et al. 2009). An important source of variation in the thermal biology of *Liolaemus* lizards is mediated by shifting behavioral strategies to exploit thermally challenging environments, instead of changing thermal preferences (Artacho et al. 2017). The mean preferred temperatures do not differ between *L. tandiliensis* (38.17 ± 1.11 °C; Villalba 2016) and *L. wiegmannii* (38.12 ± 0.83 °C; Stellatelli et al. 2013). These findings are in concordance with Moreno Azócar et al. (2013) who mention that preferred temperatures tend to be a more conservative character than *T*b in the genus *Liolaemus*. *Liolaemus tandiliensis* and *L. wiegmannii* may display different thermoregulatory strategies to achieve a certain *T*b in their contrasting thermal environments. The individuals of *L. tandiliensis* shifted between static prostrated body postures and displacements, remaining mainly exposed to full sun through the daily activity period. These lizards maintained a mean body temperature 4.23 ºC above the *T*e and used sites with micro-environmental temperatures (*T*s and *T*a) that were 2 to 3 °C higher than the mean *T*e of the Tandilia mountains. The saxicolous *L. tandiliensis* used the orientation of the walls in order to receive sufficient insolation throughout the course of the day, since individuals continuously followed the movements of sunlight through the rugged habitat. In vertical substrates, solar radiation is higher in the morning and in the late afternoon, whereas in horizontal substrates, radiation is higher around midday (Díaz et al. 1996). This situation is almost nonexistent for ground-dwelling species because a vegetated area at flat ground level

Table 3.

Generalised linear models performed on factors influencing the body posture and the exposure to sun in *L. tandiliensis* and *L. wiegmannii* in the Southeastern temperate Pampas of Argentina. Only models with strong support (i.e. ΔAIC < 2) are shown. References: Gr = age-sex group (Ju: juvenile, Ma: male or Fe: female); Hr = hour of the day; SVL = snout-vent length; *Te* = operative temperature; *Tb* = field body temperature; *w*: model weight.

Behavior trait		*L. tandiliensis*					*L. wiegmannii*			
	Model	Variables	R^2	ΔAIC	*w*	Model	Variables	R^2	ΔAIC	*w*
BODY POSTURE										
Prostrated	Best	+ SVL; − *Tb*; − *Te*	0.15	0.000	0.146	Best	+ Hr; − SVL; − *Te*	0.15	0.000	0.230
	M1	+ SVL; − *Tb*	0.12	0.332	0.124	M1	+ Hr; + Gr; − *Te*	0.16	1.005	0.139
	M2	− *Tb*	0.09	0.457	0.116	M2	+ Hr; − *Te*	0.11	1.542	0.106
	M3	− Hr; − *Tb*	0.12	0.505	0.114	M3	− SVL; − *Tb*; − *Te*	0.15	1.778	0.094
	M4	− Hr; + SVL; − *Tb*	0.14	0.742	0.101	Global	+ Hr; − SVL; + Gr; − *Tb*; − *Te*	0.17	4.790	0.021
	M5	− *Tb*; − *Te*	0.11	1.003	0.089	Null	—	0.00	8.299	0.004
	Global	− Hr; + Gr; + SVL; − *Tb*; − *Te*	0.16	6.462	0.006					
	Null	—	0.00	6.682	0.005					
Raised	Best	+ SVL; + *Tb*	0.16	0.000	0.165	Best	− Hr; + *Tb*; + *Te*	0.27	0.000	0.301
	M1	+ Gr; + *Tb*	0.19	0.365	0.137	M1	− Hr; + SVL; + *Tb*; + *Te*	0.28	1.425	0.147
	M2	+ Gr; + SVL; + *Tb*	0.21	0.649	0.119	M2	− Hr; + Gr; + *Tb*; + *Te*	0.30	1.656	0.131
	M3	+ *Tb*	0.11	1.986	0.061	M3	+ *Tb*; + *Te*	0.22	1.949	0.113
	Global	− Hr; + Gr; + SVL; + *Tb*; + *Te*	0.22	5.188	0.012	Global	− Hr; + Gr; + SVL; + *Tb*; + *Te*	0.30	4.126	0.038
	Null	—	0.00	8.411	0.002	Null	—	0.00	19.340	0.000
Other	Best	+ Gr; − SVL; + *Tb*	0.18	0.000	0.113	Best	− *Tb*; − *Te*	0.68	0.000	0.221
	M1	+ Hr; − SVL	0.12	0.220	0.101	M1	+ Gr; − *Tb*; − *Te*	0.65	1.126	0.126
	M2	+ Hr; + Gr; − SVL	0.17	0.347	0.095	M2	+ SVL; − *Tb*; − *Te*	0.71	1.238	0.119
	M3	− SVL; + *Tb*	0.11	0.898	0.072	Global	− Hr; + Gr; + SVL; − *Tb*; − *Te*	0.70	3.645	0.036
	M4	+ Gr; − SVL	0.13	1.024	0.068	Null	—	0.16	13.970	0.000
	M5	+ Hr; + Gr; − SVL; + *Tb*	0.19	1.040	0.067					

