



## Daily thermal preference variation of the sand recluse spider *Sicarius thomisoides* (Araneae: Sicariidae)

Andrés Taucare-Ríos<sup>a,b,\*</sup>, Claudio Veloso<sup>c</sup>, Mauricio Canals<sup>d</sup>, Ramiro O. Bustamante<sup>c,e</sup>

<sup>a</sup> Facultad de Ciencias, Universidad Arturo Prat, Casilla 121, Iquique, Chile

<sup>b</sup> Centro de Investigación en Medio Ambiente (CENIMA), Universidad Arturo Prat, Casilla 121, Iquique, Chile

<sup>c</sup> Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Chile

<sup>d</sup> Departamento de Medicina & Programa de Salud Ambiental, ESP, Facultad de Medicina, Universidad de Chile, Chile

<sup>e</sup> Instituto de Ecología y Biodiversidad (IEB), Facultad de Ciencias, Universidad de Chile, Santiago, Chile

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### ABSTRACT

Preferential temperature as a physiological feature is crucial for spiders, since it determines the selection of key habitats for their survival and reproduction. In this work, we study the daily and geographical variation of the preferential temperature of the spider *Sicarius thomisoides* subjected to different degrees of daily thermal oscillation in their habitats. Preferred temperatures differ between coastal and inland populations, but in both cases, there is a marked bimodality in the daily pattern of temperature preference, with two peaks per day that would be given by the changes in the hours of activity. These nocturnal spiders select higher temperatures in the evening (active period) and select lower temperatures during late morning (resting period). In laboratory, spiders have preferred temperatures that differ from those found in their habitats, so they must tolerate or compensate non-preferred temperatures by active thermoregulation in natural conditions.

### 1. Introduction

Temperature is an environmental variable capable of generating selective pressure in populations along environmental gradients, modulating the evolution of body size, metabolism, thermal tolerance and thermal preference (Castañeda et al., 2005; Dillon et al., 2009; Lardies et al., 2011; Gaitan-Espitia et al., 2014). In turn, contrasting thermal environments can determine inter-population variations in phenotypic traits (Dillon et al., 2009; Gaitan-Espitia et al., 2014; Barria and Bacigalupe, 2017).

Body temperature is an important ecophysiological variable for ectothermic organisms (Johnson and Bennett, 1996; Canals, 1998; Angilletta et al., 2002; Alfaro et al., 2013). In some cases, body temperatures are similar to environmental temperatures, while in others, individuals can find optimal temperatures via behavioral and physiological thermoregulations (Huey, 1982; Hertz and HueyStevenson, 1993; Díaz et al., 2002). In this context, preferred temperature (Tp) is important to quantifying changes of body temperature (Tb) in ectotherms; under laboratory conditions, we can simulate thermal environments existing in the field to examine thermal preferences under controlled thermal environments (Huey and Stevenson, 1979; Huey,

1991).

Thermal preferences (Tp) are obtained using a thermal gradient, in which individuals are allowed to freely choose a temperature that is then considered optimal (Canals et al., 1997; Dillon et al., 2009; Alfaro et al., 2013; Sepúlveda et al., 2014). The preference zone is a thermal interval in which the individuals could find their physiological optimum in natural habitats (Dillon et al., 2009; Stork, 2012; Alfaro et al., 2013). This physiological trait may vary with sex, body size, photoperiod and the geographic origin of populations (Castañeda et al., 2005; Stork, 2012; Alfaro et al., 2013).

Studies of daily thermal variation that indicate the range of body temperatures available to an ectotherm are important to determine how body temperatures are constrained by environmental factors (Peterson, 1987; Angilletta et al., 1999). In addition, little is known about body temperature variation during periods of inactivity (e.g., during daily torpor) vs activity periods (e.g., during reproduction or capture of prey) (Huey, 1982; Huey et al., 1989; Goldsbrough et al., 2004).

Spiders are ectothermic organisms and their activity and locomotor speed, are highly correlated with temperature (Ford, 1978; Stork, 2012; Taucare-Ríos et al., 2018). Temperature affects many aspects of a spider's life, i.e. growth, survival and reproduction (Goldsbrough et al.,

\* Corresponding author. Facultad de Ciencias, Universidad Arturo Prat, Casilla 121, Iquique, Chile.

E-mail address: [and.taucare26@gmail.com](mailto:and.taucare26@gmail.com) (A. Taucare-Ríos).

