

THERMAL PERFORMANCE OF THE CHILEAN RECLUSE SPIDER *LOXOSCELES LAETA* (ARANEAE, SICARIIDAE)

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Abstract: The study of the impact of thermal variability on the performance of individuals is important to understand microhabitat selection and the responses of organisms to different climate scenarios. In this study we explore the performance of the Chilean recluse spider, *Loxosceles laeta*, of great medical importance, measuring the activity of spiders under different temperatures in a range of usual environmental temperatures in Chile. The optimum temperature for a correct performance at speed agrees with preferred temperatures previously reported in the evening and night, in which spider bites on human usually occur. Also, the maximum estimated temperature for movement (CT_{max}) agrees with temperatures reported to suppress coordinated activity, but the minimum estimated temperature for movement (CT_{min}) is lower than in other araneomorph spiders and higher than previous reported minimum temperatures that suppress coordinated movements and lethal temperatures. High CT_{max} and low CT_{min} could be explained by adaptation of this species to arid environments with a Mediterranean climate. The performance curve suggests that *L. laeta* is adapted to high temperatures in the range of the usual indoor temperatures prevalent in human dwellings.

Key words: Araneae, Sicariidae, *Loxosceles*, thermal performance, Chile.

Desempeño térmico de la araña del rincón *Loxosceles laeta* (Araneae, Sicariidae)

Resumen: El estudio del impacto de las variaciones térmicas en el desempeño de los individuos es importante para entender la selección de microhábitats y la respuesta de éstos frente al cambio climático. Aquí exploramos el desempeño de la araña del rincón, *Loxosceles laeta*, de gran importancia médica, midiendo la actividad de las arañas en un gradiente de temperaturas habituales en Chile. La temperatura óptima para un buen desempeño en velocidad de carrera es consistente con la temperatura preferida de la araña en la tarde y la noche, coincidiendo con el período de actividad y con la hora de las mordidas en humanos de esta especie. La temperatura máxima tolerable para desplazamiento (CT_{max}) es también consistente con las temperaturas reportadas para suprimir actividad motora, pero la temperatura mínima (CT_{min}) es menor que en otras arañas y más alta que las temperaturas reportadas para suprimir la actividad coordinada y que la temperatura letal. La alta CT_{max} y la baja CT_{min} podría ser explicada como una adaptación de esta especie a ambientes áridos con clima mediterráneo. La curva de desempeño sugiere que *L. laeta* se encuentra adaptada a las temperaturas que usualmente se encuentran en el interior de las habitaciones humanas.

Palabras clave: Araneae, Sicariidae, *Loxosceles*, desempeño térmico, Chile.

Introduction

The physiology of organisms is closely related to body temperature (Huey & Stevenson, 1979; Angilletta *et al.*, 2002; Angilletta, 2009). The environmental temperature can affect the performance of different physiological features (metabolism, growth, escape velocity, etc.) (Angilletta, 2009), specifically in the case of ectothermic organisms (Angilletta *et al.*, 2002). Thermal variation is an important selective force on organisms (Jentsch *et al.*, 2007; Lalouette *et al.*, 2007; Terblanche *et al.*, 2010; Bannerman *et al.*, 2011; Bozinovic *et al.*, 2011a; Thompson *et al.*, 2013; Bozinovic *et al.*, 2016) and the study of the impact of thermal variability on the performance of individuals is important to understand the microhabitat selection and the responses of ectotherms to different climatic scenarios (Somero, 2011; Bozinovic *et al.*, 2013; Estay *et al.*, 2014; Bozinovic & Pörtner, 2015; Vasquez *et al.*, 2015; Bozinovic *et al.*, 2016). Organisms reduce physiological performance when the mean temperature is out of range of the thermal optimum.

The thermal performance curve, has been studied extensively in a variety of organisms (Bozinovic *et al.*, 2016). Several parameters have been proposed to characterize the thermal performance: the optimal temperature (T_{opt}), which corresponds to the temperature at which physiological processes are at their maximum, the minimum and maximum critical temperatures, CT_{min} and CT_{max} , which are the temperatures at which the performance of the physiological features becomes null, and the amplitude of thermal performance, TPB , thermal performance breadth, which is the range at which the organism behaves well, normally defined as a yield equal to or greater than 80% of the maximum performance (Angilletta *et al.*, 2002).

