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Thermal relationships between body temperature and environment conditions set upper distributional limits on oviparous species

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ABSTRACT

We determined the thermal biology of the oviparous *Liolaemus boulengeri* and the viviparous *Liolaemus lineomaculatus* populations localised at high and low latitude sites in Patagonia, Argentina. We present data of body temperatures in the field (T_b) and preferred temperature in the laboratory (T_{pref}), micro-environmental and operative temperatures and the effectiveness of thermoregulation. *Liolaemus boulengeri* and *L. lineomaculatus* choose different heat sources for active selection of suitable thermal micro-environments for thermoregulation, and the oviparous *L. boulengeri* is a more effective thermoregulator ($E=0.55$) than the viviparous *L. lineomaculatus* ($E=0.43$). Even when *L. boulengeri* is a better thermoregulator and both species show identical timing in the reproductive cycles, there are constraint factors that impose limitations on the southernmost distribution of the oviparous *L. boulengeri*.

1. Introduction

The relationship between thermoregulation and life history governs the course of adaptation in variable environments (Angilletta, 2009). Several lizard species are able to precisely thermoregulate in narrow ranges of temperatures (Pearson, 1954; Hertz et al., 1993; Zug et al., 2001). However, when heat sources or thermal microhabitats are scarce or ephemeral, compensatory changes can occur in behaviour and/or physiology (Niewiarowski, 2001) to maintain body temperature at a relatively high and constant level (Pearson, 1954; Hill, 1980; Zug et al., 2001). But, under thermal restrictions the costs of thermoregulation competes with the energy allocated to feed and to reproduce, and increases the risk of predation (Avery, 1978; Huey and Slatkin, 1976; Hertz and Huey, 1981; Sears, 2005).

For example, conspicuous differences exist between higher-elevation lizards regarding the extent of thermoregulation and activity period (Marquet et al., 1989). At high elevations, in tropical areas, lizards such as *Liolaemus signifer* from Perú (4300 m; Pearson, 1954) or *L. huacahuasicus* from the Cumbres Calchaquíes, Tucumán, Argentina (4000 m; Halloy and Laurent, 1988) compensate for the low air temperatures (12 °C, weather stations records) by basking and taking advantage of the high solar radiation fluxes (Pearson, 1954) or by prolonging the activity period (Carothers et al., 1989; Marquet et al., 1989). In contrast, lizards in warmer climates typically avoid sunny patches when they achieve temperatures that are close to maximal body temperatures and are inactive at midday (Hertz et al., 1993; Sinervo et al., 2010).

However, effective thermoregulation becomes uncertain at high latitudes in Patagonia probably because of short daily and seasonal activity periods, combined with low air temperatures and the almost constant high wind intensity from the west (Paruelo et al., 1998; Ibargüengoytía et al., 2010). Species such as *L. bibronii (*43 and 46°S; Medina et al., 2009), *L. sarmientoi* and *L. magellanicus* (53°S, Ibargüengoytía et al., 2010) exhibit the lowest T_b recorded for 55 populations belonging to 33 species of the genus *Liolaemus*, and behave as thermoconformers or poor thermoregulators (sensu Hertz et al., 1993; Medina et al., 2009; Ibargüengoytía et al., 2010).

The main objective of this study was to explore the intra- and interspecific differences in field body temperature (T_b), preferred

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temperatures in laboratory (T_{pref}) and the effectiveness of thermoregulation (E, sensu Hertz et al., 1993) of two populations of an oviparous *L. boulengeri* and two of the viviparous *L. lineomaculatus* localised at different latitudes and altitudes. These two species were chosen, for comparative purposes, to complete previous studies on thermal biology on liolaemids from the southernmost distributions in Patagonia, such as those of *L. bibronii* (Medina et al., 2009), *L. magellanicus* and *L. sarmientoi* (Ibargüengoytía et al., 2010). The oviparous species *Liolaemus boulengeri*, included in the *chilliensis* group, inhabits the Monte and Steppe, and the high Andean grasslands environments, and is common at elevations up to 900 m asl in the Andean valleys from Mendoza Province (36°S; Cei, 1986; Scolaro, 2005) to the coast line of Santa Cruz Province (50°S; Scolaro, 2005; Morando et al., 2007; Pincheira-Donoso et al., 2008). The viviparous *L. lineomaculatus* belongs to the *signifer* group, and it inhabits from the north-west of Patagonia in the Neuquén Province (39°S) at elevations up to 900 m asl to the high Andean grasslands in Santa Cruz Province, where it is syntopic with the southernmost lizard of the world, *Liolaemus magellanicus* (51°S; Cei, 1986; Scolaro, 2005). Even though, *Liolaemus boulengeri* and *L. lineomaculatus* belong to two different phylogenetic groups and are representative of the oviparous and viviparous modes of reproduction, they are syntopic in part of their distribution and show similar reproductive traits such as timing of reproduction, clutch size and size at sexual maturity (Medina and Ibargüengoytía, 2010). So, our main question is whether thermal physiology and behaviour compensates for differences in body size, reproductive mode and genetic load.

