# Selected body temperatures of seven species of Chilean *Liolaemus* lizards

# Temperaturas corporales seleccionadas de siete especies de lagartos Liolaemus chilenos

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### ABSTRACT

Selected body temperature (Tsel) was determined for seven species of *Liolaemus* lizards, under laboratory conditions. The objectives were to establish if there are intra- and interspecific differences in Tsel, and if these differences would be correlated with the thermal environments naturally experienced by the lizards. To analyze intraspecific differences in Tsel, I collected individuals of each species from different localities or during different months of the year. Lizards were placed in a thermal gradient without biotic or abiotic factors that would prevent thermoregulation, and their Tsels were recorded. No intraspecific differences were observed in Tsel for six of the seven species studied. However, there were interspecific differences in Tsel, and these were positively correlated with the minimum air temperature recorded during the capture period of lizards. It is not clear if this correlation actually represent an adaptive response because this argument depends on level of analysis. At the intraspecific level, lizards did not appear to exhibit an adaptive response to thermal conditions, whereas at the interspecific level lizards appeared to be responding to thermal factors in their physical environment. Results suggest that different factors are involved in the thermal biology of the species studied, at macro and microevolutionary scales. Further studies in this area may help to understand the evolution of the thermal biology of *Liolaemus* species.

Key words: adaptive response, elevation, selected body temperatures, lizards, Liolaemus, thermoregulation.

### RESUMEN

Las temperaturas corporales seleccionadas (Tsel) de siete especies de lagartos *Liolaemus*, fueron determinadas en condiciones de laboratorio. Los objetivos fueron establecer si existen diferencias intra e interespecíficas en Tsel, y si estas diferencias estarían correlacionadas con los ambientes térmicos naturales experimentados por estos lagartos. Para analizar diferencias intraespecíficas se colectaron individuos de cada especie provenientes de diferentes localidades o de distintos meses del año. Los lagartos fueron puestos en un gradiente térmicos in factores bióticos o abióticos que pudieran obstaculizar la termorregulación, y sus Tsel fueron registradas. No se observaron diferencias intraespecíficas en Tsel, en seis de las siete especies estudiadas. Sin embargo, existieron diferencias interespecíficas en Tsel, y estos valores se correlacionaron positivamente con la temperatura mínima registrada durante el período de captura de los lagartos. No esta claro si esta correlación realmente representa una respuesta adaptativa, debido a que los argumentos dependen del nivel de análisis. A nivel intraespecífico, los lagartos parecieran no exhibir una respuesta adaptativa a las condiciones térmicas, mientras que a nivel interespecífico los lagartos parecieran estar respondiendo a los factores térmicos de sus ambientes físicos. Los resultados sugieren que diferentes factores están involucrados en la biología térmica de las especies estudiadas, a escalas micro y microevolutivas. Estudios en esta área de pueden ayudar a entender la evolución de la biología térmica de especies de *Liolaemus*.

Palabras clave: respuesta adaptativa, elevación, temperaturas corporales seleccionadas, lagartos, Liolaemus, termorregulación.

### INTRODUCTION

Research concerning how lizards regulate their body temperature has been the focus of many studies (for reviews see Huey 1982, Espinoza & Tracy 1997). This is partially due to the important influence temperature has over most aspects of a lizard's life including: ecology, physiology and behavior (i.e., Bennett 1980, Spotila & Standora

1985, Espinoza & Tracy 1997). Importantly, lizards may select or be constrained to operate at different body temperatures, because biotic and/or abiotic factors can prevent thermoregulation (Huey & Slatkin 1976). These factors are called constraints for thermoregulation. Perhaps as a consequence, body temperatures measured under field conditions (FBT) tend to be variable in different populations of a species, or within a population in different seasons of the year (i.e. Hertz & Huey 1981, Christian et al. 1983, Christian & Tracy 1985, Grant & Dunham 1988, 1990, Bauwens et al. 1990, Hertz 1992, Christian & Weavers 1996). Therefore, the body temperature that a lizard voluntarily selects in a laboratory thermal gradient -the selected body temperature Tsel (Pough & Gans 1982)-, provides a reasonable estimate of what a lizard would select in the absence of constraints for thermoregulation.

