Seasonal shifts in the thermal biology of the lizard *Liolaemus tandiliensis* (Squamata, Liolaemidae)

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ABSTRACT

Small lizards can accommodate to constraints imposed by temporal changes in ambient temperature through a combination of adaptive evolution and behavioral and physiological plasticity. Thermal physiology plasticity may compensate for climate variation and favor performance while minimizing behavioral costs in sub-optimal conditions. The Tandilia's lizard, *Liolaemus tandiliensis*, occurs in an isolated mountain range of the Argentinean temperate Pampas. In this study, we compared the thermal biology of *L. tandiliensis* between late spring (December) and mid-summer (February). The habitats' thermal quality was lower in late spring than in mid-summer. The lizard's field-body temperature (Tb) was 2–3 °C higher than the operative temperature (Te). Overall, the mean preferred temperature (Tsel) was 37.4 °C [preferred range (Tset): 36.2–38.7 °C], and was similar to other *Liolaemus* species. The Tset and Tsel of females in late spring were 1.8 °C lower than in mid-summer. In the case of males, the Tsel did not vary among seasons, while the Tset had a difference of 2.5 °C between seasons. Adults were moderate thermoregulators, but females were more efficient only in late spring (E_{males} = 0.69; $E_{females}$ = 0.58), compared to mid-summer (E_{males} = 0.68; $E_{females}$ = 0.50). Juveniles did not show temporal differences in temperature preferences and had a relatively higher efficiency in late spring (E = 0.38) compared to mid-summer (E = 0.28). An increased proportion of juveniles and adults shifted their Tb near to the Tset in late spring respect to mid-summer. The adults also matched their preferred temperatures to their current body temperature. These results suggest that seasonal shifts in the thermoregulatory parameters of *L. tandiliensis* may improve their thermoregulatory efficiency. Although temporal variation in ambient temperatures might influence the thermal biology of the studied lizards, other factors such as changes in the reproductive status may have also interfered.

1. Introduction

Ectotherms thermoregulate by exchanging heat with the environment in order to maintain their body temperature within an accurate range to favor the performance of their vital functions (Stevenson, 1985; Castilla et al., 1999). Thermoregulation is a highly complex aspect because different physiological processes and behaviors are achieved at temperatures near performance optima (Huey and Slatkin, 1976; Huey and Stevenson, 1979; Angilletta et al., 2009). In lizards, thermoregulation requires fine-grained adjustments to match body temperature with physiological optima functions, such as digestion (Harlow et al., 1976), escape behavior (Bonino et al., 2011; Zamora-Camacho et al., 2015; Foster et al., 2015) or reproduction (Mathies and Andrews, 1997). Thermoregulation may reflect ecological constraints that depend on extrinsic factors, such as the availability of thermal resources, elevation, vegetation structure, the degree of exposure to the wind (Bujes and Verrastro, 2006), social interactions (Labra, 1995) or predation risk (Downes and Shine, 1998). Lizards display alternative thermoregulatory strategies depending on the climatic conditions. For example, *Liolaemus* species can temporally exchange the use of air and substrate temperature (Martori et al., 2002; Maia-Carneiro and Rocha, 2013b) or they can swap between shade areas and direct sunlight to

control their body temperature (Moreno Azócar et al., 2013). Thermoregulation may also be affected by intrinsic factors, such as body size, age, sex (Sievert and Hutchison, 1989; Huey and Pianka, 2007) or reproductive condition (Núñez, 1996; Ibargüengoytía and Cussac, 2002). For example, adults of some lizards exhibit a more accurate thermoregulation than juveniles. Large individuals can control the heat exchange by blood flow and have a high thermal inertia, which results in slow heating and cooling rates (Sagonas et al., 2013; Tang et al., 2013; Gilbert and Lattanzio, 2016).

Lizards with flexible thermal behavior are able to counteract the climatic variations (Huey et al., 2003; Díaz and Cabezas-Díaz, 2004; Caldwell et al., 2017). However, behavioral adjustments may be energetically expensive in low-quality thermal conditions (Downes and Shine, 1998; Row and Blouin-Demers, 2006; Cadena and Tattersall, 2009). The inability of lizards to thermoregulate near their preferred levels is the result of reduced thermal opportunities related to the geographical conditions and the climatic seasonality (Andrews, 1998; Grbac and Bauwens, 2001; Sepúlveda et al., 2008). To survive in environments with relatively large climatic changes, small lizards must accommodate to local variations of the ambient temperature through a combination of adaptive evolutionary traits and behavioral and physiological plasticity (Niewiarowski, 2001; Glanville and Seebacher, 2006; Basson and Clusella-Trullas, 2015). Physiological plasticity compensates climate variation and favors performance while minimizing behavioral costs in sub-optimal conditions (Hadamová and Gvoždík, 2011; Clusella-Trullas and Chown, 2014; Ortega et al., 2016). This characteristic is a reversible conditioning process that occurs over a relatively short period of time, usually days to weeks (Little and Seebacher, 2016). Physiological plasticity is called acclimatization when it is caused by changes in the natural environment, or acclimation when it is caused by changes in a single factor under controlled laboratory conditions (Huey et al., 2012).

There are two main postures regarding the degree of the thermal plasticity in lizards, the labile and the static hypotheses (Hertz et al., 1983). The labile hypothesis states that thermal physiology responds readily to directional selection (Angilletta et al., 2002). On the other hand, the static hypothesis posits that thermal physiology is evolutionary conservative and consequently, relatively insensitive to directional selection (Van Damme et al., 1990; Labra, 1998). Multiple lines of evidence suggest that some components of the thermal biology tend to be more plastic (e.g. field body temperature, preferred temperature, critical thermal minimum) than others (e.g. critical thermal maximum; Hertz et al., 1983; Tocher, 1992; Gvoždík, 2012; Muñoz et al., 2014; Leal and Gunderson, 2012). However, this will depend on the lizard's taxa. Plasticity in thermal preferences can occur within an individual's lifespan as a response to variations in the thermal environment (Gvoždík, 2012; Little and Seebacher, 2016). Species from many family of lizards can shift their preferred temperatures to favor thermoregulatory efficiency during periods of low ambient temperatures (e.g., Phrynosomatidae -Ballinger et al., 1969; Crotaphytidae -Sievert and Hutchison, 1989; Scincidae -Andrews, 1994; Agamidae -Christian and Bedford, 1995; Lacertidae -Díaz et al., 2006).

