



Thermal responses to environmental constraints in two populations of the oviparous lizard *Liolaemus bibronii* in Patagonia, Argentina

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ABSTRACT

Ectotherms change their thermoregulation behaviour according to the available temperatures, photoperiod, and radiation present in their local environment. The influences of the abiotic environment not only affect the body temperature but also most life history traits of populations. The thermal biology of one of the southernmost oviparous lizards, *Liolaemus bibronii*, was studied at high- and low-latitude sites in Patagonia, Argentina, following the methodology of Hertz et al. [1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142, 796–818]. Our results show that *L. bibronii* lives under thermal–environmental constraints, behaves as a moderate thermoregulator, and shows the lowest body temperature (28 °C) for oviparous liolaemids.

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1. Introduction

Environment influences ectotherms through the exchange of energy affecting their body temperature and the resting metabolic expenditure, which has consequences for whole-animal energy balance (Porter and Gates, 1969; Beaupre, 1995). In consequence, biophysical environments not only affect the body temperature but also the evolution of most life history traits of populations, such as the levels of activity (Avery, 1982; Lillywhite, 1987), the growth rates and body size (Cruz et al., 2005; Pincheira-Donoso et al., 2007), the timing of the reproductive events (Boretto et al., 2007), reproductive mode (Shine, 1985; Shine, 2004), diet (Espinoza et al., 2004), and survivorship (Huey, 1982).

Geographic variation results in different thermal resource availability, which generally declines with elevation and latitude (Van Damme et al., 1987) resulting in differences in properties of populations, especially those related to the thermal ecology of lizards (Andrews, 1998). Thus, limitations imposed by temperature, photoperiod, and radiation result in radically different behaviour and/or physiological performance, survival and fitness (Bogert, 1949). Several reptile populations exhibit a gradient of body temperatures across their latitudinal (Avery, 1976) or

altitudinal distribution (Hertz, 1992; Hertz and Huey, 1981; Huey et al., 2003), reflecting different thermal interactions with the environment (Garland and Adolph, 1991). In addition, lizards from cold environment possess different strategies or adaptations to harsh conditions. For example, in liolaemids, larger body size seems to correlate with higher altitude and latitude, sites with decreasing environmental temperatures (Cruz et al., 2005). However, smaller body sizes in cooler environments would be advantageous for cold-blooded vertebrates, because the heating rates are slower when body mass is greater (e.g. Shine, 1980; Pincheira-Donoso et al., 2007). Therefore, the optimal body temperatures to allow basic biological activities (e.g. feeding, reproduction) can be reached in shorter spans of times (Jaksic, 1998; Mattison, 1999). In addition, in the evolution of their trophic niches in relation to morphological and thermoregulatory traits showed that omnivorous and herbivorous species that inhabit high altitudes and latitudes tend to show small body size and low preferred metabolic temperatures (Espinoza et al., 2004). In the genus *Phymaturus*, the diet, the ability to be active over a broad thermal range, and a longer activity season can counteract the effect of body temperature on the timing and allocation of energy to growth, maturation and reproduction (Ibargüengoytía et al., 2008). Finally, parental care in reptiles also is associated with cold climates and harsh environments. In *Liolaemus elongatus*, Halloy et al. (2007) observed that mothers and their offspring occupied the same refuge for several days. This may help the neonates to conserve body heat and retain water during the cold, dry nights of Patagonia.

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The achievement and maintenance of body temperature (T_b) within a range that allows activity and optimizes physiological performance is dependent on the availability of suitable microhabitats and on the effectiveness of thermoregulation (Beaupre, 1995; Huey et al., 2003). Thermal behaviour in reptiles can result in body temperatures that closely resemble those of their environment. For example, in an absence of effective temperature regulation the thermal relationship between the environment and the organism results in a proportional function of environmental temperature (thermoconformers). However, under conditions within a restricted range involving variable internal and/or external heat loads, some reptiles are able to actively maintain higher or lower body temperatures (thermoregulators, Espinoza and Tracy, 1997; Bligh and Johnson, 2003). *Liolaemus multiformis*, for example, living at 3000 m above sea level with environmental temperatures between -9 and 13 °C is able to thermoregulate and achieve body temperatures of 37 °C with air temperatures of 13 °C (Pearson, 1954). In addition, a comparative study among three species of the genus *Phymaturus*, distributed along an altitudinal and latitudinal gradient, show that they share similar micro-environments and habits and follow the air and substrate temperatures when they are inside the rock crevices. But, these species each seem to be using predominately either heliothermy at high altitudes or thigmothermy at lower altitudes. Thus, thermoregulatory behaviours will buffer the potential impact of selection induced by geographic variation in thermal environment (Huey et al., 2003).

In Northwestern Patagonia, Argentina, the climate is dry and cold with intense westerly winds (especially in summer), snow in winter, and freezing temperatures most of the year (Cabrerá, 1976). Lizards from this region are active during spring and summer but hibernate approximately 6 months during autumn and winter (Ceí, 1986). The life histories of ectotherms that hibernate are constrained by the length of the activity season, the availability of food energy and thermal energy, and by the ability to survive over winter. In consequence, constraints on lizard life histories by climate are more severe at higher latitudes and altitudes and further constrained by the cold conditions during the activity season in the maritime climate of the Southern Hemisphere (Ibargüengoytía and Casalins, 2007).

The lizard genus *Liolaemus*, with 190 recognized species and subspecies (Morando et al., 2007), is endemic to temperate South America and is versatile and able to occupy a variety of environments ranging from the extremely arid Atacama Desert to the temperate *Nothofagus* rainforest (Donoso-Barros, 1966; Ceí, 1986, 1993; Etheridge and Queiroz, 1988; Lobo, 2001). The oviparous species are found from 9° to 50° S latitude and from sea level to 3000 m altitude, and the viviparous species from 9° to 53° S latitude and from sea level to 5000 m altitude (Duellman, 1979; Ceí, 1993; Navas, 2002; Scolaro, 2005, 2006). Studies of thermal biology of genus *Liolaemus* have reported intra- and interspecific differences in field body temperatures and thermoregulatory behaviours associated with climatic conditions, and differences in the daily activity patterns and types of substrates used (Table 1).