Group	Model	Terms				Model	Terms			
	M6	+ Hr; − SVL; + Tb	0.20	1.294	0.059					
	M7	− SVL	0.08	1.561	0.052					
	Global	+ Hr; + Gr; − SVL; + Tb; − Te	0.19	3.392	0.021					
	Null	—	0.00	7.248	0.003					
EXPOSURE TO SUN										
Full sun	Best	+ Hr; − SVL; − Te	0.33	0.000	0.270	Best	+ Hr; − SVL; − Te	0.15	0.000	0.230
	M1	+ Hr; + Gr; − Te	0.34	0.871	0.175	M1	+ Hr; + Gr; − Te	0.16	1.005	0.139
	M2	+ Hr; − Te	0.27	1.493	0.128	M2	+ Hr; − Te	0.11	1.542	0.106
						M3	+ Hr; − SVL; − Tb; − Te	0.15	1.778	0.094
	Global	+ Hr; + Gr; − SVL; − Tb; − Te	0.35	4.958	0.023	Global	+ Hr; + Gr; − SVL; − Tb; − Te	0.17	4.790	0.021
	Null	—	0.00	16.890	0.000	Null	—	0.00	8.299	0.004
Filtered sun	Best	− Hr; + Tb; + Te	0.22	0.000	0.180	Best	− Hr; + Tb; + Te	0.22	0.000	0.229
	M1	+ Tb	0.12	0.643	0.131	M1	− Hr; + SVL; + Tb; + Te	0.23	0.647	0.166
	M2	+ Tb; + Te	0.16	0.761	0.123	M2	+ Tb; + Te	0.18	0.794	0.154
	Global	− Hr; + Gr; − SVL; + Tb + Te	0.23	6.138	0.008	Global	− Hr; + Gr; + SVL; + Tb; + Te	0.25	4.065	0.030
	Null	—	0.00	5.234	0.013	Null	—	0.00	14.170	0.000
Shade	Best	− Hr; + Gr; − Tb; + Te	0.53	0.000	0.236	Best	− Hr; − Tb	0.16	0.000	0.162
	M1	+ Gr; − Tb; + Te	0.44	1.313	0.122	M1	− Tb;	0.24	1.228	0.088
	M2	− Hr; + Gr; + Te	0.42	1.860	0.093	M2	− Tb; − Te	0.09	1.754	0.067
						M3	− Hr; + Gr; − Tb	0.18	1.921	0.062
	Global	− Hr; + Gr; + SVL; − Tb; + Te	0.53	2.484	0.068	Global	− Hr; +Gr; + SVL; − Tb; − Te	0.17	6.467	0.006
	Null	—	0.00	10.390	0.001	Null	—	0.00	4.822	0.015

Table 4.

Coefficient estimates (± SE) from generalised linear models influencing the behavior traits in *L. tandiliensis* and *L. wiegmannii* in the Southeastern temperate Pampas of Argentina. References: CI: confidence interval (95%); Gr = age-sex group (Ju: juvenile. Ma: male or Fe: female); Hr = hour of the day; SVL = snout-vent length; T_e = operative temperature; T_b = field body temperature. Parameters likelihoods are model weight summed across all models that contained that parameter and are indicative of the importance of the variable. Explanatory variables with CI excluding zero are in bold.