Species from the Liolaemidae family have field-body temperatures that are adapted to ecological gradients of ambient temperature as a consequence of evolutionarily labile thermal physiology, independently of the phylogeny (Labra et al., 2009; Medina et al., 2012; Rodríguez-Serrano et al., 2009; Moreno Azócar et al., 2013; Cruz et al., 2014). Climate seasonality, together with intrinsic factors such as sex, age, and body size, are the main driving forces that induce changes in the field body temperatures of lizards (Medina et al., 2009; Maia-Carneiro et al., 2012; Maia-Carneiro and Rocha, 2013a; Maia-Carneiro and Rocha, 2013b). For example, the mean field body temperatures of some species of *Liolaemus* are 1–3 °C lower in spring than summer (*L. koslowskyi* -Martori et al., 2002; *L. occipitalis* -Bujes and Verrastro, 2006; *L. pseudoanomalus* -Villavicencio et al., 2007). However, whether the thermal preference of *Liolaemus* is evolutionarily labile or static, and which

factors influence this variable is still a matter of debate (Medina et al., 2009, 2012; Moreno Azócar et al., 2013; Gómez Alés et al., 2017). Labra et al. (2009) mention that rapid adaptive shifts in the thermal preferences of *Liolaemus* lizards may occur within a relatively narrow range of temperatures. Recent studies show that some species of *Liolaemus* have a limited acclimation capacity to adjust to new thermal conditions by physiological plasticity (Fernández and Ibargüengoytía, 2012; Kubisch et al., 2015). However, Artacho et al. (2017) found that the species *L. pictus* was thermally labile across its widespread distributional range.

The southeast (SE) Pampas of Argentina is characterized by a temperate and humid climate, with no dry season. The average environmental temperature in spring (September to December; 16 ± 3.8 °C) is around 5 °C lower than in summer (January to March; 21 ± 2.9 °C) (Burgos and Vidal, 1995; NASA, 2016). Since the *Liolaemus* species that inhabit the SE temperate Pampas concentrate their annual activity period during spring and summer (Vega, 1999; Vega et al., 2008), the seasonal change in ambient temperatures might affect their thermal biology. Therefore, the aim of this study was to assess the thermal biology of the endemic lizard *Liolaemus tandiliensis* during late spring and mid-summer in the Tandilia Mountain System of the SE temperate Pampas. We aimed to: (1) compare the operative temperature (T_e), the substrate microenvironmental temperature (T_s) and the air temperature (T_a) between late spring and mid-summer; (2) contrast the field body temperature (T_b), the preferred temperature (T_{sel}) and the descriptive indexes of thermoregulation (d_b, d_e and E, *sensu* Hertz et al., 1993) according to the sampling period and the sex-age group (juvenile, male, female); and (3) analyze which of the microenvironmental temperatures (T_s or T_a) constitute the most important heat source for body temperature regulation of the lizards. We hypothesize that seasonal variations in ambient temperatures induce shifts in the thermal biology of *L. tandiliensis*. Because the field body temperature of *Liolaemus* lizards is more labile than the preferred temperature, we predict that in late spring, individuals will have lower T_b than in mid-summer and, that they will not shift their preferred temperature. Therefore, the thermoregulatory efficiency of *L. tandiliensis* in late spring will be lower than the thermoregulatory efficiency in mid-summer.

2. Materials and methods

2.1. Species under study

The Tandilia's lizard (*Liolaemus tandiliensis*) is a recently described liolaemid lizard that belongs to the *Liolaemus alticolor-bibronii* group (Vega et al., 2008). It is a small body-sized lizard (49–58 mm snout-vent length [SVL]), endemic of the rocky grounds at elevations up to 250 m in the Tandilia mountain range of the Buenos Aires province, Argentina (Vega et al., 2008; Quinteros, 2012). *Liolaemus tandiliensis* is oviparous and has a seasonal reproductive cycle, being reproductively active from late winter to the beginning of summer (Vega et al., 2008). There is a synchronism between the climatic cycle and the reproductive cycle of the species of the *alticolor-bibronii* group that inhabit the SE temperate Pampas (Vega, unpublished data). In this sense, female lizards have yolked follicles from early September to mid-October and oviductal eggs from October to December. On the other hand, male lizards have enlarged testes from late August to November (Vega and Bellagamba, 2005; Vega et al., 2008).

2.2. Field data recordings

Fieldwork was carried out during the first weeks of February and December of 2015. Given the climatic seasonality in the Southern Hemisphere, hereafter we refer to the December sampling period as late spring and to that sampled in February as mid-summer. The data were recorded in a plot of 35 ha at Sierra de Los Difuntos -La Peregrina (37°53′S; 57°50′W), comprising part of the Tandilia mountain range

located in Buenos Aires province, Argentina. This area is part of the Tandilia mountain range from the SE of the temperate Pampas. The Tandilia mountain range is a discontinuous chain of mountains, hillocks and hills that extend along 350 km over the SE Pampas and rise between 50 m and 250 m. The landscape consists of quartzite rock patches sparsely covered with small grasses, such as *Stipa* sp., *Poa* sp., *Briza* sp. and *Paspalum* sp., and shrubs of *Baccharis* spp., *Colletia* sp. and *Discaria* sp. (Burkart et al., 1999; Cabrera, 1976). The region is located in a mid-latitude climate, with average temperatures of 19.4 °C (range 11.9–27.9 °C) in early December and 21.4 °C in February (range 15.0–30.4 °C) (NASA, 2016). The mean annual precipitation ranges from 800 to 1000 mm (Burgos and Vidal, 1995).

The individuals of *L. tandiliensis* were captured by noose during their daily activity period (9:00–18:00 h; Vega et al., 2008). A total of 140 lizards were captured (72 in late spring and 68 in mid-summer). To avoid bias related to differences in the daily lizard activity, the same sampling effort was performed in three periods of the day (morning, midday and afternoon). Immediately after capture (no more than 20 s after noosing), the lizards' body temperature (*T*b, *sensu* Pough and Gans, 1982) was measured using an ultra-thin thermocouple introduced 1 cm inside the vent. Individuals were handled by the head to avoid heat transfer (Stellatelli et al., 2013) and were marked temporally in the belly with a black non-toxic pen to avoid recaptures (*sensu* Plummer and Ferner, 2012). We registered the SVL of each lizard with a digital caliper (SC111001, Schwyz MR., Argentina; ± 0.01 mm) and the body mass with a digital pocket scale (CH02, Diamond premium MR, China; ± 0.1 g). Individuals were classified according to their age class, based on the SVL (juvenile: < 49 mm, and adults: ≥ 49 mm), and according to their sex by external sexual dimorphic characters (*sensu* Vega et al., 2008).

