

Characterization of the thermal micro-environment of *Paraphysa parvula* Pocock 1903 (Araneae: Theraphosidae), a spider from the Chilean Andes

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Abstract. We characterize, in both the laboratory and the field, the preferential thermal microenvironments of *Paraphysa parvula* (Pocock 1903) (Araneae: Theraphosidae), a mygalomorph spider that successfully inhabits the high elevation environments of the Chilean Andes. We studied 116 spiders. Their average body temperature in the field was $31.02 \pm 2.74^\circ\text{C}$, similar to the laboratory preferred temperature of $31.7 \pm 2.31^\circ\text{C}$, and higher than the ideal temperature of reproductive females, $29.34 \pm 2.81^\circ\text{C}$. In non-reproductive spiders, we found significant associations between body temperature and the temperatures of the air, substrate and rocks; however, the strongest association was between body and rock temperatures. Similar results were obtained in reproductive females, but there the best predictor of the body temperature was air temperature in the shelter. In both cases, the air temperature remained below body temperature and well below the temperature of the rocks and stones. Both situations show the importance of behavioral thermoregulation and the mechanisms of heat transfer into the microenvironment in the body temperature regulation of spiders. Conduction from the environment, heat transfer by small convection currents, and radiation from the hot stones constitute small environmental cues that allow these spiders to maintain an optimal temperature. The selection of shelters meeting specific temperature regimes appears to be a key condition for the optimization of female reproductive success and survival of females and juveniles in a high elevation environment.

Keywords: Behavioral thermoregulation, mygalomorph spiders

In ectothermic animals, the selection of temperatures can influence many aspects of life history such as aging, habitat selection, mating, and development (Canals 1998; Angilletta et al. 2002). This is especially relevant in spiders, for which thermal limits may be helpful in assessing the suitability of foraging and nesting sites, particularly for species in which the female stays in her nest with her egg sac (Hanna & Cobb 2007). The thermal biology of spiders has been poorly studied and limited to understanding the thermal tolerances of a few species and their relation to the habitat (Humphreys 1987; Schmalhofer 1999; Hanna & Cobb 2007). To the best of our knowledge, with reference to mygalomorph spiders, only the preferential temperature of *Aphonopelma* sp. has been reported (Seymour & Vinegar 1973; Schmalhofer 1999). Spiders are small, which results in a large body surface area per unit mass, making them susceptible to rapid heat loss, heat gain, and water loss. This is particularly relevant in the conditions of high temperature and low humidity that are typical of xeric environments. As ectotherms, their metabolism is temperature dependent, which means that their oxygen consumption and carbon dioxide production increase, following a power law, with increasing environmental temperature. This could conflict with the conservation of water as a result of high water exchange rates associated with high metabolic rates and increased evaporation at high environmental temperatures. This is especially critical in the mygalomorph spiders that have two pairs of book lungs with a surface area that is also large (Canals et al. 2007). Thus, the involvement of the book lungs in evaporative water loss can reach 50% (Davies & Edney 1952) or 60% (Figueroa et al. 2010). In other spiders, the relationship between temperature and evaporation

is also evident. For example, lycosid spiders of xeric environments have lower evaporation rates than those living in caves (Hadley et al. 1981), and the low evaporation rates of the widow spider *Latrodectus hesperus* Chamberlin & Ivie 1935 appears to have allowed successful colonization of desert habitats in southwestern North America (Hadley & Quinlan 1989).

The Chilean Andes are characterized by large daily and seasonal temperature variability, which, depending on the substrate, can range from several degrees below 0°C in winter to above 40°C in summer, and large changes in water vapor pressure and availability of prey for spiders (Canals et al. 2007). Under high temperature conditions, mygalomorph spiders maintain a low metabolism compared to other arthropods (Anderson 1970; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Figueroa et al. 2010) that can be supported by a low number of prey. In mygalomorphs, high temperatures can cause metabolic depression (Canals et al. 2007) or elevation of metabolism that can lead to dehydration (Figueroa et al. 2010).

