

Thermal preference of *Dysdera crocata* C. L. Koch 1838 (Araneae: Dysderidae)

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Abstract. Body temperature is the most important ecophysiological variable affecting all aspects of the performance of ectotherms. However, thermal preferences and tolerances of spiders have been studied only in 0.1% of spider species. Knowledge of thermal preferences and tolerances is necessary to describe the ecology of these animals, defining the preferred foraging sites or preferred shelters and reproductive sites. In this study we report for the first time the preferred temperature of *Dysdera crocata* C.L. Koch 1838 in the laboratory. This is an epigeal spider of Mediterranean climates with large temperature fluctuations. The preferred temperature was low: 9.12 ± 5.12 °C, and actively searched. It did not vary throughout the day.

Keywords: Woodlouse spider, micro-environments, Chile

Spiders are ectothermic animals; their energetic processes are highly correlated with the temperature of their surroundings, which has 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 & Cobb 2007). Knowledge of thermal preferences and tolerances is necessary to describe the ecology of these animals (Hertz et al. 1993), defining the preferred foraging sites or preferred shelters and reproductive sites (Hanna & Cobb 2007).

By analyzing thermal preferences and tolerances we can estimate the thermal niche, which is one of the niche dimensions. This may be assessed by means of mechanistic biophysical ecological methods not using the environment per se but rather the state of the organism, for example body temperature (T_b). T_b 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 niches of organisms mechanistically (Kearney 2006; Kearney & Porter 2009; Kearney et al. 2010; Kearney 2012).

Spiders of the genus *Dysdera* Latreille 1804 (Family Dysderidae) are ground dwellers characteristic of xerothermic forests of the Mediterranean and adjacent areas. During the day, they shelter in gravel covered by organic material or under stones, and it has been reported that at night these wandering nocturnal hunters search for woodlice (terrestrial isopods), their principal prey (Cooke 1965; Bradley 2013).

The woodlouse spider, *Dysdera crocata* C. L. Koch 1838 is originally from the Mediterranean and eastern European region (Cooke 1965) but has spread throughout the world. There are over 240 species of *Dysdera* (Platnick 2013) however only *D. crocata* is cosmopolitan. It is amenable to a wide spectrum of environmental conditions, being a common spider in regions with cold temperatures and winter snow cover (e.g., Illinois, Ohio, Great Britain, Tasmania) as well as regions of hot, dry summers and mild winters of a Mediterranean climate (e.g., southern California, Greece) (Southcott 1976; Roberts 1995; Bradley 2004; Bosmans & Chatzaki 2005; Vetter & Isbister 2006).

In Chile, *D. crocata* is mostly limited to urban areas in the central region (Mediterranean climate); it is considered to be a synanthropic spider (Taucare-Rios et al. 2013). It is an epigeal species which can be captured under stones, rocks and rotting logs that also support isopods; it is active throughout the year in a micro-environment practically isolated from light, and with constant high humidity. The temperature in this environment is affected by the fluctuations characteristic of the Mediterranean climate, varying in the year more than fifteen degrees at a depth of 10 cm in the soil (Villaseca 1990). There are no studies of the thermal biology of *D. crocata*. Because body temperature is 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 (Angilletta et al. 2002; Portner et al. 2006; Angilletta 2009; Hazell et al. 2010), the objective of this study was to determine the preferred temperature of this species.

METHODS

Animals and study area.—Twenty individuals of *D. crocata* were collected in the peri-urban zones of Santiago, Chile (32°S, 70° 40' W). They were transferred to the laboratory in the Faculty of Science of the University of Chile. Each spider was introduced into a plastic box with moist soil and isopods obtained in the capture site and maintained for one week at room temperature (20 ± 5 °C, $60 \pm 5\%$ RH) and at 10L (8:00–18:00):14D (18:00–8:00) photoperiod. All experiments were conducted in this laboratory during March 2012–October 2012.