Micro-environmental temperatures were recorded at each capture site. The substratum temperature (*T*s) was measured at ground level, and the air temperature (*T*a) at 1 cm above the ground by thermocouples connected to a digital thermometer (SC133, Schwyz MR., Buenos Aires, Argentina; ± 0.01 °C). We measured the operative temperatures (*T*e) (*sensu* Hertz et al., 1993) of each sampling period using five regular electronic devises or data loggers (DS1921G, iButton Sunnyvale ®, CA, USA) that registered temperatures every 10 min from 09:00 to 18:00 h for seven consecutive days. In the case of small lizards, such as *L. tandiliensis*, coin-shaped data logger devices can be used to estimate *T*e because shape, morphology, scale architecture and color contribute very little to temperature change (Shine and Kearney, 2001). Hence, it was not necessary to use small-sized life-like models to estimate the *T*e. The devices were placed randomly at different sites directly on top of the substrate (e.g. bare rocks, rocks covered with vegetation, cracks in rocks) within the habitat of the lizards (*sensu* Vitt and Sartorius, 1999). Mean temperatures were calculated from each data logger and used to obtain the mean *T*e of each sampling period. Therefore, we screened all the spatial and temporal microenvironmental temperatures available for thermoregulation.

2.3. Laboratory protocol and determination of preferred body temperature

The preferred body temperatures of *L. tandiliensis* were measured in the laboratory from 24 individuals (8 juveniles, 7 males, 9 females) in late spring and 24 individuals (10 juveniles, 6 males, 8 females) in mid-summer. Laboratory protocols and methodology were identical for both trials. Before the trials, lizards were kept in a glass terrarium (0.35 × 0.20 × 0.20 m, L × W × H), provided with water *ad libitum*. The photoperiod was set to resemble the daylight hours of each sampling period. Thermoregulation experiments were carried out 3–4 days after capture (*sensu* Corbalán et al., 2013; Gómez Alés et al., 2017). For the trials, lizards were placed individually in an open-top terrarium (1.50 × 0.30 × 0.18 m) with a 0.03 m sand layer on the bottom to prevent overheating. The thermal gradient was produced by a line of four overhead infrared lamps, one of 150 W, two of 100 W and one of 75 W,

set at a distance of 0.10, 0.40, 0.70 and 1.00 m respectively, at one end of the terrarium (*sensu* Stellatelli et al., 2013). The lamps were adjusted to different heights above the soil to make a linear substratum gradient from 18° to 65°C. We measured body temperatures with an ultra-thin (1 mm) thermocouple fixed in place with adhesive tape approximately 1 cm inside the vent. The thermocouple was connected to a digital thermometer (SC133, Schwyz MR., Buenos Aires, Argentina; ± 0.01 °C). After 16:00 h, the lizards buried themselves in the colder corner of the terrarium and remained inactive with a body temperature around 20 °C; for this reason, we decided to end the trials at this time of the day. The temperature of each lizard was recorded every 15 min during two consecutive days from 09:00 to 16:00 h. A period of at least 5 h is considered sufficient for individuals to reach their preferred temperature in thermoregulation trials (e.g., Medina et al., 2009; Gutiérrez et al., 2010). For each individual, we calculated the mean preferred temperature (*T*sel) and the boundaries of the set-point range of preferred temperature (lower: *T*set_lo; upper: *T*set_up), considered as the temperatures within the interquartile range that include 50% of the observations, following the protocol of Hertz et al. (1993). Once the laboratory experiments were finished, the individuals were released at the capture sites.

2.4. Effectiveness of thermoregulation

We calculated the descriptive indexes of thermoregulation following the protocol by Hertz et al. (1993). These indexes can be estimated from three independent data types: (i) the distribution of *T*e, (ii) field body temperature (*T*b), and (iii) preferred body temperature obtained in the laboratory. The first is the index of habitat thermal quality (mean *d*e), which is estimated as the mean absolute values of the deviations of each *T*e from the set-point range of preferred temperature. A relatively high value of *d*e indicates low habitat thermal quality. The second index corresponds to the accuracy of thermoregulation (mean *d*b), which is estimated as the mean absolute values of the deviations between each *T*b from the set-point range of preferred temperature. A relatively high value of *d*b indicates low accuracy of thermoregulation. The third is the index of the effectiveness of thermoregulation (*E*), that is calculated as $E = 1 - (db / de)$. The *E* index shows how close the *T*b is from *T*sel, considering the null distribution of temperature (*T*e). A given value of *E* results from a variety of different combinations of *d*b and *d*e. When *E* is close to one, the organism is considered to be an efficient thermoregulator, an *E* value close to 0 means that the organism is a thermoconformer, and when *E* is close to 0.50 the organism is considered to be a moderate thermoregulator (Hertz et al., 1993; Bauwens et al., 1996).