The mygalomorph spider *Paraphysa parvula* (Pocock 1903) successfully inhabits these high elevation environments in the Chilean Andes at altitudes above 2000 m. This species dramatically increases its rate of evaporative water loss by about 10 times when it is moved from 20 to 40°C , and 40°C appears to be upper temperature limit above which there is danger of dehydration (Figueroa et al. 2010). This spider is also sensitive to elevated carbon dioxide, which promotes opening of the spiracles and evaporative water loss (Davies & Edney 1952; Figueroa et al. 2010). Under the conditions of high summer temperatures of the Andean highlands, these spiders face the possibility of losing water and should seek temperate environments and oxygenated shelter under rocks or bushes.

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Table 1.—Distribution of body mass (mb) of *Paraphysa parvula* spiders captured in the field.

| mb (g) | N (%) |
|---------|-----------|
| 0.0–0.5 | 64 (55.2) |
| 0.5–1.0 | 30 (25.9) |
| 1.0–2.0 | 9 (7.8) |
| 2.0–4.0 | 5 (4.3) |
| 4.0–6.0 | 3 (2.6) |
| 6.0–8.0 | 5 (4.3) |

In this article, we studied and characterized the preferential thermal microenvironments of *Paraphysa parvula* in the laboratory and the field. Specifically, we studied the preferred temperature in both situations and analyzed whether the selection of shelters was related to the selection of specific thermal microenvironments.

METHODS

Animal model, capture, and maintenance of individuals.—The animal model was *Paraphysa parvula* (Pocock 1903) (Araneae: Theraphosidae), an inhabitant of the central mountains (elevations above 2000 m) of the Chilean Andes. It is a crepuscular and nocturnal spider, although males of this species occasionally can be seen at noon. During the day, it can be found in shelters under flat stones. Its reproductive period occurs between December and January. The body mass of adults ranges between 6–10 g.

All animals used in this study came from a population from the central Andes of Chile (Farellones: 33° 21' S 70° 20' W) at about 2400 m above sea level. The capture area is dominated by low shrubs, mainly *Chuquiraga oppositifolia*, *Ephedra chilensis*, and *Acaena splendens* (Rosaceae) and numerous small rocks. Once captured, animals were brought to Santiago (550 m) and kept in boxes with natural light and photoperiod.

Field activities.—In the field, we defined 20 quadrats of 5×5 m. In each quadrat, all the stones were lifted and potential shelters were explored. We conducted all observations between 11:00 and 18:00 hours, when the temperature was highest. When a spider was found, its body temperature (Tb) was recorded with a type K thermocouple, which was attached dorsally between the cephalothorax and abdomen. We also recorded air temperature (Ta) in the shade at 1 m height, the temperature of the nearest rock (Tr) and soil temperature (Tt). All animals were weighed (mb) using a digital balance (± 0.01 g). We studied a total of 116 individuals under this protocol.

Subsequently, a second sampling was performed during the reproductive season, exclusively focused on adult females with egg sacs; we studied 15 spiders (mb = 5.33 ± 1.54 g). The procedure was similar to that described above, except that as

we found them under shelters, we noted whether the temperature in the shade corresponded to the temperature of the shelter. When a spider was detected, Tb, Ta, Tr and Tt were recorded.

Laboratory.—Seven adult females and 20 juveniles of various developmental stages were selected for the experimental study of preferred temperature (mb ranged between 0.4–11.4 g). We created a thermal gradient from 10° to 70° C in an opaque plastic cylinder 70 cm long and 5 cm in diameter, with a continuous record of temperature at four equidistant points using K-type thermocouples. The spiders were introduced individually into the gradient and they were neither watched nor perturbed during the trial. They could move freely, selecting their temperature for three hours, enough time to establish a thermal equilibrium with the environment. At the end of the experiment, we removed the subjects and within the first 10 s recorded the body temperature with a type K thermocouple attached dorsally between the cephalothorax and abdomen, using a digital thermometer (EXTECH Instruments, model AE15). That recorded temperature was considered as the behavioral preferred temperature.

Analysis.—We calculated descriptive statistics of body temperature for the three situations: preferred temperature in the laboratory, operating temperature, and field temperature of females of reproductive age. These temperatures were compared with one way ANOVA. We then performed regression analysis between mass and body temperature.