Behaviour trait	Variable	*L. tandiliensis*			*L. wiegmannii*		
		Coefficient ± SE	CI	Parameter likelihood	Coefficient ± SE	CI	Parameter likelihood
BODY POSTURE							
Prostrated	Intercept	6.930 ± 3.310	0.451; 13.400	—	2.250 ± 3.300	-- 4.210; 8.710	—
	Hr	– 0.067 ± 0.113	– 0.289; 0.155	0.40	**0.446 ± 0.172**	**0.108; 0.784**	**1.00**
	T_e	– 0.047 ± 0.078	– 0.201; 0.107	0.40	**– 0.154 ± 0.077**	**– 0.305; – 0.001**	**0.96**
	Gr (Ju)	– 0.040 ± 0.118	– 0.272; 0.192	0.09	0.721 ± 1.130	– 1.500; 2.940	0.32
	Gr (Ma)	0.031 ± 0.105	– 0.175; 0.237	0.09	0.108 ± 0.275	– 0.432; 0.648	0.32
	SVL	0.021 ± 0.029	– 0.036; 0.080	0.48	– 0.029 ± 0.037	– 0.103; 0.045	0.51
	T_b	**– 0.179 ± 0.081**	**– 0.338; – 0.020**	**0.97**	– 0.022 ± 0.044	– 0.110; 0.065	0.30
Raised	Intercept	– 14.000 ± 6.760	– 27.300; – 0.775	—	– 14.800 ± 5.810	– 26.200; – 3.470	—
	Hr	– 0.003 ± 0.032	– 0.067; 0.060	0.19	– 0.345 ± 0.225	– 0.786; 0.095	0.87
	T_e	0.009 ± 0.029	– 0.048; 0.067	0.18	**0.321 ± 0.120**	**0.085; 0.557**	**1.00**
	Gr (Ju)	0.763 ± 1.370	– 1.920; 3.450	0.52	– 0.421 ± 0.766	– 1.920; 1.080	0.21
	Gr (Ma)	0.814 ± 1.050	– 1.230; 2.860	0.52	– 0.157 ± 0.308	– 0.761; 0.448	0.21
	SVL	0.058 ± 0.066	– 0.072; 0.189	0.62	0.009 ± 0.019	– 0.028; 0.048	0.24
	T_b	0.261 ± 0.149	– 0.030; 0.553	0.95	0.166 ± 0.115	– 0.059; 0.392	0.82
Other	Intercept	2.640 ± 4.900	– 6.980; 12.300	—	31.900 ± 19.300	– 5.910; 69.800	—
	Hr	0.095 ± 0.132	– 0.163; 0.353	0.48	– 0.172 ± 0.322	– 0.803; 0.460	0.38
	T_e	0.008 ± 0.036	– 0.062; 0.079	0.26	– 0.377 ± 0.323	– 1.010; 0.257	0.86