2.5. Statistical analyses

We used the Mann-Whitney *U* test (α < 0.05) to compare the *T*e between both sampling periods, because assumptions of normality and homogeneity of variance were not fulfilled, even after data transformation (Zar, 1984). To assess the effect of the sampling period (late spring, mid-summer) and sex-age group (juvenile, male, female) on the thermoregulatory parameters of *L. tandiliensis*, we used generalized linear models (GLMs; Crawley, 2007). The GLMs with Gamma error structure and inverse function were constructed considering sampling period and sex-age group as explanatory variables (fixed factors), and *T*s, *T*a, *T*b, *T*sel, *T*set_lo and *T*set_up as response variables. We applied the bootstrap method with 1000 iterations on the data matrix of the indexes *d*b, *d*e, and *E* (Hertz et al., 1993). The indexes were compared using GLMs with Gaussian error structure and identity function with *d*b, *d*e and *E* as response variables, and sampling period and sex-age group as explanatory factors (Crawley, 2007). We also used GLMs with Gamma error structure and inverse function to explore possible associations between *T*b, micro-environmental temperatures (*T*s and *T*a) and body mass (Crawley, 2007). All statistical analyses were carried out using R software, version 3.1.3 (R Core Team, 2015).
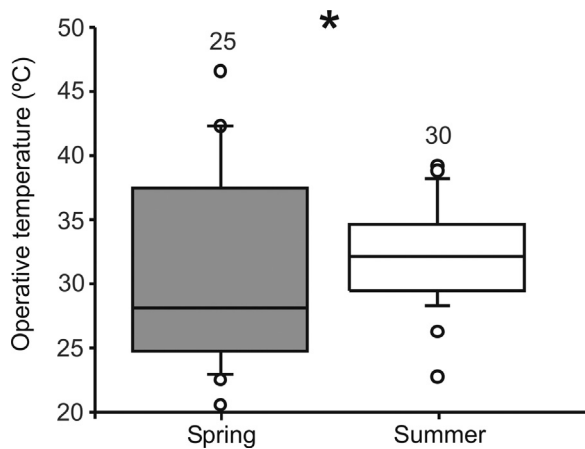
Fig. 1. Operative temperature (Te) of the Tandilia Mountains in late spring (early December) and mid-summer (February) during the daily activity period (09–18 h) of *Liolaemus tandiliensis*. Horizontal bar denotes median, vertical bar denotes range, upper-lower boundary of boxes denotes quartile, circles denote outliers. Asterix (*) indicates interseasonal differences in mean values (Mann-Whitney test: $P < 0.001$), and the numbers indicate sample sizes.

3. Results

3.1. Seasonal comparison of thermoregulatory parameters within each sex-age group

The median of the Te was lower in late spring than in mid-summer, with a difference of 4 °C (Mann-Whitney test: $U = 446762.00$, $P < 0.001$; Fig. 1). In both sampling periods, we registered low frequencies of Te that had values within the set-point range of the preferred temperature of the lizards (Fig. 2A–C). Nevertheless, we found relatively higher de values in late spring than in mid-summer (Tables 1 and 2). The Tb was significantly different between both sampling periods in adult lizards, but not in juveniles (Tables 1 and 2). The mean Tb of the adult individuals was lower in late spring than in mid-summer, with a difference of 2.4 °C and 3.6 °C in males and females, respectively (Tables 1 and 2, Fig. 2B, C). The microenvironmental temperatures (Ts and Ta) at the capture sites of juveniles and females were lower in late spring than in mid-summer. However, there were no differences between Ts and Ta at the capture sites of males between late spring and mid-summer (Tables 1 and 2). In late spring, the mean $Tset_{lo}$ of the adults was lower than that the mean $Tset_{lo}$ of mid-summer, with a difference between seasons of 2.5 °C and 1.8 °C in males and females, respectively (Tables 1 and 2; Fig. 2B, C). The preferred temperature was significantly different between seasons only in females. In this case, the mean value of $Tsel$ in late spring was 1.8 °C lower than the $Tsel$ in mid-summer (Tables 1 and 2; Fig. 2C). The highest frequencies of individuals that had body temperatures near the set-point range of preferred temperature occurred in late spring (Tables 1 and 2, Fig. 2A–C). Therefore, the effectiveness of thermoregulation, both in juvenile and adult lizards, was high during the late spring sampling period.

3.2. Comparison of thermoregulatory parameters among sex-age groups

Late spring. The Tb of *L. tandiliensis* did not differ between the different age and sex groups (Tables 1 and 2). Also, the preferred temperature and the boundaries of the set-point range of $Tsel$ did not differ among sex and age groups (Tables 1 and 2, Fig. 2A–C). The Ts and Ta differed only between juveniles and males. In this case, the mean values of Ts and Ta of males were higher (4.3 °C and 3.4 °C, respectively) than those of juveniles (Tables 1 and 2). The accuracy of thermoregulation had intraspecific differences. The db values suggest that the frequencies of Tb deviated from the set-point range of preferred temperature were highest in juveniles followed by females and males (Tables 1 and 2;

Fig. 2A–C). The deviation of Te from the set-point range of preferred temperature was higher in juveniles than in adults, and greater in males than in females ($de_{juveniles} > de_{females} > de_{males}$) (Tables 1 and 2, Fig. 2A–C). Males were more effective thermoregulators than females, and females were more effective thermoregulators than juveniles, since $E_{males} > E_{females} > E_{juveniles}$ (Tables 1 and 2).

Mid-summer. The mean Tb of juveniles was 2.1 °C lower than the Tb of males and 2.9 °C lower than the Tb of females (Tables 1 and 2). The $Tsel$ and the set-point range of preferred temperature did not differ among juveniles, males and females (Tables 1 and 2). The Ts differed only between juveniles and females, being the mean Ts of females 3 °C higher than that of juveniles (Tables 1 and 2). There were no differences in Ta between sex-age groups (Tables 1 and 2). The accuracy of thermoregulation was significantly different among sex-age groups. In this case, juveniles had the highest db values, followed by females and males. There were no differences among mean de values of juveniles, males and females (Tables 1 and 2; Fig. 2A–C). Males were more effective thermoregulators than females, and females were more effective than juveniles, since $E_{males} > E_{females} > E_{juveniles}$ (Tables 1 and 2).

### 3.3. Relationship between body temperatures, body size and microenvironmental temperatures

The Tb of juveniles in late spring was only related to Ts, whereas the Tb in summer was positively related to Ts and Ta (Table 3). We found no relationship between the body mass and the Tb of juveniles in late spring or mid-summer. However, when we pooled the data from both sampling periods we found a positive relation between the body mass and the Tb (Table 3). The Tbs of males was positively related to Ts and Ta in both sampling periods (Table 3). In females, the Tb was positively related to Ts and Ta in late spring, whereas in mid-summer, the Tb of females was positively related to Ts but not to Ta (Table 3). Overall, the Ts and Ta for all the sex-age group data were positively related in both sampling periods (Table 3). There was no statistically significant effect of body mass on the Tb of adults (Table 3).