Preferred temperature.—After a week of acclimation, twenty individuals (11 females and nine males; $m_b = 102.29 \pm 60.88$ mg) were exposed to a temperature gradient between 2 ± 2.56 °C and 50 ± 0.89 °C established in a plastic cylinder oriented horizontally with the extremes halfway submerged in a thermoregulated chamber 1.20 m long \times 0.25 m wide \times 0.25 cm high. This chamber had a thermoregulated heater in one end and a cold point in the other, generating a thermal gradient between the end points (Fig. 1). The gradient was closely linear with a temperature of 19.3 ± 5.10 °C in the

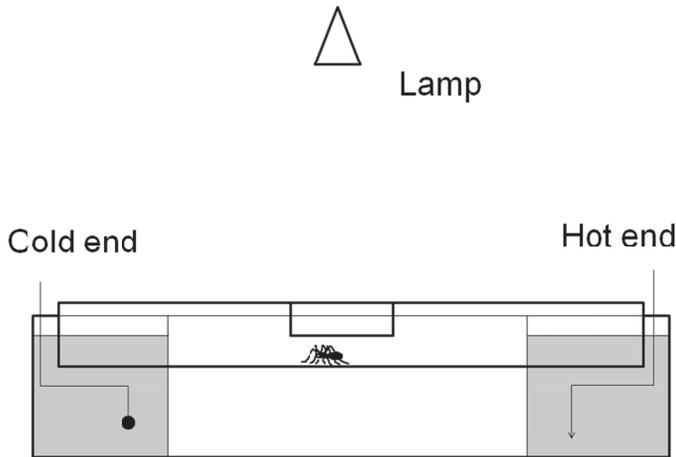


Figure 1.—Experimental temperature gradient apparatus used to measure preferred temperatures of *Dysdera crocata*. Thermoregulated water baths in grey. Infrared lamp at 2.5 m.

center. Prior to the beginning of the experiments, the thermal gradient was calibrated with thermocouples installed every 5 cm. The hot/cold ends of the gradient were always switched between trials to account for potential side biases.

The spiders were exposed individually for 65 min. This was repeated twice in the morning (09:00, 12:00) and twice in the twilight-night period (18:00, 20:00). The experiments were conducted in an isolated room illuminated with artificial light in the two morning experimental hours and with only an infrared lamp positioned perpendicular to the gradient at a distance of 2.5 m in the two twilight-night periods. Individuals were deposited in the center of the chamber and allowed five minutes of settling. Then the temperature of the spiders was measured at the midpoint of the cephalothorax with an infrared thermometer every five minutes 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 12 temperatures chosen by the spiders (t_i : one every 5 minutes) in the periods was obtained. These were recorded starting at 9:00, 12:00, 18:00 and 20:00. With these temperature records, frequency histograms of the chosen temperatures were constructed. For each individual the mean preferred temperature (T_p) in each hour was calculated (the average of the 12 values).

Analysis and statistics.—The temperatures chosen by the spiders (t_i) were characterized with frequency histograms. The normality of the distributions was tested with the Shapiro-Wilks test (W). The initial and t_i temperatures were compared using the Friedman test (Fr), with *a posteriori* multiple comparisons. Sex differences were analyzed with the Mann-Whitney test (U), and the correlation between initial temperature and the temperature at the end of the trials were evaluated with the Spearman correlation coefficient (R).

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 (T_p). Considering that each individual was studied at four different hours (repeated measures design) and the non-normal distribution of the data, a non-parametric Friedman test for dependent samples was performed, with T_p the response

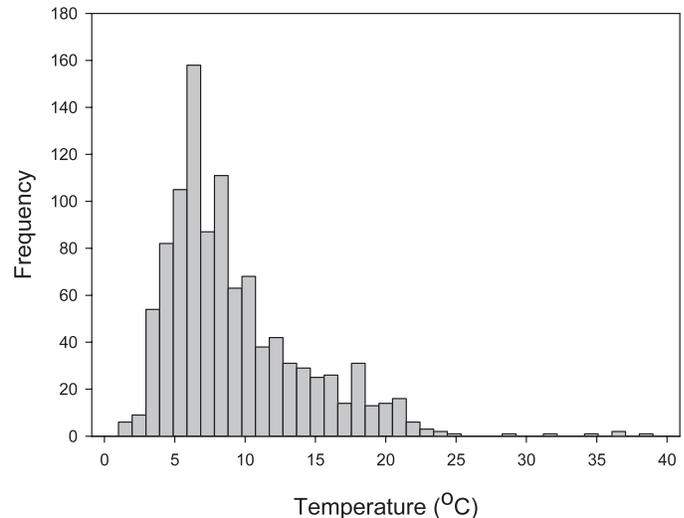


Figure 2.—Frequency histogram of preferred temperatures for *Dysdera crocata*.

variable and the four experimental times (9:00, 12:00, 18:00 and 20:00) as the factors.