Liolaemus bibronii inhabits the Monte, Steppe, and high Andean grassland, and is common at high elevation up to 3000 m in the Andean valleys from southern San Juan Province (32° S) to the coastline of Santa Cruz Province (51° S; Scolaro, 2005; Morando et al., 2007). *L. bibronii* together with *Liolaemus boulengeri* are the southernmost oviparous liolaemids (Scolaro, 2005) resulting in an appealing model for the study of environmental constraints and the evolution of differences in life history and thermoregulation, particularly in the cold environments of Patagonia.

In this work, we present a comparative study of two populations of *L. bibronii*, providing the first data on field and

selected body temperatures, thermoregulation behaviour, micro-environments and climate of one of the southernmost oviparous *Liolaemus*. Results are discussed considering 33 populations of 19 species of oviparous liolaemids and 22 populations of 15 species of viviparous liolaemids.

2. Materials and methods

2.1. Study area and materials

Field work was performed in two locations in Patagonia, Argentina: Esquel (Chubut Province, $43^\circ 01'S$, $70^\circ 47'W$, 626 m asl) and Perito Moreno (Santa Cruz Province, $46^\circ 37'S$, $71^\circ 15'W$, 263 m asl) from February 2005 to March 2007. Lizards ($N = 88$ in Esquel and $N = 47$ in Perito Moreno) were caught by hand or loop from 9 to 18 h only when active (outside the burrows, performing any behaviour related to feeding and/or breeding activities; sensu Ibargüengoytía and Cussac, 2002). Lizards were killed for further research in reproductive biology by intraperitoneal administration of sodium thiopental, fixed in Bouin's solution for 24 h, and preserved in 70% ethanol. The specimens are stored at the Department of Zoology at Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina (CRUB-UNC).

2.2. Data recorded

Monthly means of temperature, humidity, and wind velocity during the activity season (September–April) were obtained for the last 10 yr from the National Meteorological Service, Argentinean Air Force. The air temperatures of Esquel were corrected for differences in altitude (-6 °C/Km; Fernández-García, 1996) from temperatures obtained at the Esquel National Airport (797 m asl). The photoperiod data were obtained from the Argentinean Manual for pilots (1991).

The micro-environmental temperatures were recorded at capture sites: substratum temperature in the Sun (T_{ss}) and in the shade (T_{ssh} , TES TP-K03 substrate probe), air temperature at 1 cm above the ground (T_a , TES TP-K02 gas probe). Thermocouples were connected to a TES 1302 thermometer (TES Electrical Electronic Corp., Taipei, Taiwan, ± 0.01 °C). Wind velocities (Turbo meter, ± 0.1 m/s), humidity (Micro-meteorological Station, Lutron LM-8000), and luminescence (Luximeter Extech model 401025, \pm lux) were also recorded in the micro-environments.

The operative temperature (T_e , sensu Bakken, 1992; Hertz, 1992) as the product of the interactions between biophysical and morphological factors that influence an ectotherm's T_b , were measured from 9 to 18 h when lizards were active using 12 copper models set at a variety of microsites within *L. bibronii* habitat. The models were connected to three data loggers (HOBO) each with four thermocouples, and the micro-environmental temperatures were recorded every 5 min. The mean temperatures from each model were used to obtain the daily T_e in order to describe the “null” distribution of T_b expected in non-regulating animal. Twelve mean values of T_e were obtained for each field site and their average was used to compare the T_e between the populations by Mann–Whitney test. The models were designed using simultaneous comparisons of the body temperatures (T_b) of live *L. bibronii* to that of copper models of varying sizes and colours. Catheter probes TES TP-K01 were used simultaneously to register the temperatures of both the models and the lizards. The calibration experiments were made during 3 consecutive hours and half of the time was in full Sun and the other half was in shade. The best-fit model was a flat-black copper cylinder with

Table 1Body (T_b) and selected body temperature (T_{sel}), latitude ($^{\circ}$ S), longitude ($^{\circ}$ W), and altitude (m) of oviparous and viviparous *Liolaemus* populations and species.