The flexibility of lizards' thermal physiology has been a matter of debate (i.e., Hertz et al. 1983, Crowley 1985, Van Damme et al. 1990). An important component is whether or not Tsel changes as function of the environment thermal conditions. Simply put, can lizards alter their Tsel as an adaptive response or is this trait evolutionary "hard-wired"?. Comparisons across lizards of the same genus indicate both, that congeners may have similar or different Tsel (i.e. Bennett & John-Alder 1986, Christian & Weavers 1996). At the intraspecific level, studies have reported that there exist differences in Tsel and FBT among and within populations for some lizards species. In these studies, both Tsel and FBT are lower in lizards that naturally experience lower air temperatures (Mueller 1969, Mayhew & Weintraub 1970, Patterson & Davies 1978, Van Damme et al. 1986, 1987). However, other studies have shown that conspecifics exposed to different thermal conditions exhibit similar Tsel, in spite of differences in FBT (Huey & Webster 1976, Van Damme et al. 1989, 1990, Báez & Cortés 1990). Thus, it is appear that the relationship

between Tsel and FBT is species specific, and generalizations to unstudied taxa would be inappropriate.

With more than 150 species (Etheridge 1995) the lizard genus Liolaemus (Tropiduridae), is very diverse in arid and semiarid South America, with more than 60 species broadly distributed in Chile (Veloso & Navarro 1988). Some species have vast geographic distributions, and thus are exposed to a wide range of climatic conditions. Such species are suitable to study if their Tsel change under different climatic conditions. The mean Tsel of the genus is around the 34-36 °C (Valencia & Jaksic 1981, Marquet et al. 1989, Cortés et al. 1992, Nuñez 1996) and results obtained for L. nitidus (Valencia & Jaksic 1981, Cortés et al. 1992), indicate that this species has intraspecific variation in Tsel, which may be interpreted as an adaptive response. The FBT values for Chilean Liolaemus seem to depend on the elevational and latitudinal distribution of the species (Fuentes & Jaksic 1981, Valencia & Jaksic 1981, Jaksic & Schwenk 1983, Marquet et al. 1989, Cortés et al. 1992, Nuñez 1996, Carothers et al. 1997, Carothers et al. 1998). These studies suggest that some Liolaemus might respond adaptively, changing their body temperatures, as function of the ambient thermal conditions. In order to further test this prediction, I measured Tsel in seven species of Liolaemus. I first examined intraspecific differences in Tsel by measuring populations from different thermal environments. Next, I determined if there were interspecific differences in Tsel, or if the species I studied had Tsel near 34-36° C, like other members of the genus. Finally, I determined if Tsel values within and among species, were related to the thermal conditions the animals experienced during their period of capture.

### MATERIALS AND METHODS

Six of the seven *Liolaemus* species studied were from Mediterranean environments (Di

Castri & Hajek 1976) and one, *L. fabiani*, was from the Atacama desert (Atacama Salt flat). Table 1 lists these species and the geographic distribution of the different populations examined. This table also includes air temperatures for the month in which the animals were captured. These values only constitute a rough estimate of

### TABLE 1

# List of the *Liolaemus* species studied and collection localities. The month, locality (Latitude °S; Longitude AW) and the elevation (m) of each population, are indicated. Mean maximum (Max) and minimum (Min) temperatures, the populations experienced at that capture locality.

Lista de las especies de *Liolaemus* estudiadas y las localidades de colecta. Se indican el mes, localidad (Latitud °S; Longuitud °W) y elevación (m) de cada población. Temperaturas máximas (Max) y mínimas (Min), que experimentaron las poblaciones en el lugar de captura.

