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Wind Decreases Microhabitat and Body Temperatures in Populations of Endangered Brazilian Sand Lizards

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***Abstract*.—Increasing temperatures from climate change threatens the Brazilian Sand Lizard (*Liolaemus lutzae*) with extinction. Nevertheless, thermal restrictions on both the time available to be active and thermoregulation could be relieved by cooling winds. Here, we used original and literature data of juvenile and adult *L. lutzae* to investigate interactions among body size, body temperature, thermal microhabitat, and wind speed across four populations of this species. Body temperatures were correlated with microhabitat temperatures. The thermal flexibility of *L. lutzae* favors suitable operation of life functions despite changing body temperatures and climatic conditions within and across populations. Winds decreased air and body temperatures and the quality of thermal microhabitats for thermoregulation under mild environmental temperatures, which could negatively affect lizard activity. Large lizards (mainly adult males) seemed to have greater resistance to heat loss by wind than smaller individuals (mostly juveniles and adult females). Therefore, restrictions on activity levels and microhabitat and body temperatures of *L. lutzae* by high environmental temperatures may be even greater for larger-sized adults because of increased vulnerability to overheating. Under a warming climate, however, increased winds could be beneficial by decreasing heat load, especially for larger lizards.**

Key Words.—body size; Liolaemidae; *Liolaemus lutzae*; microhabitat temperatures; thermal ecology; thermal flexibility; thermoregulation; wind speed

Introduction

Wind has been shown to alter both microhabitat and body temperatures of lizards (Fuentes and Jaksic 1979; Bujes and Verrastro 2006; Ariani et al. 2011) decreasing rates of activity, body temperatures, and microhabitat temperatures used for thermoregulation (Medina et al. 2009; Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015; Ortega et al. 2016). Under mild environmental temperatures, wind may jeopardize activities and the regulation of body temperatures of lizards (Medina et al. 2009; Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015), which might compromise carrying out activities (Medina et al. 2009; Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015; Ortega et al. 2016). Wind, however, might be beneficial in counteracting the effects of climate change by decreasing high body temperatures of lizards and their microhabitats. Such positive effects from wind may also be important to compensate for the continuous damage to vegetation and habitat loss (Rocha et al. 2009a,b; Maia-Carneiro and Rocha 2013a), which might jeopardize thermoregulation by exposing individuals to excessively high temperatures.

Wind decreases activity rates and both microhabitat and body temperatures in the Brazilian Sand Lizard (*Liolaemus lutzae*; Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015). Body temperatures of *L. lutzae* are also affected by age due to an increase in body sizes, with older, large-sized lizards warmer than younger, smaller ones likely because of the greater capacity of heat conservation of larger bodies (thermal inertia; see Maia-Carneiro and Rocha 2013b). Because of that, small juveniles may be active mostly when wind speeds are low, whereas large adults may be active mainly under high wind speeds (Maia-Carneiro et al. 2017). Winds are frequent in the coastal sand plains near the sea (Restingas) in the state of Rio de Janeiro, southeastern Brazil (Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015), where *L. lutzae* lives (Rocha et al. 2009a, b; Maia-Carneiro and Rocha 2013c). When coming from the sea, the wind directly affects the *L. lutzae* habitat, without any obstacles, which might enhance its effects on these lizards.

Liolaemus lutzae is distributed in three main populations (Rio de Janeiro, Araruama, and Cabo Frio) along sand beaches isolated from each other by geographical barriers (Ariani et al. 2013). The species is considered to be endangered based on predictions of the effect of climate change (Sinervo et al. 2010). Here, we used data from the Cabo Frio population (Praia do Foguete and Praia do Peró) and from the Araruama population (Praia Grande and Maricá). We refer to the term population, however, as corresponding to each locality where data were collected. We used original and literature data (Maia-Carneiro and Rocha 2013b; Almeida-Santos et al. 2015) of juveniles and adult female and male *L. lutzae* to investigate relationships among body size, microhabitat temperature, body temperature, and wind speed across four populations. Previous analyses revealed intricate interactions among thermal microhabitats, body temperatures, and wind speed affecting daily and seasonal activities and thermoregulation in a *L. lutzae* population (Maia-Carneiro et al. 2012, 2017; Maia-Carneiro and Rocha 2013b,d). We assessed original and literature data to deepen the investigation by pursuing a more comprehensive insight on influences of wind and body size on thermal microhabitats and body temperatures in *L. lutzae*. Such data integration allowed us to evaluate the thermal biology of the species across populations, which contrasts with analyses of individual populations as it has been done in the past. We discuss how our findings relate to potential responses and vulnerabilities of individuals, populations, and the species to the warming caused by climate breakdown.

