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Article in *Zoologia (Curitiba Impresso)* · February 2010

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Thermoregulation and activity pattern of the high-mountain lizard *Phymaturus palluma* (Tropiduridae) in Chile

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ABSTRACT. Behavioral and physiological mechanisms of thermoregulation in ectotherms are conditioned by thermal constraints. These mechanisms may be even more restrictive when environmental conditions are unfavorable for individuals, especially when sexual dimorphism segregates the sexes spatially. In order to understand behavioral and physiological regulation mechanisms, we investigated the thermal biology of *Phymaturus palluma* (Molina, 1782), a sexually size dimorphic, high-mountain lizard that inhabits extreme climatic conditions. *P. palluma* showed a bimodal activity pattern, a major peak in the morning (11:00-13:30h) and in the afternoon (15:30-18:00 h). The lizards were more active when substrate temperatures were between 25 and 28° C. The highest abundance was found around 27° C (between 11:00-12:30). Females showed greater activity than males in the early morning. Sub-adults and juveniles did not show differences in their activity pattern. There was a positive relationship between body temperature and air and substrate temperatures, suggesting typically thigmothermal regulation.

KEY WORDS. Age classes; daily activity; sexual dimorphism.

Thermoregulation influences physiological, behavioral and ecological features in ectotherms (AVERY 1982, BAUWENS *et al.* 1996, SEEBACKER & FRANKLIN 2005). Behavioral mechanisms allow temperature regulation, including changes in activity times, the selection of thermally appropriate microhabitats, and postural adjustments (PORTER & GATES 1969, HUEY & SLATKIN 1976, DUNHAM *et al.* 1989, ADOLPH 1990, ADOLPH & PORTER 1993, HERTZ *et al.* 1993, BAUWENS *et al.* 1996, TRACY & CHRISTIAN 1996, MELVILLE & SCHULTE 2001, SEARS 2005). In lizards, thermoregulatory behavior and microhabitat selection are correlated because the thermal microclimates vary in space (BARTLETT & GATES 1967, ROUGHGARDEN *et al.* 1981, MELLA 2007), promoting intra and interspecific differences (MARQUET *et al.* 1989, ADOLPH 1990, CORTÉS *et al.* 1992, HERTZ *et al.* 1994, VERRASTRO & BUJES 1998, LABRA *et al.* 2001, 2008, LABRA & VIDAL 2003).

In most animal groups, sexual differences in morphological characters (sexual dimorphism) is a common phenomenon, particularly in body size. The direction of this difference, i.e., whether males or females are larger, differs between animal groups; in vertebrates males typically constitute the sex with larger body size (SCHOENER *et al.* 1982, SHINE 1986, FAIRBAIRN 1990,

1997, ANDERSSON 1994). Several proximate mechanisms have been proposed to explain sexual dimorphism, such as differential mortality of sexes (STAMPS 1993) and different growth rates of sexes (WATKINS 1996); however, natural or sexual selection remains the ultimate mechanism explaining sexual dimorphism (SHINE 1986, ANDERSON 1994, WATKINS 1998). In species with sexual dimorphism, thermal behavior and microhabitat use have many ecological implications due to the displacement of sexes to favorable or unfavorable thermal sites (SCHEERS & VAN DAMME 2001, VIDAL *et al.* 2002) or they may determine a highly variable daily pattern (WINNE & KECK 2004, RADDER *et al.* 2005).

Phymaturus palluma (Molina, 1782) is a high-mountain, ovoviviparous, saxicolous and herbivorous lizard (DONOSO-BARROS 1966, LAMBOROT & NAVARRO 1984) that inhabits niches between 31°S and 38°S in Chile (DONOSO-BARROS 1966, VIDAL 2008). This lizard is exposed to harsh environments with cold and snowy winters and it hibernates throughout the winter and part of spring and autumn (DONOSO-BARROS 1966), which is a particular thermal strategy to enable it to withstand these environments. *Phymaturus palluma* shows sexual size dimorphism (HABIT & ORTIZ 1994), and during the reproductive season (November to March,