2004; Glover, 2013). However, thermal preferences in spiders have been poorly studied around the world, especially in environmental gradients with different climatic conditions (Schmalhofer, 1999; HannaCobb, 2007; Stork, 2012).

The sand recluse spider *Sicarius thomisoides* (Sicariidae) lives in desert biomes located in Chile, characterized by high temperatures during the day and low temperatures at night. These spiders are nocturnal animals and are thus inactive during the day (Magalhães et al., 2017; Taucare-Ríos et al., 2017). This species hunt under rocks in arid environments with sandy substrate. They are considered as sit-and-wait predators, waiting for prey and ambushing from their shelters, although they can also be seen stalking at night. They mainly consume coleopterans, myriapods and other spiders (Magalhães et al., 2017).

Previous studies provide strong evidence of microhabitat selection by this species, selecting rocks larger than 40 cm and with temperatures between 25 and 30 °C (Taucare-Ríos et al., 2017). During the summer, adults copulate and females lay eggs under these rocks (Magalhães et al., 2017; Taucare-Ríos et al., 2018). Females of *S. thomisoides* are sedentary, but move looking for suitable rocks to lay a hide their egg sacs, while the males move when searching for females. Experimentally, the locomotor performance of this species has been measured during the reproductive period, with an optimum temperature ( $T^{\circ}opt$ ) of  $25.33 \pm 2.65$  °C,  $CT_{min} = 6.56 \pm 1.72$  °C and  $CT_{max} = 44.23 \pm 4.92$  °C. Under rocks, these spiders would find temperatures close to the optimum performance that would favor reproduction and protect them from critical temperatures (Taucare-Ríos et al., 2018).

In this study, we examined thermal preferences ( $T_p$ ) of the spider *S. thomisoides* (Araneae: Sicariidae) under controlled lab conditions. We evaluated individuals from three populations located on the coast (characterized by low mean diurnal range), and three populations far from the coast (with high mean diurnal range). We expected to find differences in the preferential temperature related to the period of activity and the geographic location of the populations.

## 2. Material and methods

### 2.1. Animals and study area

Adult individuals (males and females) were captured in different locations along the known distribution of the species. Coastal habitats with low daily variation include: Iquique (20.126°S, 70.921° W; Mean diurnal range: 7.8 °C), Punta de Choros (29.144°S, 71.274°W; Mean diurnal range: 9.1 °C) and Maitencillo (32.31°S, 71.270°W; Mean diurnal range: 10.05 °C). Inland habitats with high daily variation were: Canchones (20.255°S, 69.334°W; Mean diurnal range: 13.9 °C), Vicuña (30.01°S, 70.42°W; Mean diurnal range: 11.8 °C) and Lo Prado (33.26°S, 70.43°W; Mean diurnal range: 17.6 °C) (temperatures obtained by <https://es.climate-data.org/>). The specimens were housed in plastic boxes (250 cm<sup>3</sup>) and transferred to the laboratory of Ecophysiology of Invertebrates, University of Chile in the Faculty of Sciences, Santiago of Chile and were fed with a single larva of *Tenebrio molitor* (Insecta, Coleoptera) every week, with a photoperiod of 12L: 12D under laboratory conditions (Night:  $22.57 \pm 1.47$  °C; Day:  $26.52 \pm 2.31$  °C) for 3 weeks before beginning the experiments.

### 2.2. Laboratory thermal preferences

The specimens were exposed to a temperature gradient in a plastic cylinder submerged halfway in water inside a thermo-regulated chamber of 1.20 m long x 0.25 m wide x 0.5 cm high. At one end of the chamber, a thermoregulator was placed with a heater and at the other end a cold point, with ice water generating a temperature gradient between 8 °C and 45 °C, monitored by thermocouples. The spiders were exposed individually for 1 h to said gradient. Individuals were randomly placed inside the chamber and their body temperature was measured with an IR (Extech, model IRT600) thermometer pointing towards the

cephalothorax of the spider at a distance of 15 cm every 5 min for 1 h following Alfaro et al. (2013). This was repeated twice during the morning (at 10:00 and 12:00) and twice at evening (at 18:00 and at 20:00) to evaluate if there are differences in the selection of temperatures during the day. Here, preferred temperature ( $T_p$ ) was defined as the mean temperature obtained from the thermal gradient. The  $T_p$  for each habitat was represented by a frequency histogram. Before the experiments, body mass of spiders was measured with an analytical balance (Shimadzu, AUX 220,  $\pm 1$  mg).