Populations	T_b population	T_b species	T_{sel} population	T_{sel} species	Latitude	Longitude	Altitude
<i>Oviparous</i>							
<i>L. nitidus</i> ^a			35 ± 1.3(5)		30.39	71.4	200
<i>L. nitidus</i> ^a	34.9 ± 1(6)	35.25	36.2 ± 1.3(7)	35.70	33.21	70.19	1985
<i>L. nitidus</i> ^b	35.4 ± 0.9(14)				33.04	71.37	100
<i>L. chiliensis</i> ^c	34.09 ± 2.2(8)	34.09			33.49	70.12	1800
<i>L. fuscus</i> ^b	33.7 ± 0.9(17)				33.04	71.37	50
<i>L. fuscus</i> ^b	35.6 ± 1.1(11)	34.79		35.30	33.35	70.3	1000
<i>L. fuscus</i> ^d	36 ± 0.6(8)		35.3 ± 0.3(5)		33.35	70.23	890
<i>L. lemniscatus</i> ^b	33.9 ± 0.5(33)				33.04	71.37	50
<i>L. lemniscatus</i> ^b	35.9 ± 0.9(22)	34.83		35.20	33.04	70.3	1000
<i>L. lemniscatus</i> ¹			35.5 ± 0.8(8)		33.32	70.57	500
<i>L. lemniscatus</i> ¹			34.3 ± 1.5(6)		33.23	70.3	950
<i>L. lemniscatus</i> ¹			35.8 ± 0.8(5)		33.27	70.42	600
<i>L. lemniscatus</i> ^d	35.1 ± 0.4(25)		35.2 ± 0.3(19)		33.35	70.23	890
<i>L. monticola</i> ^b	35.4 ± 0.8(26)	35.83		36.80	33.04	70.3	1000
<i>L. monticola</i> ^d	36.7 ± 0.4(13)		36.8 ± 0.3(10)		33.35	70.23	890
<i>L. tenuis</i> ^d	36.9 ± 1.8(7)	36.9	37.2 ± 0.1(4)	37.2	33.35	70.23	890
<i>L. t. tenuis</i> ^a			37.2 ± 0.1(4)	37.2	33.17	71.11	600
<i>L. t. punctatissimus</i> ^a			36.7 ± 1.1(3)	36.7	37.28	72.21	130
<i>L. nigromaculatus</i> ^b	34.8 ± 0.8(25)	34.80			33.04	71.37	50
<i>L. platei</i> ^b	35.3 ± 0.7(13)	35.59			33.04	71.37	50
<i>L. platei</i> ^b	37.5 ± 1(2)				33.04	70.3	1000
<i>L. bibronii</i> [*]	28.3 ± 0.48(86)	28.09	34.08 ± 0.56(46)	34.11	43.01	70.47	622
<i>L. bibronii</i> [*]	27.7 ± 0.56(47)		34.14 ± 0.41(47)		46.37	71.15	263
<i>L. alticolor</i> ^e	29.1 ± 1.2(23)	29.10			19.42	68.49	4500
<i>L. constanzae</i> ^f	30.79 ± 0.81(17)	30.79	34.31 ± 0.22(11)	34.31	26.46	68.14	2400
<i>L. fabiani</i> ^f	29.78 ± 0.49(13)		30.03 ± 0.61(11)		26.46	68.14	2400
<i>L. fabiani</i> ¹		31.25	32.7 ± 1.1(15)	31.98	26.46	68.14	2300
<i>L. fabiani</i> ^f	31.76 ± 0.28(37)		33.03 ± 0.36(10)		26.46	68.14	2300
<i>L. sanjuanensis</i> ^g	30.1 ± 5.2(29)	30.10			31.22	67.58	2994
<i>L. olongasta</i> ^h	32.1 ± 3.9(55)	32.10			31.19	68.41	700
<i>L. pseudoanomalus</i> ⁱ	31.98 ± 3.9(98)	31.98			31.19	68.41	700
<i>L. koslowskyi</i> ^j	34.76 ± 2.8(30)	34.76			28.49	66.57	1200
<i>L. occipitalis</i> ^k	30.89 ± 4.4(270)	30.89			30.24	50.17	0
<i>Viviparous</i>							
<i>L. belli</i> ^a	34.2 ± 1.1(9)		35.31(15)		33.2	70.19	2300
<i>L. belli</i> ^a	32.7 ± 2(34)	33.01	36 ± 0.7(5)	35.12	33.06	70.24	3200
<i>L. belli</i> ^a			33.9 ± 1.2(6)		36.04	70.3	2100
<i>L. p. pictus</i> ^a		31.80	35.4 ± 0.7(6)	34.31	41.06	72.3	1000
<i>L. p. pictus</i> ^a	31.8 ± 2.5(16)		33.8 ± 1.7(13)		35.36	71.05	1150
<i>L. schroederi</i> ^a	31.6 ± 3.8(10)		34.6 ± 1.5(6)	34.9	35.36	71.05	1150
<i>L. schroederi</i> ^a		33.24	35.5 ± 0.6(3)		33.2	70.19	2300
<i>L. schroederi</i> ^b	35.3 ± 0.8(8)				33.4	71.06	2000
<i>L. nigroviridis</i> ^b	35.9 ± 0.4(80)	35.90			33.4	71.06	2000
<i>L. p. chiloensis</i> ^a			34.4 ± 1.8(5)	34.40	42.24	73.47	200
<i>L. pictus argentinus</i> ^l	33.2(8)	33.20			41.1	71.3	700
<i>L. elongatus</i> ^l	33.2(29)				41.1	71.3	700
<i>L. elongatus</i> ^l	29.8(40)	31.15		29.9	41.6	71.7	800
<i>L. elongatus</i> ^m	30.27 ± 0.76(41)		29.9 ± 0.32(14)		41.5	70.5	970
<i>L. parvus</i> ^a	32 ± 2.5(16)	32			33.22	69.29	3700
<i>L. magellanicus</i> ^o	27 ± 0.7(20)	27			53.24	69.19	76
<i>L. nigroroseus</i> ^f	33.89 ± 0.71(8)	33.89	34.74 ± 0.24(8)	34.74	26.46	68.14	2400
<i>L. huacahuasicus</i> ^p	32(25)	32			30.11	67.4	4500
<i>L. islugensis</i> ^e	28.2 ± 1.3(41)	28.20			19.42	68.59	4000
<i>L. ornatus</i> ^e	30.7 ± 1.3(24)	30.70			19.42	68.59	4000
<i>L. jamesi</i> ^e	29.1 ± 2.2(9)	29.10			19.42	68.49	4500
<i>L. ruibali</i> ^q	24.4 ± 6.2(12)	24.4			31.1	69.46	3000
Genus <i>Liolaemus</i>	32.4 ± 0.48(45)		34.5 ± 0.4(28)				

Mean and sample size (N) is indicated.

^a Labra (1998).^b Fuentes and Jaksic (1979).^c Carothers et al. (1997).^d Labra and Bozinovic (2002).^e Marquet et al. (1989).^f Labra et al. (2001).^g Acosta et al. (2004).^h Cánovas et al. (2006).ⁱ Villavicencio et al. (2007).^j Martori et al. (2002).^k Bujes and Verrastro (2006).^l Iburgüengoytia and Cussac (2002).^m Iburgüengoytia (2005).ⁿ Quinteros et al. (2008).^o Jaksic and Schwenk (1983).^p Halloy and Laurent (1988).^q Villavicencio et al. (2006).

* Present study.

dimensions of 90 × 20 mm (correlation T_b vs. model, $r = 0.98$, $N = 36$, $P < 0.0001$).

