

Effect of thermal acclimation on preferred temperatures in two mygalomorph spiders inhabiting contrasting habitats

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Abstract. Variations in the preferred temperatures during the rest periods of *Grammostola rosea* Walckenaer and *Paraphysa parvula* Pocock, two mygalomorph spiders occupying different habitats in central Chile, are analyzed. The former inhabits arid and semi-arid lowland near plant communities, composed of shrubs (evergreens with small leathery leaves) and small trees; the latter is found in the central mountains of the Chilean Andes, above 2000 m.a.s.l. The preferred temperatures of these spiders at different times of day and exposure to cold (15 °C) and warm (25 °C) acclimation temperatures are compared. Body mass does not affect the preferred temperature of the larger spider *G. rosea*, although *P. parvula*, a spider with half of the body mass of *G. rosea*, shows a decrease in preferred temperature with body mass. This can be explained by a higher plasticity and thermal sensitivity of the smaller species as result of increased surface : volume ratio. The preferred temperature increases with the hour of the day under both acclimation conditions in *P. parvula* and in cold-acclimated *G. rosea*, which is likely associated with crepuscular and nocturnal behaviour in both species. *Grammostola rosea* shows temperature preferences lower than those of *P. parvula* under both acclimation conditions. The increase of the acclimation temperature from 15 to 25 °C results in an increment of 2–3 °C in the preferred temperature of *P. parvula* but only 0.2 °C in that of *G. rosea*. Two contrasting lifestyle strategies are found: a small mygalomorph spider with phenotypic plasticity and adaptation to the fluctuating environment of high altitude, and a large mygalomorph spider with higher thermal inertia adapted to the more stable environment of lowlands.

Key words. Acclimation, mygalomorph, preferred temperature, spider.

Introduction

Mygalomorph spiders are ectotherm predators that depend upon thermal micro-environments for energy saving, reproduction and capture of their prey (Greenstone & Bennett, 1980; Humphreys, 1987; Schmalhofer, 1999; Canals *et al.*, 2007; Figueroa *et al.*, 2010; Veloso *et al.*, 2012). However, thermoregulatory behaviour, thermal tolerance and preferred temperatures are only studied in less than 1% of the species

of spiders (Humphreys, 1987), and the species that inhabit temperate environments are less well known (Schmalhofer, 1999). Studies of thermal biology of spiders are limited to understanding the thermal tolerances of a few species and their relationship with the habitat (Humphreys, 1987; Schmalhofer, 1999; Frick *et al.*, 2007; Hanna & Cobb, 2007). In particular, in mygalomorph spiders, only the preferred temperatures of *Aphonopelma* sp. and *Paraphysa parvula* are reported (Seymour & Vinegar, 1973; Shillington, 2002; Veloso *et al.*, 2012).

Information regarding thermal preferences is necessary to assess the suitability of thermal habitats and to describe the thermal ecology of a species (Hertz *et al.*, 1993; Canals,

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1998). For example, during the mating season, although females of the tarantula *Aphonopelma anax* remain fossorial at stable temperatures below 40 °C, male tarantulas abandon their burrows and search actively for females. Consequently, they experience fluctuating temperatures, particularly during the day, during which they thermoregulate effectively. However, at night, they are exposed to environmental temperatures in the range of this preferred temperature: 22.1–31.3 °C (Shillington, 2002). In *Peucetia viridians* (Oxyopidae), different mean temperatures at death (lethal temperatures) in gravid (49.4 °C), postparturient females (47.2 °C) and male spiders (46.9 °C) suggest different preferred temperatures depending on the sex and gravidity condition (Hanna & Cobb, 2007). Studies on the influence of temperature on foraging activity and prey handling in the burrowing spider *Seothyra* sp. (Eresidae) show that this species can forage at web temperatures above 65 °C by moving between the hot surface and the cooler burrow, supporting the hypothesis that web design and thermoregulatory behaviour enable it to hunt under extreme thermal conditions (Lubin & Henschel, 1990).