### 2.3. Statistical analysis

Previously, we tested for normality and homoscedasticity using the Kolmogorov-Smirnov and Levene tests, respectively. For each individual the average temperature of thermal preference ( $T_p$ ) was calculated for each hour (the average of the twelve values). A repeated measures ANOVA was performed, with  $T_p$  as the response variable and the origin of the populations (coast vs inland) and the four experimental times as factors. An *a posteriori* test of Tukey was performed to check the differences between the means. To record environmental temperatures ( $T_e$ ) in the origin locality, thermochron iButton temperature loggers ACR Mark ( $\pm 0.5$  °C) were placed under rocks where spiders were found. The devices were active for a month measuring temperature all day every 30 min in each location during January 2016 (mid-summer) with an average time of sunrise: 6:43 a.m. and sunset: 20:08 p.m. To compare laboratory thermal preferences ( $T_p$ ) and environmental temperatures ( $T_e$ ) in each habitat, a Student's t-test was used ( $p < 0.05$ ).

## 3. Results

A total of 107 individuals were studied (86 females and 21 males), with female body mass at  $0.52 \pm 0.18$  g and male body mass at  $0.47 \pm 0.14$  g. We did not find correlation between mass and preferred temperature ( $n = 107$ ,  $r = 0.091$ ,  $p = 0.35$ ). Considering the populations studied, the estimated average preferred temperature ( $T_p$ ) for this species is approximately  $25.50 \pm 3.52$  °C (Table 1). The results show that thermal preference ( $T_p$ ) obtained in the laboratory varies depending on the time (hour) of the day (ANOVA repeated measures two factors,  $F_{3, 312} = 148.44$ ,  $p < 0.001$ ) and habitat ( $F_{1, 104} = 71.118$ ,  $p < 0.001$ ) (Fig. 1). No interaction between time and habitat was found ( $F_{3, 312} = 1.93$ ,  $p < 0.12$ ). In addition, no differences were found between sexes in preferred temperatures (Student's t-test =  $-0.92$ ,  $df = 106$ ,  $p = 0.36$ ). Spiders prefer approx. 20–25 °C in the morning and approx. 25–30 °C in the evening, individuals tends to avoid temperatures below 10 °C and above 40 °C. We observed that spiders stop moving when staying for a long time at low temperatures near or below 15 °C.

In all populations,  $T_p$  increased during the evening and histograms have bimodal distribution in both habitats, possibly related to differences in activity time, however, it is more noticeable in inland

**Table 1**  
Preferred temperatures ( $T_p$ ) for different locations and period of day.

Locality	Time			
	10	12	18	20
Iquique (17)	20.56 ± 3.22	20.47 ± 3.36	25.53 ± 2.87	26.95 ± 2.90
Punta de Choros (20)	17.73 ± 4.93	19.84 ± 4.28	25.47 ± 4.53	25.8 ± 3.23
Maitencillo (18)	18.8 ± 2.58	20.5 ± 3.24	28.88 ± 2.78	30.17 ± 3.61
Canchones (15)	22.69 ± 3.16	23.79 ± 4.10	34.21 ± 4.16	36.36 ± 3.45
Vicuña (17)	23.06 ± 5.62	25.54 ± 7.42	27.9 ± 6.26	28.78 ± 5.91
Lo Prado (20)	21.06 ± 3.67	23.07 ± 5.6	34.2 ± 3.26	34.06 ± 2.31

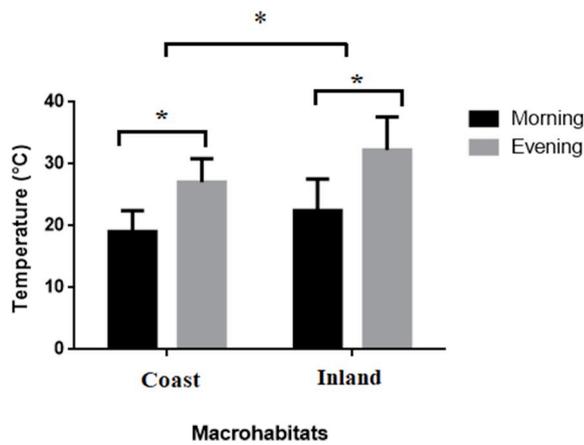


Fig. 1. Thermal preferences of *S. thomisoides* (Mean  $\pm$  SD) in different habitats. \* indicates significant differences. Morning: 10:00–12:00hrs; Evening: 18:00–22:00hrs.