Body temperature (sensu Pough and Gans, 1982) was taken only in active lizards using a catheter probe TES TP-K01, 1.62 mm diameter introduced ca. 1 cm inside the cloaca. Individuals were handled by the head to avoid heat transfer and temperature was recorded before 20 s of handling. Time of day at capture was also recorded.

The snout-vent length (SVL, vernier caliper ± 0.02 mm) and body mass (BW, 10-g Pesola spring scale ± 0.5 g; ovigerous lizards and those with tail damage were excluded) were registered for each lizard. Reproductive condition and sex was determined by autopsy and histology of the gonads. Adults were distinguished from juveniles by the presence of gametogenesis.

2.3. Laboratory experiments

Experiments were performed with a sub-sample of lizards for Esquel ($N = 46$) and for Perito Moreno ($N = 47$) to obtain a selected body temperature (T_{sel}) range and mean. In addition, we measured the set-point range (T_{set}) as the central 50% of all T_b 's selected in the laboratory. There are solid neurophysiological bases (Baber and Crawford, 1977; Firth and Turner, 1982) to support that ectotherms regulate between upper and lower set-point temperatures rather than around a single T_b and that the set-point range in lizards and fishes represent the natural settings caused by the hypothalamic thermostat (Hertz et al., 1993).

Experiments were conducted from 3 to 7 days after capture. Lizards were placed individually in open-top terraria (200 × 45 × 8 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 terrain to make a lineal substratum gradient from 15 to 69 °C. Temperatures were taken using ultra-thin (1 mm) catheter thermocouples located approximately 10 mm inside the cloaca and taped at 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). All measurements were taken in a non-invasive way so as to not interfere with the normal activities of lizards. The duration of the experiments was chosen considering the time that *L. bibronii* and several other liolaemids (*Liolaemus lineomaculatus*, *L. boulengeri*, *L. elongatus*, and *Liolaemus fitzingeri*, unpublished data) reach the preferred temperature during thermoregulation trials. The air temperatures of the laboratory at the beginning and at the end of the experiments were also recorded.

The mean T_{sel} 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_{sel} for each population and for the species. In order to measure the average degree to which *L. bibronii* experienced T_b outside the set-point range, the mean of the absolute values obtained from the deviations of T_b from T_{set} of each individual was calculated (individual deviation = d_b).

The index of the average thermal quality of a habitat from the organism's perspective (d_e) was calculated as the deviation of mean T_e for each population, with respect to the mean of minimum and maximum T_{set} for the population. The effectiveness of temperature regulation: $E = 1 - (\text{Mean } d_b / \text{Mean } d_e)$ was also calculated.

2.4. Comparison with other *Liolaemus*

Data from the literature on field and selected body temperature for 34 populations of 20 oviparous species and for 22 populations of 15 viviparous species of *Liolaemus* were used for comparison with *L. bibronii* (Table 1). We present data for more than one population per species when these populations represented sites differing in latitude or elevation. If the same T_b or T_{sel} was given for a range of latitudes and altitudes, the highest latitude and altitude was selected for the analyses. If latitude or elevation were not given for particular sites, these data were determined by searching the locality by Google Earth Plus. For mean, ranges, and analyses of tendencies in the thermal biology of the genus the weighted mean for each species was used. Since we did not find in the bibliography differences between sexes, reproductive state, or adult and juveniles, the overall mean for each population was used.

2.4. Statistical analyses

Normality and variance-homogeneity assumptions were tested using the Kolmogorov-Smirnov and Levene tests. When the assumptions were violated, non-parametric tests and median values were used. Means are given ± 1 SE.

3. Results

3.1. Climate from national meteorological service

The paired comparison of the monthly mean air temperatures and wind velocities were significantly higher in Perito Moreno than in Esquel, but the humidity did not show differences (Pair t -test, t_{air} temperature, $\gamma = -14.098$, $P < 0.001$, t_{wind} , $\gamma = -9.310$, $P < 0.001$; $t_{humidity}$, $\gamma = 1.19$, $P = 0.272$, Table 3).

3.2. Micro-environmental temperatures

Substrate temperature in the Sun (T_{ss}) was higher than the rest of the micro-environmental temperatures (T_{ssh} , T_a) in both sites, and was also higher than *L. bibronii* T_b from Esquel. In addition, in both sites the T_b was higher than the air temperature and the substrate temperature in the shade (Table 2).

The micro-environmental temperatures T_a , T_{ss} , and T_{ssh} were higher in Esquel than in Perito Moreno (Mann-Whitney,

Table 2

Comparisons among mean (paired t -test, t) or median (Mann-Whitney, T) of body (T_b) and micro-environmental temperatures (°C): substratum temperature in the Sun (T_{ss}) and in the shade (T_{ssh}), air temperature at 1 cm (T_a) within Esquel and Perito Moreno populations.

	T_{ss}	T_{ssh}	T_a	P
<i>Esquel</i>				
$T_{ss} = 33.48 \pm 0.89$ (73)				
$T_{ssh} = 22.15 \pm 0.65$ (69)	$t = 18.02^*$			< 0.005
$T_a = 24.97 \pm 0.59$ (87)	$T = 7926^*$	$T = 4554^*$		< 0.005
$T_b = 28.33 \pm 0.48$ (86)	$T = 7209^*$	$T = 3469^*$	$T = 8962^*$	< 0.001
<i>Perito Moreno</i>				
$T_{ss} = 29.57 \pm 1.07$ (47)				
$T_{ssh} = 19.99 \pm 0.50$ (47)	$T = 3090^*$			< 0.05
$T_a = 22.64 \pm 0.70$ (47)	$T = 1628^*$	$T = 1866^*$		< 0.05
$T_b = 27.7 \pm 0.56$ (47)	$T = 2131$	$t = 10.24^*$	$T = 1607^*$	= 0.05 < 0.001

Sample size (N) and significance $P < 0.05$ as * are indicated.

