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RESEARCH ARTICLE

Thermal tolerance and preferred temperature of the Andean Chilean tarantula *Euathlus walteri* (Araneae: Theraphosidae)

Tolerancia y preferencia térmica de la tarántula andina chilena *Euathlus walteri* (Araneae: Theraphosidae)

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ABSTRACT

Mygalomorph spiders are ectothermic organisms reliant on temperature for movement, prey capture, and reproductive success. The species *Euathlus walteri*, is endemic to northern Chile and inhabits cold and high-altitude regions. This study investigates the preferred body temperature and the parameters of the locomotor thermal performance curve in females and large juveniles of *E. walteri* in a controlled laboratory setting. We identified their preferred temperature ranges and examined the correlation between laboratory temperatures and burrow temperatures. The results indicate a preference for warmer temperatures (around 34°C) than the environment temperatures where this species live, actively avoiding colder temperatures. No significant differences in thermal preference were observed between morning and evening periods. We found an optimum temperature of 22 ± 2.0°C, lower thermal limit (LTL) of -1.11 ± 0.76°C and upper thermal limit (UTL) of 44.94 ± 1.79°C. Our preliminary results suggest that individuals that live in this cold environment seek warmer temperatures to compensate for the reduced opportunity to find favorable temperatures in their habitat. Furthermore, our results suggest that locomotor performance is significantly affected by low temperatures and that spiders might select shelters with temperatures that allow them to approach their physiological optimal temperature.

Keywords: Chile, desert, locomotor performance, microhabitat, tarantula.

RESUMEN

Las arañas migalomorfas son organismos ectotérmicos que dependen de la temperatura para su desplazamiento, la captura de presas y su éxito reproductivo. La especie *Euathlus walteri* es endémica del norte de Chile y habita en regiones frías y de gran altitud. Este estudio investiga la preferencia térmica y los parámetros de la curva de desempeño térmico de juveniles grandes y hembras adultas de *E. walteri* en un entorno controlado de laboratorio. Identificamos sus rangos de temperatura preferidos y examinamos la correlación entre la temperatura de laboratorio y las temperaturas de las madrigueras. Los resultados indican una preferencia por temperaturas más cálidas (cercanas a los 34 °C) que las temperaturas donde habita la especie, evitando activamente las temperaturas más frías. No se observaron diferencias significativas en la preferencia térmica entre los períodos matutinos y vespertinos. Encontramos una temperatura óptima de 22 ± 2,0 °C, un límite térmico inferior (LTI) de -1,11 ± 0,76°C y un límite térmico superior (LTS) de 44,94 ± 1,79°C. Nuestros resultados

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preliminares sugieren que los individuos que viven en este ambiente frío buscan temperaturas más cálidas para compensar la menor oportunidad de encontrar temperaturas favorables en su hábitat. Además, sugerimos que el rendimiento locomotor se ve significativamente afectado por las bajas temperaturas y que las arañas seleccionan refugios cuyas temperaturas les permiten acercarse a la temperatura fisiológica óptima.

Palabras clave: Chile, desierto, microhábitat, rendimiento locomotor, tarántula.

Temperature influences foraging behavior, movement, and reproduction in ectothermic organisms (Peterson *et al.* 1993; Huey & Berrigan 2001; Angilletta 2006). In this regard, thermal preference (T_{pref}) and thermal tolerance are frequently utilized to investigate the thermal ecology of these species (Hertz *et al.* 1993; Angilletta *et al.* 1999; Huey & Berrigan 2001; Angilletta 2006). Typically, frequency histograms are used to assess thermal preferences (Hertz *et al.* 1993; Frick *et al.* 2007; Labra *et al.* 2009; Sepulveda *et al.* 2014; Alfaro *et al.* 2013; Taucare-Ríos *et al.* 2020; Schwerdt *et al.* 2020). On the other hand, upper and lower thermal limits are derived from a thermal performance curve (TPC) (Huey & Slatkin 1976; Huey & Kingsolver 1989). These are defined as the upper and lower critical temperature at which an animal must maintain thermal balance and survive (Huey & Kingsolver 1989; Angilletta 2006; Terblanche *et al.* 2007). In essence, both thermal preferences (T_{pref}) and thermal limits are effective indicators of the fundamental thermal niche (Hutchinson 1957; Kearney & Porter 2009).