populations (Fig. 2A–B). Temperatures under rocks account for a similar pattern obtained in the laboratory with a marked daily thermal variation (Fig. 3). There are significant differences between  $T_p$  and  $T_e$ , depending on the time of activity. In coastal locations, environmental temperatures ( $T_e$ ) are higher than preferred temperatures ( $T_p$ ) during the morning (Student's t-test,  $t = -3.77$ ,  $gl = 218$ ,  $p < 0.05$ ), while in the evening  $T_p$  is higher than  $T_e$  (Student's t-test,  $t = 9.15$ ,  $gl = 214$ ,  $p < 0.05$ ) (Fig. 4A). On the other hand, inland locations have higher morning  $T_p$  than  $T_e$  (Student's t-test,  $t = 3.07$ ,  $gl = 214$ ,  $p = 0.002$ ) and higher evening  $T_p$  than evening  $T_e$  (Student's t-test,  $t = -11.25$ ,  $gl = 214$ ,  $p < 0.05$ ) (Fig. 4B).

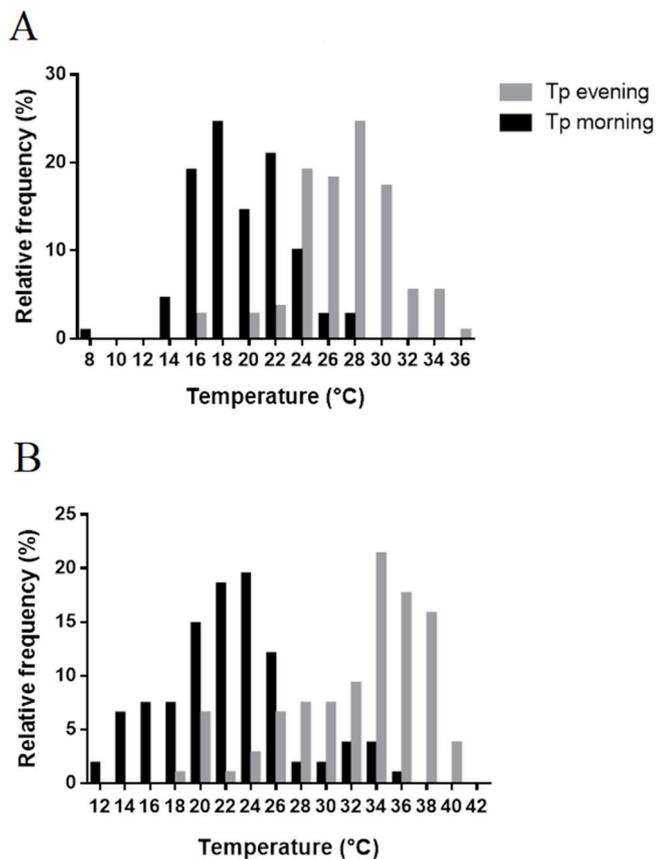


Fig. 2. A–B. Frequency histogram of preferred temperatures (percentage of all recordings) for *Sicarius thomisoides* in different habitats. A. Coast locations; B. Inland locations.

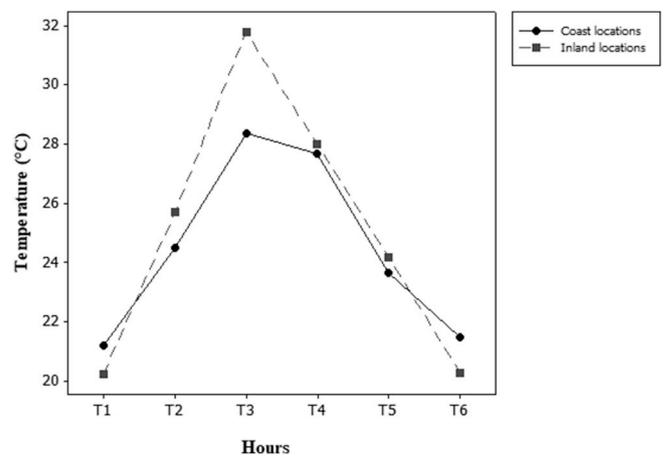


Fig. 3. Daily temperature variation for different habitats where *Sicarius thomisoides* were found. Abbreviation: T1 (0600–1000), T2 (1000–1400), T3 (1400–1800), T4 (1800–2200), T5 (2200–0200), T6 (0200–0600).