Spiders can regulate their body temperature by behavioural mechanisms, including, orientation (mostly in orb weavers), changing position in burrows, restricting activities and evaporative cooling (Shillington, 2002). Some spiders have also been shown to select retreat sites in accordance with the thermal properties of the environment (Hammerstein & Riechert, 1988). Species from different environments typically also have different thermal preferences (Pulz, 1987; Schmalhofer, 1999) and these may vary seasonally (Schmalhofer, 1999), with the breeding season (Hanna & Cobb, 2007; Veloso *et al.*, 2012) or during the day, as in other ectotherms (Canals *et al.*, 1997). However, acclimation temperatures are reported to have no effect on the thermal preferences of araneomorph and mygalomorph spiders (Sevacherian & Lowrie, 1972; Seymour & Vinegar, 1973). In the present study, variations in the preferred temperatures during the rest periods of *Grammostola rosea* Walckenaer and *P. parvula* Pocock, two mygalomorph spiders of central Chile with different habitats, are analyzed. The former inhabits arid and semi-arid lowland near sclerophyll forests (evergreens shrubs with small leathery leaves) and the latter inhabits the central mountains of the Chilean Andes, comprising a variable environment in which the environmental temperature can vary in the range 0–40 °C and where the substrate surface temperature can exceed 60 °C (Veloso *et al.*, 2012). The temperature preferences at different times at different times of day are compared in spiders exposed to low and high acclimation temperatures. It is expected that acclimation of the preferred temperature will be found in the spider of a smaller body size that inhabits a more variable environment.

Materials and methods

Two species of the family Theraphosidae: *G. rosea* ('Chilean rose tarantula') and a population of *P. parvula* were studied. *Grammostola rosea* is a species of arid and semi-arid areas of Chile. The adult has a body mass of 12–22 g (Canals *et al.*, 2007). It digs shelters near trees and rocks and displays a

crepuscular and nocturnal activity. The small mygalomorph spider *P. parvula* can be found in the mountains at altitudes above 2000 m.a.s.l. It is a small animal with a body mass of approximately 6–10 g. Its behaviour and activity rhythms are similar to those of *G. rosea*.

The specimens of *G. rosea* were obtained from a breeding culture in Santiago, Chile (550 m.a.s.l.). They were raised at environmental temperatures typical of their distribution area. The individuals of *P. parvula* were obtained from a population in the central Andes of Chile (Farellones, 33°21'S 70°20'W) at approximately 2400 m.a.s.l. The area of capture was dominated by low shrubs, mainly *Chuquiraga oppositifolia*, *Ephedra chilensis* and *Acaena splendens* (Rosaceae), as well as numerous small rocks.

Ten adult individuals of *G. rosea* (five females and five males) with a body mass 10.31 ± 2.05 g (mean \pm SD) and 12 adult individuals of *P. parvula* (body mass 4.78 ± 1.14 g; one male and 11 females) were acclimated for 3 weeks at a constant temperature of 15 ± 1 °C (cold acclimation) in a thermo-regulated chamber. Individual spiders were then placed in the centre of a thermal gradient with temperatures varying between 15 and 50 °C, comprising the range that both species can experience in their natural environments. The apparatus consisted of a brass chamber (100 × 30 × 40 cm), the bottom of which was filled with sand. Under the sand, the hot end had a copper coil heater and the cold end was left at the ambient temperature of the chamber. At approximately 0.5 mm from the surface of the sand, five thermocouples were installed equidistant to record the temperatures continuously, showing a decreasing temperature gradient from 50 ± 5 °C at the hot end to 15 ± 5 °C at the cold end. Spiders were introduced individually into the gradient at 08.00 h (± 30 min) and maintained for 10 h, allowing the free movement of individuals, even when they climbed the walls of the gradient chamber. The spiders were allowed 2 h to acclimate to the gradient, and then the body temperature of individuals was recorded every 2 h (at 10.00, 12.00, 14.00, 16.00 and 18.00 h) with an infrared thermometer (model IR201; Extech Instruments, Nashua, New Hampshire), installed 10 cm from the surface of the body of the animal, allowing measurement of the temperature at one point on the surface of the spider (usually the midpoint between the cephalothorax and the abdomen). The measurement accuracy of the infrared thermometer was studied previously by comparing the measurements of the soil temperature with this device and the measurement obtained with a copper thermocouple. The body temperature was measured three times at each observation and averaged. This value estimated the preferred temperature at this particular hour of the day (T_p). Only values of spiders at rest were considered. Temperatures recorded from spiders that were actively moving were discarded. After the first series of experiments, spiders were allowed to rest for 1 week at room temperature. These same individuals were then acclimated for 3 weeks at 25 ± 2 °C (warm acclimation). Subsequently, they were subjected to a second experimental series in the thermal gradient chamber under the same conditions as those used in the first experimental trials. Throughout the experiment, the

animals were kept in individual boxes with food (*Tenebrio molitor* larvae) and water available *ad libitum*. Before each experiment, animals were weighed on an electronic balance (± 0.01 g).