4. Discussion

The endemic lizard *Liolaemus tandiliensis* is an active moderate thermoregulator, with values of mean field body temperature (Tb) 2–3 °C above the mean environmental temperatures of the Sierra de Los Difuntos-La Peregrina (Tandilia Mountain range of the southern Pampas). The daily environmental temperatures of this ecosystem had marked temporal differences since the mean operative temperature (Te) during the daily activity period of the lizards was 1.3 °C lower in late spring (early December) compared with that of mid-summer (February). The Tandilia Mountain range is a poor thermal quality habitat for *L. tandiliensis*, because of the relatively high magnitude of the deviations of Te from the observed lizards' thermal preference. The Tb values of *L. tandiliensis* were similar to those of other congeneric species that also occur in the SE temperate Pampas, such as *L. gracilis*, *L. multimaculatus* and *L. wiegmannii* (Vega, 1999; Labra et al., 2008). Additionally, the field body temperature of *L. tandiliensis* ($\overline{X} = 33.96$ °C, SD $= 4.10$ °C) was similar to the Tb of other *Liolaemus* species that occur in different regions of Argentina and Chile ($\overline{X} = 32.31$ °C, SD $= 4.51$ °C; Medina et al., 2012; Moreno Azócar et al., 2013). In general, closely related lizard species tend to have similar body temperatures, even when living in different habitats (Andrews, 1998; Andrews et al., 1999; Huey et al., 2003). Despite the observed temporal variation in the Tb of *L. tandiliensis*, this species resembles its congeners probably through phylogenetic affinity. However, local factors may also promote variations of thermoregulatory parameters within a relatively narrow range (Rodríguez-Serrano et al., 2009; Robles and Halloy, 2016; Duran et al., 2017).

Our results raised several interesting questions after observing intraspecific temporal variations in thermoregulatory parameters. In
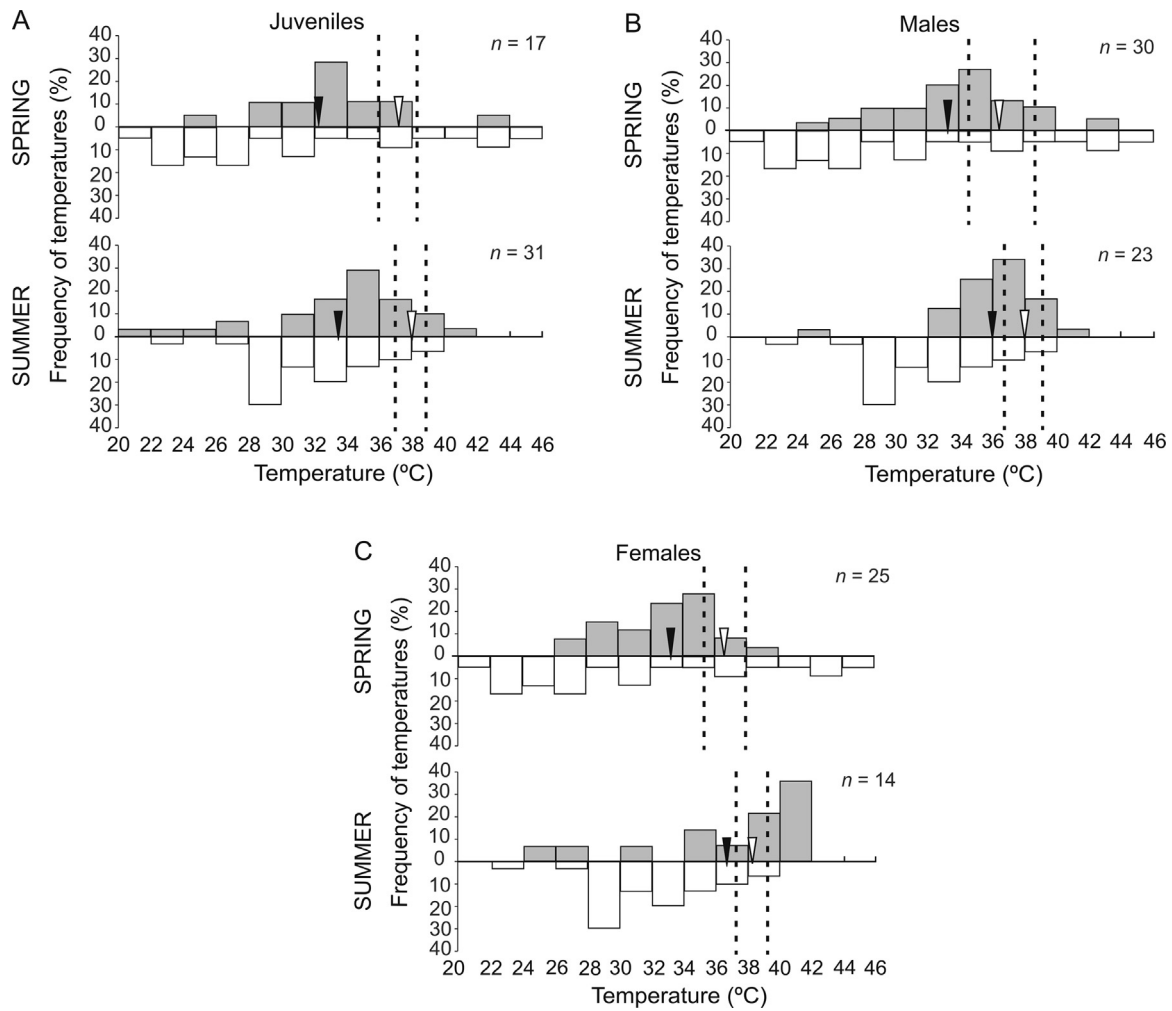
Fig. 2. Distribution of field body temperature (Tb, grey bars) of juveniles (A), males (B) and females (C) of *Liolaemus tandiliensis* and operative temperature (Te, white bars) of the habitat in the Tandilia Mountains of the SE temperate Pampas during late spring (early December) and mid-summer (February). References: grey arrows, median field body temperature (Tb); white arrows, median preferred temperature ($Tsel$); vertical dashed lines, set-point range of preferred temperature; and "n", the number of registers.

Table 1
Thermoregulatory parameters of *Liolaemus tandiliensis* in late spring (early December) and mid-summer (February).