Materials and Methods

Study areas and data collection.—We used data available in Maia-Carneiro and Rocha (2013b) and Almeida-Santos et al. (2015) and data we collected and present here for the first time. Data from previous studies (see Maia-Carneiro and Rocha 2013b; Almeida-Santos et al. 2015) were collected using the same methods as we report here. We located individuals using Visual Encounter Surveys throughout the day. We recorded the snout-vent length (SVL) with calipers (to 1 mm) and body temperature (T_b) using a quick-reading thermometers (°C) inserted into the cloaca of each lizard. At each capture location, we measured air temperatures (T_a) 1 cm above the sites occupied by the lizards, substrate temperatures (T_s), and wind speeds (W_s) using a digital anemometer (m/s).

The data we collected and those in Maia-Carneiro and Rocha (2013b) are means of wind speed experienced by juveniles and means of air and substrate temperatures and wind speed experienced by adult female and male *L. lutzae* from the Restinga of Praia Grande (22º57'S, 42º02'W), municipality of Arraial do Cabo, state of Rio de Janeiro, southeastern Brazil. We collected during 9 d in the drier and colder season (June, July, and September) and 7 d in the rainy and warmer season of 2011 (November and December). Data for Almeida-Santos et al. (2015) were collected at Barra de Maricá, Praia do Foguete, Praia Grande, and Praia do Peró, Brazil, from late February to early April 2012 (the number of sampling days were not presented). We also used means of wind speeds and air and substrate temperatures of adult and juvenile *L. lutzae* from Almeida-Santos et al. (2015). That study provided values of body temperatures for juveniles and adult females and males and microhabitat temperatures and wind speeds grouping all individuals of the same location. We considered the means of microhabitat temperatures and wind speeds grouping all individuals as approximations of thermal microhabitats and winds experienced by juveniles and adult females and males. In this case, we used the same mean values calculated for all individuals for juveniles and adult females and males in the statistical analyses.

We used arithmetic means in the analyses to match the data presented here with those available in the literature. We used minimum sizes at maturity to define age classes as juveniles, adult females, or adult males (Rocha 1992). We identified males and females according to the following morphological characters (Rocha 1996): (1) males have the cloacae transversally straight in the anterior edge and females have them in V shape; (2) males have precloacal pores and females do not have them; (3) the ventral surface of the thighs is whitish yellow in adult males and white in adult females; and (4) males have ventral scales enlarged and arranged in rows near the cloaca and females have smaller scales arrayed irregularly.

Statistical procedures.—Given the non-normality and heteroscedasticity of data, we used the non-parametric Spearman's Rank Correlations using pooled data from all populations. We performed pairwise correlations using the variables as follows: $T_b \times T_a$; $T_b \times T_s$; $T_a \times W_s$; $T_s \times W_s$; $T_b \times W_s$; SVL × T_a; SVL × T_s; SVL × T_b; SVL × W_s. To test if wind speed explained variations of body temperatures factoring out the effects from thermal microhabitats, we calculated the residuals from simple Linear Regression of $T_b \times T_a$ and $T_b \times T_s$ and correlated them with W_s. Also, to evaluate if body sizes contributed to variations of body temperatures disregarding the effects from thermal microhabitats, we correlated the residuals of $T_b \times T_a$, $T_b \times T_s$, and $T_b \times W_s$ with SVL. We assumed a significance level of 0.05.

Results

Body temperatures correlated positively to air temperatures (r_s = 0.565; P = 0.014; Fig. 1) but was not significantly correlated with substrate temperatures (P = 0.053; Tables 1 and 2). Wind speed was not significantly correlated with T_s (P = 0.276) or the residuals of $T_b \times T_a$ (P = 0.122) but significantly decreased air temperatures (r_s = -0.486; P = 0.041) and body temperatures of lizards (r_s = -0.560; P = 0.016; Fig. 2). Wind speed also interacted negatively with the residuals of $T_b \times T_s$ (i.e., controlling the effect from T_s on T_b the wind decreased body temperatures; r_s = -0.505; P = 0.033; Fig. 2). There were no significant correlations between SVL and T_b (P = 0.227), SVL and T_a (P = 0.587), SVL and T_s (P = 0.937), SVL and W_s (P = 0.480), and the residuals from the regression of $T_b \times T_s$ and SVL (P = 0.173; Tables 1 and 2). The residuals of $T_b \times T_a$ also were not significantly correlated with SVL (P = 0.056), but the residuals of $T_b \times W_s$ were positively correlated with SVL (r_s = 0.567; P = 0.014; Fig. 3, Tables 1 and 2).