Ectothermic animals tend to select environments that optimize their fitness relative to temperature (Hanna & Cobb 2007; Hughes & Grand 2000). It is generally understood that these organisms reside in areas that align with their preferred temperature ranges (Taucare-Ríos *et al.* 2020). For spiders, this knowledge is particularly important for assessing the suitability of foraging and nesting habitats, especially for species where females and juveniles remain within their shelters (Hanna & Cobb 2007; Veloso *et al.* 2012; Schwerdt *et al.* 2020; Montes de Oca *et al.* 2020; Taucare-Rios *et al.* 2020). In this framework, tarantulas predominantly occupy their burrows for extended periods (Alvarez *et al.* 2016), choose these burrows based on the thermal characteristics of their habitat and therefore can be ideal models for study thermal ecology (Riechert & Tracy 1975; Veloso *et al.* 2012; Alfaro *et al.* 2013; Schwerdt *et al.* 2020).

Thermal ecology determines where spiders seek to select temperatures that allow them to maximize their locomotor performance (Taucare-Ríos *et al.* 2018; Orellana *et al.* 2020; Schwerdt *et al.* 2020), which is directly associated with feeding, mating behaviors, habitat selection and predator avoidance (Huey & Stevenson 1979; Shillington, 2002; Booster *et al.* 2015; Silva-Pereyra *et al.* 2019; Schwerdt *et al.* 2020). Therefore, the effect of different temperatures on locomotor activity has proven to be extremely relevant for these arthropods (Shillington, 2002; Stork 2012, 2020; Taucare-Ríos *et al.* 2018; Orellana *et al.* 2020; Schwerdt *et al.* 2020).

The species *Euathlus walteri* Taucare-Ríos, Plaza & Pérez-Miles, 2025, is an endemic tarantula that inhabits the high Andean steppe at elevations above 4.000 m a.s.l. in northern Chile (Taucare-Ríos *et al.* 2024). This species has low abundances, a restricted distribution and occupies shallow burrows constructed under stones close to the vegetation (Taucare-Ríos *et al.* 2024). The geographic range that this species inhabits is characterized by a dry and cold climate (Luebert & Pliscoff 2006; Meteoblue 2024). Relative humidity remains at very low levels due to the great water vapor absorption capacity of the air mass. The intensity of dry periods tends to vary across geographic areas and has a strong influence on the vegetation where this spider lives (Dillon & Rundel 1990).

In this study, we estimated preferred body temperature and thermal tolerance of the endemic spider *E. walteri*, analyzing whether the habitat temperatures are related to the selection of laboratory temperatures. Firstly, we (1) estimated the preferred body temperatures of *E. walteri* under laboratory conditions, (2) evaluated the relation between temperature and locomotor performance through a thermal performance curve and 3) compared preferred temperatures and field temperatures.

Field activities and laboratory conditions. In the field we actively searched for spiders during a two-hour period (12:30-14:30). The capture permission and the low abundance of the species allowed us to collect a limited number of individuals. We captured only six individuals (three females and three large juveniles) from a population from northern of Chile (Altos de Pica: 20°21.414' S, 69°01.053' W) at 4.017 m above sea level. Individuals were found under rocks hidden in their burrows (Fig. 1). The climatic data of the site studied (meteorological station data extracted each one hour), is characterized by an annual rainfall between 50 and 100 mm, a mean annual temperature of 3.3°C and a high daily thermal oscillation (daily average maximum: 14°C; daily average minimum: -5 °C) (Meteoblue 2024). When a spider was found, we measured burrow temperature for 10 seconds with a mini temperature meter (UNI-T UT333, resolution: 0.1 °C) placed between the burrow and the rock to prevent heat loss. Also, we measured the shaded air temperature at tarantula height (approximately 2 cm above the ground).

All individuals of *E. walteri* used here were maintained in the laboratory for 3 weeks before experiments. Individuals were kept at an ambient temperature of 20.4 ± 1.8°C, RH: 60.6 ± 8.4 under a 12 h light: 12 h dark photoperiod and were housed individually in a plastic terrarium with water provision. Spiders were fed once a week with *Tenebrio* sp. larvae except during the experimental period. The body mass (M_b) of each specimen was measured using a digital balance with a precision of 0.001 g.