	LATE SPRING			MID-SUMMER			OVERALL
	Juv	Mal	Fem	Juv	Mal	Fem	
Te		30.7 ± 7.4 (25)			32.0 ± 3.9 (30)		31.2 ± 5.8 (55)
Tb	32.2 ± 4.32 (17)	33.4 ± 3.5 (30)	33.0 ± 3.0 (25)	33.7 ± 4.7 (31)	35.8 ± 3.0 (23)	36.6 ± 5.1 (14)	33.9 ± 4.1 (140)
Ts	29.0 ± 5.0 (17)	33.3 ± 4.2 (30)	31.1 ± 4.3 (25)	33.2 ± 4.5 (31)	33.3 ± 3.8 (23)	36.2 ± 5.9 (14)	32.6 ± 4.8 (140)
Ta	29.1 ± 6.5 (17)	32.5 ± 5.0 (30)	30.1 ± 5.2 (25)	32.0 ± 3.6 (31)	32.3 ± 2.8 (23)	34.6 ± 3.0 (14)	31.7 ± 4.7 (140)
$Tset_{lo}$	36.0 ± 1.6 (8)	34.3 ± 2.7 (7)	35.6 ± 1.7 (9)	36.9 ± 1.4 (10)	36.8 ± 1.8 (6)	37.4 ± 0.6 (8)	36.2 ± 1.9 (48)
$Tsel$	37.0 ± 1.6 (8)	36.5 ± 2.6 (7)	36.7 ± 1.5 (9)	37.9 ± 1.0 (10)	38.2 ± 1.7 (6)	38.5 ± 0.5 (8)	37.4 ± 1.7 (48)
$Tset_{up}$	38.2 ± 1.5 (8)	38.7 ± 1.7 (7)	38.0 ± 1.6 (9)	38.9 ± 0.7 (10)	39.1 ± 1.4 (6)	39.3 ± 0.2 (8)	38.7 ± 1.3 (48)
db	4.5 ± 3.2 (17)	1.8 ± 2.5 (30)	3.0 ± 2.8 (25)	3.7 ± 4.2 (31)	1.6 ± 2.5 (23)	2.7 ± 3.9 (14)	2.8 ± 3.4 (140)
de	7.3 ± 4.7 (17)	6.1 ± 4.2 (30)	7.2 ± 4.7 (25)	5.1 ± 3.5 (31)	5.1 ± 3.5 (23)	5.6 ± 3.7 (14)	6.0 ± 4.2 (140)
E	0.38	0.69	0.58	0.28	0.68	0.50	0.51

The values correspond to mean ± standard deviation with the number of samples between brackets. References: Te, operative temperature; Tb, field body temperature; Ts, substrate temperature; Ta, air temperature; $Tsel$, mean preferred body temperature; $Tset_{lo}$, lower limit of the set-point range of preferred temperature; $Tset_{up}$, upper limit of preferred temperature; de, index of thermal quality of the habitat; db, index of accuracy of thermoregulation; E, index effectiveness of thermoregulation.

Table 2

Comparisons of thermoregulation parameters. Fixed factors contrasts resulted from generalized linear models (GLMs) testing the effect of sampling period (late spring: early December; mid-summer: February) and sex-age group (juvenile, male, female) of *L. tandiliensis* on thermoregulatory parameters.

Variable	Parameter	Intercept	INTER-SEASONAL COMPARISON			INTRA-SEASONAL COMPARISON					
			Late spring vs Mid-summer			Late spring			Mid-summer		
			Juv	Mal	Fem	Juv vs Mal	Juv vs Fem	Mal vs Fem	Juv vs Mal	Juv vs Fem	Mal vs Fem
T_b	Estimate	0.030	−0.001	−0.002	−0.003	−0.001	−0.001	0.000	−0.002	−0.002	−0.000
	df	134	134	134	134	134	134	134	134	134	134
	P	< 0.001*	0.214	< 0.05*	< 0.05*	0.315	0.532	0.686	< 0.05*	< 0.05*	0.596
T_s	Estimate	0.034	−0.004	−0.000	−0.004	−0.004	−0.002	0.002	−0.000	−0.002	−0.002
	df	134	134	134	134	134	134	134	134	134	134
	P	< 0.001*	< 0.05*	0.966	< 0.05*	< 0.05*	0.121	0.079	0.908	< 0.05*	0.077
T_a	Estimate	0.033	−0.003	−0.000	−0.004	−0.003	−0.001	0.002	−0.000	−0.002	−0.002
	df	134	134	134	134	134	134	134	134	134	134
	P	< 0.001*	< 0.05*	0.882	< 0.05*	< 0.05*	0.456	0.063	0.829	0.095	0.160
$T_{set_{lo}}$	Estimate	0.028	−0.001	−0.002	−0.001	0.001	0.000	−0.001	0.000	−0.000	−0.000
	df	42	42	42	42	42	42	42	42	42	42
	P	< 0.001*	0.284	< 0.05*	< 0.05*	0.071	0.686	0.139	0.926	0.556	0.546
T_{sel}	Estimate	0.027	−0.000	−0.001	−0.001	0.000	0.000	−0.000	0.000	−0.000	−0.000
	df	42	42	42	42	42	42	42	42	42	42
	P	< 0.001*	0.240	0.061	< 0.05*	0.532	0.719	0.767	0.733	0.462	0.748
$T_{set_{up}}$	Estimate	0.026	−0.000	−0.000	−0.001	−0.000	0.000	0.000	0.000	−0.000	−0.000
	df	42	42	42	42	42	42	42	42	42	42
	P	< 0.001*	0.213	0.551	0.052	0.451	0.848	0.339	0.806	0.560	0.781
d_b	Estimate	2.828	1.117	0.174	0.034	2.719	1.727	0.991	1.776	0.645	−1.131
	df	5994	5994	5994	5994	5994	5994	5994	5994	5994	5994
	P	< 0.001*	< 0.001*	0.235	0.816	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*
d_e	Estimate	7.052	1.816	0.947	1.660	1.603	0.102	0.901	0.134	−0.054	−0.188
	df	5994	5994	5994	5994	5994	5994	5994	5994	5994	5994
	P	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	0.580	< 0.001*	0.468	0.771	0.309
E	Estimate	0.580	0.902	0.034	0.080	−0.313	−0.205	0.0803	−0.371	−0.216	0.155
	df	5994	5994	5994	5994	5994	5994	5994	5994	5994	5994
	P	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*

References: T_e, operative temperature; T_b, field body temperature; T_s, substrate temperature; T_a, air temperature; T_{sel}, mean preferred body temperature; $T_{set_{lo}}$, lower limit of the set-point range of preferred temperature; $T_{set_{up}}$, upper limit of the set-point range of preferred temperature; d_e, the index of thermal quality of the habitat; d_b, the index of accuracy of thermoregulation; E, the index effectiveness of thermoregulation; df, degree of freedom; P, probability value (α = 0.05); asterixs (*), statistically significant differences.