IBARGÜENGOYTÍA 2008) it forms hierarchic systems in which dominant males have a more extensive home range than females and juveniles (HABIT & ORTIZ 1996a,b). The spatial segregation in *P. palluma* may reflect differences in thermal strategies (VIDAL *et al.* 2002, LABRA *et al.* 2008) because males would have access to better resources than females and juveniles. To understand the behavioral and physiological thermal mechanisms used by *P. palluma* in response to spatial segregation, we analyzed intersexual and age differences in daily activity patterns. If the rigorous environment exerts selection pressure on the thermoregulatory traits in this species, and if also dimorphism determines the quality of the microhabitat used, then we expect to find that males and females have differences in their thermoregulatory ability. We expect that females and juveniles, being at a thermal disadvantage compared to males, will be more efficient in the use of space and in their thermoregulatory ability.

MATERIAL AND METHODS

The study was performed during November-March (austral spring and summer) in 1986-1987 and in 2002-2004 in Laguna del Laja National Park, Chile (37°20'S, 71°18'W, 1700 m.a.s.l.). To investigate the activity patterns of *P. palluma*, we established linear transects during the entire daily activity period of lizards (08:30 to 20:30 h). These transects were walked in opposite directions to minimize the probability of repeated counts of the same individual. For each lizard observed, sex, age class, and time of day were recorded. Additionally, one hundred and seven lizards (56 females and 51 males) were collected and thermal data were recorded. Upon capture, the following temperatures were recorded: body (cloacal, T_b), air (10 cm above the substrate, T_a), and substrate (in contact with the surface, T_s) with a Cu-Constantan thermocouple (Cole Parmer® thermometer, $\pm 0.1^\circ\text{C}$). Sex and body size (snout-vent length, SVL) were recorded for each lizard. Body classes were defined as juveniles (males and females: 48.7-64.0 mm), subadults (males: 65.0-84.0 mm and females: 65.0-80.0 mm) and adults (males: >84.0 mm and females: >80.0 mm) according to HABIT & ORTIZ (1996a).

Differences in SVL between sexes and age classes were analyzed by two-way Analysis of Variance (ANOVA), followed by HSD-Tukey tests (ZAR 1999). Prior to ANOVA, homogeneity of variance and normality were tested by the Levene and Kolmogorov-Smirnov tests, respectively (SOKAL & ROHLF 1996). A two-way ANCOVA was used to investigate T_b differences between sexes and age classes, using SVL as covariate. Variation in daily activity patterns between sexes was analyzed by a G test (ZAR 1999). Data were pooled in four blocks of three hours. The relationship between the frequency of individuals and T_a and T_s was analyzed by Pearson correlation (SOKAL & ROHLF 1996). The thermoregulatory ability was estimated from the variance of T_b , and from the slopes of the linear regressions (SOKAL & ROHLF 1996) between T_b and T_a and between T_b and T_s (HUEY 1982, PEREZ-MELLADO & RIVA 1993). A slope equal to one indicates that animals are completely thermoconformers (BÁEZ & CORTÉS 1990).

RESULTS

Body size (SVL) differed significantly between sexes ($F_{1,98} = 3.55$, $p < 0.05$) and among age classes ($F_{2,98} = 393.57$, $p < 0.001$, Tab. I). All age classes were different (HSD-Tukey tests, $p < 0.001$). Contrary to the expected, T_b did not show significant differences between sexes ($F_{1,98} = 0.355$, $p > 0.05$) or among age classes ($F_{2,98} = 1.06$, $p > 0.05$). Lizards had a bimodal daily activity pattern; the frequency recorded in the morning (11:00-13:30 h) was greater than in the afternoon (15:30-18:00 h), and the highest activity was observed at around 25° to 28° C (Fig. 1).