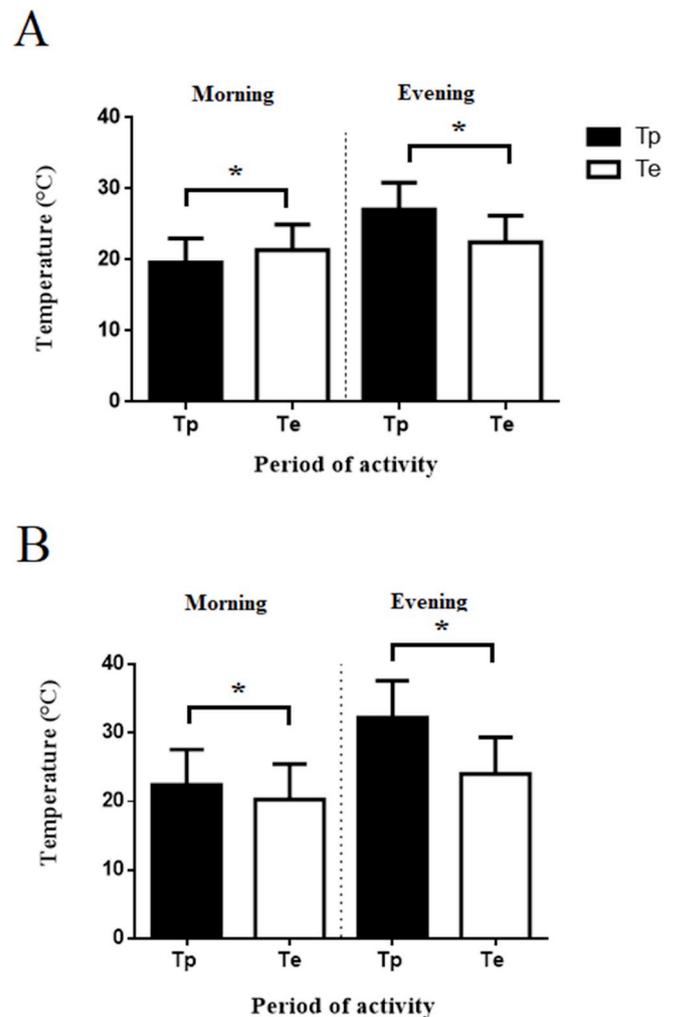


Fig. 4. Preferred temperatures ( $T_p$ ) vs environmental temperature ( $T_e$ ) for different habitats (Mean  $\pm$  SD). A. Coast locations; B. Inland locations \* indicates significant differences. Morning: 10:00–12:00hrs; Evening: 18:00–22:00hrs.

#### 4. Discussion

The results obtained suggest that *Sicarius thomisoides* is an eurythermal species with a large amplitude of thermal niche, capable of moving over a wide range of temperatures. The field temperatures obtained by the sensors move within a smaller range but are contained within the thermal niche found in the laboratory (niche realized vs. fundamental niche) (Hutchinson, 1957; Kearney et al., 2010).

The differences in Tp between coastal and inland locations may lie in the daily thermal variation to which spiders are subjected in their habitats. High temperatures during evenings and low temperatures during mornings might be more marked in inland populations, because rock temperatures should be warmer or cooler than in coast locations. Higher evening Tp reflect that *S. thomisoides* leaves the sheltered area beneath rocks at night and moves over the sides of the rocks as well as under the rocks as it hunts. On the other hand, low temperatures in the mornings may favor the decrease physiological activity in these spiders by reducing body temperature and metabolic rate (i.e. torpor), which reduces water loss, important for survival in desert environments (Geiser, 2004). Histograms show a strong bimodal distribution for thermal preferences, agreeing with Canals et al. (1997) and Alfaro et al. (2013) regarding nocturnal spiders that spend much of their lives under rocks. This daily variation in Tp has been found in both arthropods and small nocturnal vertebrates (Canals et al., 1997; Angilletta et al., 1999; Alfaro et al., 2013). Alfaro et al. (2013) found that *Loxosceles laeta* (Sicariidae), a species with nocturnal habits and belonging to the same family, selects low temperatures during mornings and high temperatures during the evening. Thus, the bimodality of the frequency histograms might reflect the drastic change in their thermal preferences during the hours of activity (Alfaro et al., 2013). The increase of Tp during the evening may be directly related to the thermoregulatory capacity of these spiders (Angilletta et al., 1999; Alfaro et al., 2013). For example, some nocturnal lizards tend to increase their body temperature before starting their activity at night, where high daytime body temperatures would help in digestion, maintenance, growth, reproduction, foraging and other physiological processes that are temperature dependent (Angilletta et al., 1999).