$Z_{T_{ssh}} = -2.96$, $N = 116$, $P < 0.0003$; $Z_{T_{ss}} = -2.89$, $N = 120$, $P < 0.004$; $Z_{T_a} = -2.54$, $N = 134$, $P < 0.01$), but wind velocity, humidity, and luminescence were lower in Esquel (Mann-Whitney, $Z_{wind} = -5.80$, $N = 133$, $P < 0.0001$; $Z_{humidity} = -7.07$, $N = 88$, $P < 0.0001$; $Z_{luminescence} = -2.20$, $N = 118$, $P < 0.024$).

3.3. Body temperature, size, and weight

In Esquel, the T_b ranged from 14 to 35.6 °C (Fig. 1) and showed a significant and positive relationship with T_a (stepwise regression, $F_{1,39} = 11.97$, $P < 0.001$, Fig. 2), but there was no relationship with SVL, BW, wind, luminescence, T_{ss} , T_{ssh} , or humidity ($P > 0.05$).

In the lizards from Perito Moreno, the T_b ranged from 19.8 to 35.4 °C (Fig. 1), and showed a significant and positive relationship with T_{ssh} and a negative relationship with wind (stepwise regression, $F_{T_{ssh} \ 1,44} = 13.94$, $P < 0.001$; $F_{wind \ 2,44} = 16.16$, $P < 0.001$), but there was no relationship with SVL, BW, luminescence, T_{ss} , or humidity ($P > 0.05$).

There were no significant differences between T_b values of lizards from Esquel and Perito Moreno (Table 3) including date of capture as the only significant covariable in the model. The mean T_b values of ovigerous and non-ovigerous females of

both populations were compared and were not significantly different (t -test, $t_{18} = -0.08$, $P = 0.9$), nor were T_b values between adult males and non-ovigerous females including date of capture as the only significant covariable in the model (ANCOVA, $F_{1,44} = 0.007$, $P = 0.9$).

3.4. Operative temperatures and selected body temperature

The T_e from Esquel (range = 7.7–43 °C, $N = 106$) was higher than in Perito Moreno (13.4–37.4 °C, $N = 83$, Table 3).

In Esquel the absolute T_{sel} ranged from 19.54 to 38.9 °C. Mean T_{sel} values were not significantly different among non-ovigerous, ovigerous females, males or juveniles (ANCOVA, $F_{3, \ 46} = 1.40$, $P = 0.4$), including air temperature in the laboratory at the end of the experiment as the only significant covariable. T_b was significantly lower than mean T_{sel} (pair t -test, $t_{45} = -7.42$, $P < 0.001$). In the individuals from Perito Moreno, the absolute T_{sel} ranged from 26.6 to 38.5 °C and mean T_{sel} for adult males was higher than for adult females (non-ovigerous; ANOVA, $F_{3,47} = 3.49$, $P < 0.05$). The T_b was significantly lower than mean T_{sel} (pair t -test, $t_{46} = -9.36$, $P < 0.001$). There was no significant difference between populations in T_{sel} including SVL as covariate (Table 3).

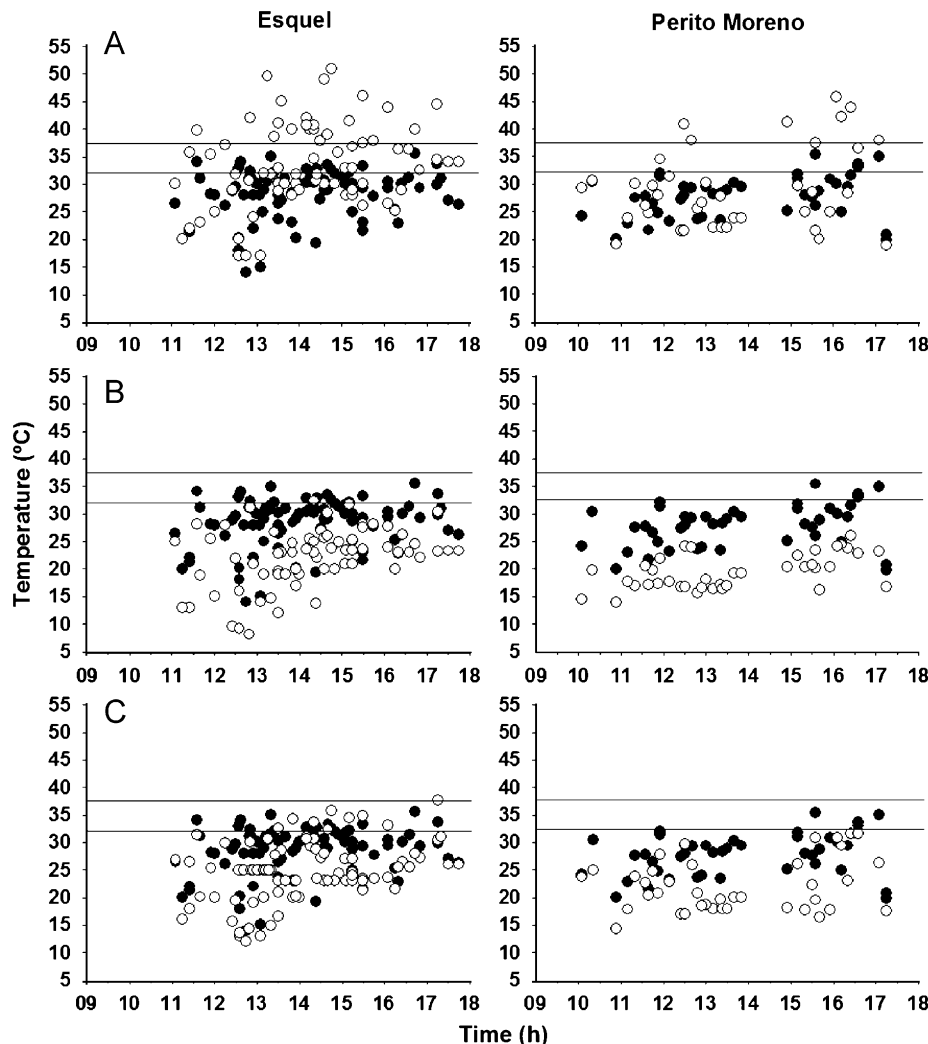


Fig. 1. Body temperatures (black dots) and micro-environmental temperatures (white circles): substrate in the sun (T_{ss} , panel A), in the shade (T_{ssh} , panel B) and air (T_a , panel C) temperature vs. time (h) of *Liolaemus bibronii* in two populations, Esquel and Perito Moreno. The lines indicate the lower and upper set-points of the selected body temperature (T_{sel}).