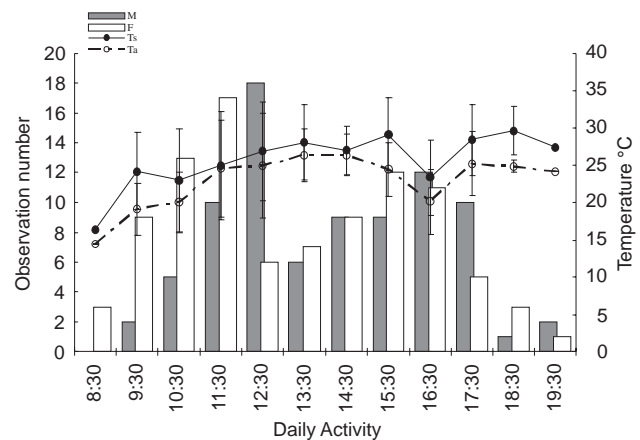
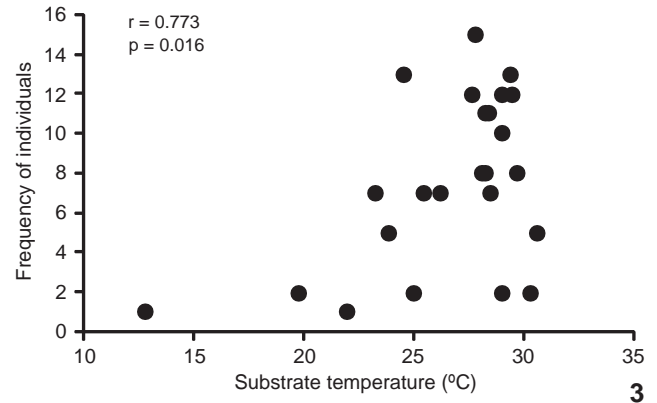
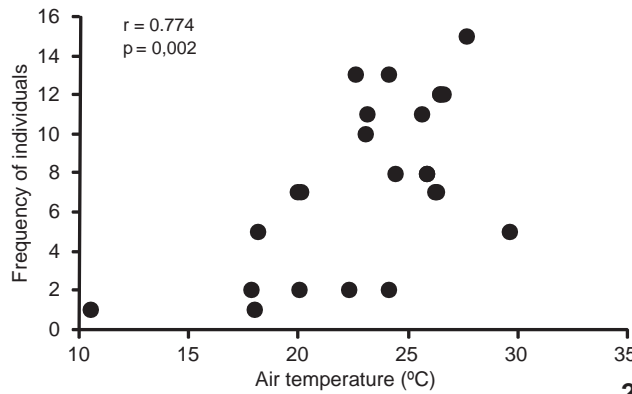


Figure 1. Daily activity pattern of males (black bar) and females (white bar) of *Phymaturus palluma*. Mean values and standard deviation of air temperature (T_a , dashed line) and substrate temperature (T_s , solid line) are indicated.

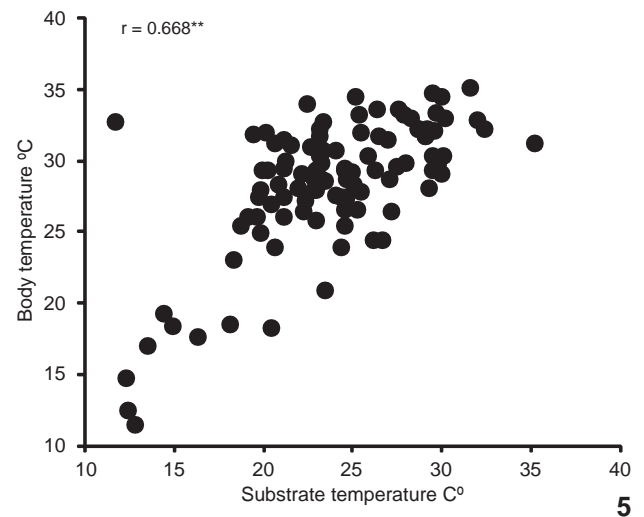
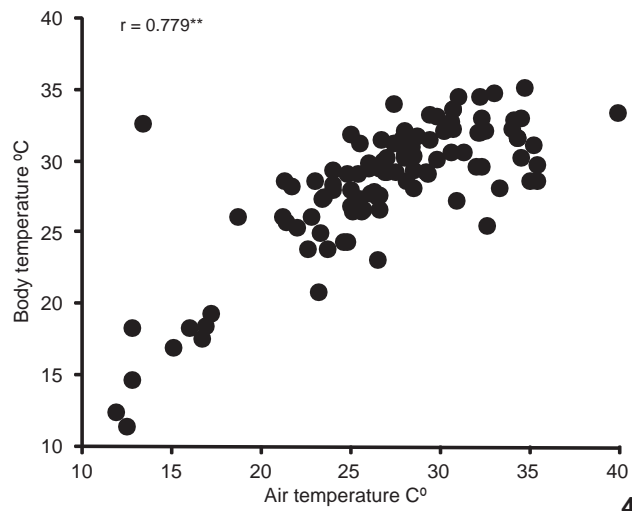
The number of lizards observed at different times of day varied significantly. Females emerged earlier than males, when T_a and T_s had not exceeded 20° C ($\chi^2 = 10.6$, $p < 0.05$), whereas males were only active when the temperature was about 27° C (12:30-13:30 and 16:00-17:00 h). The frequency of individuals was positively correlated with $T_a - T_s$ (Figs 2 and 3). Furthermore, significant relationships were found between T_b and T_a (Fig. 4) and between T_b and T_s (Fig. 5). The thermoregulatory ability estimated showed that *P. palluma* is a thermodependent species because the slopes were positively related.