Environmental temperature (Te) and preferred temperature (Tp) are different, in which case these spiders must tolerate non-preferred temperatures if it is unable to behaviorally or physiologically keep body temperature (Tb) within Tp. On the other hand, some spiders show sophisticated behavioral and physiological temperature regulation (Humphreys, 1987) very similar to that found in other small ectothermic organisms (Humphreys, 1978; Sabo, 2003; Frick et al., 2007). One of the suggested mechanisms for *S. thomisoides* is the active selection of microhabitat in suitable rocks that have ideal temperatures to maximize their performance without falling into thermal stress (Taucare-Ríos et al., 2018).

We found that preferred temperature ( $25.50 \pm 3.52$  °C) is very similar to the performance optimum temperature (Topt) of this species in the reproductive period ( $25.33 \pm 2.65$ °C, Taucare-Ríos et al., 2018). Therefore, the temperature found in the laboratory would be related to the optimum temperature that *S. thomisoides* look for to reproduce in natural conditions. Some studies coinciding with our results, showing that thermal preferences would match the optimum temperature for maximizing the fitness in ectotherms, affecting reproductive success in their habitats (Angilletta et al., 2002; Martin and Huey, 2008).

Temperature is important for the selection of reproductive sites in spiders because thermal conditions influence egg viability and clutch size. Females could benefit if they can moderate their body temperature through microhabitat selection within a range optimal of temperatures (Li and Jackson, 1996; Rittschof, 2012). Females of *S. thomisoides* might prefer lower temperature in the morning (the spider's resting phase) as a means of reducing energy expenditure. By selecting microhabitats with lower Te, spiders reduce metabolic rate, which would allow females to expend less energy/resources on maintenance and, conversely, allocate

more resources/energy to reproduction. If these spiders select large rocks in the field, they have a thermoregulatory advantage, since large rocks reduce the impact of extreme temperatures during the day (Huey et al., 1989). The upper surfaces of the rocks would be warmer due to an accumulation of heat load during the day while sun exposed. This would explain inactivity during mornings and the increase in activity during evenings (Huey et al., 1989; Angilletta et al., 1999).

On the other hand, the absence of differences in thermal preferences between spiders of different sexes would possibly account for a similar use of microhabitats under field conditions, which has also been seen in other ectotherms (Anaya-Rojas et al., 2010). In this scenario, individuals could compete for the availability of shelters with high thermal quality, favoring territoriality and the struggle for the use of the same microhabitat (Huey et al., 1989; Díaz et al., 2006; Taucare-Ríos et al., 2017).

The preferred temperatures are not directly related to the type of climate in which the spiders are found, but they might be linked to the daily thermal variations (Huey and Stevenson, 1979; Huey et al., 1989; Sepúlveda et al., 2014; Alfaro et al., 2013). In this sense, there are doubts about the ecological significance of the thermal preference measured in the laboratory since in some cases they coincide with the temperature found in the field, while in other cases they do not (Humphreys, 1977; Huey and Bennett, 1987; Kinzner et al., 2019).

Another aspect to consider is the methodological limitations in the short 1-h measurement used in this study, since some studies of thermal preference have indicated that reliable results cannot be obtained until the animals have been in the temperature gradient for several days (Huey and Bennett, 1987; Dillon et al., 2009). Our results should be viewed with caution; however, similar studies conducted in small arthropods such as insects and spiders with short intervals measurements (60–90 min) have had valid results in laboratory conditions (Castañeda et al., 2005; Alfaro et al., 2013; Kinzner et al., 2019).

In conclusion, the sand recluse spider *S. thomisoides* is a species that selects a wide range of temperatures. Preferred temperatures differ between coastal and inland populations, but in both cases, there is a marked bimodality that would be given by the daily thermal variation and changes in the hours of activity. Under laboratory conditions, spiders have preferred temperatures that differ from those found in their habitats, so they must tolerate or compensate non-preferred temperatures by active thermoregulation. Thermal compensation is more likely, since these spiders are capable of selecting thermally suitable rocks in nature.