3.5. Effectiveness of temperature regulation

In Esquel, the minimum and the maximum mean T_{set} was $31.9 \pm 1^\circ\text{C}$ and $37.70 \pm 0.36^\circ\text{C}$, respectively ($N = 46$, Fig. 2). Most of the T_b 's (74%; $N = 34$) were lower than the minimum T_{set} , the 24% ($N = 11$) were included in the set-point range, and 2% ($N = 1$) were higher than the maximum T_{set} .

In Perito Moreno, the minimum and the maximum mean T_{set} was $32.3 \pm 0.89^\circ\text{C}$ and $37.7 \pm 0.20^\circ\text{C}$, respectively ($N = 47$, Fig. 2). Again, most of the T_b 's (79%) were lower ($N = 37$) than the minimum T_{set} ; 21% ($N = 10$) were included in the set-point range and none were above it. The index of d_e was significantly higher in Perito Moreno than in Esquel but the d_b did not show differences between populations (Table 3).

3.6. Comparison with other Liolaemus

There were not significant differences in T_b or T_{sel} between oviparous and viviparous populations described in Table 1 (ANOVA, $F_{T_b, 1, 31} = 1.58$, $P = 0.22$; $F_{T_{sel}, 1, 15} = 0.51$, $P = 0.49$). Neither were significant differences between T_b and T_{sel} of oviparous and viviparous lizards (paired t -test, $t_{12} = -2.10$, $P > 0.05$). In consequence, both reproductive modes were joined for subsequent analyses.

There was a significant relationship between T_b of the populations and latitude and altitude (forward regression, $F_{2, 47} = 7.08$, $P < 0.002$; $y = 38.94 - 0.14 \times \text{latitude} - 0.001 \times \text{altitude}$), but there were not a significant relationship between T_{sel} of the populations and latitude (correlation, $r^2 = 0.09$, $P > 0.61$, $N = 28$) or altitude ($r^2 = 0.26$, $P > 0.18$, $N = 28$).

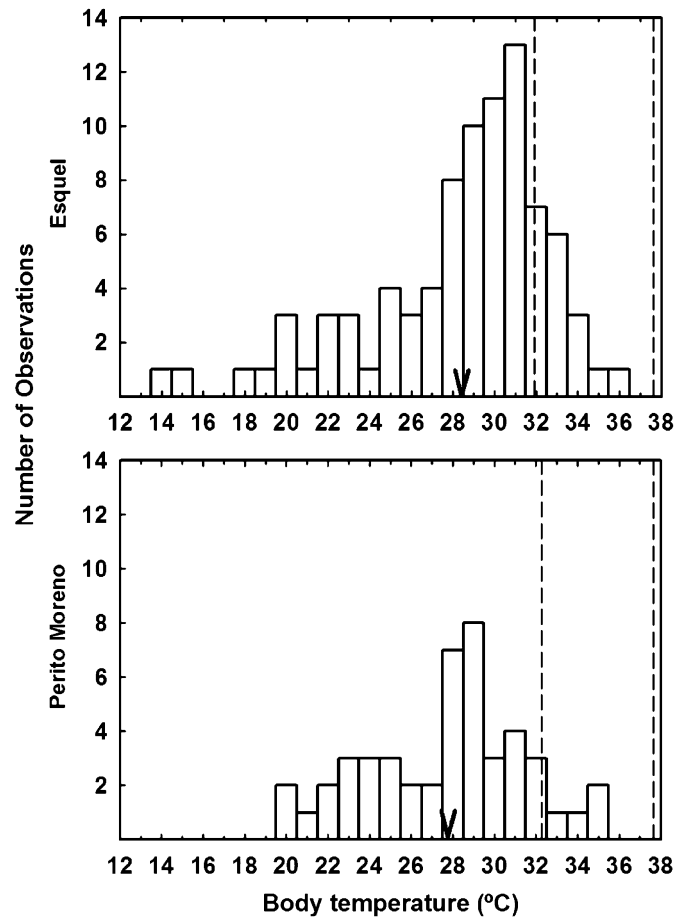


Fig. 2. Distribution of body temperatures (T_b) at capture of *Liolaemus bibronii* (bars) in Esquel and Perito Moreno. The arrows show the mean T_b and the dashed lines indicate the lower and upper set-points of the selected body temperature (T_{set}).

Table 3

Comparisons between Esquel and Perito Moreno in mean (ANCOVA, F ; Pair t -test, t) or median (Mann–Whitney, T) selected body temperatures (T_{sel} , $^\circ\text{C}$) and indices *sensu* Hertz et al. (1993): operative temperature (T_e), absolute values obtained from the deviations of T_b from T_{set} of each individual (d_b), index of the average thermal quality of an habitat (d_e) and the effectiveness of temperature regulation (E).

Locality	T	Wind	H	T_b	T_{sel}	T_e	d_b	d_e	E
Esquel	$10.33 \pm 3.48(8)$	$22.68 \pm 3.51(8)$	$53.28 \pm 5.96(8)$	$28.33 \pm 0.48(86)$	$34.08 \pm 0.56(46)$	$22.56 \pm 0.76(107)$	$4.76 \pm 0.67(46)$	8.42	0.44
Perito Moreno	$11.77 \pm 3.5(8)$	$30.35 \pm 5.7(8)$	$56.36 \pm 8.82(8)$	$27.7 \pm 0.56(47)$	$34.08 \pm 0.56(46)$	$20.03 \pm 0.56(83)$	$5.98 \pm 0.67(47)$	10.87	0.45
Comparisons	$t_7 = -14.10^*$	$t_7 = -9.31^*$	$t_7 = 1.19$	$F_{1, 133} = 1.40$	$F_{1, 93} = 0.04$	$T = 7179^*$	$T = 2007.5$		

Temperature (T), humidity (H , %), and wind velocity (wind, $\text{Km}^* \text{h}^{-1}$) obtained from the National Meteorological Service, Argentinean Air Force, sample size (N) and significance $P < 0.05$ as * are indicated.