Discussion

Body temperatures of *L. lutzae* increased with the air and substrate temperatures across populations of the species. Although the correlation between body and substrate temperatures had marginal significance, the fact that wind speed did not correlate with T_s and correlated negatively with T_b after removing the effect from T_s demonstrates the importance of substrates as thermal sources for *L. lutzae*. Like other congeneric species (Labra et al. 2009; Medina et al. 2012; Rodríguez-Serrano et al. 2009), *L. lutzae* are active under variable climatic conditions within and among populations (Rocha 1995; Maia-Carneiro et al. 2012, 2017; Maia-Carneiro and Rocha 2013d; Almeida-Santos et al. 2015), demonstrating flexible thermal biology. Body temperatures influence physiological and ecological processes of relevance for lizards (Adolph and Porter 1993; Brown et al. 2004; Rocha et al. 2009c) and in turn are affected by microhabitat temperatures (Adolph and Porter 1993; Rocha et al. 2009c; Maia-Carneiro et al. 2012, 2017; Maia-Carneiro and Rocha 2013d; Almeida-Santos et al., 2015). The thermal flexibility of *L. lutzae* and other *Liolaemus* species (Rocha 1995; Labra et al. 2009; Medina et al. 2009, 2012; Maia-Carneiro and Rocha 2013d) likely favors suitable operation of life functions despite changing body temperatures and

Table 1. Means of snout-vent length (SVL; mm), body temperatures (T_b; ºC), air temperatures (T_a; ºC), substrate temperatures (T_s; ºC), and wind speeds (W_s; m/s) for Brazilian Sand Lizard (*Liolaemus lutzae*) juveniles, adult females, and adult males from four populations in the State of Rio de Janeiro, southeastern Brazil. The following symbols refers to the source of the data: * Almeida-Santos et al. 2015; Δ Maia-Carneiro and Rocha 2013a; ‡ original data. Seasons in which data were collected in Praia Grande are indicated by a C (= colder season) and a W (= warmer season).

Trait	Barra de Maricá*	Praia do Foguete*	Praia do Peró*	Praia Grande*	Praia Grande^C	Praia Grande^W
SVL of juveniles	42.1	43.6	40.3	38.7	43.9^Δ	51.4^Δ
SVL of females	61.6	59.8	58.5	56.8	55.2^Δ	57.2^Δ
SVL of males	72.8	74.1	68.5	67.8	65.8^Δ	68.5^Δ
T_b of juveniles	31.8	31.5	33.9	33.4	30.8^Δ	31.1^Δ
T_b of females	33.2	31.3	34.9	32.5	31.4^Δ	32.2^Δ
T_b of males	33.1	31.9	34.2	34.6	33.2^Δ	33.6^Δ
T_a of juveniles	27.4	26.9	30.8	29.9	28.5^Δ	30.2^Δ
T_a of females	27.4	26.9	30.8	29.9	28‡	29.5‡
T_a of males	27.4	26.9	30.8	29.9	27.5‡	30.2‡
T_s of juveniles	33	33	33.7	33.9	31.2^Δ	35.3^Δ
T_s of females	33	33	33.7	33.9	30.9‡	33.6‡
T_s of males	33	33	33.7	33.9	31.5‡	35‡
W_s of juveniles	4.4	4.9	2.3	2.4	4.3‡	5.4‡
W_s of females	4.4	4.9	2.3	2.4	5.0‡	4.5‡
W_s of males	4.4	4.9	2.3	2.4	5.5‡	5.1‡