The relationships between preferred temperature, body mass and time of day for each species at each acclimation temperature were examined using regression analysis. The mean preferred temperature for each individual was estimated taking the mean of all temperatures measured (τ_p). Finally, the differences between species and the effect of acclimation temperature on preferred temperature were analyzed by repeated-measure analysis of variance, using the residuals of a regression between preferred temperature and hour as the dependent variable and temperature as the repeated variable because the preferred temperature varied with the hour of the day.

Results

Preferred temperature and body mass

Grammostola rosea did not show a relationship between body mass and the preferred temperature after cold acclimation (slope $\beta = 0.24$, $R^2 = 0.09$; $F_{1,8} = 0.07$, $P = 0.80$) or warm acclimation ($\beta = 0.15$, $R^2 = 0.003$; $F_{1,8} = 0.28$, $P = 0.61$). Similar results were found for cold-acclimated *P. parvula* ($\beta = -1$, $R^2 = 0.15$; $F_{1,10} = 1.82$, $P = 0.21$) but, in warm-acclimated *P. parvula*, a negative correlation between preferred temperature and body mass was found ($\beta = -1.35$, $R^2 = 0.46$; $F_{1,10} = 8.67$, $P = 0.014$) (Figs 1 and 2).

Preferred temperature and time of day

The body mass of each species not varied between the two acclimation temperatures. This result allowed us to

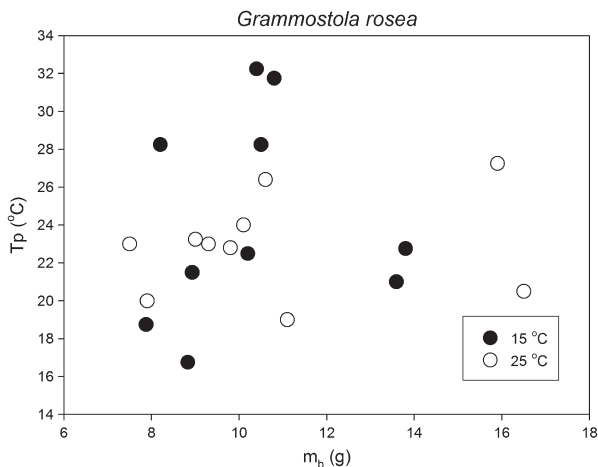


Fig. 1. Variations of preferred temperatures (T_p) with body mass (m_b) in the large mygalomorph spider *Grammostola rosea* for two acclimation conditions. The slopes of regression lines (not represented) were not different from 0.

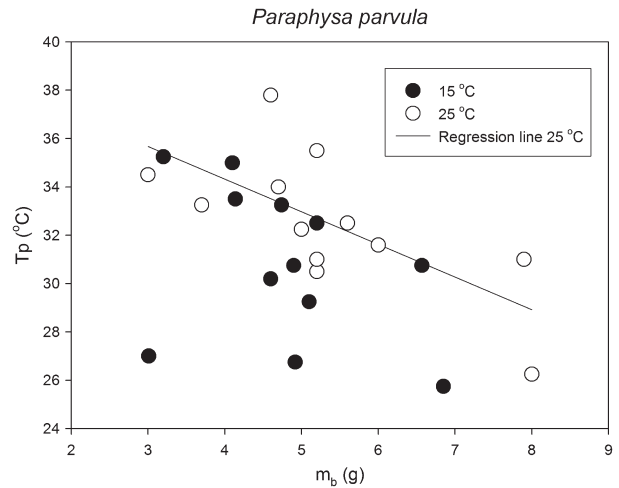


Fig. 2. Variations of preferred temperatures (T_p) with body mass (m_b) in the smaller mygalomorph spider *Paraphysa parvula* for two acclimation conditions. Only the regression line at 25 °C is plotted.

analyze the relationship between preferred temperature and time of day in which this was chosen without mass effects. In cold-acclimated *G. rosea*, a variation throughout the day in the preferred temperature was observed, gradually increasing towards evening ($R^2 = 0.162$; $F_{1,48} = 9.28$, $P = 0.03$). However, this increment was not evident in the same individuals when they were warm acclimated ($R^2 = 0.025$; $F_{1,48} = 1.21$, $P = 0.28$). *Paraphysa parvula* showed increases in preferred temperatures towards evening when the individuals were cold acclimated ($R^2 = 0.40$; $F_{1,58} = 38.14$, $P = 0.0001$) and warm acclimated ($R^2 = 0.39$; $F_{1,56} = 35.20$, $P = 0.002$) (Figs 3 and 4).

