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**BODY TEMPERATURES OF TWO  
VIVIPAROUS *LIOLAEMUS* LIZARD  
SPECIES, IN PATAGONIAN RAIN  
FOREST AND STEPPE**

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The genus *Liolaemus*, with at least 160 known species, is broadly distributed from the highlands of Peru and Bolivia to Tierra del Fuego, and from the Pacific islands of Chile to coastal Brazil (Cei, 1986). *Liolaemus elongatus* and *Liolaemus pictus* are distributed along an east-west precipitation gradient from the Patagonian steppe to the rainforest and they are sympatric in the transition zone located along the east of the Andes. *Liolaemus elongatus* is a saxicolous, viviparous, medium- to large-sized lizard (23 - 90 mm snout-vent length, adults and juveniles included). This species is distributed from San Juan to Chubut and is associated with steppe environments (Cei, 1986), but it has been found in the rainforest-steppe transition, in a very humid, cloudy microhabitat, syntopic with *Liolaemus pictus* (Ibargüengoytía & Cussac, 1998). *Liolaemus pictus* is a viviparous, medium-sized lizard (23-75 mm snout-vent length, adults and juveniles included) that lives in temperate habitats from sea level to moderate elevations (1600 m), in leaf-litter and under logs (Donoso-Barros, 1966).

We have shown previously that *L. elongatus* has an annual or biennial female reproductive cycle, while *L. pictus* has a biennial or triennial female reproductive cycle. As there is a strong association between the rate of embryonic development and temperature (Heulin, Osenegg & Lebouvier, 1991; Gilbert, 1994; Andrews, Mathies, Qualls & Qualls, 1999), we suggested that the low frequency of reproduction observed in these species is related to a short, cold, active season which constrains opportunities for thermoregulation, in turn affecting vitellogenesis and embryonic development (Ibargüengoytía & Cussac, 1996; 1998).

In the present work, we report the body temperatures at capture of lizards from two sympatric populations of *L. elongatus* and *L. pictus* in a rainforest site, and of a steppe population of *L. elongatus* alone. In an effort to

understand the relationship between environmental temperature and reproduction, the objectives of this preliminary study were to determine (1) the general thermobiology characteristics of the two species; (2) whether there are intraspecific differences between a steppe and a rainforest population of *L. elongatus*; and (3) whether reproductive status is related to body temperature in *L. elongatus*.

Measurements were made on *L. pictus* (eight lizards) and *L. elongatus* (16 lizards) from sympatric populations occupying a rocky promontory on the eastern shore of lake Moreno (rainforest site) near San Carlos de Bariloche, Río Negro, Argentina (41° 10' S; 71° 30' W, 700 m above sea level), from September 1996 to April 1997. Another *L. elongatus* population was studied in the steppe (53 lizards) in San Carlos de Bariloche (41° 6' S, 71° 7' W, 800 m above sea level), from September 1997 to February 1998 and from October 2000 to February 2001. Animals were caught by noose, toe clipped for identification upon recapture, and subsequently released.

The cloacal temperature (CT) was considered equivalent to body temperature (*sensu* Pough & Gans, 1982) and was measured using a catheter probe (TES TP-K01, 1.62 mm diameter) introduced about 1 cm inside the cloaca. The animals were handled by the legs to minimize heat transfer and temperature was recorded within 20 sec. of handling.

The temperatures of active and non-active individuals were measured, the latter caught only in the steppe site. Active individuals were defined as lizards found outside the burrows, performing any behaviour related to feeding and/or breeding activities. Non-active individuals were captured inside rock crevices and their temperatures show the thermal consequences of avoiding predation risk and/or the absence of adequate environmental conditions for activity.

We recorded the date and time of collection, snout-vent length (SVL, using a vernier calliper) and microenvironmental temperatures. The temperature of the substratum ( $T_s$ ) was measured using a TES TP-K03 probe; air temperature ( $T_a$ ) was measured 1 cm above the ground, in the case of lizards in activity, or inside the crevice, in the case of non-active individuals, using a TES TP-K02 gas probe. Thermocouples were connected to a TES 1302 thermometer (TES Electrical Electronic Corp., Taipei, Taiwan).

Maximum juvenile SVL was taken as 54 mm for *L. elongatus* and 49 mm for *L. pictus*, following Ibargüengoytía & Cussac (1996; 1998). Sex was determined in both species from the precloacal pores which are present only in males (Cei, 1986). Lizards were assigned to one of four reproductive categories: (1) juveniles; (2) adult males; (3) adult, non-pregnant females; and (4) pregnant females (recognized by their swollen body; Smith, 1997). The swollen body can be recognized from the beginning of pregnancy as these species are mainly lecithotrophic and the recently-ovulated oocytes are similar in size to the fetuses in advanced pregnancy (Crocco, 2001).

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TABLE 1. Cloacal temperature ( $T_c$ ) and environmental temperatures ( $T_a$  and  $T_s$ ) of *L. elongatus* and *L. pictus* from the rain forest and steppe sites. \* indicates the significance of either paired Student's *t*-test or Wilcoxon Signed Ranks Test ( $P < 0.01$ ).