Species	Population	Month	Locality	(m)	Elevation Max	Temperature °C <sup>(1)</sup> Min
L. bellii	Farellones	Jan.	33°20';70°19'	2 300	19.6	8.4 <sub>a</sub>
	Farellones	Oct.	33°20';70°19'	2 300	11.7	$2.5_{a}^{-}$
	Los Vientos	Jan.	33°06';70°24'	3 200	22.1	$9.1_{b}^{(2)}$
	El Maule	Jan.	36°04';70°30'	2 100	17.5	$6.5^{(2)}_{c}$
L. fabiani	Atacama	Jan.	26°46':68°14'	2 300	28.5	8.1 <sub>d</sub>
	Salt Flat	May	26°46';68°14'	2 300	22.1	1.8 <sub>d</sub>
		Aug.	26°46';68°14'	2 300	22.0	$0.4_{d}$
		Nov.	26°46';68°14'	2 300	27.3	5.6 <sub>d</sub>
L. lemniscatus	San Carlos	Jan.	33°23';70°30'	950	27.8	10.6 <sub>e</sub>
	Santiago	Oct.	33°27';70°42'	600	24.6	7.3 <sub>c</sub>
	C. Barriga	Oct.	33°32';70°57'	500	21.0	5.9 <sub>f</sub>
L. nitidus	Curva 20 <sup>(3)</sup>	Mar.	33°21';70°19'	1 985	25.3	8.3 <sub>e</sub>
	Fray Jorge	Oct.	30°39';71°40'	200	23.8	8.6 <sub>c</sub>
L. p. pictus	Osorno	Oct.	41°06';72°30'	1 000	16.0	4.9 <sub>a</sub>
L. p. pictus	Vilches	Oct.	35°36';71°05'	1 1 50	15.0	3.4 <sub>g</sub>
L. p. chiloensis	Chiloé	Feb.	42°24';73°47'	200	20.1	9.6 <sub>a</sub>
L. schroederi	Vilches	Oct.	35°36';71°05'	1 1 50	15.0	3.4 <sub>e</sub>
	Farellones	Oct.	33°20';70°19'	2 300	11.7	3.4 <sub>g</sub> 2.5 <sub>a</sub>
L. t. tenuis	El Pangue	Jan.	33°17';71°11'	600	27.2	13.8 <sub>f</sub>
L. t. punctatissimus	Los Angeles	Mar.	37°28';72°21'	130	24.7	9.5 <sub>f</sub>

(1) Source of information: a = Dirección Meteorológica de Chile. B = Rodríquez (1971), data from La Invernada  $(35^{\circ}44'S;70^{\circ}47'W; 1 325 m)$ . c = Ulriksen et al. (1979), data from Cristo Redentor  $(32^{\circ}50'S;70^{\circ}04'W; 3850 m)$ . d = Ramírez (1971), data from San Pedro de Atacama (22°55'S;68°12'W; 2400 m). e = Anuario Meteorológico de Chile (1989). f = Hajek and Di Castri (1975). g = Anuario Agrometeorológico de Chile (1992).

Fuentes de información: a = Dirección Meteorológica de Chile. b = Rodríquez (1971), datos provenientes de La Invernada  $(35^{\circ}44'S;70^{\circ}47'W; 1\ 325\ m)$ . c = Ulriksen et al. (1979), datos provenientes de Cristo Redentor  $(32^{\circ}50'S;70^{\circ}04'W; 3850\ m)$ . d = Ramírez (1971), datos provenientes de San Pedro de Atacama (22°55'S;68°12'W; 2400 m). e = Anuario Meteorológico de Chile (1989). f = Hajek and Di Castri (1975). g = Anuario Agrometeorológico de Chile (1992).

(2) Data from the literature were transformed to obtain an estimation of the thermal conditions where lizards were collected. This was done considering that by each 100 m of elevation, air temperature decreases  $0.47 \text{ }^{\circ}\text{C}$  (Rodríquez 1971).

Los datos de la literatura fueron transformados para obtener una estimación de las condiciones térmicas donde los lagartos fueron colectados. Se considero que por cada 100 m de elevación, la temperatura ambiente disminuye 0.47 °C (Rodríquez 1971).

(3) Site located about 25 Km NW in the road to Farellones.

Sitio ubicado aproximadamente a 25 Km NE en el camino a Farellones.

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the air temperature to which the lizards were exposed because they were obtained from the literature. Hence these records do not correspond to the air temperatures of the microhabitats used by individual animals.