The spider *Loxosceles laeta* (Nicolet, 1849) is a species of great importance for its ability to produce severe necrotic arachnidism with its bite. *L. laeta* is found within human dwellings, usually in dark corners, cracks, closets, clothing and bath towels, but can sometimes be found outdoors. It is a

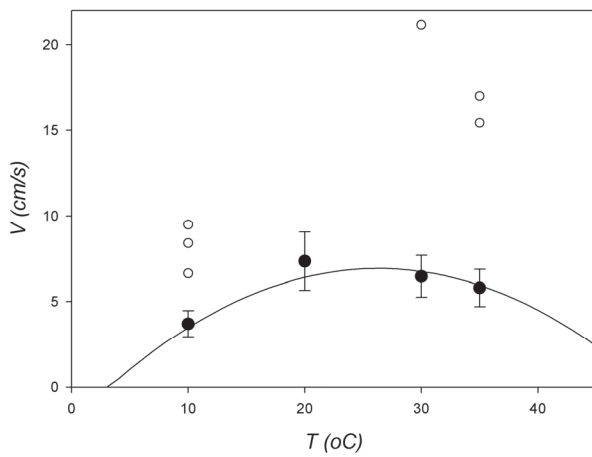


Fig. 1. Thermal performance curve of *Loxosceles laeta*. *V* is the speed and *T* the environmental temperature. The continuous line is the estimated quadratic polynomial average curve, black circles are the observed average speed, white circles are outlier values and the bars are the 95% confidence intervals at each temperature.

solitary nocturnal spider (Solís *et al.*, 2018) that feeds on flies, moths, and other small arthropods (Taucare-Ríos *et al.*, 2013; Canals & Solís, 2014; Canals *et al.*, 2015). *L. laeta* is associated with high temperatures and low amounts of precipitation. The distribution of *L. laeta* in Chile is from the Arica and Parinacota Region (18°28' 30''S 70° 18' 52''W) to the Los Lagos Region (41°28' 18''S 72° 56' 12''W) (Canals *et al.*, 2016). Its thermal preference has been established in the laboratory (Alfaro *et al.*, 2013). However, the preferred substrate temperature when spiders are exposed to sub-lethal and lethal temperatures represent extreme situations. In this study we explore the performance of spiders in a more physiological way, measuring the activity of spiders under different temperatures in a range of usual environmental temperatures in Chile.

Material and methods

Thirty-five individuals of *L. laeta*, 10 males (body mass, Mb = 106.4 ± 29.0 mg, average ± standard deviation) and 25 females (Mb = 144.4 ± 63.1 mg), were maintained at environmental temperature of 20 ± 3 °C in the Invertebrate Eco-physiology Laboratory of the Faculty of Sciences of the University of Chile. All the experiments were performed in the same laboratory during activity hours of this species (Solís *et al.*, 2018). To obtain the performance curve, the spiders were exposed to temperatures of 10, 20, 30 and 35° C for 20 minutes in a 20 cm transparent acrylic chamber immersed in a thermoregulated bath (Lab-Tech LCB-R20). After this, the spiders were removed and placed in a 1m polycarbonate cylinder that served as a "track" of a meter with graph paper. The distance of the first displacement in the cylinder was measured and the time occupied in this movement was obtained with a chronometer, estimating the movement speed (V_{ij}). The spiders were randomly selected for the trials and each spider was measured only once after the exposition to each temperature, leaving a waiting period of one day between each experiment. After each experiment the experimental cylinder was carefully cleaned with water with commercial detergent and then, to avoid any remaining detergent, was washed with distilled water.

Effects of sex and temperatures on the speed were studied with repeated measures ANOVA. The thermal performance curve was estimated with the velocity data and the corresponding temperatures, obtaining the temperature at which the maximum speed is produced. A quadratic polynomial curve (Angilletta, 2006), was fitted by means of a mixed-effects model with a random intercept.

$$V_{ij} = \beta_0 + \beta_1 * Temperature_j + \beta_2 * Temperature_j^2 + b_{0i} + \varepsilon_{ij}$$

Where $i = \{1, \dots, 35\}$ and $j = \{1, \dots, 4\}$; b_{0i} corresponds to random effects and indicates the change in velocity when individual i is measured. The free access statistical software R3.6.2 (lme4 library) was used for data processing and subsequent analysis. Once the temperature and the maximum speed were obtained according to this adjustment, we proceeded to obtain the values of 80% of the maximum speed from the marginal model and the two corresponding temperatures.

Results

The speed was different at different temperatures ($F_{3,99} = 10.77$, $p < 0.001$), without clear differences between sexes ($F_{1,33} = 3.78$, $p = 0.06$) or sex-temperature interaction effects ($F_{3,99} = 1.37$, $p = 0.26$).