Interspecific differences and the effect of acclimation temperature on the preferred temperature

Grammostola rosea showed preferred temperatures lower than those of *P. parvula* for both acclimation conditions ($F_{1,105} = 39.44$, $P < 0.001$). The increase of the acclimation temperature from 15 to 25 °C resulted in a significant effect on preferred temperature of each species ($F_{1,105} = 5.96$, $P = 0.002$) with an interaction effect between species and acclimation temperature ($F_{1,105} = 4.19$, $P = 0.04$). Female and male spiders showed similar mean preferred temperatures: 24.6 ± 4.1 and 22.7 ± 3.0 , respectively ($F_{1,7} = 0.34$, $P = 0.7$). The acclimation temperature and interaction effects were the result of an increase of the mean preferred temperature in *P. parvula*: $\tau_p = 27.58 \pm 8.27$ °C when cold acclimated (median = 28 °C, mode = 26 °C, range 25.75–35.25 °C) and 29.94 ± 6.29 °C when they were warm acclimated (median = 31 °C, mode = 33 °C, range 26.25–37.8 °C) ($P = 0.007$). However, the mean preferred temperatures for *G. rosea* were similar for both acclimation temperatures: $\tau_p = 22.64 \pm 6.34$ °C when cold acclimated (median = 21 °C, mode = 20.18 °C, range 18.75–32.25 °C) and 22.82 ± 3.64 °C when warm acclimated (median = 23 °C, mode = 23 °C, range

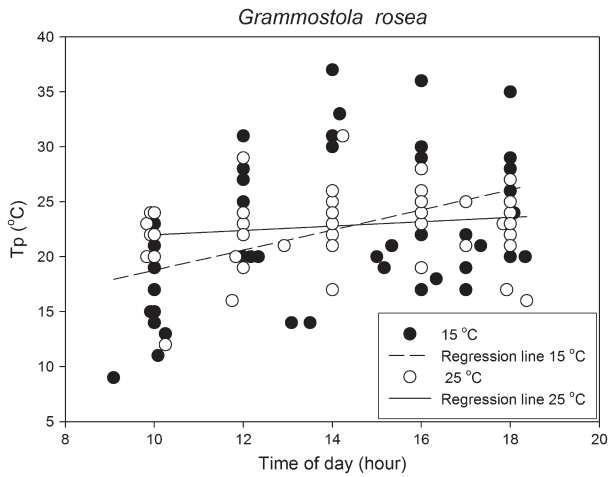


Fig. 3. Variations of preferred temperatures (T_p) during day in *Grammostola rosea* for two acclimation conditions. Regression lines at the two acclimation temperatures are plotted.

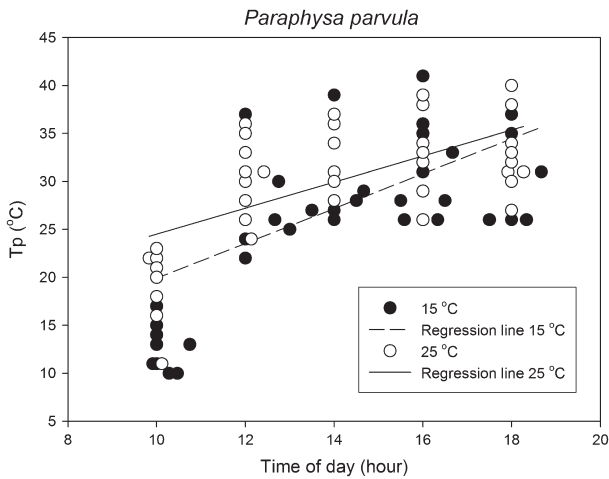


Fig. 4. Variations of preferred temperatures (T_p) during the day in *Paraphysa parvula* for two acclimation conditions. Regression lines are plotted.

19.00–27.25 °C) ($P = 0.99$), despite the small differences in mode and median values. The interquartile range, which represents 50% of the observed T_p values, was 26–34 and 29–34 °C for *P. parvula* at acclimation temperatures of 15 and 25 °C, respectively, and 19–33 °C and 21–24 °C for *G. rosea* at acclimation temperatures of 15 and 25 °C, respectively (Fig. 5).