4. Discussion

The field body temperature of *L. bibronii* in both populations (28°C) was the lowest of the oviparous *Liolaemus* species (29 – 37°C , Table 1) and lower than in most lizards (34 – 36°C ; Andrews et al., 1999). Nevertheless, the T_b values were similar to the southernmost viviparous lizards in the world, *Liolaemus magellanicus* (27°C ; Table 1). Instead, the selected body temperatures (34°C) were similar to the rest of the liolaemids (34 – 36°C ; Labra, 1998 and 30 – 37°C this study; Table 1), and significantly higher than the body temperature in the field. There were no differences between the field and selected body temperatures between populations at different latitude. However, the indexes obtained by the comparison among operative and field body with the selected body temperatures showed that *L. bibronii* is a moderate thermoregulator living under thermal–environmental constraints in both populations, but especially at the higher-latitude site.

Ectotherms living at high latitudes and altitudes often exhibit lower and more variable activity body temperatures, and they thermoregulate less precisely than conspecific or congeneric populations living at lower elevations or latitudes (Brattstrom, 1965; Hertz and Nevo, 1981; Vial, 1984; Crowley, 1985; Bauwens et al., 1990). This is the case of the populations *Anolis* lizards from Puerto Rico in which species living at higher altitude have lower T_b than the populations at lower altitude (Hertz, 1992). However, there is a complex interplay among biotic and abiotic factors resulting in different responses among ectotherms (Ibargüengoytia et al., 2008). *L. bibronii* populations showed similar field body temperatures even when in Perito Moreno there are lower micro-environmental and operative temperatures, and a greater wind velocity suggesting different behavioural or physiological mechanisms to compensate for these environmental constraints. Accordingly, *L. bibronii* populations differed in the way that T_b related to the micro-environmental and operative temperatures (T_e) evidencing different behaviours for heat acquisition.

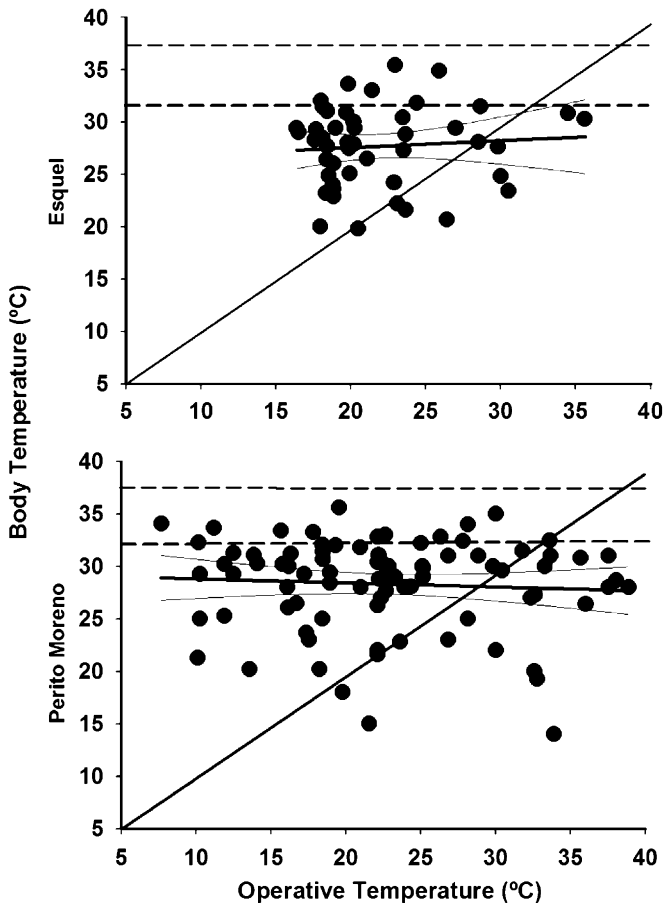


Fig. 3. Body vs. operative temperatures in Esquel and Perito Moreno. The lower and upper set-points of the selected body temperature (dashed lines) and $y = x$ relationship (solid lines). The regression and 95% confidence intervals are indicated.

Various behavioural mechanisms can alter rates of heat exchange and produce T_b 's that differ from a random sample of T_e 's like modulation of activity times, the selection of thermally appropriate microhabitats, and postural adjustments (Pearson, 1954; Hertz and Huey 1981; Van Damme et al., 1989). When environmental temperatures are low, basking behaviour is more frequent and has an important effect on T_b , especially when T_e is low (Van Damme et al., 1987; Bauwens et al., 1996). In both populations of *L. bibronii* the operative temperatures (T_e) were below the minimum set-point range (T_{set}), but this was more evident in Perito Moreno (Fig. 3). In Esquel, even when ground temperatures were greater than in Perito Moreno, the T_b was lower than the substratum temperature in the Sun (T_{ss}) suggesting an heliothermic behaviour. In contrast, in Perito Moreno the body temperature follows the substrate, showing that this population may use predominantly thigmothermy (Fig. 2). The maintenance of similar T_b 's at different latitudes suggest that lizards from Perito Moreno have to spend more time to find appropriate micro-environments for thermoregulation, which in turn will result in a decrement in the time available to feed, and reproduce, as well as causing a greater exposure to predators (Avery, 1976; Huey and Slatkin, 1976; Hertz and Huey, 1981).