The six *Liolaemus* species from Mediterranean habitats were captured from October to March of 1988 and 1989, whereas L. fabiani was captured over the four seasons of the year (1995-1996). Lizards were transported to the laboratory and kept in terraria (91 x 37 x 21 cm) with a photoperiod of 11L:13D. To determine thermal instead of light selection, the whole terraria was illuminated by an incandescent lamp, and as a source of heat a 250 W infrared lamp was placed above one end of the terrarium. This set up allowed to establish a thermal gradient ranging from 19  $\pm$  0.2 °C (SE) to 55.3  $\pm$  2.1 °C. Water was provided ad libitum and food (larvae and adults of Tenebrio molitor), was provided one day before the beginning of the experiments. Measurements were recorded for no longer than two weeks after capture to avoid acclimation to laboratory conditions.

Data were gathered during the light phase, for three to four consecutive days, following one day of acclimation to the terrarium. Only adults were used and no gender distinctions were made. Body temperature (cloacal) of each lizard was obtained hourly using a copper-constantan type T thermocouple and a Sensortek thermometer model Bat-12 ( $\pm$  0.1 °C). Animals were caught by hand and their temperatures were recorded within one minute after capture. To minimize heat transfer from the hand to the lizards, they were seized by the neck. Mean Tsel values of each animal were used to calculate the populational or monthly Tsel. For some populations, it was possible to obtain FBT for individuals active during sunny days, in the same period in which Tsels were measured. FBT were recorded within one minute after capture a lizard, inserting in the cloaca a quick-reading Schultheis thermometer. Only adults were measured.

Wilcoxon test or Kruskal-Wallis test with an a posteriori multiple range test,

were used because inspection of the data found that Tsel values were not normally distributed (Zar 1984). Spearman rank correlations were used to evaluate relationships between Tsel and ambient temperature. Tsel data pooled by species were normally distributed. An one-way ANOVA with an a-posteriori Tukey's test for multiple comparisons was used to perform interspecific comparisons in Tsel (Zar 1984).

### RESULTS

Table 2 shows thermal values obtained for the populations of *Liolaemus* studied. The desert inhabitant, L. fabiani did not exhibit seasonal differences in Tsel. In addition, its seasonal Tsel was not correlated with the maximum or minimum ambient air temperature naturally experienced by lizards ( $r_s = 0.12$ , p = 0.67, n = 15, for both relationship). With the exception of L. bellii, species from the Mediterranean environments did not exhibit intraspecific differences in Tsel (see Table 2). In L. bellii a positive correlation was found between its Tsel and the maximum and minimum air temperature ( $r_s = 0.63$ , p< 0.05, n = 26, for both relationships).

The differences in monthly FBT obtained for L. bellii from the Farellones population (January-October) were marginally significant (Z= 2.41, p= 0.06). Comparisons between Tsel and FBT recorded in the same month for this species at this locality were statistically different (Z = 2.94, p = 0.003 and Z = 2.41, p = 0.02,for January and October, respectively). In both cases, FBT was lower than Tsel. Similar trends were obtained for those species for which records of FBT were available (see Table 2, L. nitidus: Z = 2.01, p = 0.04; L. pictus: Z = 2.44, p = 0.01 and *L.* schroederi: Z = 1.94, p = 0.049).

Differences in patterns of daily Tsel during the light phase for populations of *L. bellii* were evident, particularly when

### TABLE 2

Mean values for selected body temperatures (Tsel) and field body temperatures (FBT) in °C, n = sample size of *Liolaemus* species studied. Below thermal values of the species, test statistic and the probability (P) values of the intraspecific comparisons; Mean = Average Tsel value of the species. Common subscripts in a column denote values that do not differ significantly. Values are mean ± standard deviation.

Valores promedios de las temperaturas corporales seleccionadas (Tsel) y las temperaturas corporales de actividad en terreno (FBT) en °C, n = tamaño muestral de las especies de *Liolaemus* estudiadas. Bajo los valores térmicos de las especies, los valores de las pruebas estadísticas y la probabilidad (P), de las comparaciones intraespecíficas. Subscriptos iguales en una columna indican valores que no difieren significativamente. Los valores se entregan como promedio ± desviación estándar.