Discussion

Several studies report the importance of behavioural thermoregulation in spiders, as well as the mechanisms of heat transfer into the microenvironment for body temperature regulation. Conduction from the environment, heat transfer by small convection currents and radiation from hot stones all

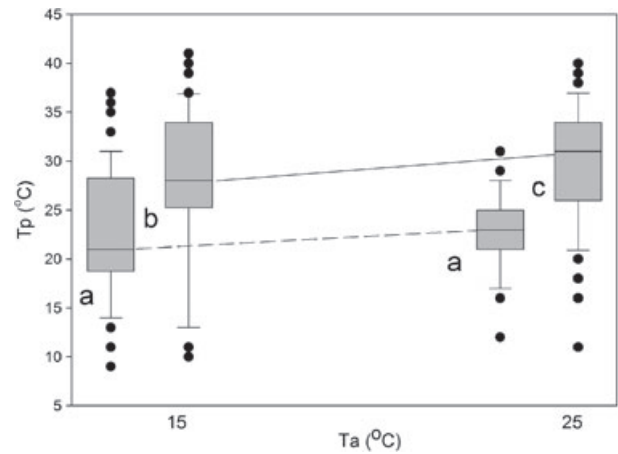


Fig. 5. Distribution of preferred temperatures of *Paraphysa parvula* (continuous line) and *Grammostola rosea* (segmented line) for two acclimation conditions. The median line in each box represents the median preferred temperatures; the box indicates 25 and 75 percentiles (interquartile range); bars show 10 and 90 percentiles; and points indicate the outliers. Different lowercase letters represent significant differences among groups in multiple comparisons with Tukey's test ($\alpha = 0.05$). T_a , acclimation temperature.

allow spiders to maintain a physiologically appropriate temperature. In this context, the selection of shelters that meet specific temperature conditions appears to be a key condition for the optimization of female reproductive success and the survival of females and juveniles (Schmalhofer, 1999; Canals *et al.*, 2007; Figueroa *et al.*, 2010; Veloso *et al.*, 2012). The species in the present study show preferred temperatures in the range of those reported for other mygalomorph spiders. For example, in the American tarantula *Aphonopelma* sp., shelter temperatures between 27 and 35 °C are reported (Seymour & Vinegar, 1973). The mean preferred temperature in the present study for warm-acclimated *P. parvula* (32.51 ± 2.90 °C) is close to the body temperature reported for animals of the same population captured in the field (31.02 ± 2.74 °C) and the preferred temperature of 31.7 ± 2.31 °C in the laboratory (Veloso *et al.*, 2012). The study by Veloso *et al.* (2012) was conducted during the spring, a time of high temperatures that are very similar to the acclimation temperature. There is no effect of body mass on the preferred temperature in *G. rosea*, which coincides with the findings described for *P. parvula* in the field over a body mass range from 0.5 to 2 g (Veloso *et al.*, 2012).

Although cold-acclimated *P. parvula* do not show body mass effects, warm-acclimated individuals show a decrease in preferred temperature at heavy body mass. This contrasts with reports for Lycosidae spiders (Sevacherian & Lowrie, 1972; Humphreys, 1975, 1977, 1978; DeVito & Formanowicz, 2003). For example, juveniles of two *Pardosa* species show preferential temperatures that are lower than those of adults (Sevacherian & Lowrie, 1972) and juveniles of the riparian spider *Pirata sedentarius* survive longer than adults when exposed to the same thermal stress (DeVito & Formanowicz, 2003).

The upper limit of preferred temperature (approximately 37 °C) is lower than the temperature at which water loss increases sharply in this species (40 °C) (Figuroa *et al.*, 2010) and, as expected, is lower than the maximum critical temperature (i.e. the maximum temperature at which an animal can display coordinated locomotory behaviour) as reported for *Aphonopelma* sp. (43 °C; Shillington, 2002). Compared with species of labidognathan spiders, the preferred temperatures of *P. parvula* are in the upper part of the range, similar to those of some of the Lycosidae, such as *Pardosa pullata* and *Pardosa sierra*, which are hunters from temperate zones similar to the species employed in the present study (Sevacherian & Lowrie, 1972).