Gr (Ju)	− 1.510 ± 1.990	− 5.410; 2.380	0.57	—	—	—
Gr (Ma)	− 0.607 ± 0.814	− 2.200; 0.988	0.57	1.290 ± 2.570	− 3.740; 6.320	0.32
SVL	− 0.130 ± 0.092	− 0.310; 0.050	0.92	0.049 ± 0.087	− 0.122; 0.221	0.37
*T*b	0.049 ± 0.070	− 0.088; 0.187	0.47	−0.704 ± 0.389	− 1.470; 0.058	1.00
EXPOSURE TO SUN						
Full sun						
Intercept	17.000 ± 5.650	5.920; 28.100	—	2.250 ± 3.300	− 4.210; 8.710	—
Hr	**0.533 ± 0.267**	**0.009; 1.060**	0.96	**0.446 ± 0.172**	**0.108; 0.784**	**1.00**
*T*e	**− 0.656 ± 0.210**	**− 1.070; − 0.245**	1.00	− 0.154 ± 0.077	**− 0.305; − 0.001**	**0.96**
Gr (Ju)	0.036 ± 0.516	− 0.974;1.050	0.34	0.721 ± 1.130	− 1.500; 2.940	0.32
Gr (Ma)	− 0.498 ± 0.807	− 2.080; 1.080	0.34	0.108 ± 0.275	− 0.432; 0.648	0.32
SVL	− 0.035 ± 0.047	− 0.129; 0.058	0.52	− 0.029 ± 0.037	− 0.103; 0.045	0.51
*T*b	− 0.014 ± 0.036	− 0.086; 0.057	0.25	− 0.022 ± 0.044	− 0.110; 0.065	0.30
Filtered sun						
Intercept	− 16.400 ± 7.150	− 30.400; − 2.360	—	− 14.300 ± 5.470	− 25.000; − 3.570	—
Hr	− 0.171 ± 0.257	− 0.676; 0.333	0.44	− 0.235 ± 0.224	− 0.673; 0.203	0.69
*T*e	0.219 ± 0.209	− 0.191; 0.629	0.70	0.244 ± 0.109	**0.030; 0.457**	**1.00**
Gr (Ju)	− 0.020 ± 0.063	− 0.146; 0.104	0.03	− 0.215 ± 0.446	− 1.090; 0.660	0.14
Gr (Ma)	0.014 ± 0.051	− 0.086; 0.115	0.03	− 0.098 ± 0.207	− 0.505; 0.307	0.14
SVL	0.010 ± 0.021	− 0.032; 0.053	0.29	0.017 ± 0.029	− 0.040; 0.075	0.35
*T*b	0.259 ± 0.177	− 0.087; 0.605	0.88	0.180 ± 0.109	− 0.033; 0.393	0.89
Shade						
Intercept	− 20.400 ± 11.300	− 42.600; 1.850	—	8.120 ± 5.140	− 1.960; 18.200	—
Hr	− 0.506 ± 0.482	− 1.450; 0.439	0.71	− 0.234 ± 0.264	− 0.751; 0.283	0.61
*T*e	0.893 ± 0.480	− 0.048; 1.830	1.00	− 0.033 ± 0.061	− 0.153; 0.086	0.34
Gr (Ju)	1.020 ± 2.080	− 3.050; 5.090	0.63	—	—	—
Gr (Ma)	2.910 ± 3.220	− 3.400; 9.230	0.63	0.208 ± 0.460	− 0.693; 1.110	0.25
SVL	0.017 ± 0.047	− 0.075; 0.112	0.31	− 0.002 ± 0.011	− 0.024; 0.020	0.16
*T*b	− 0.196 ± 0.181	− 0.550; 0.159	0.74	− 0.174 ± 0.152	− 0.472; 0.124	0.73

provides sunny and shaded patches during the entire day (Scheers & Van Damme 2002). Additionally, the relatively low conductivity and the slow heat absorption of irregular rock surfaces in contrast with other substrates, such as sand (Martins et al. 2014), reduces the amount of contact and heat transference between the rock and the body of the lizards and, finally, the efficiency of conduction (Bakken 1989). The lizard *L. tandiliensis* gains thermal energy by both direct radiation (heliothermy) and conduction (thigmothermy) because its body temperature was related to both micro-environmental temperatures sources (*T*s and *T*a). It is possible that *L. tandiliensis* uses air or substrate temperatures as a source of heat, alternately depending on the environmental conditions, as do other species of *Liolaemus* (Bujes & Verrastro 2006; Ibargüengoytía et al. 2010).