DISCUSSION

Thermal behavior and microhabitat selection are usually correlated with the spatial and temporal variability in thermal resources (PORTER *et al.* 1973, LABRA & VIDAL 2003). *Phymaturus palluma* showed a high thermoconformism, although many species that occur in highly fluctuating habitats are thermoregulators (VIDAL *et al.* 2002, IBARGÜENGOYTÍA 2005). This species has activity patterns limited in time and a long hibernation period due to being exposed to extreme seasonal changes. Energetic



Figures 2-3. Frequency of lizards in relation to (2) air temperature and (3) substrate temperature in *Phymaturus palluma*.



Figures 4-5. Relationship between (4) body and air temperature (T_b - T_a), and (5) body and substrate temperature (T_b - T_s) in *Phymaturus palluma*. r and $p < 0.01$ are indicated by **.

Table I. Descriptive statistics (mean \pm standard deviation) of body size – snout-vent length (SVL, mm), body temperature (T_b), air temperature (T_a) and substrate temperature (T_s) of females and males of different age classes for *P. palluma*. (n) Sample size.

Age classes	Sex	n	SVL	T_b	T_a	T_s
Adults	Females	28	90.3 \pm 3.6	27.4 \pm 4.8	25.9 \pm 5.7	23.3 \pm 4.4
	Males	31	91.4 \pm 4.9	28.7 \pm 4.8	26.5 \pm 5.0	24.8 \pm 4.3
Subadults	Females	13	70.8 \pm 4.1	28.6 \pm 2.2	29.0 \pm 5.5	24.1 \pm 4.7
	Males	8	72.1 \pm 3.5	30.9 \pm 5.3	24.1 \pm 6.7	25.2 \pm 4.5
Juveniles	Females	13	56.8 \pm 6.4	28.8 \pm 5.1	27.2 \pm 6.5	23.8 \pm 5.1
	Males	11	57.1 \pm 5.4	29.4 \pm 5.0	26.6 \pm 6.2	22.6 \pm 5.4

costs are high in these cases, forcing individuals to maintain body temperature near the temperature of the environment (CRUZ *et al.* 2009). These ecological constraints may be compensated by behavioral thermoregulation (HERTZ & HUEY 1981,

VAN DAMME *et al.* 1989, LEMOS-ESPINAL & BALLINGER 1995, HUEY *et al.* 2003). It is well known that lizards from cooler habitats can compensate the high cost of thermoregulation by increasing basking time and using microhabitats differentially (HERTZ &

HUEY 1981, CHRISTIAN *et al.* 1983, DUNHAM *et al.* 1989, ADOLPH & PORTER 1993, 1996, BAUWENS *et al.* 1996). Additionally, lizards can change body posture and/or body orientation to the sun (BAUWENS *et al.* 1996, GVO•DIK 2002), and change activity patterns (VAN DAMME *et al.* 1989, BAUWENS *et al.* 1996).

Phymaturus palluma showed a clear sex difference in activity patterns, but not in T_b . The overall, mean body temperature of *P. palluma* was 29° C. This temperature is similar to that reported by IBARGUENGOYTÍA (2005) for *P. patagonicus* Koslowsky, 1898 although LABRA & VIDAL (2003) reported temperatures around 22° C for *P. palluma*. They pointed out that the low body temperature is a consequence of constraints to thermoregulation. In this context, *P. palluma* was found basking on rocks with the body surface exposed to the substrate. This may indicate that heat surface accounts for a greater percentage of body temperature variance, and suggests a predominantly thigmotherm behavior such as that found in *P. patagonicus* (IBARGUENGOYTÍA 2005).