The preferred temperatures of both species are shown to vary during the day. They increase under both of the acclimation conditions in *P. parvula* and in the cold acclimation of *G. rosea*. The preferred temperature of a species may be affected by many factors. For example, *Geolicosa godeffroyi*, a burrowing Australian wolf spider, has a preferred temperature between 32 and 36 °C, although the preferred temperature is reduced to approximately 30 °C by a lack of food or water in females that are carrying egg sacs, as well as in mature males (Humphrey, 1978). Diurnal changes in the preferred temperature have been established in other arthropods, such as Hemiptera (Canals *et al.*, 1997), although these are clearly not established in spiders. In the Texas tan tarantula *Aphonopelma anax* (Theraphosidae), a preferred temperature variation between 22 and 31.3 °C (with no evidence of a nocturnal/diurnal pattern) is reported (Shillington, 2002). However, body temperatures are higher in the evening than in the morning (30.3 versus 28.8 °C, respectively), which is consistent with the present findings in *P. parvula* and cold-acclimated *G. rosea*. The latter species, when acclimated to 25 °C, does not show an increase in its preferred temperature throughout the day, maintaining a temperature near to 22–23 °C. This might be a result of both mygalomorph species appearing to show a preference for low temperatures near to the acclimation temperature at the beginning of the experiments, then gradually moving to higher temperatures. For example, cold-acclimated *P. parvula* and *G. rosea* choose temperatures near 20 °C at 10.00 h but warm-acclimated spiders choose temperatures higher than 20 °C, although they are always placed at the midpoint of the gradient between 15 and 50 °C.

A clear increase of approximately 2 °C in the preferred temperature of *P. parvula* is found when the spiders are warm acclimated, contrasting with the thermal preferences in *P. sierra* and *Pardosa ramulosa* (Sevacherian & Lowrie, 1972) and the critical thermal maximum in *Aphonopelma* sp. (Seymour & Vinegar, 1973). This effect is evident in terms of both the mean and median preferred temperatures. However, *G. rosea* does not show a clear effect of acclimation temperature. This might be the result of a lower plasticity and higher thermal inertia in this larger mygalomorph spider. In this sense, the variation in thermal sensation from 15 to 25 °C may be different for small and large spiders.

It is reported that diurnally active spiders prefer higher temperatures than species that are active nocturnally, and

that they also have a higher critical thermal maxima because they experience higher temperatures (Pulz, 1987; Schmalhofer, 1999). However, the diurnal spiders *Misumenops asperatus* and *Misumenops formosipes* (Araneae, Thomisidae) prefer temperatures that are 3–5 °C higher than nocturnal spiders and also have higher critical maxima (Schmalhofer, 1999). This provides indirect evidence of a relationship between the temperature experienced and the preferred temperatures, and also is consistent with the findings of the present study.

It is striking that the maximum ranges for both mygalomorph species under both conditions of acclimation are very similar, and the maximum physiological tolerance ranges are possibly not affected. In *P. parvula*, stress conditions from loss of water are manifest above 30 °C, and specimens of this species can be found at 37 °C in the wild (Figuroa *et al.*, 2010; Veloso *et al.*, 2012). Under normal feeding conditions, *G. rosea* does not show an apparent physiological distress at temperatures of 30 °C (Canals *et al.*, 2008).

The results of the present study show that the two species examined increase their respective preferred temperatures in the evening behaviourally, which is possibly related to their crepuscular and nocturnal activities, during which time the rate of metabolism and the speed of physiological reactions need to be increased to capture prey. However, the temperatures and thermal preferences are not measured during the night. In this regard, differences in mean body temperatures between day and night are not reported in *Aphonopelma anax*, although variability during the day (29.8 ± 0.7 °C), more than two-fold greater than nocturnal variability (29.4 ± 0.3 °C) (Shillington, 2002). The present results also show that, although *G. rosea* and *P. parvula* exploit similar thermal patches, they have differences in their preferred temperatures, which are higher in *G. rosea*. Although, within each species, there are no differences related to body mass, the interspecific differences can be attributed in part to the large interspecific difference in size because *P. parvula* is a smaller species (4.78 g versus 10.31 g of *G. rosea*). This is associated with a higher specific mass metabolism (Canals *et al.*, 2008, 2012; Figuroa *et al.*, 2010), higher plasticity and probably higher thermal sensation in the smaller species as a result of an increased surface/volume ratio. The plasticity may be associated with the seasonal environment that the species inhabits. The population of *P. parvula* in the present study comprises a high Andean population from an area that has a dry climate in the spring and summer, with high temperatures for at least 4 months, reaching over 40 °C in some areas, which may also be conditioning the choice with respect to higher temperatures. The lower acclimation response in *G. rosea* suggests a limited plasticity of thermal limits, which may be a result of inhabiting the lowlands of Santiago, where temperature and temperature fluctuations are smaller.

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