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Thermal niche overlap of the corner recluse spider *Loxosceles laeta* (Araneae; Sicariidae) and its possible predator, the spitting spider *Scytodes globula* (Scytodidae)

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ABSTRACT

Loxoscelism is a health problem caused by the bite of spiders of the genus *Loxosceles*. In Chile all cases are attributable to *Loxosceles laeta*. It has been suggested that the spitting spider *Scytodes globula* may be a predator of *L. laeta* and control its population, which is only possible if they share the microhabitat. This study compared the thermal preferences and tolerances of the two species. Later, spiders acclimated to 15 °C and 25 °C were exposed to decreasing and increasing temperatures to determine the lower and upper critical temperatures. The preferred temperatures were lower during the morning, but there were no differences between the species. The thermal niche breadths were similar for the species, with a large overlap. Both species showed tolerance to extreme temperatures, but *L. laeta* showed greater tolerance to low temperatures. Both species showed acclimation of the lower critical temperatures to changes in acclimation temperatures. The similarity of preferred and tolerated temperatures was partly an expected fact, since the species share the same macrohabitat; these spider species are very common in domestic environments of central Chile. However, the results imply that their microhabitat choices are also very similar, indicating a high probability of meeting and predation, which could have important consequences in loxoscelism epidemiology.

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1. Introduction

Loxoscelism is a health problem caused by the bite of spiders of the genus *Loxosceles* (Araneae, Sicariidae). The cases in America are attributed to *Loxosceles laeta* Nicolet 1849, and *Loxosceles reclusa* Gertsch and Mulaik 1940 in the United States, *Loxosceles gaucho* Gertsch 1940 in Argentina, *Loxosceles intermedia* Mello-Leitão 1934 in Brazil and *Loxosceles rufescens* (Dufour 1820) in Mediterranean areas (Gertsch, 1967; Gertsch and Ennik, 1983; Reyes et al., 1991; Vetter, 2008).

In Chile all necrotic arachnidism is attributed to the corner recluse spider, *L. laeta* (also called Chilean recluse), a species which may be preyed upon by the “tiger spider”: *Scytodes globula* Nicolet 1849 (Araneae, Scytodidae); the biology of these species is not well known (Fernandez et al., 2002; Canals et al., 2004, 2008).

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Spiders are ectothermic animals; their energetic processes are highly correlated with the temperature of their surroundings, with consequences in energy conservation, reproduction and prey capture. However, thermal preferences and tolerances of spiders have been studied only in 0.1% of spider species (Humphreys, 1987; Schmalhofer, 1999; Hanna and Cobb, 2007). Knowledge of thermal preferences and tolerances is necessary to describe the ecology of these animals (Hertz et al., 1993). This is particularly relevant in spiders in which the thermal limits allow defining the preferred foraging sites or preferred shelters and reproductive sites (Hanna and Cobb, 2007).

By analyzing thermal preferences and tolerances we can estimate the thermal niche, which is one of the niche dimensions. The niche is defined as a multidimensional combination of biotic and abiotic variables required for a species to survive and reproduce. This concept includes the potential (or fundamental) niche, which describes the set of conditions that a population could occupy (i.e. maximum tolerances), and the realized niche that describes the actual set of conditions under which a population exists and persists over time (i.e. preferred temperatures) (Hutchinson, 1957, 1976; Jaksic and Marone, 2007). Mechanistic

biophysical ecological methods to assess the niche have been used to quantify the interactions of organisms with their environment; not using the environment *per se* but rather the state of the organism, for example body temperature (Tb). Tb drives an organism's physiological state; thus it is crucial to quantify patterns of body temperature if we are to link controlled laboratory conditions with those in the field. The principles of these models provide a robust approach to determining mechanistically niches of organisms (Kearney, 2006, 2012, Kearney and Porter 2009, Kearney et al., 2010). Body temperature is perhaps the most important ecophysiological variable affecting all aspects of the performance of ectotherms, including locomotion, immune function, sensory input, foraging ability, courtship and rates of feeding and growth (Johnson and Bennett 1996; Portner et al., 2006; Angilletta et al., 2002; Angilletta, 2009). During the exposition to a broad range of temperatures the relationship between performance and temperature is described by a curve in which the thermal optimum is the Tb at which performance is maximum, and the critical thermal limits are the minimum (CTmin) and maximum (CTmax) body temperatures that permit performance (Angilletta et al., 2002). Traditional analyses of thermal tolerance ranges are carried out as determinations of upper and lower thermal tolerance limits, CTmax and CTmin. These extreme limits to thermal stress are found beyond the window of aerobic scope for activity, allowing estimation of their acclimation ability and their thermal tolerance ranges (Boher et al., 2010). Thermal

thresholds are also important in the determination of insect distribution and abundance in response to climate change (Hazell et al., 2010).