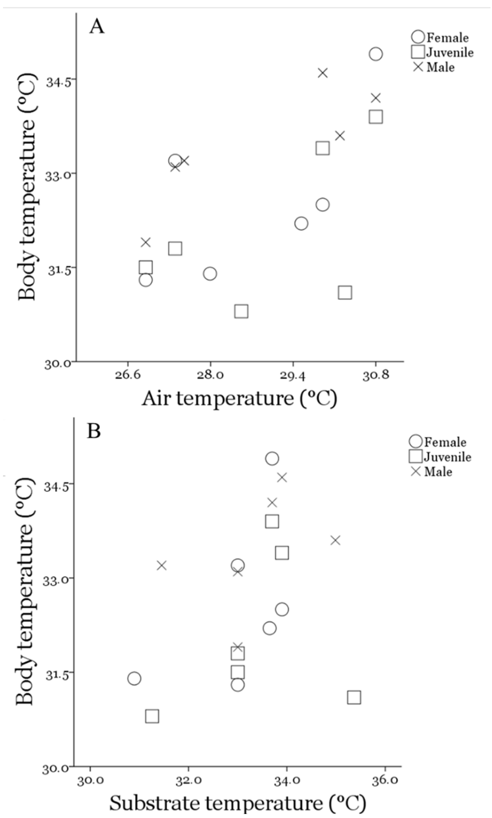

Figure 1. Associations of body temperature (°C) with (A) air temperature (°C) and (B) substrate temperature (°C) across four populations of Brazilian Sand Lizards (*Liolaemus lutzae*) in the State of Rio de Janeiro, southeastern Brazil. Symbols indicate juveniles (□), adult females (○), and adult males (×). Data points matching each of the populations are presented in Tables 1 and 2.

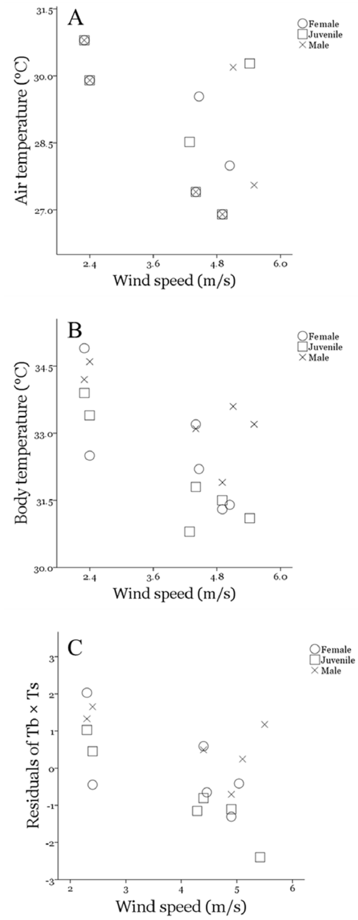

Figure 2. Associations of (A) air temperatures (°C), (B) body temperatures (°C), and (C) residuals of $T_b \times T_s$ (°C) of Brazilian Sand Lizards (*Liolaemus lutzae*) with wind speed across four populations in the State of Rio de Janeiro, southeastern Brazil. Symbols indicate juveniles (□), adult females (○), and adult males (×). Data points matching each of the populations are presented in Tables 1 and 2.

climatic conditions within and across populations.

For most correlations, body temperatures of large-sized *L. lutzae* (mainly adult males) were higher than smaller lizards (mostly juveniles and adult females), suggesting that larger individuals had greater resistance to heat loss than smaller ones under similar microhabitat temperatures and wind speeds (Maia-Carneiro and Rocha 2013b; Maia-Carneiro et al. 2017). Body temperatures of adult males tended to be higher and varied less with increasing wind speeds. In contrast, body temperatures of adult females and juveniles were lower and had more pronounced alterations under similar winds. This may derive from differential properties of thermal inertia (capacity to keep heat) of *L. lutzae* adult males, adult females, and juveniles. After controlling for the effects of T_a (at a significance level of 0.056) and W_s on T_b, the body temperatures of *L. lutzae* tended to increase with body sizes. This is supported by indications of large *L. lutzae* having higher body temperatures (Maia-Carneiro and Rocha 2013b) and of winds influencing its daily and seasonal activities, with small individuals active mainly at low wind speeds, thereby avoiding heat loss, and large individuals active mostly during high-speed winds preventing overheating (Maia-Carneiro et al. 2017). Under warming temperature due to climate change, restrictions on levels of activity and microhabitat and body temperatures of *L. lutzae* by high environmental temperatures (Sinervo et al. 2010; Maia-Carneiro et al. 2017) may be even greater for larger-sized adults as it seems already ongoing (Maia-Carneiro et al. 2017; this study) because of increased vulnerability to overheating.