Species	Habitat	Cloacal temperature ( $T_c$ )	N	Environmental temperatures	$T_c$ vs $T_a$ or $T_s$
<i>Active lizards:</i>					
<i>L. elongatus</i>	Rain forest	33.2	29	$T_a=23.3$	$Z=4.63^*$
			29	$T_s=27.7$	$Z=4.18^*$
<i>L. elongatus</i>	Steppe	29.8	40	$T_a=20.0$	$Z=5.22^*$
			40	$T_s=25.3$	$Z=3.42^*$
<i>L. pictus</i>	Rain forest	33.2	8	$T_a=24.6$	$Z=2.53^*$
			7	$T_s=30.2$	$Z=1.35$
<i>Inactive lizards:</i>					
<i>L. elongatus</i>	Steppe	11.7	18	$T_a=11.9$	$t=1.0$
			17	$T_s=11.3$	$t=0.5$

Regression analysis, paired Student *t*-test, and one-way analysis of variance (ANOVA), were used in the analyses. Assumptions of normality and homogeneity of variance were tested using the Kolmogorov-Smirnov test and Levene's test, respectively. When parametric assumptions were not met, non-parametric Spearman's correlation coefficient, Mann-Whitney Rank Sum Test (MW) and Kruskal-Wallis H (KW) tests were used.

Cloacal temperature in *L. elongatus* from the rainforest was not significantly correlated with SVL ( $r_s=0.09$ ,  $n=27$ ,  $P>0.62$ ), but was positively and significantly correlated with both  $T_s$  and  $T_a$  ( $r_{s(T_s)}=0.60$ ,  $r_{s(T_a)}=0.54$ ,  $n=29$ ,  $P<0.001$ ). Cloacal temperature was, on average, significantly higher than both  $T_a$  and  $T_s$  (Table 1, Fig. 1).

Cloacal temperature of active, thermoregulating *L. elongatus* from the steppe site showed a negative rela-

tionship with SVL ( $r_s=-0.28$ ,  $n=69$ ,  $P<0.01$ ) and a positive relationship with both  $T_s$  and  $T_a$  ( $r_{s(T_s)}=0.49$ ,  $r_{s(T_a)}=0.44$ ,  $n=69$ ,  $P<0.001$ ). The cloacal temperature was significantly higher than the environmental temperatures (Table 1, Fig. 1). Cloacal temperatures of non-active *L. elongatus* from the steppe site showed a significant relationship with  $T_s$  and  $T_a$  (regression,  $F_{2,14}=33.08$ ,  $P<0.001$ , Fig. 1) but they did not show a significant relationship with SVL ( $P>0.9$ ). Cloacal temperature of non-active *L. elongatus* did not differ either from  $T_a$  or from  $T_s$  (Table 1).

*Liolaemus pictus* cloacal temperature was not significantly related to SVL,  $T_s$  or  $T_a$  ( $r_{s(SVL)}=0.38$ ,  $r_{s(T_s)}=0.07$ ,  $r_{s(T_a)}=0.54$ ,  $n=7$ ,  $P>0.3$ ). However, cloacal temperature was significantly greater than  $T_a$  (Table 1, Fig. 1).

Data from *L. elongatus* showed no significant difference among sex and reproductive categories, either in the rain forest (KW:  $H_{3,17}=2.09$ ,  $P>0.55$ ), or in actively thermoregulating (KW:  $H_{2,54}=2.54$ ,  $P>0.28$ ) or non-active *L. elongatus* from the steppe (ANOVA:  $F_{1,15}=1.161$ ,  $P>0.29$ ). Nevertheless, there was a tendency for pregnant females to have somewhat lower cloacal temperatures (Fig. 2).

Cloacal temperatures of *L. elongatus* from the steppe site were significantly lower than those of the same species from the rain forest (ANOVA:  $F_{1,68}=6.46$ ,  $P<0.013$ ), taking into account  $T_s$  as a significant covariable in the model ( $P<0.001$ ). Residuals obtained from the regression of cloacal temperature versus  $T_s$  were calculated and compared in Fig. 2.

The data show that *L. elongatus* and *L. pictus* body temperatures in activity were higher than environmental temperatures up to approximately 35 °C, beyond which body temperature no longer increased. Body temperatures which are higher than microhabitat temperatures are also known in other lizard species, such as *Liolaemus multiformis* (Pearson & Bradford, 1976), *Kentropyx calcarata* (Vitt, 1991), *Ameiva ameiva* (Vitt & Colli, 1994) and *Sceloporus jarrovi* (Smith & Ballinger, 1994a). The relationships between body and environ-