FIGURE 1. Study site of *Euathlus walteri* in northern Chile. A. Habitat where individuals were found. B. Burrow built under rock. C. Female of *Euathlus walteri* found in burrow. / Sitio de estudio de *Euathlus walteri* en el norte de Chile. A. Hábitat donde los individuos fueron hallados. B. Madriguera construida bajo roca. C. Hembra hallada en madriguera.

Thermal preference. A thermal gradient from 8 to 40°C was generated in a glass container measuring 50 cm long × 20 cm wide × 20 cm high without substrate. This container had a thermoregulated heater (100 W) on one side and a cold point on the other (cooling gels), creating a thermal gradient between the endpoints. This gradient was calibrated and checked before and during each experiment. Individuals were exposed for one hour to the thermal gradient at different times of day: morning (10:30-11:30h) and evening (19:30-20:30 h). The spiders were free to move for 30 minutes to select their preferred temperature. Then the body temperature of each individual was recorded every five minutes with an infrared thermometer (EXTECH Instrument, model IR267; IR accuracy: ± 0.2 °C) for one hour. The measurements were obtained from the midpoint of the carapace. After each experiment the glass container was carefully cleaned with ethanol and then, to avoid any remaining, was washed with distilled water.

Critical thermal limits and locomotor performance. The thermal tolerance thresholds of spiders, including both the upper and lower limits, were assessed by observing the loss of their righting reflex under extreme temperature conditions. In this study, we quantified rollover speed, which is defined as the velocity at which spiders return from an upside-down position to an upright one, to develop a thermal performance curve (Castañeda *et al.* 2005; Bozinovic *et al.* 2016; Taucare-Ríos *et al.* 2018). Each spider was placed in a sealed plastic tube and subjected to a programmable thermostatic bath for 20 minutes at a range of temperatures (0, 10, 20, 30 and 40°C) on different days, ensuring that each spider was assessed at only one temperature per day. The spiders were randomly selected for the different treatments, but the maximum and minimum temperatures were measured at the end of the experiment after a few days of rest to avoid the cumulative effect of temperatures. After 20 minutes for each temperature, we evaluated rollover speed for 5 minutes. Rollover speed is the inverse of the time it took an individual to right itself (Rollover Speed = 1 / (time to right itself). The longer it takes for an individual to right itself, the slower its rollover speed will be (Bozinovic *et al.* 2016). The spiders were grasped laterally from the prosoma with long forceps and turned upside down. Individuals were placed individually in an inverted position on a flat surface (Fig. 2). We observed how long it takes to turn around and the rollover speed was taken as the inverse of this value. There is only one rollover speed value per spider. The spiders were recorded with a camera, and their speed was calculated from this record. If an animal was unable to right itself within this time (5 minutes), it was considered to have null performance (rollover speed = 0) (Bozinovic *et al.* 2016). To create the TPC, we calculated the average rollover speed at the respective temperatures. We compared the fit of several functions (Angilletta 2006) that could describe spider performance using the AIC criterion (Table 1). In this context, the parameters of the TPC, including lower thermal limit (LTL) and upper thermal limit (UTL) were determined through a polynomial quadratic regression model. T_{opt} is defined as the temperature at which the spider achieves its maximum speed, while P_{max} indicates the rollover speed at T_{opt}. The numerical values for LTL and UTL were obtained at the points where the TPC intersects the temperature axis (u = 0) (Gaitán-Espitia *et al.*, 2014). The tolerance range (TR) was calculated using the formula TR = LTL – UTL (Schwerdt *et al.* 2020).