Niche overlap is useful to estimate the probability of encounter between species, such as predator-prey interactions between two species. Thus for there to be regulation by a predator on a prey population, niche overlap must exist. This is the case, for example, that may occur with the corner recluse spider *L. laeta* and its potential predator *S. globula*. The predation and control of populations of *L. laeta* by *S. globula* could have important consequences in the epidemiology of loxoscelism.

L. laeta is a solitary spider of domestic habitats, found within households usually in dark corners, cracks, closets, clothes and bath towels, but sometimes can be found outdoors. It has been suggested that its activity is preferentially nocturnal and that high temperatures are a factor that favoring its development (Schenone, 1998, 2003, 2004, 2001). With respect to diet, in Chile it has been reported that this spider feeds on flies, moths and other small arthropods (Levi and Spielman, 1964, Schenone, 1998, 2003, 2004, Schenone et al., 1970, 1989, 2001, Parra et al., 2002). From medical point of view the epidemiology of loxoscelism incidents coincides with nocturnal activity, since incidents are common in the twilight and night hours. Also epidemiology suggests larger spider populations and great activity in summer (Schenone, 1998, 2003, 2004, 2001).

A potential predator of *L. laeta* in Chile is *S. globula* Nicolet 1849. It is a solitary spider that belongs to the family *Scytodidae*, which includes a group of spiders known as spitting spiders with recognized arachnophagic habits (Gilbert and Rayor, 1985; Bowden, 1991). During predation these spiders spit an adhesive substance through their chelicerae, immobilizing their prey (Foelix, 1996; Araujo et al., 2008). There is little knowledge about its environmental preferences. It is active during twilight and night and desiccation tolerances are similar to those of *L. laeta* (Canals et al., 2013). *S. globula* is distributed in South America in Chile, Bolivia, Argentina, Brazil and Uruguay. Like *L. laeta*, this species is common in human dwellings and gardens of houses of central Chile (Fernandez et al., 2002).

While there are references that suggest predation on *L. laeta* by *S. globula*, there are few studies that support this (Fernandez et al.,

2002). For example, Ramirez (1999) and Ades and Ramirez (2002) produced encounters between *S. globula* and three species of *Loxosceles*: *L. laeta*, *L. gaucho* and *L. intermedia*; they found that within thirty minutes of the meeting, virtually all individuals of *L. laeta* were alive, although they were victims of the adhesive substance and wrapped in silk lines. Of the 22 predation events recorded, in three occasions the defense of *L. laeta* caused leg autotomy in *S. globula* and in two instances it was *L. laeta* who preyed on *S. globula*.

In this study we determined the thermal limits and the niche overlap of these species, considering that interactions between these two species are possible if they share the microhabitat (Canals, 2011).

2. Material and methods

2.1. Animals and study area

Forty five *S. globula* and thirty five *L. laeta* were collected from houses in the peri-urban zones of Santiago, Chile (32°S, 70°40' W). They were transferred to the laboratory at the University of Chile, Faculty of Science, fed a single *Tenebrio molitor* (Insecta; Coleoptera) larva every two weeks and exposed to 12 L:12D photoperiod. All experiments were conducted on these laboratory spiders during the period August 2011–August 2012.

