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

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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 27º 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, Meville & 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 (Schneider et al. 1982, Shine 1986, Fairbairn 1990, Anderson 1994, 1997). 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,
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 (37º20’S, 71º18’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, *Tb*), air (10 cm above the substrate, *Ta*), and substrate (in contact with the surface, *Ts*) with a Cu-Constantan thermocouple (Cole Parmer® thermometer, ± 0.1°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 *Tb* 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 *Ta* and *Ts* was analyzed by Pearson correlation (SOKAL & ROHLF 1996). The thermoregulatory ability was estimated from the variance of *Tb*, and from the slopes of the linear regressions (SOKAL & ROHLF 1996) between *Tb* and *Ta* and between *Tb* and *Ts* (HUEY 1982, PEREZ-MELLADO & RIVA 1993). A slope equal to one indicates that animals are completely thermoformers (BÁEZ & CORTÉS 1990).

RESULTS

Body size (SVL) differed significantly between sexes (*F*<sub>1,98</sub> = 3.55, *p* < 0.05) and among age classes (*F*<sub>2,98</sub> = 393.57, *p* < 0.001, Tab. I). All age classes were different (HSD – Tukey tests, *p* < 0.001). Contrary to the expected, *Ts* did not show significant differences between sexes (*F*<sub>1,98</sub> = 0.355, *p* > 0.05) or among age classes (*F*<sub>2,98</sub> = 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.](image)

The number of lizards observed at different times of day varied significantly. Females emerged earlier than males, when *Tb* and *T*<sub>a</sub> had not exceeded 20°C (*χ<sup>2</sup> = 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*<sub>a</sub>-*T*<sub>s</sub> (Figs 2 and 3). Furthermore, significant relationships were found between *T*<sub>b</sub> and *T*<sub>a</sub> (Fig. 4) and between *T*<sub>s</sub> and *T*<sub>a</sub> (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, IRARGÜENGÖYTA 2005). This species has activity patterns limited in time and a long hibernation period due to being exposed to extreme seasonal changes. Energetic...
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 &
they emerge from their refuges and warm up at different rates
h. In general, lizards are cool in the early morning just after
als were active between 11:00-13:30 and between 15:30-18:00
lizards had a bimodal daily activity pattern and most individu-
tern and morphology. In fact, females are darker and more flat-
reptiles are able to warm faster and maintain higher body tem-
plays an important role in thermoregulation, because darker
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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 (Schers & 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
Tb, 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 use 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 hier-
archical social system that induces mainly behavioral adjust-
ments 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
(Ibargueynotí 2005). According to Stevenson (1985), behav-
ioral mechanisms contribute to changes in Tb that may be four to five times greater than those provided by physiological mechanisms. This is because behavior is seemingly more plastic than physiology.

Huey 1981, Christian et al. 1983, Dunham et al. 1989, Adolphi &
Porter 1993, 1996, Bauwens et al. 1996). Additionally, lizards can change body posture and/or body orientation to the sun
(Bauwens et al. 1996, Gvozdi 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 Tb. The overall, mean body temperature of P. palluma was 29° C. This temperature is similar to that
reported by Ibargueynotí (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
(Ibargueynotí 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 (Ibargueynotí 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, Ibargueynotí 2005, Labra et al. 2008). We did
not find variation in Tb 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 tem-
peratures (Crisp et al. 1979, Bittner et al. 2002, Lutterschmidt et al.
2003, Randriamahazo & 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 (Eschler 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 Ibargueynotí (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
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