Statistical analysis. Residuals were analyzed for normality and heteroscedasticity. Here, preferred temperature (T_{pref}) was defined as the mean temperature obtained from the thermal gradient. The T_{pref} was represented by a frequency histogram. We calculated 25th and 75th percentiles of the preferred temperature distribution. These values represent the temperatures most frequently selected within a given environment. We compared the preferred temperature between the morning and evening periods using a paired t-test. Additionally, we compared T_{pref} and burrow temperatures using paired t-test. A Pearson correlation was performed between body mass and preferred temperature. Considering that each individual was studied at five different temperatures (repeated measures design) and the non-normal distribution of the data, a non-parametric Friedman test for dependent samples was performed with rollover speed as the response variable and the five experimental temperatures as factors. When differences in the means were significant at the $p<0.05$ level, they were also tested with a posteriori Tukey's test (HSD). All these analyses were performed using the PAST software version 4.03 (Hammer *et al.*, 2001). Data are presented as means ± SE.

TABLE 1. Comparison of functions used to describe the thermal performance curves of *Euathlus walteri*. / Comparación de funciones utilizadas para describir las curvas de rendimiento térmico de *Euathlus walteri*.

Function	AIC	r2
Gaussian	31	0.96
Quadratic	**30.2**	**0.98**
Cubic	31.5	0.94
Exponential	31.7	0.16