2.2. Preferred temperature

Twenty one individuals of *L. laeta* (15 females and 6 males; $m_b = 156.46 \pm 69.91$ mg) and 25 individuals of *S. globula* (15 females, 10 males, $m_b = 58.8 \pm 27.43$ mg) were kept at room temperature for three weeks ($20 \pm 5^\circ\text{C}$, $60 \pm 5\%$ RH). Then each individual was exposed to a temperature gradient between 2 ± 2.56 and $50 \pm 0.89^\circ\text{C}$ established in a plastic cylinder halfway submerged in a thermoregulated chamber 1.20 m long $\times$ 0.25 m wide $\times$ 0.25 cm high. This had a thermoregulated heater in one end and a cold point in the other, generating a thermal gradient between the end points. The gradient was closely linear with a temperature of $19.3 \pm 5.10^\circ\text{C}$ in the center. Prior to the beginning of the experiments, the thermal gradient was calibrated with thermocouples installed every 5 cm.

The spiders were exposed individually for 1 h 5 min. This was repeated twice in the morning (09:00, 12:00) and twice in the twilight-night period (18:00, 20:00). Individuals were deposited in the center of the chamber and allowed five minutes of setting. Then the temperature of the spiders was measured at the mid-point of the cephalothorax every five minutes with an infrared thermometer for one hour. Prior to the experimental trial, the body mass of spiders was measured with an analytical balance (Shimadzu, AUX 220, ± 1 mg).

For each individual a record of the twelve temperatures chosen by the spiders (1 every 5 min) at 9:00, 12:00, 18:00 and 20:00 was obtained. With these temperature records, frequency histograms of the chosen temperatures were constructed. For each individual the mean preferred temperature (Tp) in each hour was calculated (the average of the twelve values).

2.3. Minimum and maximum critical temperatures

Minimum critical (CTmin) and maximum critical (CTmax) temperatures, corresponding respectively to minimum and maximum temperatures in which coordinated motor activity stopped (Vollmer and Mac Mahon, 1974; Schmalhofer, 1999) were determined using two groups of ten spiders. One group was first acclimated at 15°C and the other at 25°C for two weeks.

Each individual was then placed in a transparent plastic chamber which was exposed to decreasing temperatures from 20 °C to –10 °C with a cooling rate of 3 °C/minute. This chamber had a thermocouple and a wooden stem which allowed recording temperature and the mechanical stimulation of the spider, respectively. This experiment continued until the spider stopped coordinated motor activity, defined as the moment in which the spider did not respond to mechanical stimulation with the wooden stem. The temperature at which this occurred was recorded (CTmin). The spider was then exposed to 20 °C to recuperate it, and then it was returned to the acclimation temperature again. Subsequently and after at least two days of rest the maximum critical temperature was determined. A completely recovered spider with normal motor activity was deposited in a chamber similar to that used in CTmin experiments. This chamber was immersed in a thermo-regulated bath with temperatures that were increased from 20 °C to 50 °C at a rate of 5 °C/min to determine CTmax. As in the case of CTmin, the experiment was stopped when there was cessation of response to mechanical stimulation. Also, when possible in the last experiment a temperature that we called flight temperature (Th) was measured. This was defined as the temperature in which the spider showed a clear change in its motor activity manifested by quick movements around the container.

2.4. Analysis and statistics

The temperatures chosen by the spiders were characterized with frequency histograms. The normality of the distributions was tested with Kolmogorov–Smirnov test (K–S) and a two sample K–S test was used to compare the distributions. The niche breadth of each species was estimated with Levins's index (Jaksic and Marone, 2007): $B = (1/\sum p_i^2)$, where p_i is the proportion of use of temperature i . Furthermore the standardized Levin index was estimated: $Ba = (1/\sum p_i^2) - 1/n - 1$, where n is the number of temperatures elected in intervals of 1 °C (Colwell and Futuyma, 1971). The index values range from 0 to 1, values < 0.6 indicate a temperature election dominated by few temperatures (stenothermic specialist) and values > 0.6 indicate a generalist election of temperatures (eurythermic) (Krebs, 1989; Labropoulou and Eleftheriou, 1997).

Then to assess the similarity in thermal preferences of the species, the niche overlap was calculated with Pianka's index: $O_{jk} = \sum p_{ij}p_{ik} / \sqrt{\sum p_{ij}^2 \sum p_{ik}^2}$, where j and k represent *L. laeta* and *S. globula* and “ i ” the temperature. This index varies between 0 and 1, with 0 being null overlap and 1 complete overlap (Pianka, 1973).