Species		Population	Month	Tsel	n	FBT	n
L. bellii		Farellones	Jan.	$36.1 \pm 0.4_{a}$	8	$34.2 \pm 1.1$	9
		Farellones	Oct.	$34.4 \pm 1.3$	7	$32.7 \pm 2.01$	34
		Los Vientos	Jan.	$36.0 \pm 0.7$	5		
		El Maule	Jan.	$33.9 \pm 1.2^{\circ}_{h}$	6		
	Test			$Z = 15.46^{\circ}$		Z = 1.84	
	P-value			P = 0.002		P = 0.06	
	Mean			$35.1 \pm 1.0$	26		
L. fabiani		Atacama	Jan.	$33.3 \pm 1.0$	4		
		Salt Flat	May	$32.1 \pm 0.9$	3		
			Aug.	$33.6 \pm 1.0$	2		
			Nov.	$32.3 \pm 1.2$	6		
	Test			Z = 4.12			
	P- value			P = 0.25			
	Mean			$32.7 \pm 1.1$	15		
L. lemniscatus		San Carlos	Jan.	$34.3 \pm 1.5$	6		
		Santiago	Oct.	$35.8 \pm 0.8$	5		
		C. Barriga	Oct.	$35.5 \pm 0.8$	8		
	Test			Z = 3.49			
	P-value			P = 0.18			
	Mean			$35.2 \pm 1.2$	19		
L. nitidus		Curva 20	Mar.	$36.2 \pm 1.0$	7	$34.9 \pm 1.0$	6
		Fray Jorge	Oct.	$35.0 \pm 1.3$	5		
	Test			Z = 1.21			
	P-value			P = 0.22			
	Mean			$35.7 \pm 1.2$	12		
L. p. pictus		Osorno	Oct.	$35.4 \pm 0.7$	6		
L. p. pictus		Vilches	Oct.	$33.8 \pm 1.7$	13	$31.8 \pm 2.5$	16
L. p. chiloensis	_	Chiloé	Feb.	$34.4 \pm 1.8$	5		
	Test			Z = 5.04			
	P- value			$\mathbf{P} = 0.08$			
	Mean			$34.3 \pm 1.6$	24		
L. schroederi		Vilches	Oct.	$34.6 \pm 1.5$	6	$31.6 \pm 3.8$	10
	-	Farellones	Oct.	$35.5 \pm 0.6$	3		
	Test			Z = 0.65			
	P- value			P = 0.52	0		
	Mean			$34.9 \pm 1.3$	9		
L. t. tenuis L. t. punctatisismus		El Pangue	Jan.	$37.2 \pm 0.1$	4		
		Los Angeles	Mar.	$36.7 \pm 1.1$	3		
	Test			Z = 0.52			
	P- value			P = 0.60			
	Mean			$37.0 \pm 0.7$	7		

(1) Body temperatures obtained from the La Parva population (Bozinovic, Novoa and Veloso, pers. comm.), located at 20 km NE of Farellones (33°35'S; 70°32'W; 2 800 m).

Temperaturas corporales obtenidas de la población de la Parva (Bozinovic, Novoa and Veloso, pers. comm.), localizada a 20 km NE de Farellones (33°35'S; 70°32'W; 2 800 m).

the seasonal patterns obtained from Farellones population were compared (Fig.1). During January (summer), body temperatures were higher with less variance than in October (spring). A different pattern of daily Tsel is observed in *L. fabiani*. Tsel is attained gradually between 0900 and 1200 hr (Fig.1), thereafter, and between 1300 and 1700 h, Tsel was maintained at about 33 °C.