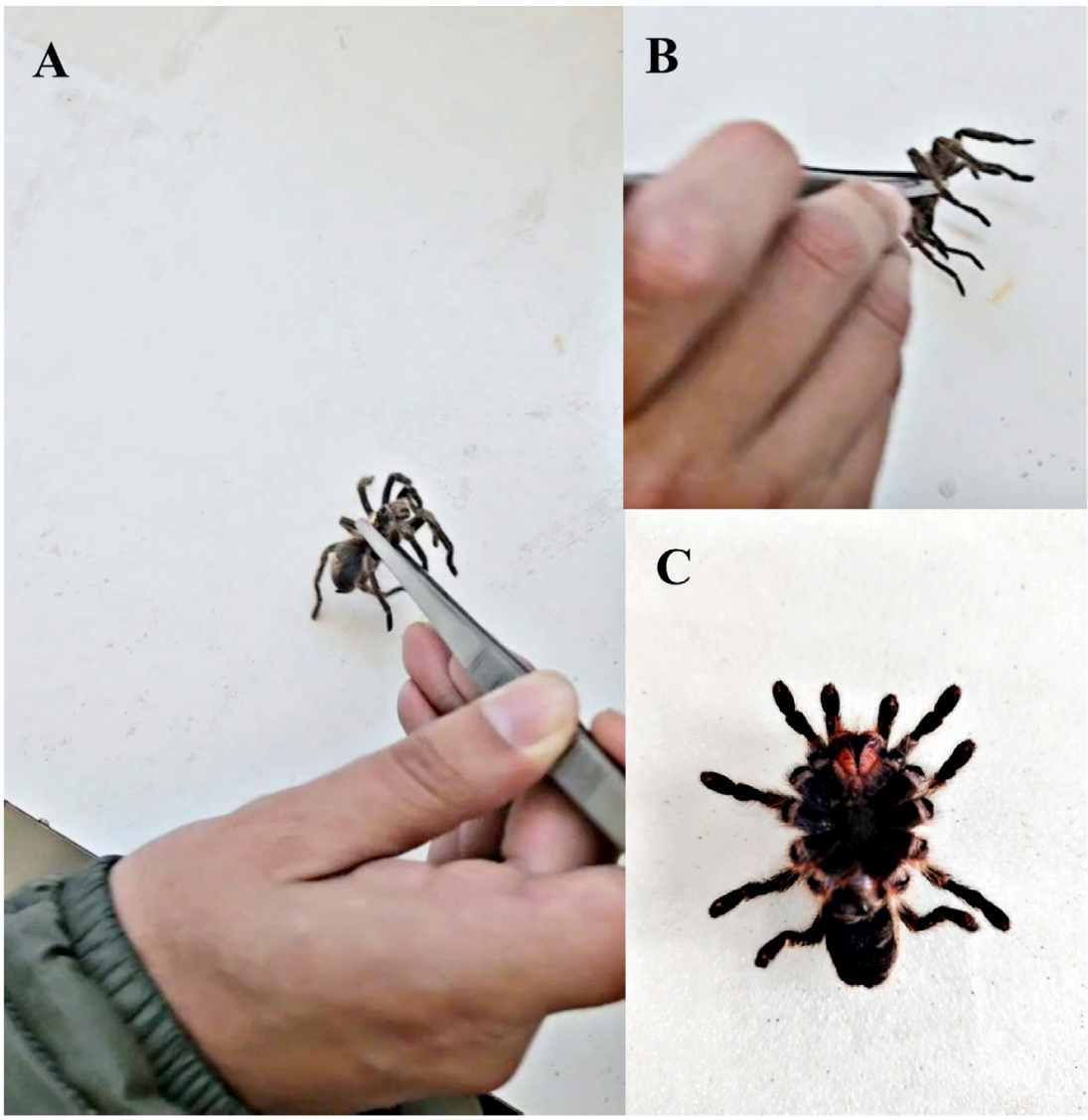

FIGURE 2. Manipulation of spiders during thermal performance experiments. A. The individual is grasped laterally with the forceps from the prosoma. B. The individual is turned upside down. C. Final position of the spider after the turn. / Manipulación de las arañas durante experimentos de desempeño térmico. A. Se sujeta al individuo lateralmente con las pinzas desde el prosoma. B. Se gira al individuo boca abajo. C. Posición final de la araña tras el giro.

On average, the individuals of *E. walteri* weighed 4.13 ± 2.04g. Individuals of *E. walteri* were able to move freely during the experiments until they remained in a warmer preferred zone. The T_{pref} obtained was 33.61 ± 2.28°C with T_{pref} 25 of 32.45°C and the T_{pref} 75 of 35.27°C. Therefore, individuals spent more time in the 33-35°C temperature range (Fig. 3). We did not find any significant differences in T_{pref} between morning and evening periods (morning = 33.08 ± 1.76°C and evening = 34.14 ± 2.02°C; paired t-test, = 0.69, $p > 0.05$). The T_{pref} were higher than burrow temperature (T_{pref} = 33.61 ± 2.28°C; burrow temperature = 20.14 ± 2.83°C; paired t-test, = -9.61, $p < 0.0001$) and burrow and air temperatures were different (burrow temperature = 20.14 ± 2.83°C; air temperature = 14.8 ± 0.83°C; paired t-test, = 33.009, $p < 0.0001$) (Fig. 4). We did not find any significant correlation between the body mass and the preferred temperature (Pearson correlation: $r = 0.14$, $p > 0.05$).

We recorded a T_{opt} of 22 ± 2.0°C, LTL of -1.11 ± 0.76°C, and UTL of 44.94 ± 1.79°C. The P_{max} was 4.38 ± 1.09 s^{-1} and TR was 46.04 ± 3.12 °C. The results showed that the performance of the spiders was significantly different across the different temperatures (Friedman test = 14.5, $p < 0.05$). Performance decreased at 0 and 10°C, but no statistical difference was found between them. Also, differences were found only between 0/10°C vs. 20°C and 20/30°C vs 40°C (Tukey's test, $p < 0.05$). Individuals exhibited the greatest performance between 20 and 30°C and the slowest at 0 and 40°C (Fig. 5).

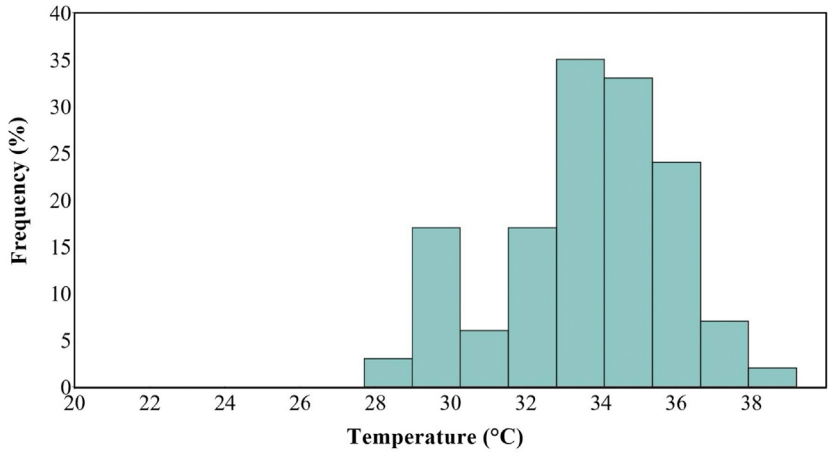

FIGURE 3. Frequency histogram of preferred temperatures (percentage of all recordings) for *E. walteri*. / Histograma de frecuencia de temperaturas preferidas (porcentaje de todos los registros) para *E. walteri.*