#### Author statement

I have decided to upload the preferential temperature data of the spider studied.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2019.102465>.

#### References

- Angilletta, M.J., Montgomery, L.G., Werner, Y.L., 1999. Temperature preference in geckos: diel variation in juveniles and adults. *Herpetologica* 55 (2), 212–222.
- Angilletta, M.J., Niewiarowski, P.H., Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* 27 (4), 249–268.
- Alfaro, C., Veloso, C., Torres-Contreras, H., Solis, R., Canals, M., 2013. Thermal niche overlap of the brown recluse spider *Loxosceles laeta* (Araneae; Sicariidae) and its

- possible predator, the spitting spider *Scytodes globula* (Scytodidae). *J. Therm. Biol.* 38, 502–507.
- Anaya-Rojas, J.M., Serrano-Cardozo, V.H., Ramirez-Pinilla, M.P., 2010. Diet, microhabitat use, and thermal preferences of *Ptychoglossus bicolor* (Squamata: Gymnophthalmidae) in an organic coffee shade plantation in Colombia. *Papeis Avulsos Zool. (São Paulo)* 50 (10), 159–166.
- Barria, A.M., Bacigalupe, L.D., 2017. Intraspecific geographic variation in thermal limits and acclimatory capacity in a wide distributed endemic frog. *J. Therm. Biol.* 69, 254–260.
- Canals, M., Solís, R., Valderas, J., Ehrenfeld, M., Cattán, P.E., 1997. Preliminary studies on temperature selection and activity cycle of Chilean vectors of the Chagas disease. *J. Med. Entomol.* 34 (1), 11–17.
- Canals, M., 1998. Thermal ecology of small animals. *Biol. Res.* 31, 367–374.
- Castañeda, L.E., Lardies, M.A., Bozinovic, F., 2005. Interpopulational variation in recovery time from chill coma along a geographic gradient: a study in the common woodlouse, *Porcellio laevis*. *J. Insect Physiol.* 51, 1346–1351.
- Díaz, F., Sierra, E., Re, A.D., Rodríguez, L., 2002. Behavioural thermoregulation and critical thermal limits of *Macrobrachium acanthurus* (Wiegman). *J. Therm. Biol.* 27, 423–428.
- Díaz, J.A., Monasterio, C., Salvador, A., 2006. Abundance, microhabitat selection and conservation of eyed lizards (*Lacerta lépida*): a radiotelemetric study. *J. Zool.* 268, 295–301.
- Dillon, M.E., Wang, G., Garrity, P.A., Huey, R.B., 2009. Thermal preference in *Drosophila*. *J. Therm. Biol.* 34, 109–119.
- Ford, 1978. Locomotory activity and predation strategy of the wolf spider, *Pardosa amentata* (Clerck) (Lycosidae). *Anim. Behav.* 26, 31–35.
- Frick, H., Kropf, C., Nentwig, W., 2007. Laboratory temperature preferences of the wolf spider *Pardosa riparia* (Araneae, Lycosidae). *Bull. Br. Arachnol. Soc.* 14, 45–48.
- Gaitan-Espitia, J.D., Bacigalupe, L.D., Opitz, T., Lagos, N.A., Timmermann, T., Lardies, M.A., 2014. Geographic variation in thermal physiological performance of the intertidal crab *Petrolisthes violaceus* along a latitudinal gradient. *J. Exp. Biol.* 217, 4379–4386.
- Geiser, F., 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* 66, 239–274.
- Glover, N., 2013. The habitat preferences of web building spiders. *Plymouth Stud. Sci.* 6 (1), 363–375.
- Goldsbrough, C.L., Hochuli, D.F., Shine, R., 2004. Fitness benefits of retreat-site selection: spiders, rocks, and thermal cues. *Ecology* 85, 1635–1641.
- Hanna, C.H.J., Cobb, V.A., 2007. Critical thermal maximum of the green lynx spider *Peucea viridans* (Araneae, Oxyopidae). *J. Arachnol.* 35, 193–196.
- Hertz, P., Huey, R., Stevenson, R., 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142, 796–818.
- Huey, R.B., Stevenson, R., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Integr. Comp. Biol.* 19, 357.
- Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles. In: Gans, C., Pough, F.H. (Eds.), *Biology of the Reptilia*, vol. 12. Academic Press, London, England, pp. 25–91.
- Huey, R.B., Bennett, A.F., 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41, 1098–1115.
- Huey, R.B., Peterson, C.R., Arnold, S.J., Porter, W., 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70, 931–944.
- Huey, R.B., 1991. Physiological consequences of habitat selection. *Am. Nat.* 137, 91–115.
- Humphreys, W.F., 1977. Variables influencing laboratory energy budgets of *Geolycosa godeffroyi* (Araneae). *Oikos* 28, 225–233.
- Humphreys, W.F., 1978. The thermal biology of *Geolycosa godeffroyi* and other burrow inhabiting Lycosidae (Araneae) in Australia. *Oecologia* 31, 319–347.
- Humphreys, W.F., 1987. Behavioral temperature regulation. In: *Ecophysiology of Spiders*. (W. Nentwig. Springer-Verlag, Berlin, pp. 56–65.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22, 415–427.
- Johnson, I.A., Bennett, A.F., 1996. *Animals and Temperature*. Society for Experimental Biology Seminar Series, vol. 59. Cambridge University Press, Cambridge, p. 419.
- Kearney, M., Simpson, S.J., Raubenheimer, D., Helmuth, B., 2010. Modelling the ecological niche from functional traits. *Phil. Trans. R. Soc.* 365, 3469–3483.
- Kinzner, M.T., Kinzner, M.C., Kaufmann, R., Hoffman, A.A., Arthofer, W., Schlick-Steiner, B.C., Steiner, F.M., 2019. Is temperature preference in the laboratory ecologically relevant for the field? The case of *Drosophila nigrosparsa*. *Glob. Ecol. Conserv.* <https://doi.org/10.1016/j.gecco.2019.e00638>.
- Lardies, M.A., Muñoz, J.L., Paschke, K.A., Bozinovic, F., 2011. Latitudinal variation in the aerial/aquatic ratio of oxygen consumption of a supratidal high rocky-shore crab. *Mar. Ecol.* 32, 42–51.
- Li, D.Q., Jackson, R.R., 1996. How temperature affects development and reproduction in spiders: a review. *J. Therm. Biol.* 21, 245–274.
- Magalhães, I.L.F., Brescovit, A.D., Santos, A.J., 2017. Phylogeny of Sicariidae spiders (Araneae: Haplogynae), with a monograph on neotropical Sicarius. *Zool. J. Linn. Soc.* 179, 767–864.
- Martin, L., Huey, R., 2008. Why “Suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. *Am. Nat.* 171, 102–118.
- Peterson, C., 1987. Daily variation in the body temperatures of free-ranging garter snakes. *Ecology* 68, 160–169.
- Rittschof, C.C., 2012. The effects of temperature on egg development and web site selection in *Nephila clavipes*. *J. Arachnol.* 40, 141–145.
- Sabo, J.L., 2003. Hot rocks or no hot rocks: overnight retreat availability and selection by a diurnal lizard. *Oecologia* 136, 329–335.
- Schmalhofer, V.R., 1999. Thermal tolerances and preferences of the crab spiders *Misumenops asperatus* and *Misumenoides formosipes* (Araneae, Thomisidae). *J. Arachnol.* 27, 470–480.
- Sepúlveda, R., Taucare-Ríos, A., Veloso, C., Canals, M., 2014. Thermal preference of *Dysdera crocata* Koch 1838 (Araneae: dysderidae). *J. Arachnol.* 42 (3), 299–302.
- Stork, R., 2012. Intraspecific variation in the thermal biology of *Rabidos arabida* (Araneae: Lycosidae) (Walckenaer) from the mountains of Arkansas. *Environ. Entomol.* 41, 1631–1637.
- Taucare-Ríos, A., Claudio, V., Bustamante, R.O., 2017. Microhabitat selection in the sand recluse spider (*Sicarius thomisoides*): the effect of rock size and temperature. *J. Nat. Hist.* 51, 2199–2210.
- Taucare-Ríos, A., Veloso, C., Bustamante, R.O., 2018. Thermal niche conservatism in an environmental gradient in the spider *Sicarius thomisoides* (Araneae: Sicariidae): implications for microhabitat selection. *J. Therm. Biol.* 78, 298–303.