We found that wind decreased air and body temperatures across *L. lutzae* populations. Heat is removed from lizards directly as indicated by negative correlations of wind speeds with body temperatures

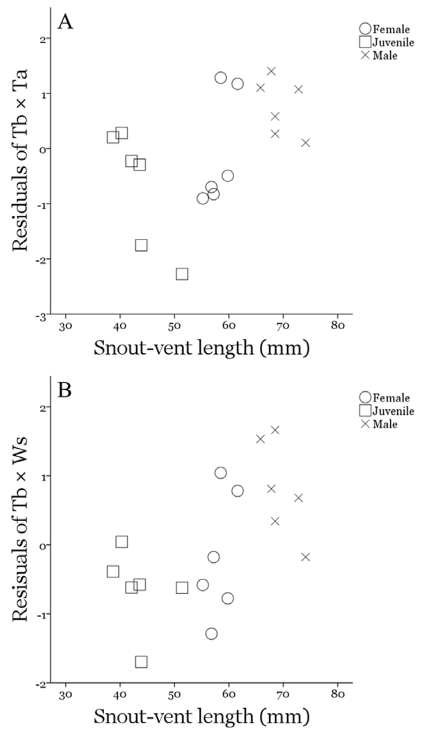

Figure 3. Associations of (A) the residuals from Linear Regression of $T_b \times T_a$ and of (B) $T_b \times W_s$ with snout-vent length (mm) across four populations of Brazilian Sand Lizards (*Liolaemus lutzae*) in the State of Rio de Janeiro, southeastern Brazil. The variables T_b and T_a are in °C and W_s is in m/s. Symbols indicate juveniles (□), adult females (○), and adult males (×). Data points matching each of the populations are presented in Tables 1 and 2.

(Medina et al. 2009; Maia-Carneiro et al. 2012; Ortega et al. 2016) and with the residuals from $T_b \times T_s$, and indirectly as supported by decreasing air temperatures by action of winds (Almeida-Santos et al. 2015; Ortega et al. 2016; Maia-Carneiro et al. 2017). Besides other factors influencing *L. lutzae* body temperatures, such as body size (Maia-Carneiro and Rocha 2013b), behavioral thermoregulation (Maia-Carneiro et al. 2012, 2017; Maia-Carneiro and Rocha 2013d), and habitat features (Rocha et al. 1988; Maia-Carneiro et al. 2012, 2017), rates of heat gain and heat loss of lizards, as well as of their microhabitats, are partly determined by a combination of incoming of solar energy allowing heating and the cooling by winds (Rocha 1995; Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015). Under typical environmental temperatures, winds can cool down microhabitat temperatures and body temperatures of lizards, which may decrease lizard activity and negatively affect their thermoregulation (Medina et al. 2009; Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015). Under high temperatures, as may become common with climate change, winds might help to moderate temperatures favoring lizard activity, the quality of thermal microhabitats, and suitable body temperatures (Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015). The operation of physiological and ecological functions that rely on activity levels and microhabitat and body temperatures (Adolph and Porter 1993; Brown et al. 2004; Rocha 2009c) may be facilitated by cooling winds (Maia-Carneiro et al. 2012, 2017; Almeida-Santos et al. 2015), which may favor the permanence of *L.* lutzae under climate warming. Nevertheless, benefits from winds may be interrupted if air masses heat up. If winds remain cool, however, they might favor the conservation of these lizards as they allow them to compensate for negative impacts of warming on levels of activity and microhabitat and body temperatures.

Table 2. Air and substrate temperatures (ºC) of adult female and male Brazilian Sand Lizards (*Liolaemus lutzae*) and wind speed (m/s) recorded at capture points for juveniles and adult females and males during two seasons in Praia Grande, State of Rio de Janeiro, southeastern Brazil. Abbreviations are n = number of observations and SD = standard deviation.

	Colder season			Warmer season		
Data	n	Mean ± SD	Range	n	Mean ± SD	Range
Air temperature						
Adult females	23	28.0 ± 3.1	24–36.2	42	29.5 ± 0.9	22.6–35.4
Adult males	15	27.5 ± 1.9	24.4–31	28	30.2 ± 2.1	25.0 – 34.4
Substrate temperature						
Adult females	23	30.9 ± 5.1	22.8–46.6	42	33.6 ± 5.7	22.0–48.0
Adult males	15	31.5 ± 3.8	25–41.4	28	35 ± 5.5	24.0–43.6
Wind speed						
Juveniles	95	4.3 ± 1.9	0–9.6	18	5.4 ± 1.9	2.6–9.0
Adult females	23	5.0 ± 1.9	1.2–7.9	42	4.5 ± 2.0	0–8.0
Adult males	15	5.5 ± 2.1	0–8.7	28	5.1 ± 1.4	2.2–7.2

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