Univariate and multiple regressions of Tb against substrate temperatures (Ta, Tr, and Tt) were performed, the latter with stepwise (backward) selection. We performed correlation analysis between these variables.

RESULTS

We studied 116 spiders with body masses between 0.02–8.0 g (Table 1). The body temperature was $31.02 \pm 2.74^\circ\text{C}$ (average \pm standard deviation), which was similar to the laboratory preferential temperature, $31.7 \pm 2.31^\circ\text{C}$, and higher than the preferential temperature of reproductive females, $29.34 \pm 2.81^\circ\text{C}$ ($F_{2,99} = 51.65$, $p = 0.028$; Table 2). Correlation between temperature and body mass was not significant in the laboratory ($F_{1,25} = 0.21$, $p > 0.05$), in field non-reproductive spiders ($F_{1,59} = 0.33$, $p > 0.05$), or in reproductive females ($F_{1,12} = 0.60$, $p > 0.05$) (Figs. 1–3).

In non reproductive spiders, significant regressions between Tb and Ta (Slope $\beta = 0.69$; $r^2 = 0.33$; $F_{1,114} = 58.22$, $p < 0.001$); Tb and Tr ($\beta = 0.46$; $r^2 = 0.53$; $F_{1,114} = 126.59$, $p < 0.001$) and Tb and Tt ($\beta = 0.32$; $r^2 = 0.40$; $F_{1,114} = 77.68$, $p < 0.001$) were found (Fig. 4). All these variables were correlated (Table 3), and when a stepwise multiple regression was performed, the selected model was $Tb = 11.02 + 0.46 Tr$. Similar results were obtained in reproductive females: Tb and

Table 2.—Preferred body temperature in the laboratory and in the field in non-reproductive and reproductive individuals ($^\circ\text{C}$). Different letters indicate significant differences ($\alpha = 0.05$) in multiple comparisons.

| | Laboratory | Non reproductive (field) | Reproductive females (field) |
|-------------------------|-------------------|--------------------------|------------------------------|
| Mean \pm S.D. | $31.70 \pm 2.31a$ | $31.02 \pm 2.74a$ | $29.34 \pm 2.81b$ |
| 95% confidence interval | 30.78–32.61 | 30.32–31.72 | 27.71–30.96 |
| Range | 26.2–36.8 | 24.4–37.0 | 23.1–33.0 |
| Median | 31.8 | 31.4 | 29.95 |

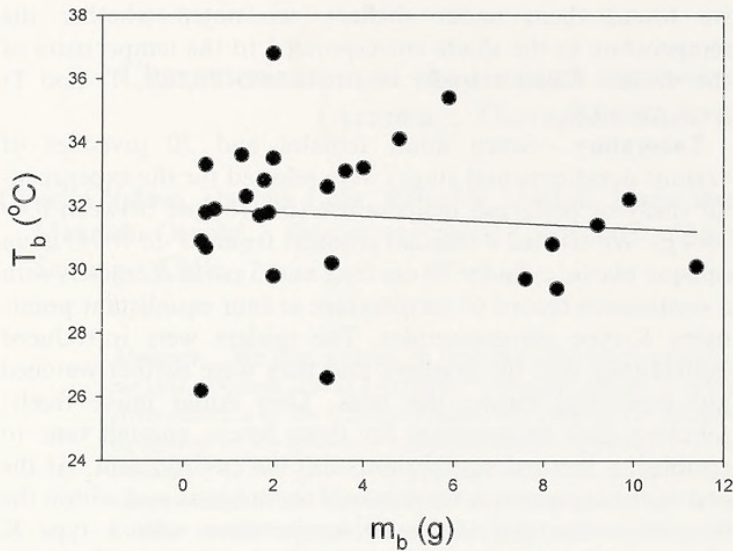


Figure 1.—Variation of the preferred body temperature (T_b) of *P. parvula* as a function of body mass (m_b) in the laboratory. The line is the estimated linear regression.