2. Materials and Methods

2.1. Study area and materials

Two populations of *L. boulengeri* and two populations of *L. lineomaculatus* were studied in Patagonia, Argentina. In Esquel (Chubut Province), *L. boulengeri* was captured at a low elevation (43°01′S, 70°47′W, 626 m asl) and *L. lineomaculatus* at a high elevation (42°52′S, 71°12′W, 1400 m asl). In Perito Moreno (Santa Cruz Province) both species were captured in syntopy (46°37′S, 71°15′W, 263 m asl). Lizards (in Esquel: *L. boulengeri*, $N=98$; *L. lineomaculatus*, $N=76$; in Perito Moreno: *L. boulengeri*, $N=62$; *L. lineomaculatus*, $N=86$) were caught by hand or noose only when active (9 to 18 h), outside the burrows or performing any behaviour related to feeding and/or breeding activities, from February 2005 to March 2008.

2.2. Air temperatures and illuminance conditions of localities

Air temperatures and illuminance were recorded on the ground every 30 min during the activity season (from September to May) in the three localities. Data loggers were placed (Hobo Pendant, Temperature and Illuminance Data Logger) in similar conditions and exposed to solar radiation throughout the day.

2.3. Micro-environmental conditions at capture sites

In order to determine the main heat source used by the lizards (thigmothermy vs heliothermy) the substratum temperature in the sun (T_{ss}) and in the shade (T_{ssh}), and the air temperature at 1 cm above the ground (T_a) were recorded at each capture site, hereafter called micro-environmental temperatures. Temperatures were registered using thermocouples for substrate TES TP-K03 and air TES TP-K02, respectively, and they were connected to a TES 1302 thermometer (TES Electrical Electronic Corp., Taipei, Taiwan, ±0.03 °C). Wind velocity (Turbo meter, ±0.1 m/s), humidity (Micro-meteorological station, Lutron LM-8000) and illuminance (Luximeter Extech model 401025, ±lux) were also recorded at capture microsites. Time of day at capture was also recorded.

2.4. Determination of operative temperatures

Operative temperatures (T_e, sensu Bakken, 1992; Hertz, 1992) were recorded to describe the "null" distribution of body temperatures (T_b) expected in non-regulating animals integrating biophysical and morphological factors that influence an ectotherm's T_b. The appropriate model was designed using simultaneous comparisons of the body temperatures (T_b) of live lizards with that of copper models of varying sizes and colours. To choose the best model catheter probes TES TP-K01 were used simultaneously to register the temperatures of both the models and the lizards. The calibration experiments were conducted during 3 consecutive hours with half of the time in full sun and the other half in the shade. The best model was chosen by comparing the R^2 obtained from the correlation between each model and T_b. The best-fit model corresponded to a flat-black copper cylinder of 90 mm long × 20 mm wide × 2 mm thick, sealed at the ends. The correlation between T_b and T_{model} was significant (Lineal Regression, $F_{1,\ 50}=428.56$, $R^2=\ 0.897$, $P<0.001$) and the R^2 range was from 0.87 to 0.97 (±1 °C), considered acceptable in numerous previous studies (Beaupre, 1995; Dorcas et al., 1997; Dzialowski, 2005; Angilletta, 2009).

2.5. Lizards body temperatures

Body temperature (sensu Pough and Gans, 1982) was taken using a catheter probe TES TP-K01 (1.62 mm diameter) introduced ca. 1 cm inside the cloaca. Individuals were handled by head to avoid heat transfer and temperature was recorded within 10 s of handling.

2.6. Laboratory protocol and experiments

Experiments were performed 3 to 7 days after capture of lizards from Esquel (*L. boulengeri*, $N=44$; *L. lineomaculatus*, $N=63$) and from Perito Moreno (*L. boulengeri*, $N=46$; *L. lineomaculatus*, $N=69$) to obtain a preferred body temperature (T_{pref}). Lizards were placed individually in open-top terrarium (200 × 45 × 20 cm) each with a sand floor and a thermal gradient produced by a line of four infra-red lamps above (one of 250 W, two of 150 W and one of 100 W). The lamps were adjusted to different heights above the terrarium to make a linear substratum gradient from 15° to 65 °C. Temperatures were taken using ultra-thin (1 mm) catheter thermocouples located approximately 10 mm inside the cloaca and taped to the base of the lizard's tail to prevent the thermocouple from being dislodged during the experiment. The temperature of each lizard was obtained every 10 min for 5 h, by connecting the thermocouple to a TES 1302 thermometer (TES Electrical Electronic Corp., Taipei, Taiwan, ±0.01 °C). The duration of the experiments was chosen considering the time during which *L. boulengeri* and *L. lineomaculatus* reach their preferred temperature during thermoregulation trials. The mean T_{pref} and the minimum and maximum set-point temperatures (T_{set}, the temperatures bounding the interquartile range, the middle 50% of the observations, for each lizard) were obtained for each lizard and were used to estimate the range and mean T_{pref} for each population and for the species.

2.7. Effectiveness of thermoregulation

The effectiveness of temperature regulation: $E=1-(\text{Mean } d_b/\text{Mean } d_e)$ was obtained. The d_b was calculated as the mean of the