To analyze differences in thermal preferences of the species, the temperatures chosen were averaged for each hour so that each experimental time was represented by a single value (Tp). Then a repeated measures ANOVA was performed, with Tp the response variable and the species and the four experimental times (repeated measure: 9:00, 12:00, 18:00 and 20:00) as the factors. Sphericity was tested with the Mauchly test. Multiple comparisons were performed with the Tukey test.

Critical temperatures and flight temperature were analyzed with two-way ANOVA, in which species and acclimation temperatures were the factors. Before all analyses the normality (K–S) and homocedasticity (Bartlett) of data was tested.

3. Results

3.1. Preferred temperature

Preferred temperatures were similar for the two species ($F_{1,44}=0.23$, $p=0.64$). Both species preferred cooler temperatures in the morning than in the evening ($F_{3,132}=17.92$, $p<0.001$), with

no significant interaction between species and the time of day ($F_{3,132}=0.46$, $p=0.71$) (Fig. 1). For *S. globula* Tp at 9:00, 12:00, 18:00 and 20:00 h were, respectively: 15.88 ± 3.87 °C, 18.12 ± 7.77 °C, 21.31 ± 5.67 °C, 20.96 ± 4.91 °C and for *L. laeta* these were 16.70 ± 5.91 °C, 19.62 ± 6.5 °C, 22.89 ± 6.35 °C and 22.93 ± 5.70 °C. We did not find differences between males and females: $F_{4,19}=0.75$, $p=0.57$ for *S. globula* and $F_{4,16}=1.85$, $p=0.17$ for *L. laeta*)

The frequency distribution of temperatures chosen by *L. laeta* and *S. globula* was different. While *L. laeta* had a bi-modal distribution with peaks of choice at 19 °C and 39 °C, the distribution for *S. globula* was unimodal (Fig. 2). Both distributions were different from a normal distribution (Shapiro–Wilks test 0.927 and 0.989, $p<0.01$, for *L. laeta* and *S. globula* respectively) and the distributions of the two species were different (K–S=0.0772, $p<0.001$)

Niche breaths and standardized breaths of the species were similar: $B=23.2$ and 26.1 , and $Ba=0.62$ and 0.61 for *S. globula* and *L. laeta*, respectively, suggesting a eurythermal status. The niche overlap was $O_{jk}=0.852$.

3.2. Critical temperatures

Minimum critical temperatures for *L. laeta* were: CTmin = -4.84 ± 2.46 °C acclimated to 15 °C and -3.44 ± 3.13 °C at 25 °C. These were lower than those of *S. globula*, CTmin = -3.85 ± 1.70 °C at 15 °C and -0.39 ± 2.13 °C at 25 °C ($F_{1,41}=7.87$, $p=0.008$). In addition minimum critical temperatures were warmer for spiders acclimated to the higher temperatures (25 °C) ($F_{1,41}=11.34$, $p=0.002$) (Fig. 3).

Maximum critical temperatures of *L. laeta* were: CTmax = 48.1 ± 2.8 °C and 48.6 ± 2.7 °C for the spiders acclimated to 15 °C and 25 °C, respectively. These were higher than those of *S. globula*: CTmax = 46.5 ± 2.4 °C and 43.5 ± 2.0 °C in the spiders acclimated to 15 °C and 25 °C, respectively ($F_{1,38}=19.28$, $p<0.001$) and an interaction effect between species and acclimation temperature was detected ($F_{1,38}=5.26$, $p=0.03$). While the upper critical temperature of *L. laeta* remained similar, that of *S. globula* decreased at higher acclimation temperature (Fig. 3).

The flight temperatures of *L. laeta* were Th = 39.5 ± 5.9 °C and 39.2 ± 5.1 °C; and for *S. globula* they were Th = 36.8 ± 4.2 °C and 36.5 ± 3.6 °C in the spiders acclimated to 15 °C and 25 °C, respectively. No differences between species ($F_{1,27}=2.3$, $p=0.14$) or between acclimation temperatures were found ($F_{1,27}=0.03$, $p=0.85$).