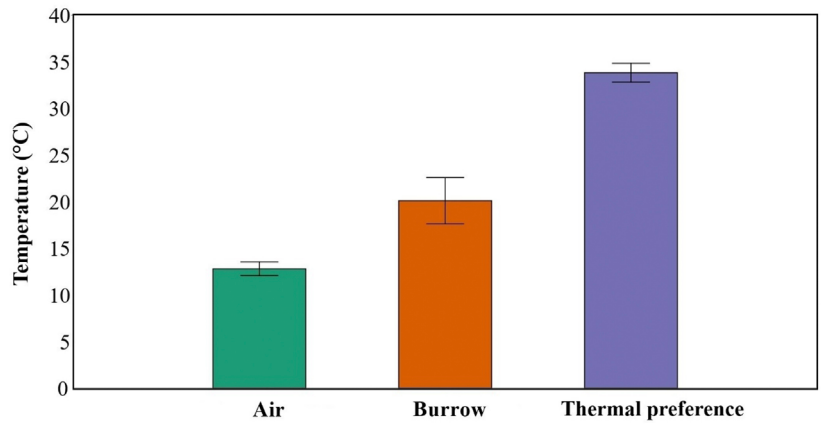

FIGURE 4. Comparison between field and laboratory temperatures selected by *E. walteri.* Means ± SE. / Comparación entre las temperaturas de campo y de laboratorio seleccionadas por *E. walteri*. Medias ± EE.

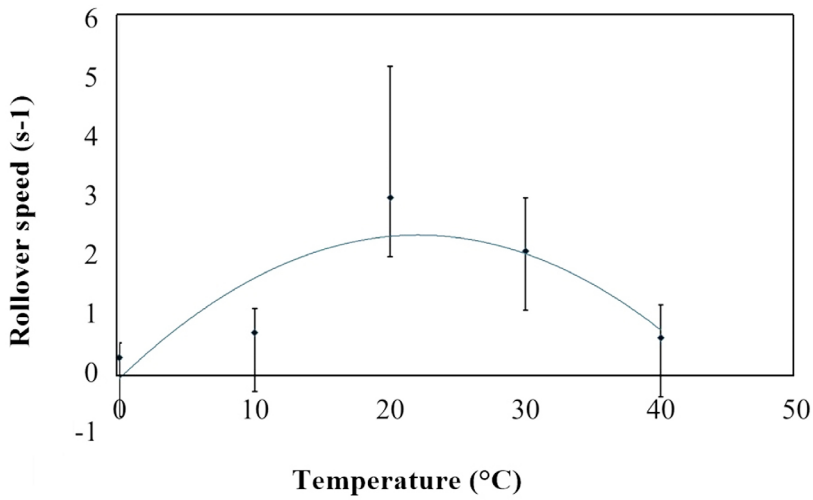

FIGURE 5. Thermal performance curve of *E. walteri*. The continuous line is the estimated quadratic polynomial average curve, black circles are the observed average speed, and the bars are the 95% confidence intervals at each temperature. / Curva de rendimiento térmico de *E. walteri*. La línea continua es la curva promedio polinomial cuadrática estimada, los círculos negros son la velocidad promedio observada y las barras son los intervalos de confianza del 95% a cada temperatura.