Body temperature is often influenced by activity time (PAULISSEN 1999) and the daily thermal cycle (WINNE & KECK 2004) to maximize prey ingestion, digestive efficiency, reproduction and growth (IBARGUENGOYTÍA 2005). We found that *P. palluma* lizards had a bimodal daily activity pattern and most individuals were active between 11:00-13:30 and between 15:30-18:00 h. In general, lizards are cool in the early morning just after they emerge from their refuges and warm up at different rates until they have reached the body temperature at which they will remain active for the rest of the day (HABIT & ORTIZ 1996b, PAULISSEN 1999, IBARGUENGOYTÍA 2005, LABRA *et al.* 2008). We did not find variation in T_b among age classes; the hierarchical social behavior of *P. palluma* (HABIT & ORTIZ 1994) could imply changes in microhabitat use and the time spent, however, this was not determined in the field.

Several studies have pointed out that skin color in lizards plays an important role in thermoregulation, because darker reptiles are able to warm faster and maintain higher body temperatures (CRISP *et al.* 1979, BITTNER *et al.* 2002, LUTTERSCHMIDT *et al.* 2003, RANDRIAMHAZO & MORI 2005). In many vertebrates, males tend to be more colorful than the females, particularly during the reproductive season (COOPER *et al.* 1983, COOPER 1988, WATKINS 1997), whereas females tend to have the same colors as the substrate, decreasing the risk of predation, especially during pregnancy (ENDLER 1978, COOPER & GREENBERG 1992, ANDERSON 1994, WATKINS 1997, CUADRADO 2000, MACEDONIA *et al.* 2000). Males and females of *P. palluma* showed sexual dimorphism in color pattern and morphology. In fact, females are darker and more flattened than males (DONOSO-BARROS 1966), thus they increase their area-volume relationship, being able to gain heat faster than the males. This agrees with IBARGUENGOYTÍA (2005) who suggested that females of *P. patagonicus* have a greater control over heating than males, indicating some physiological control over heat gain and loss. On the other hand, the intersexual differences in daily activity patterns may be explained because dominant males have

to patrol an extensive home range to maintain the harem (FERGUSON 1970, WALDSCHMIDT & TRACY 1983). In addition, an extensive home range allows them to have access to a greater availability of thermal microhabitats for foraging activities than the females and juveniles (SCHEERS & VAN DAMME 2001, VIDAL *et al.* 2002). Thus, females must display activities earlier to diminish the pressure of dominant males on microhabitat selection (BAUWENS *et al.* 1996, MELVILLE & SCHULTE 2001). Females emerge earlier than males, possibly to occupy favorable microhabitats and increase a thermal opportunity for thermoregulatory behavior. Although our results did not show age class differences in T_b , a clear temporal niche separation between males and females is obvious in *P. palluma*. The hierarchical social behavior of this lizard appears to influence intraspecific differences in microhabitat selection and in the time spent engaging in thermoregulatory behavior and foraging activities (LABRA *et al.* 2008).

In conclusion, our data support the hypothesis that daily activity patterns differ among sexes but not among age classes in *P. palluma*. Sex differences may probably be due to the hierarchical social system that induces mainly behavioral adjustments for thermal processes. We suggest that *P. palluma* uses a wide display of behaviors (but not physiological regulation) that allows individuals to thermoregulate above the ambient temperature, as has been found for *P. patagonicus* in Argentina (IBARGUENGOYTÍA 2005). According to STEVENSON (1985), behavioral mechanisms contribute to changes in T_b that may be four to five times greater than those provided by physiological mechanisms. This is because behavior is seemingly more plastic than physiology.

ACKNOWLEDGEMENTS

We thank to Hector Ibarra-Vidal by the field assistance. This study was partly funded by NSF PIRE 05-533 to EH and PV and DIUC 205.113.067-1sp of the Universidad de Concepción.

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Submitted: 04.III.2009; Accepted: 18.I.2010.

Editorial responsibility: Kleber del Claro