In *L. wiegmannii*, the display of raised and prostrated body postures combined with shuttling between full sun and filtered sun patches was the main thermoregulatory behavioral mechanism. Active shifts between prostrated and raised body postures allow individuals to regulate conductive heating exchange in order to maintain a steady-state body temperature during the daily activity period. Individuals of *L. wiegmannii* were observed to be less exposed to full sun and remained more frequently in filtered sun areas to avoid over-heating. This species searched for micro-environmental temperatures (*T*s, *T*a) about 3 to 6 °C lower than the mean *T*e of the sand dune habitat to maintain its body temperature 4.79 ºC below the *T*e. Shuttling, understood as moving back and forth between fully sun and shaded patches, is an additional mechanism of behavioral thermoregulation used by *L. wiegmannii* (Block et al. 2013). Sand lizards used partially shaded sites in the warmest periods of the day and adopted raised postures to promote heat loss via wind movement, as do other species that move from open to shaded areas to prevent overheating in the warmer periods of the day (Bujes & Verrastro 2008; Block et al. 2013; Maia-Carneiro & Rocha 2013). The *T*b of *L. wiegmannii* in sand dunes was closer to the temperature of the substrate rather than to that of the air, as also previously described by Block et al. (2013) and Stellatelli et al. (2013).

Despite the differences in the thermoregulatory behavioral strategy adopted by *L. tandiliensis* and *L. wiegmannii*, we observed a common set of variables explained by the body postures and the degree of exposure to the sun in both species. Prostrated body posture was negatively related to *T*e and *T*b, and positively with Hr. This body posture is usually displayed to increase the body surface area that is in contact with the substrate and therefore, allows the lizard to gain heat by conduction when heat absorption by convection is negligible because of low environmental temperatures during the early hours of the day (Martín et al. 1995; Bauwens et al. 1996). On the other hand, raised body posture was positively related to *T*e. By raising its body off the ground, a lizard minimises the conduction with the substrate and exposes itself to lower air temperatures and higher wind speeds, increasing the convective heat loss at times of high soil temperatures (Porter et al. 1973; Losos 1987). Muth (1977) empirically determined heating rates as a function of posture given the same set of environmental conditions. The prostrated posture maximises the heating rate, while the elevated posture minimises it. The exposure to full sun was positively related to the hour of the day and negatively with the *T*e, while the permanence in filtered sun patches was positively related to *T*e. Lizards selected the fully sun-exposed sites especially during the early morning and late afternoon, when warm sunlit spots were less available, thus improving heat gain at times of relatively low environmental temperatures (Grbac & Bauwens 2001; Bujes & Verrastro 2006). Consequently, as body and environmental temperatures increased, lizards prevented overheating by moving towards semi-shaded patches that

offer a mosaic of lights and shadows, as also reported by others (Huey & Pianka 1977; Labra et al. 2001).

The findings of this study confirm our predictions, since we found evidence that *L. tandiliensis* and *L. wiegmannii* combined different sets of postural adjustments and microhabitat path selection according to climate variation and this allowed to buffer changes in *T*b. Our results provide quantitative evidence to support Bogert's (1949) statement that narrow variations in the field body temperature within a genus must reflect the effectiveness of behavioral thermoregulation, which enables congeneric species to maintain similar body temperatures in diverse thermal conditions. Environmental gradients offer diverse challenges that prompt lizards to find different ways to adjust their thermoregulation. It is possible that the gradient of temperatures from the Atlantic coastal dunes to the inland Tandilia mountains appears to be not harsh enough to impose limitations for behavioral thermoregulation, at least during the summer, and consequently might not promote changes in *T*b. *Liolaemus tandiliensis* and *L. wiegmannii* maintained their *T*b near to their preferred thermal range, and therefore behaved as moderately efficient thermoregulators according to their index of effectiveness of thermoregulation (E) that was reported in previous studies ($E_{L.\ wiegmannii}$ = 0.58–0.70, Stellatelli et al. 2013; $E_{L.\ tandiliensis}$ = 0.50–0.68, Villalba 2016). *Liolaemus* populations from different altitudes may adjust thermoregulation to compensate the differences in the availability of thermal microenvironments and in wind intensity by using different behaviors and heat sources (Medina et al. 2011). In this sense, our study provides an integrative framework about the role of behavior that may define certain patterns of the thermal biology of some species of *Liolaemus*. Hence, it contributes to the understanding of the evolutionary mechanisms that mould the patterns of thermal biology at a broader scale, and in turn will help to predict the responses of some species to different types of environmental pressures.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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