T_a ($\beta = 0.53$; $r^2 = 0.79$; $F_{1,12} = 51.30$, $p < 0.001$); T_b and T_r ($\beta = 0.21$; $r^2 = 0.34$; $F_{1,12} = 7.81$, $p < 0.016$) and T_b and T_t ($\beta = 0.38$; $r^2 = 0.47$; $F_{1,12} = 12.52$, $p < 0.001$) (Fig. 5). All variables were correlated (see Table 2); the multiple regression selected the model $T_b = 14.51 + 0.43 T_a$. The body temperatures of the non-reproductive and reproductive spiders were lower than T_r and T_t , lower than T_a in non-reproductive spiders, and similar to the T_a of reproductive females in shelters (Figs. 4, 5; Table 4).

DISCUSSION

The preferred temperature of non-reproductive *P. parvula* spiders was about 31°C in the laboratory and in the field. Although the difficulty of extrapolating from the laboratory to the field has been noted (Humphreys 1977), our results were very consistent; the mean, median and range were fully matched (see Table 2). The means and ranges were similar to

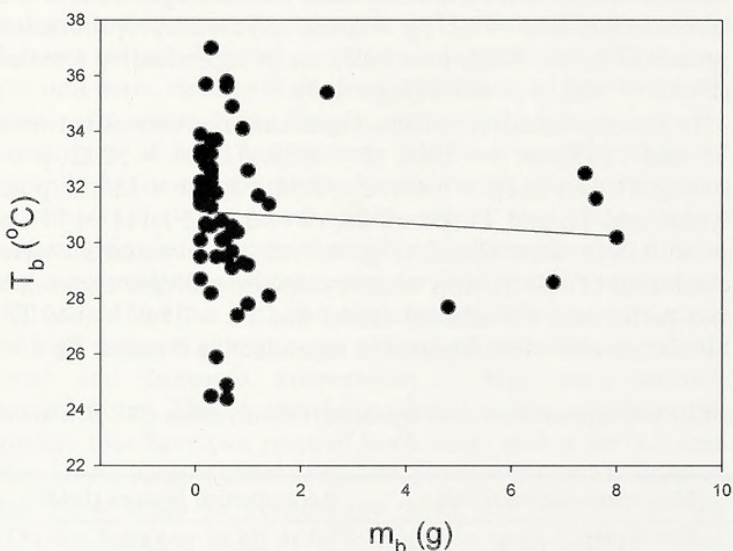


Figure 2.—Variation in preferred body temperature (T_b) in non-reproductive individuals of *P. parvula* as a function of body mass (m_b) in the field. The line is the estimated linear regression.

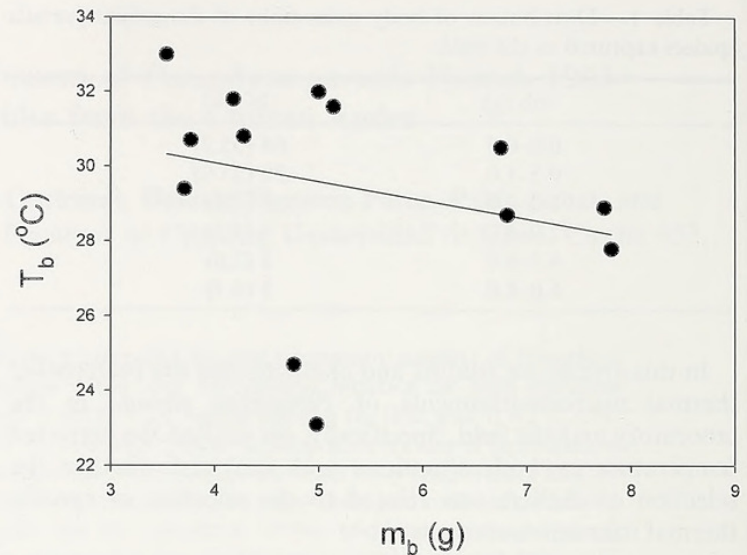


Figure 3.—Variation of the preferred body temperature (T_b) in reproductive females of *P. parvula* as a function of body mass (m_b) in the field. The line is the estimated linear regression.

the preferred temperature reported for the American tarantula *Aphonopelma* sp.; shelter temperatures between 27 and 35°C were reported for this species (Seymour & Vinegar 1973). Although there was great variability in body temperature in the juveniles (with low body mass), we found no significant effect of mass on the temperature preferences. This result contrasts with that reported for lycosid spiders (Sevacherian & Lowrie 1972; Humphreys 1975; 1978; De Vito & Formanowicz 2003). For example, Sevacherian & Lowrie (1972) found that juveniles of two *Pardosa* species showed optimal temperatures lower than adults, and De Vito & Formanowicz (2003) found that juvenile riparian spiders (*Pirata sedentarius* Montgomery 1904) exposed to thermal stress survived better than adults.