There were considerable differences between the mean Tsel among some of the species studied ( $F_{(6,105)} = 11.82$ , p = 0.0001, ANOVA). The a-posteriori Tukey tests revealed that *L. fabiani* had significantly lower Tsel than the other species (with p values between 0.0002 to 0.016). *Liolaemus pictus* also had a significantly lower Tsel than did *L. tenuis* (p = 0.004). Collectively, mean Tsel values of the species were positively correlated with the mean minimum air temperature ( $r_s$ 

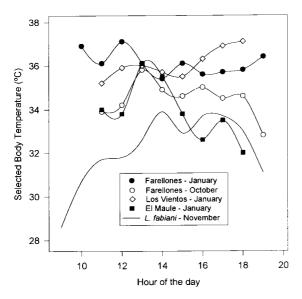


Fig. 1: Mean selected body temperatures (Tsel) of *Liolaemus bellii* populations during the light phase as a function of time. Data points represent the average of all lizards measured from each population. The Tsel of *L. fabiani* measured in November is also included.

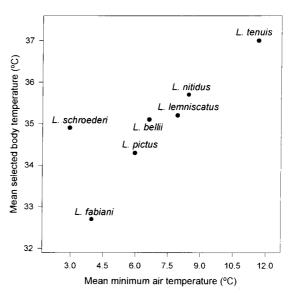
Temperaturas corporales seleccionadas (Tsel) promedios de *Liolaemus bellii* medidas durante la fase lumínica, en función de tiempo. Los puntos representan el promedio de todos los lagartos medidos en cada población. Se incluye además Tsel de *L. fabiani*, medidas en noviembre.

= 0.89, p=0.007, n=7; see Fig. 2), and with mean air temperature ( $r_s = 0.75$ , p = 0.05, n = 7). However, no correlation was found between mean Tsel values and mean maximum air temperature ( $r_s = 0.39$ , p = 0.38, n=7) or with the range between mean maximum and minimum air temperature at which lizards were exposed during capture ( $r_s = 0.071$ , p = 0.88, n = 7).

### DISCUSSION

### Intraspecific Comparisons of Tsel

Six of the seven species of *Liolaemus* studied did not exhibit intraspecific differences in Tsel. This suggests that individuals of a species from different climatic conditions do not show a response to the thermal environments naturally experienced. Lizards may have evolutionary "hard-wired" Tsel, even if the apparent constraints on thermoregulation are removed. Moreover,



*Fig. 2:* Mean selected body temperatures (Tsel) of seven *Liolaemus* species as function of the mean minimum air temperature the lizards experienced at the period when they were captured.

Temperaturas corporales seleccionadas de siete especies de *Liolaemus* en función de la temperatura ambiental mínima promedio, experimentada por los lagartos durante el período de sus capturas. subspecies of *L. pictus* and *L. tenuis* exposed to different thermal conditions had similar Tsel values. Hence, these results (with the exception of those obtained for *L. bellii*), are more consistent with the non-flexible view of the thermal physiology in reptiles (Hertz et al. 1983, Van Damme et al. 1990). Although these results indicate that these lizards might not respond adaptively to their thermal environments, one must consider both the diversity of this genus and the small sample size in some cases.

The intraspecific differences in Tsel exhibited by L. bellii may be related to the environmental temperatures to which the populations were exposed. Lizards are know to respond to changes in the thermal environment with both behavioral and physiological adjustments (Hertz et al. 1983). In L. bellii, variations in daily thermoregulatory patterns can be interpreted as an adaptive behavioral response. Its physiological thermal adaptation is supported by inter- and intrapopulational differences in Tsel, and by the correlations between Tsel and air temperatures. A decreased Tsel under low air temperatures may have selective advantages. A low Tsel can be maintained for a longer period each day, with a concomitant decrease in the energy demands and food requirements. In fact, the observed seasonal difference in Tsel of 2 °C in the Farellones population of L. bellii (October vs. January) represents a reduction of nearly 17% in metabolic expenditure (Andrews & Pough 1985). A similar reduction in metabolism is obtained if the predicted energy expenditure of the El Maule population is compared with that of Los Vientos and Farellones populations (all measured in January).

Interpopulational differences in Tsel may also be a consequence of genetic differentiation among populations (Sinervo 1990). Populations of the species that inhabit only high elevations in Los Andes, such as *L. bellii* (Veloso & Navarro 1988), are known to have higher genetic variation

because of lower gene flow than populations of the low-elevation species (Espejo 1989). Hence, it is likely that the interpopulational differences in the Tsel for L. bellii may have a genetic basis. This might explain why only L. bellii exhibited intraspecific differences in Tsel. Even if populations of L. bellii were under selective pressures similar to those of species from low elevation, L. bellii is still more likely to exhibit intraspecific differences in its thermal biology because this species lives under conditions that foster intraspecific differentiation (i.e., isolation on mountain tops). However, genetic studies would be required to determine the extend to which phenotypic plasticity and genetic differentiation, contribute to the interpopulation variation of Tsel in L. bellii.