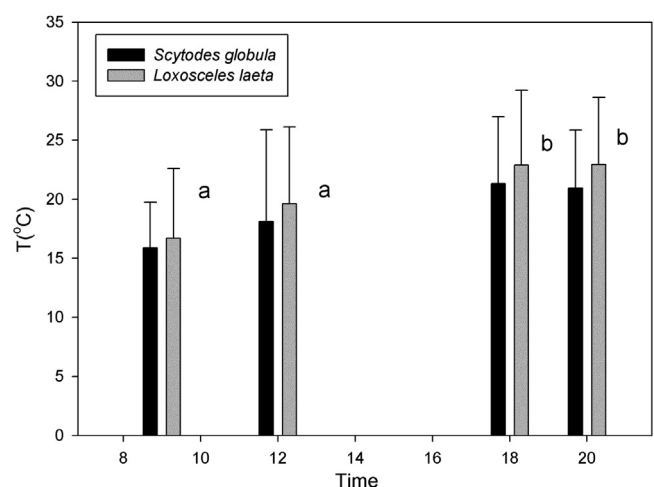


Fig. 1. Preferred temperatures of *S. globula* and *L. laeta* at different times of the day (mean and standard deviation). Different letters indicate significant differences ($\alpha=0.05$) in Tukey multiple comparisons.

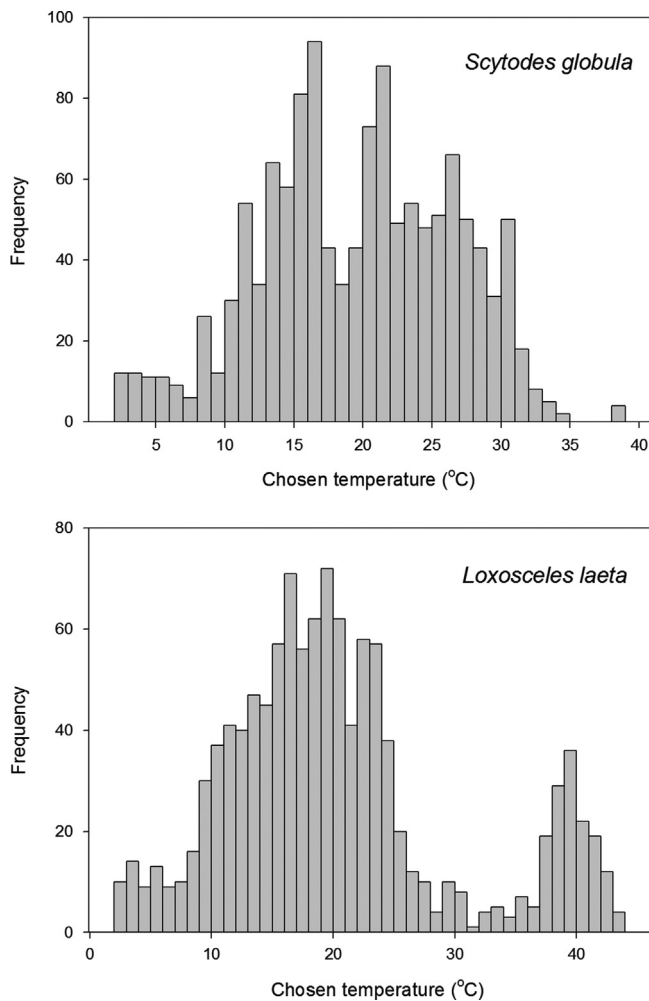


Fig. 2. Frequency histogram of preferred temperatures for *L. laeta* and *S. globula*.

4. Discussion

Thermal tolerances and preferences facilitate the description of the ecology of a species and assessment of the suitability of the habitat (Hertz et al., 1993). According to Sevacherian and Lowrie (1972) individual limits and physiological processes determine the conditions in which an organism can survive and adapt successfully to a particular environment (Fisher and Vasconcellos-Neto, 2003). In this study it was found that *L. laeta* and *S. globula* had very similar preferred temperatures, which is in agreement with finding the two species in similar environments, particularly in domestic habitats in central Chile (Schenone et al., 1970, 1989, 1975). Both species preferred higher temperatures in twilight hours, which is probably related to the crepuscular and nocturnal activity reported for these genera (Fisher and Vasconcellos-Neto, 2003; Gilbert and Rayor, 1985; Bowden, 1991). In Chile, although there are no studies of the activity rhythm for these species, there are numerous reports that suggest crepuscular and nocturnal activity (Vetter, 2008). This also coincides with the epidemiological data reported for loxoscelism. Schenone (1998, 2003, 2004, 2001) found a higher prevalence of bites by *L. laeta* on humans while sleeping and dressing (70.6%) than while performing daytime activities. In nocturnal hours (22:00–6:00 h) and in morning-afternoon (6:00–14:00 h) 73.7% of the bites occur.