The model had a good fit ($F_{3,103} = 40.9$, $p < 0.0001$; $R^2 = 0.39$ and a marginal $R^2 = 0.2$), with $\beta_0 = -2.065$ ($F_{1,103} = 3.38$, $p = 0.069$), $\beta_1 = 0.684$ ($F_{1,103} = 22.3$, $p < 0.001$), $\beta_2 = -0.013$ ($F_{1,103} = 11.5$, $p < 0.001$) (Fig. 1).

The fix effects had a marginal $R^2 = 0.2$, which represents the variability explained by the temperatures, but also a conditional $R^2 = 0.39$, indicating an increase of 0.19 points (= 0.39-0.2) in the explanation of the variability originated in the individual variability (including sex) in performance curve. The non-explained variability (= 1-0.39 = 0.61) may be explained by other factors not considered in this study such as nutritional condition, metabolic rate, behavioral aspects like motivation, among others.

The maximum predicted speed (V_{max}) the optimal temperature (T_{opt}) and the temperature breadth in which the predicted speed of spiders will be equal to or greater than 80% of V_{max} ($V_{80\%}$) are shown in Table I.

Table I. Speed and temperature parameters extrapolated from the performance curve: V_{max} : population average maximal speed, T_{opt} : temperature at which spiders reach V_{max} , $T_{i80\%}$: temperatures at which 80% of V_{max} is reached, $i = 1, 2$, CT_{min} and CT_{max} : extreme temperatures at which speed equals 0 (no movement).

V_{max}	6.67 cm/s
T_{opt}	25.5 °C
$T_{180\%}$	15.6 °C
$T_{280\%}$	35.5 °C
CT_{min}	3.2 °C
CT_{max}	49.4 °C

Discussion

The thermal preferences of spiders have been studied in less than 1% of the species (Alfaro *et al.*, 2013; Canals *et al.*, 2013); they are necessary to describe the thermal niche of these species and their acclimatization to global climate change. This is especially relevant in species of medical importance such as *L. laeta*, in which the thermal limits help to

define the foraging, reproductive and resting sites (Hanna & Cobb, 2007) where accidental bites can occur in humans.

In araneomorph spiders preferred temperatures between 16 and 27 °C in some species of Agelenidae (Pulz, 1987), Clubionidae (Almquist, 1970) and Lycosidae (Almquist, 1970; Sevacherian & Lowrie, 1972; Pulz, 1987) have been reported. In a previous study focused in the election of temperature by *L. laeta*, the preferred temperatures reported at different hours were between 17-23°C, higher at evening and night, the activity hours of this species (Alfaro *et al.*, 2013). The optimum temperature for good speed performance (T_{opt}) found in our study agrees with this range (Alfaro *et al.*, 2013) and with the activity period of this spider (Solís *et al.*, 2018). Also, the epidemiology of loxoscelism incidents coincides with its activity period, since incidents are common in night hours, occurring 70.6 % of the accidents during the hours of sleep and when getting up in the morning (Schenone, 2004).

In the study of Alfaro *et al.* (2013) the reported CT_{min} ranged between -4.84 °C and CT_{max} 48.6 ± 2.7 °C at 15 °C-25 °C. However, this study estimated the critical temperature at which the spiders did not respond to mechanical stimulation. Our study used a different approach, centered on the activity of the spiders, measuring the running speed at different temperatures. The estimated CT_{max} (49.4 °C) is very close to previous estimations with spiders exposed to high temperatures, however CT_{min} (3.2 °C) is higher than that estimated by the cessation of coordinated activity in cold (Alfaro *et al.*, 2013).

The CT_{max} was above the TL50 reported for *L. intermedia* (42 °C) and *L. laeta* (40 °C) (Fisher & Vasconcellos-Neto, 2003). This is probably associated with the adaptation of *L. laeta* to arid and semi-arid environments in Chile, characterized by high temperatures (Canals *et al.*, 2013, 2015b,c) taking into account that temperature is one of the most important niche axes in this species (Canals *et al.*, 2016).

The CT_{min} was lower than those reported for other araneomorph species, between 6.8 and 11.1 °C (Schmalhofer, 1999), which can be explained by the adaptation to the Mediterranean climate of Chile, which has important seasonal and latitudinal temperature variation. The CT_{min} was higher than that to suppress coordinated activity reported by Alfaro *et al.* (2013) and lethal lower temperature (TL₅₀) of -7 °C reported for *L. laeta*. This was an expected result, because our study estimated the average temperature at which a null speed is expected, representing the temperature at which the spiders would avoid moving.

Recent studies show that the main variable associated with the distribution of *L. laeta* in Chile is the human footprint (Canals *et al.*, 2016). The performance curve suggests that *L. laeta* is adapted to high temperatures in the range of usual indoor temperatures of human dwellings.

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