Our results provide preliminary evidence of a preference for warm temperatures in *Euathlus walteri* demonstrating physiological plasticity in this endemic species (Hodgson and Schwanz 2019; Llewelyn *et al.* 2016). Although these spiders live in cold, high-altitude environments, they seek to maximize their performance in warmer temperatures. According to this hypothesis, individuals from cold environments select higher T_{pref} to compensate for fewer opportunities to find warm temperatures in their original thermal habitat (Llewelyn *et al.* 2016; McElroy 2014). This phenomenon appears to be quite common in tarantulas that live in cold environments. For example, *Euathlus condorito* (misidentified as *Paraphysa parvula*), which inhabits the central mountains (elevations above 2000 m, annual mean temperature: 3.2°C) selected warm preferred temperatures close to 32°C under laboratory conditions (Veloso *et al.* 2012; Alfaro *et al.* 2013). In our case, *E. walteri,* that lives in Andean environments of northern Chile (elevations above 4000 m, annual mean temperatures: 3.3°C) selected preferred temperature close to 34°C. In this sense, phenotypic flexibility allows organisms to match and increase their performance under changes in high altitude conditions (Hammond *et al.* 2001). Also, the higher T_{pref} could reflect phylogenetic inertia in Theraphosidae species that live in mountains and cold habitat from South America. Species such as *Grammostola vachoni* in Argentina and *Euathlus condorito* in the Andes Mountain range of Chile show similar responses to environmental changes (Veloso *et al.* 2012; Alfaro *et al.* 2013; Schwerdt *et al.* 2020). Phylogenetic inertia means that these species would retain evolutionary adaptations of high altitude: a greater phenotypic flexibility in both physiological and morphological traits (Hammond *et al.* 2001; Bacigalupe *et al.* 2004).

The Chilean high plateau has large daily temperature ranges. Here, the mean soil temperature varied between 2.5 and 12.8°C (Norambuena *et al.* 2011). In this sense, we don't find differences in T_{pref} between the morning and evening periods (i.e. daily temperature variation), suggesting that temperatures inside the burrow are stable. In fact, the optimal temperature (T_{opt} = 22 ± 2.0 °C) is quite similar to the temperature found inside burrows (20.14 ± 2.83°C), so these spiders select shelters where they can maximize their performance avoiding extreme ambient temperatures. The presence of vegetation can influence soil temperature, as vegetation can reduce solar radiation reaching the soil and therefore lower the temperature. Similar studies have highlighted the importance of microhabitats as a thermal buffer for wandering spiders with sit-and-wait hunting strategies (Veloso *et al.* 2012; Taucare-Ríos *et al.* 2018; Schwerdt *et al.* 2020). Females, being sedentary and having limited mobility, could protect themselves inside the burrows

from high daily temperature variations (Veloso *et al.* 2012; Schwerdt *et al.* 2020). Therefore, we suggest that females of this species would only be active when temperatures do not affect its locomotor capacity (above 10°C and below 40°C) and are close to their optimal temperature.

High elevations can experience sudden daily temperature fluctuations, including freezing temperatures and high temperatures with intense solar radiation (Canals *et al.* 2007; Frei *et al.* 2014; Gonzales *et al.* 2022). In this sense, Andean plants and arthropods show high tolerance to such abrupt temperature variations at high altitudes (Frei *et al.* 2014; Gonzales *et al.* 2022). Therefore, the capacity for plastic responses varies in relation to the physiological tolerance of these organisms at different altitudes (Gonzales *et al.* 2022). Here, we found a strong thermal resistance range (TR) with LTL of -1°C and UTL of 45°C. In this regard, Figueroa *et al.* (2010) point out that in Theraphosidae, temperatures exceeding 45°C led to massive water loss, resulting in the collapse of the spiders' movement capacity, while at low temperatures the spiders quickly reduce their speed and stop moving (Schwerdt *et al.* 2020). Therefore, the role of burrows in avoiding these extreme temperatures would be key for these spiders. Interestingly in our case, this spider could survive at temperatures below zero. Maybe, this resistance to sub-zero temperatures may be an adaptation of the genus *Euathlus* to cold, high-altitude climates in Chile (Cubillos *et al.* 2018).

Although the results of this study suggest high physiological plasticity in this species, they should be interpreted with caution. An important limitation of this study was the low number of specimens studied, which prevents us from extrapolating the thermal ecology of the species throughout its distribution range. The low population densities of the species made it difficult to obtain more specimens for the experiments. In this sense, field constraints can limit data collection in such unique ecological context. However, our results highlight the importance of the microhabitat and its thermal conditions for the survival of this endemic species. Therefore, the removal and disturbance of their natural environments can have serious consequences for their survival. Studying plasticity in response to high-altitude environments in these spiders can help us understand how these organisms cope with new environments conditions, especially in the context of climate change. It can also aid in managing future conservation efforts for this species from northern Chile.

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