Preferred temperatures for *L. laeta* and *S. globula* were in the range described for other araneomorph species, but in the lower part of the range. Variation in preferred temperature throughout the day has been reported in other arthropods (Canals et al., 1997)

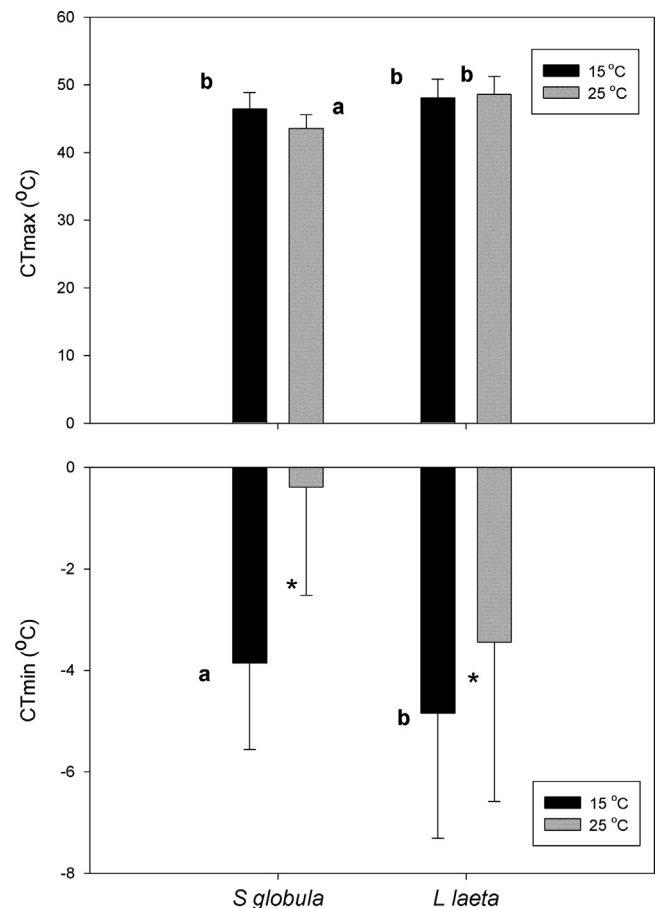


Fig. 3. Lower critical temperatures (CTmin) and upper critical temperatures (CTmax) for *S. globula* ($n=10$) and *L. laeta* ($n=10$) at two acclimation temperatures (mean $\pm$ standard deviations). In CTmin different letters indicate significant differences between species and asterisks indicate differences between acclimation temperatures ($\alpha=0.05$). In CTmax different letters indicate significant differences ($\alpha=0.05$).

and recently in mygalomorph spiders with crepuscular and nocturnal activity (Alfaro et al., 2012), but it had not been reported for araneomorph spiders. The temperatures chosen in the evenings are in the lower range of preferred temperatures of other araneomorph spiders. For example these temperatures are between 23 and 23.5 °C in Agelenidae (Pulz, 1987), between 16 and 22.3 °C in Clubionidae (Almqvist, 1970) and between 19.2 and 26.2 °C in Lycosidae (Almqvist, 1970; Sevacherian and Lowrie, 1972; Pulz, 1987). However preferred temperatures in the morning were slightly lower than the inferior limit of this range. This is consistent with lower preferred nocturnal temperature as reported by Schmalhoffer in Thomisidae (1999). Another example is *Euophrys frontalis* (Salticidae) of daytime activity, whose Tp is 27.5 °C (Almqvist, 1970), compared to *Clubiona trivialis* (Clubionidae), whose activity is nocturnal and has Tp of 16 °C.