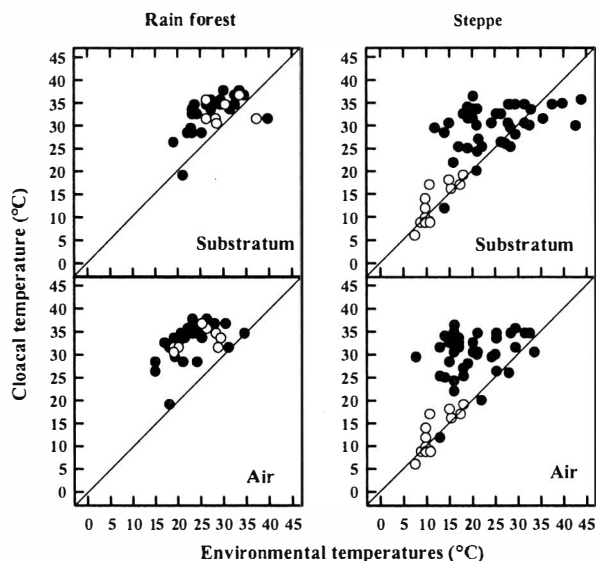


FIG. 1. Cloacal temperature versus the environmental temperatures; substratum temperature (upper panels), air temperature (lower panels). *Liolaemus elongatus* (filled circles) and *L. pictus* (open circles) from the rain forest (left panels) and active (filled circles) and non active (open circles) *L. elongatus* from the steppe site (right panels).

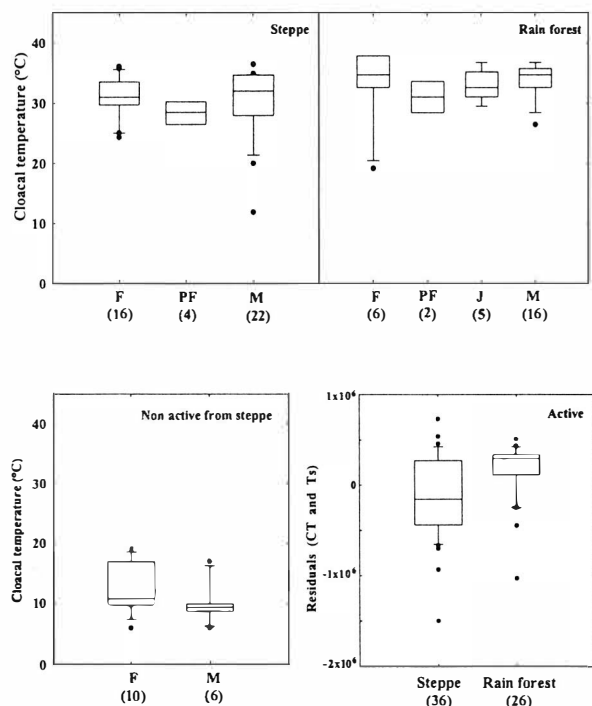


FIG. 2. Cloacal temperatures at capture (CT) of active *L. elongatus* from steppe and rain forest (top), cloacal temperature of male and female non-active individuals from steppe (lower left), and cloacal temperature (residuals of the regression versus substratum temperature,  $T_s$ ) from steppe and rain forest active individuals (lower right). F: females, PF: pregnant females, J: juveniles, M: males. Median, quartiles and data outside 10th and 90th percentiles are indicated. In brackets are the numbers of observations.

mental temperatures of *L. elongatus*, particularly in the steppe, indicate thermoregulation abilities. Although an individual was captured basking with a cloacal temperature of 11 °C, most of the lizards with body temperature lower than or equal to 20 °C were found in their burrows. This result probably reflects a severe constraint imposed by predation risk.

Although annual means of minimum, maximum and daily mean temperatures for Patagonia show that heat availability is higher in the steppe than in the rainforest (Correa, 1998), we recorded lower cloacal temperatures of *L. elongatus* from the steppe, even when the effect of substrate temperature was removed from the analyses. This difference may be attributable to differences in habit in the two environments, and reinforces the hypothesis of plasticity in the thermo-responses of *L. elongatus*.

The most commonly cited immediate benefit of viviparity in reptiles is that pregnant females can hasten embryonic development via thermoregulation and partially compensate for a short active season (Shine, 1985). Accordingly, it has been predicted that pregnant females should select higher and/or less variable body temperature than would non-pregnant females and adult males (Charland & Gregory, 1990). One postulated benefit of moderating body temperature during pregnancy is to enhance embryo survival, since high incubation temperatures are detrimental to embryonic development (Mathies & Andrews, 1997). We failed to find signifi-

cant differences among sex categories in cloacal temperature of *L. elongatus* in any of the localities. Nevertheless, there was a tendency for pregnant females to show lower cloacal temperatures than the other individuals. A similar pattern was observed in the viviparous lizard *Sceloporus jarrovi* (Smith & Ballinger, 1994a) and in the oviparous *Sceloporus virgatus* (Smith & Ballinger, 1994b), and was attributed to different microhabitat use in order to avoid the predation risk associated with carrying embryos or eggs and to maximize developmental success (Smith & Ballinger, 1994a).

In the light of our results we propose that under the restrictive environmental conditions of Patagonia, major differences arise between the body temperatures of active and non-active individuals. The former are able to thermoregulate, and pregnant females show a (non-significant) tendency to maintain this stability by choosing lower temperatures and, in consequence, lengthening the pregnancy. If this hypothesis could be confirmed, a causal link for the low female reproduction frequency observed in *L. elongatus* and *L. pictus* would be established. Further studies are necessary to advance in the thermobiology of these species.

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