Data from other studies on Tsel in L. nitidus (Valencia & Jaksic 1981, Cortés et al. 1992), suggested that this species may respond adaptively to its thermal environment. However, Tsel values recorded for L. nitidus in this study do not support this hypothesis and are similar to values measured by Valencia & Jaksic (1981). The lower Tsel values obtained by Cortés et al. (1992) -not only for L. nitidus-, cannot be attributed to geographical differences in the populations studied. These investigators studied a population of L. nitidus located near (about 90 Km) to the Fray Jorge population analyzed in this study. Differences might be related to the fact that contrarily to Valencia & Jaksic (1981) and this study, Cortés et al. (1992) obtained Tsel values as the average between maximum and minimum body temperatures, recorded at the moment at which a lizard retreats from the heating or cooling site, respectively. Hence, this is not Tsel accordingly to Pough & Gans (1982).

## Interspecific Comparisons of Tsel

Comparisons across species, indicated significant differences in Tsel among these lizards. This difference is mainly attributable to *L. fabiani* which had a significant lower Tsel than the other

species. This is noteworthy considering L. fabiani lives in the Atacama desert where it experiences the highest insolation recorded in South America (Ochsenius 1982). In fact, under field conditions L. fabiani can be found active on a substrata with temperatures near 47 °C, but it maintains a mean FBT of 32.5 °C (Navarro & Veloso, unpubl.). If Tsel values reflect the "thermal history" of the species (Dial & Grismer 1992), and assuming the mean Tsel value for Liolaemus near 34-36 °C, it is possible that L. fabiani has experience a different thermal history than the other Liolaemus studied. Perhaps L. fabiani speciated before the Atacama region became an extreme desert, at a time when this region had lower temperatures and higher humidity (Graf 1994). An alternative explanation is that L. fabiani belongs to another genus, so its Tsel should be unrelated to the Liolaemus Tsel values. Although a recent revision places L. fabiani in Liolaemus (Etheridge 1995), the taxonomic position of the species has been controversial (Laurent 1984, Cei 1986, Frost & Etheridge 1989).

With the exception of L. fabiani and L. tenuis, the mean Tsel values of the species studied were similar to the 34-36 °C reported for other Chilean Liolaemus (Valencia & Jaksic 1981, Marquet et al. 1989, Nuñez 1996, but see Cortés et al. 1992). Tsel would be a relatively conserved trait in these species, as it has been shown for other lizards genera (Bennett & John-Alder 1986, Huey & Bennett 1987 -but see Garland et al. 1991 for a reanalysis of these data-, Espinoza & Tracy 1997). However, the specific Tsel values obtained in this study were significantly correlated with the average minimum air temperature recorded where the lizards were collected. Even though these air temperatures do not correspond to the ones of the microhabitat used by animals, at interspecific level the Liolaemus species studied appear to exhibit an adaptive responses to their macro thermal environments, though, this adaptive response appears to occur over a small range of body temperatures  $(34 - 36^{\circ} C)$ . It is not clear why Tsel in these species is correlated with minimum air temperature. It has been suggested that lizards can use behavioral mechanisms to avoid extremely high but not low air temperatures (Carothers et al. 1997, but see Espinoza & Tracy 1997). An adaptive response to low air temperatures might be accomplished through physiological adaptations, such as shifts toward lower values of Tsel or other traits of their thermal biology.

The different results obtained at intra and interspecific levels regarding thermally adaptive responses in *Liolaemus* suggest that different factors are involved in the thermal biology at micro and macroevolutionary scales. These differences illustrate that more information about the thermal biology of members this lizards genus is needed, with the aim of analyzing these evolutionary processes and shedding light up some of the hypothesis proposed in this study.

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