Regarding thermal preferences, both species had standardized thermal niche breadth values slightly greater than 0.6, a value that has been proposed as limit between specialist and generalist species (Krebs, 1989). Thus *L. laeta* and *S. globula* would be predominantly eurythermal species, which is consistent with the broad tolerance polygons. Although they had similar amplitudes, the frequency histograms of chosen temperatures were different; *L. laeta* showed bi-modality, which reveals a more marked change in their preferred temperatures in hours of activity. The thermal niche overlap was extensive ($O_{jk}=0.852$) between these species, which implies a similar choice of thermal microenvironments.

The lower critical temperatures for these species were low, but higher than lower lethal temperatures reported for other species, between -6.8 and -11.1 °C in araneomorph spiders (Schmalhofer, 1999). This was because in this study, the critical temperature for the suppression of the activity was measured instead of the lethal temperature. Except for two individuals, the spiders studied here recovered quickly from the treatments. For the same reason, the values reported in this study are higher than the lethal lower temperatures (TL₅₀) of -7 °C reported for *L. laeta* and *L. intermedia* (Fisher and Vasconcellos-Neto, 2003) and -9 °C reported for *L. reclusa* (Cramer and Maywright, 2008). *L. laeta* showed greater tolerance to low temperatures than *S. globula*.

Maximum critical temperatures were very high and only comparable to those reported for *Cyrtophora citricola* (46 °C) (Pulz, 1987) and *Lycosa carolinensis* (46 °C) (Moeur and Ericksen, 1972). These temperatures were in the range reported as lethal for other araneomorph spiders, which is generally about 47 to 48 °C (Schmalhofer, 1999). These are also above the TL₅₀ reported for *L. intermedia* (42 °C) and *L. laeta* (40 °C) (Fisher and Vasconcellos-Neto, 2003). This is probably related to the methodology of raising the temperature at a rate of 5 °C per minute (short time) without maintaining the spiders for prolonged periods at high temperatures. The use of a slower ramping would have resulted in different values. For example, this effect has been reported to lower lethal temperatures in *L. reclusa*. Thus, while it has been reported that the TL₅₀ of *L. reclusa* exposed for a short time to low temperature is -9 °C, but when exposed for a long time only 30% survived at -2 °C and none survived at -5 °C (Cramer and Maywright, 2008). Flight temperatures appear to be a better estimator of tolerance and critical temperatures have values similar to those described for other spiders, however unfortunately this measure is less objective because it is expressed by a high increase in motor activity which is not clearly present in all spiders.

The maximum critical temperature of *L. laeta* did not vary with acclimation, while that of *S. globula* declined slightly at 25 °C. By contrast, minimum critical temperatures of both species were higher when these were acclimatized to higher temperatures. Although it has been reported that no acclimation temperatures affect thermal tolerances in araneomorph spiders (Lycosidae) and mygalomorph spiders (Sevacherian and Lowrie, 1972; Seymour and Vinegar, 1973), recent studies have reported acclimatization of preferred temperatures in the mygalomorph spider *Paraphysa parvula* (Alfaro et al., 2012) and our study showed acclimation of minimal critical temperatures in both species. Our results agree with those reported for other arthropod lethal limits such as those of insects, where the variation in the upper lethal limit is much less than the variation in the lower lethal limit (Addo-Bediako et al., 2000). In this regard it has been proposed that the responses to heating and cooling mechanisms obey different mechanisms and these are decoupled (Boher et al., 2010).

The niche breadth estimated here is a proxy of the realized thermal niche, but body temperature is only one dimension of the niche hyperspace that is constrained by other factors such as water loss, desiccation tolerance and energy requirements; thus despite the great overlap shown in thermal niche, they may differentiate in the other niche axes. However this is not the case. Both spiders are nocturnal, live in similar habitats and have similar water loss rates and mass specific metabolic rate (Canals et al., 2013).

In summary, *L. laeta* and *S. globula* from a thermal standpoint had very similar characteristics. The estimated niche overlap through preferred temperatures overlap was considerable, which is consistent with the overlap in the thermal tolerances. This was partly an expected fact, since both species share the macro-habitat and these spider species are very common in domestic environments of central Chile. However, these characteristics imply that

their micro-habitat choices are also very similar, indicating a high probability of meeting, allowing predation interactions between both species (Canals and Solís, 2013). This could have important consequences in loxoscelism epidemiology. If *S. globula* predaes *L. laeta*, it could become a weapon of biological control of the *L. laeta* populations.

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