Table 3

Relationships among body, microenvironmental temperatures and body mass. Results from generalized linear models (GLMs) testing the effect of substrate and air temperatures (T_s and T_a) and body mass (BM) over the field body temperature of individuals (T_b).

		LATE SPRING				MID-SUMMER				OVERALL			
		Estimate	R^2	df	P	Estimate	R^2	df	P	Estimate	R^2	df	P
Juveniles													
T_b vs BM	Intercept	0.025		15	< 0.001*	0.028		29	< 0.001*	0.0284		46	< 0.001*
	Interaction	0.003	0.11	15	0.196	0.001	0.09	29	0.085	0.0012	0.10	46	< 0.050*
T_b vs T_s	Intercept	0.045		15	< 0.001*	0.049		29	< 0.001*	0.0470		46	< 0.001*
	Interaction	−0.000	0.36	15	< 0.050*	−0.000	0.37	29	< 0.001*	−0.0005	0.37	46	< 0.001*
T_b vs T_a	Intercept	0.036		15	< 0.001*	0.050		29	< 0.001*	0.0417		46	< 0.001*
	Interaction	−0.000	0.08	15	0.234	−0.000	0.27	29	< 0.001*	−0.0003	0.17	46	< 0.050*
T_s vs T_a	Intercept	0.056		15	< 0.001*	0.063		29	< 0.001*	0.059		46	< 0.001*
	Interaction	0.000	0.65	15	< 0.001*	−0.001	0.82	29	< 0.001*	−0.000	0.69	46	< 0.001*
Males													
T_b vs BM	Intercept	0.031		28	< 0.001*	0.031		21	< 0.001*	0.0308		51	< 0.001*
	Interaction	−0.000	0.02	28	0.400	−0.000	0.03	21	0.397	−0.0004	0.03	51	0.174
T_b vs T_s	Intercept	0.045		28	< 0.001*	0.037		21	< 0.001*	0.0417		51	< 0.001*
	Interaction	−0.000	0.35	28	< 0.001*	−0.000	0.20	21	< 0.050*	−0.0003	0.25	51	< 0.001*
T_b vs T_a	Intercept	0.039		28	< 0.001*	0.041		21	< 0.001*	0.0387		51	< 0.001*
	Interaction	−0.000	0.21	28	< 0.050*	−0.000	0.21	21	< 0.050*	−0.0003	0.17	51	< 0.050*
T_s vs T_a	Intercept	0.053		28	< 0.001*	0.065		21	< 0.001*	0.055		51	< 0.001*
	Interaction	−0.000	0.80	28	< 0.001*	−0.001	0.87	21	< 0.001*	−0.000	0.79	51	< 0.001*
Females													
T_b vs BM	Intercept	0.034		23	< 0.001*	0.037		12	< 0.001*	0.0310		37	< 0.001*
	Interaction	−0.001	0.11	23	0.096	−0.003	0.19	12	0.086	−0.0004	0.01	37	0.412
T_b vs T_s	Intercept	0.046		23	< 0.001*	0.041		12	< 0.001*	0.0447		37	< 0.001*
	Interaction	0.000	0.63	23	< 0.001*	−0.000	0.30	12	< 0.050*	−0.0004	0.51	37	< 0.001*
T_b vs T_a	Intercept	0.038		23	< 0.001*	0.038		12	< 0.001*	0.0404		37	< 0.001*
	Interaction	−0.000	0.24	23	< 0.050*	−0.000	0.06	12	0.380	−0.0003	0.22	37	< 0.050*
T_s vs T_a	Intercept	11.679		23	< 0.050*	0.065		12	< 0.001*	0.055		37	< 0.001*
	Interaction	0.645	0.58	23	< 0.001*	−0.001	0.53	12	< 0.001*	−0.000	0.61	37	< 0.001*

References: R^2, coefficient of determination; df, degree of freedom; P, probability value (α = 0.05); asterixs (*), statistically significant differences.

agreement with our prediction, we found that the Tb of *L. tandiliensis* varied according to the sampling period. In this regard, we found that the Tb of adults (males and females) was about 2.4–3.6 °C lower in late spring than in mid-summer. This temporal difference in the lizards' Tb is probably a mechanism to avoid the high cost of thermoregulatory behavior during periods of low thermal quality (Downes and Shine, 1998; Row and Blouin-Demers, 2006; Cadena and Tattersall, 2009). In general, year-round active species of areas with pronounced climatic seasonality tend to have a lower Tb during the cooler months compared to the Tb in the warmer months (Huey and Pianka, 1977; Grbac and Bauwens, 2001; Navarro-García et al., 2008; Maia-Carneiro et al., 2012). The differences in the regulated body temperature may reflect differential costs associated with thermoregulation in different thermal environments (Sears and Angilletta, 2015; Caldwell et al., 2017).

Liolaemus tandiliensis gained heat both from sun irradiation (heliothermy) and by conduction from the substrate (tigmothermy), since its Tb was positively related with the substrate temperature (Ts) and air temperature (Ta). In some particular cases, such as juveniles in late spring and females in mid-summer, substrate temperature constituted the most important heat source for thermoregulation. This assumption relies on the fact that the GLMs analyses showed an exclusive and positive relationship between Tb and Ts, but we did not observe a significant interaction between Tb and Ta. It is also possible that *L. tandiliensis* uses air or substrate temperatures as a temporal source of heat, depending on the environmental conditions, as other *Liolaemus* lizards that opportunistically use both strategies of heat exchange based on the fluctuating thermal properties of the environment (Martori et al., 2002; Bujes and Verrastro, 2006). Behavioral thermoregulation through the selection of different microenvironments seems to be flexible enough to partially cope with the environmental constraints of most of the studied species of *Liolaemus* that are efficient thermoregulators despite climatic adversity (Medina et al., 2009; Gutiérrez et al., 2010; Moreno Azócar et al., 2013; Valdecantos et al., 2013; Villalba, 2016). However, microenvironmental temperatures are not the only heat sources that can be used to achieve a certain Tb, as this will depend on behavioral and physiological adjustments, interactions with other environmental variables (e.g. radiation, wind speed), heat-transfer processes (radiation, convection, conduction), and the lizards' characteristics (size, color, and shape) (Stevenson, 1985; Clusella-Trullas et al., 2009; Moreno Azócar et al., 2016).