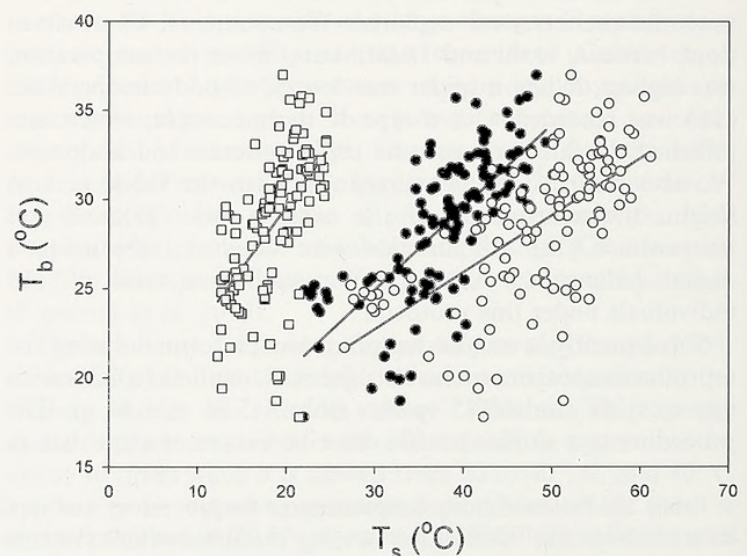


Figure 4.—Variation in body temperature (T_b) in non-reproductive individuals of *P. parvula* as a function of the substrate temperatures (T_s) in the field. White squares indicate air temperature (T_a), black circles indicate rock temperature (T_r) and white circles indicate soil temperature (T_t). The lines indicate the estimated linear regressions.

Table 3.—Correlations between body temperature (Tb) and the temperature of the air (Ta), rocks (Tr) and ground (Tt) for non-reproductive individuals (bold, above diagonal) and reproductive females (below diagonal).

| | Tb | Ta | Tr | Tt |
|----|------|-------------|-------------|-------------|
| Tb | | 0.58 | 0.73 | 0.64 |
| Ta | 0.90 | | 0.6 | 0.67 |
| Tr | 0.63 | 0.48 | | 0.82 |
| Tt | 0.71 | 0.55 | 0.79 | |

The upper limit of preferred temperature was about 37° C, lower than the temperature at which water loss increases sharply in this species (Figueroa et al. 2010), and as expected, lower than the maximum critical temperature (maximal temperature at which an animal can display coordinated locomotory behavior) reported for *Aphonopelma* sp. (43° C). Compared to other species of labidognathan spiders, preferred temperatures of *P. parvula* are in the upper range, similar to some lycosids such as *Pardosa pullata* (Clerck 1757) (Pulz 1987) and *Pardosa sierra* Banks 1898 which, like our studied species, are diurnal and nocturnal hunters from temperate zones (Sevacherian & Lowrie 1972). The preferred temperature of females carrying an egg sac was about 3°C lower than the temperature of choice for non-reproductive animals, as was the lower limit of the preferred range of temperatures, while the upper limit decreased 1–2 °C. Higher optimal temperatures have been reported for lycosid females carrying egg sacs (Norgaards 1951; Sevacherian & Lowrie 1972), lower (Humphreys 1978) or equal (Norgaard 1951; Vlijmen et al. 1963; Frick et al. 2007) to those of non-reproductive individuals. High preferential temperatures could accelerate the development of the offspring; however, it has also been reported that high temperatures lead to retarded development in lycosids (Li & Jackson 1996). In our species the preferential temperature of non-reproductive individuals is high, and the choice of a higher