Accordingly, the average degree to which *L. bibronii* experienced T_b outside the set-point range of selected body temperature in the laboratory (d_b), was high in the two populations but particularly at the higher latitude ($d_{bEsquel} = 4.76$; $d_{bP. Moreno} = 5.98$). In contrast, the viviparous *L. elongatus* and

Phymaturus tenebrosus that inhabit rock promontories in the Patagonian steppe sympatric in part of their distribution with *L. bibronii*, show a much lower d_b (1.94 and 2.29, respectively). This difference results from a combination of a higher field body (30.27 and 28.95 °C, respectively) and a lower selected body temperatures (mean 29.9 and 31.13 °C) compared with *L. bibronii* (28 and 34 °C). These differences may be caused by the interaction of different factors. *L. elongatus* and *P. tenebrosus* populations studied were at lower latitudes (41.5 °S), they are larger viviparous lizards and they use the thermal inertia of the rocks. Moreover, the low T_{sel} in these species has been attributed to the advantages of maintaining a stable body temperature during pregnancy, a trait typical of viviparous lizards under cold environments (Ibargüengoytia and Cussac, 2002; Ibargüengoytia, 2005) exemplified by the scincid lizards, *Bassiana duperreyi* and *Eulamprus heatwolei* (Shine, 2004).

In addition, we found differences between the operative temperatures (T_e) and the set-point range ($d_e = 8.42$ – 10.87 °C) showing that *L. bibronii* must thermoregulate carefully to achieve the selected body temperature in the laboratory. This is especially true in Perito Moreno, where the habitat has a significantly lower average thermal quality (Table 3). The difference found for *Liolaemus* at different latitude, shows a parallel with the studies of three *Anolis* populations in an altitudinal gradient but at similar latitude in Puerto Rico. The populations at high elevations experience a scarcity of microclimatic conditions ($d_e = 9.2$ °C; 1130–1150 m) while at lower altitudes there is a greater variety ($d_e = 0.07$ – 5.3 °C; 5–210 m; Hertz et al., 1993).

The comparison between the average degree to which *L. bibronii* experienced T_b outside the set-point range (d_b) and the corresponding d_e , in both populations, indicates an active selection of the microhabitats they used and confirms the presence of thermoregulatory behaviours in *L. bibronii* (sensu Hertz et al., 1993). The effectiveness of temperature regulation is similar in the two populations ($E_{Esquel} = 0.44$, $E_{P. Moreno} = 0.45$) and, compared to other species that thermoregulate effectively—such as *Podarcis hispanica atrata* ($E = 0.95$, Bauwens et al., 1996) and the thermoconformer *Anolis gundlachi* (from $E = 0$ – 0.21 , Hertz et al., 1993)—*L. bibronii* could be considered a moderately effective thermoregulator, as is *Anolis cristatellus* populations at high elevations ($E = 0.46$ – 0.50 , Hertz et al., 1993).

The thermal factors play a major role in the distribution of reptiles by effects upon activity and hence the ability to obtain energy to grow and reproduce (Porter and Tracy, 1983). The versatile genus *Liolaemus* has radiated widely, using habitats differing markedly in physiognomy, altitude, and therefore in exposure to climatic factors (Fuentes and Jaksic, 1979). The present review shows that *Liolaemus* exhibits high interspecific variability in T_b , which decreases with greater latitude and altitude, and this is evidenced by restrictions on thermoregulatory mechanisms meant to cope with environmental conditions. In contrast, T_{sel} does not, suggesting that the preferred body temperature is a conservative parameter in the genus in agreement with other studies (Valencia and Jaksic, 1981; Marquet et al., 1989; Labra, 1998). However, we fail to find differences between T_b and T_{sel} in a paired test, probably because the comparative data of T_b and the corresponding T_{sel} of *Liolaemus* are scarce (Table 1).

The relationship between the physical environments at potential nest sites, reproductive characteristics of egg laying, delayed oviposition, and viviparity have been found to be more relevant in the distributional limits of the *Liolaemus* than have been the effects of low temperatures at high elevations, *per se* (Carothers et al., 1997). This is the case for 10 species of *Liolaemus* studied along an altitudinal transect in Chile, which did not show differences in the body temperatures, but none of the oviparous species (such as *L. chiliensis*, *L. fuscus*, *L. lemniscatus*, *L. monticola*,

L. nitidus, and *L. tenuis*) occur above 2400 m elevation. In contrast, all of those species whose ranges extend beyond this limit (*L. altissimus*, *L. leopardinus*, *L. nigroviridis*, and *L. schroederi*) are viviparous. These species might easily survive the thermal environment but apparently cannot successfully reproduce likely due to the effects of the cold soil decreasing incubation periods and developmental rates compared to those apparently required for oviparity (Carothers et al., 1997).

The oviparous *L. bibronii*, living at latitudes up to 50°S showed low body temperatures comparable to those observed in *L. magellanicus*, a viviparous lizard living as far south as 53°S. Low environmental temperatures could result in prolonged incubation periods, and consequently, severe reductions in the survival of eggs and hatchlings (Strijbosch et al., 1980), but timing in the development of offspring could be adjusted by thermoregulatory behaviour of the mother, an option afforded by viviparity. In contrast, with oviparity, eggs raised at low temperatures may have delayed hatching and may not hatch before the onset of winter resulting in high egg mortality (Andrews, 2000). This is also the case of *Dipsosaurus dorsalis* in which the geographic range is limited by climatic constraints on egg incubation (Muth, 1980). In the ovigerous females of *Liolaemus* species, the temperature that eggs experience in the nest would be the limiting factor for development, especially in *L. bibronii*, a species whose nests would likely experience a mean air temperature of 12 °C (at 43–46°S latitude) or lower at the southern extent of its distribution (50°S). *Liolaemus* at high latitudes in South America have a short activity season, and following emergence from hibernation, earlier oviposition dates and earlier hatch dates would be required for better survival, rates of maturation, and subsequent reproduction (see Shuter and Post, 1990). The low field body temperature compared with the selected body temperature and the decline of the thermal quality of the environments for thermoregulation with increasing latitude for one of the southernmost lizards provides evidence of high thermal restraints especially for oviparous lizards in Patagonia Argentina.

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