Overall, in both sampling periods, the mean preferred body temperature of *L. tandiliensis* ($Tsel = 37.4$ °C) was near the range of preferred temperatures registered for other species of *Liolaemus* ($Tsel = 34$–37 °C; Medina et al., 2009; Cruz et al., 2014). Contrary to our prediction, we observed changes in the thermal preferences of *L. tandiliensis*, particularly in adults depending on the sampling period (late spring or mid-summer). The variation in the preferred body temperature was observed not only by changes in the central tendency (mean) but also in the lower limit of the set-point range of preferred temperature ($Tset_{lo}$). Overall, the percentage of *L. tandiliensis* individuals that reached Tb within the set-point range of preferred temperature resulted higher in late spring (juveniles = 12%; males = 40%; females =16%) than in mid-summer (juveniles = 9%; males = 26%; females = 14%). Also, the thermoregulatory efficiency of *L. tandiliensis* was higher in late spring ($E = 0.55$) than in mid-summer ($E = 0.48$), despite there was a higher deviation of Te from the $Tset$ range in late spring (December $de \sim 7$) than in mid-summer (February $de \sim 5$). Reptiles can compensate for temporal changes in ambient temperature either by shifting their body temperature to the preferred range (thermoregulation *per se*) or by shifting their preferred range to match their body temperature (acclimatization, Little and Seebacher, 2016), as observed in this study. Our results are in agreement with Labra et al. (2009) and Artacho et al. (2017) who proposed that the adjustment of vital functions in some *Liolaemus* lizards is mediated by narrow changes in thermal preferences to exploit thermally challenging environments.

Sex and body mass affected the thermoregulatory efficiency of *L.*

tandiliensis. In both sampling periods, males had the highest thermoregulatory efficiency ($E_{summer} = 0.68$; $E_{spring} = 0.69$), followed by females ($E_{summer} = 0.50$; $E_{spring} = 0.58$) and juveniles ($E_{summer} = 0.28$; $E_{spring} = 0.38$). This may be explained by the fact that adults of *L. tandiliensis* exploited better quality thermal patches than juveniles, based on the measurements of microenvironmental temperatures (Ts and Ta). The effect of body mass on Tb was only observed in juvenile lizards that had a positive relationship between Tb and body mass. Relatively large juveniles had higher Tb and used warmer microhabitats when compared with the small-sized juveniles. This is in agreement with other authors, who found that the thermal physiology of small lizards may vary ontogenetically as a function of the morphological changes that occur in an individual's lifespan (Xu and JI, 2006; Tang et al., 2013; Gilbert and Lattanzio, 2016). Small-sized lizards have lower thermal inertia because they have a low surface to volume ratio, which in turn increases their susceptibility to heat exchange (Carothers et al., 1997; Garrick, 2008). Juveniles of *L. tandiliensis* might be more susceptible to heat loss than adults in the relatively cool ambient of the Tandilia Mountains. Smaller lizards can also be considered thermoconformers because equilibration time is related to body size. In this sense, the body temperature of small ectotherms tends to equilibrate with the operative temperature within a relatively short time (Seebacher and Shine, 2004).

Although to some degree the variation in the thermal biology of *L. tandiliensis* may originate from temporal fluctuations of the ambient temperature (i.e. thermal constraints associated with the sampling period), changes in the reproductive status may also interfere, as it was observed in other reptile species (Isaac and Gregory, 2004; Rodríguez-Díaz and Braña, 2012). In this study, the females of *L. tandiliensis* showed evidence of seasonal changes in their reproductive condition. The abdominal palpation, along with the fact that in late spring the mean body mass was 19% higher than the mean body mass measured in mid-summer, suggested that females were ovigerous in December but not in February. *Liolaemus tandiliensis* and other liolaemids that inhabit the SE Pampas have annual and seasonal reproductive cycles that start from late winter (August-September) until the beginning of summer (October-December; Vega and Bellagamba, 2005; Vega, 1999; Vega et al., 2008). Most *Liolaemus* species have annual female reproductive cycles, except those that present multiennial cycles in cold harsh environments (Medina and Ibargüengoytía, 2010; Fernández et al., 2015). In temperate environments, the reproductive cycles of lizards are characteristically seasonal, alternating periods of reproductive activity and brumation, in which males and females synchronize their ovary and testes cycles during the year (Cruz-Elizalde and Ramírez-Bautista, 2016). The synchronism between the reproductive cycle and the climatic cycle plays a vital role in liolaemids from temperate climates since it maximizes the growth of neonates during summer in order to reduce the risk of perishing in winter (Ibargüengoytía, 2008). Changes in the physiological state due to reproduction may induce shifts in the thermoregulatory parameters of lizards (Mathies and Andrews, 1995; Labra and Bozinovic, 2002). Ovigerous females of many species of lizards select low Tbs and thermoregulate with a greater precision to maintain a stable temperature for the correct development of the embryos (Braña et al., 1993; Rodríguez-Díaz and Braña, 2012; Cruz et al., 2014). On the other hand, males select moderate temperatures to stimulate testicular enlargement and spermiogenesis (Licht et al., 1969; Ibargüengoytía and Cussac, 1998; Gribbins, 2010).

5. Conclusion

Our results allow us to conclude that *L. tandiliensis* lizards shift their thermal parameters (Tb, $Tsel$, $Tset_{low}$ and db) in two different periods of the year, precisely in late spring and mid-summer. The thermoregulatory parameters lability may improve the thermoregulatory efficiency against the constraints imposed by seasonal changes related to the environmental thermal regime, and possibly with variations in the

physiological status according to the endogenous cycle of the individuals. Although the temporal variation of ambient temperatures influences the thermal biology, it is important to take into account that other factors, such as changes in the reproductive status may have also interfered in our results. The main objective of this study was to analyze if the thermal biology of *L. tandiliensis* varied between two different periods of the year considering that ectotherms acclimatize over a relatively short period of time, usually days to weeks. Therefore, the extrapolation of our results to larger temporal scales should be made with caution. We believe that further studies are needed in order to elucidate the main factors that drive intraspecific changes in the thermal biology of *L. tandiliensis*.

Acknowledgements

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