Table 4.—Body temperature (Tb) of non-reproductive individuals and reproductive females of the spider *P. parvula*, and the temperature of the air (Ta), rocks (Tr) and ground (Tt). Results are shown as mean \pm standard deviation.

| | Non-reproductive individuals | Reproductive females |
|---------|------------------------------|----------------------|
| Tb (°C) | 31.02 \pm 2.34 | 29.84 \pm 2.81 |
| Ta (°C) | 18.46 \pm 3.49 | 27.97 \pm 4.65 |
| Tr (°C) | 37.66 \pm 6.46 | 43.98 \pm 8.15 |
| Tt (°C) | 48.03 \pm 8.22 | 55.13 \pm 5.26 |

temperature by reproductive females could have an effect on water loss or produce a metabolic depression in the offspring.

Both in non-reproductive animals and in the reproductive females, the body temperature change per degree C of temperature change in the physical environment (Ta, Tr and Tt) was less than 1° C, which was associated with slopes lower than 1 in all simple regressions. This indicates that *P. parvula* thermoregulated behaviorally, seeking shelters that allowed them to maintain temperatures varying less than in the environment. Ambient temperature (Ta), that of the nearest rock (Tr) and soil temperature (Tt) were strongly correlated with the body temperature of spiders, but while the temperature of soil and rock varied between 30–60° C, body temperature of spiders remained between 27.71–32.61° C. This is similar to results reported for *Aphonopelma* sp., in which the temperature of the soil adjacent to the entrances of their caves reached 55° C, while the temperature of the shelter was only 36° C, maintaining the area adjacent to the spider usually between 27.2–30.0° C (Seymour & Vinegar 1973). The air temperature at one meter in the shade ranged from 15–25° C for non-reproductive spiders, while air temperature in the shelters of reproductive females varied between 18–32° C. In both cases, the air temperature remained below body temperature and well below the temperature of the rocks and stones.

In the non-reproductive animals, the model that best explained an animal's body temperature was the temperature of the surrounding rocks. For the females in their shelters under rocks, it was not the surface temperature of the stones that best explained the body temperature, but rather the air temperature in the shelter. Both situations show the importance of mechanisms of heat transfer into the microenvironment on the body temperature regulation of spiders. The processes of conduction from the environment, heat transfer by small convection currents, and radiation from the hot stones constitute small environmental cues that allow these spiders to maintain an optimal 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 survival of females and juveniles in a high altitude environment.

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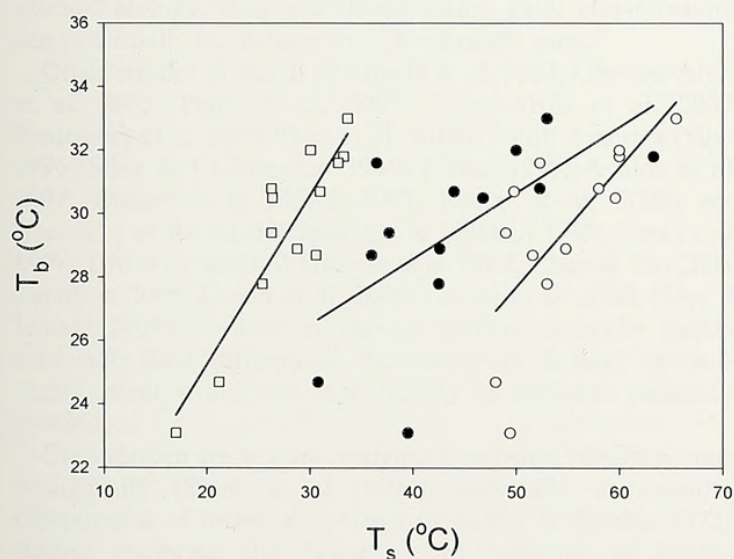


Figure 5.—Variation in body temperature (Tb) in reproductive females of *P. parvula* as a function of the substrate temperatures (Ts) in the field. White squares indicate temperature of the refuge (Ta), black circles indicate rock temperature (Tr) and white circles indicate soil temperature (Tt). The lines indicate the estimated linear regressions.

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