RESULTS

The preferred temperature over all individuals and experimental hours was $9.12^\circ \pm 5.12^\circ \text{C}$, with median and mode 8.0° and 6.0°C , respectively. This was not related to sex ($U = 35$, $P = 0.29$) or to the body mass of the spiders ($R = 0.11$, $P > 0.05$). The distribution had a skewness of 1.47 and a kurtosis of 0.32 (Fig. 2) and was different from a normal distribution ($W = 0.884$, $P \ll 0.001$). The body temperature at the end of the experiment was correlated with the body temperature at the beginning of each experimental trial ($R = 0.299$, $P < 0.05$), but the variance explained was very small ($R^2 = 0.09$) and preferred temperatures changed quickly with respect to the initial preference. Initial body temperature was different than temperatures chosen in the following minutes in the experimental trials ($Fr_{80,13} = 146$, $P \ll 0.001$) (Fig. 3). There was a mean displacement of 5.9 ± 5.7 cm every five minutes.

No differences among T_p were found comparing the four experimental hours ($Fr_{20,3} = 5.82$, $p = 0.121$) (Fig. 4).

DISCUSSION

Thermal 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 & Lowrie (1972), individual limits and physiological processes determine the conditions in which an organism can survive and adapt successfully to a particular environment.

Preferred temperatures for *D. crocata* were low compared to the range described for other araneomorph species. For example these temperatures are between 23° and 23.5°C in Agelenidae (Pulz 1987), between 16° and 22.3°C in Clubionidae (Almquist 1970) and between 19.2° and 26.2°C in Lycosidae (Almquist 1970; Sevacherian & Lowrie 1972; Pulz 1987). However there are reports of low preferred temperatures in other species. For example, preferred temperatures of some species of Linyphiidae have been reported; 4.1

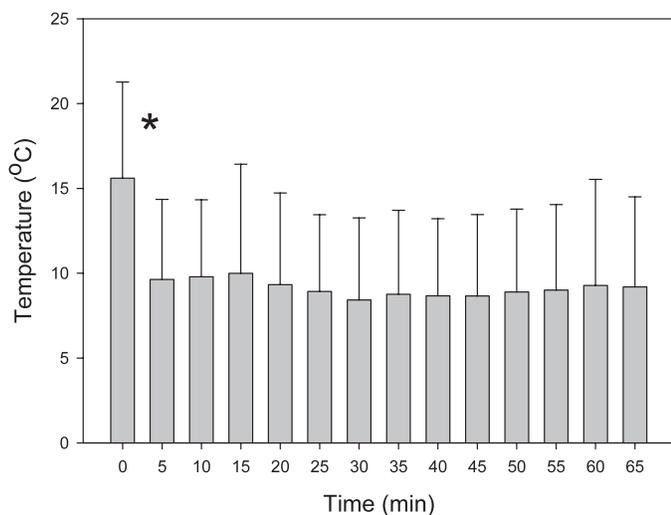


Figure 3.—Changes in body temperature over time in all experimental series. The asterisk indicates that the initial temperature was different than all others in a posteriori multiple comparisons.

°C in *Bolephthyphantes* (= *Bolyphantes*) *index* (Thorell 1856) (Pulz 1987) and 1.2 °C in *Macrargus rufus* (Wider 1834) (Almquist 1970). The preferred temperature of *D. crocata* is probably associated with temperatures that are usually found in their habitat under stones, dried leaves and organic material.

In Santiago, Chile, in the location where the specimens were captured, the soil temperature can vary more than 15 °C, with the lowest temperatures in the months of April to September (winter), where temperature at 10 cm depth can reach 8 °C. The lowest temperatures are reached at night, which coincides with the activity period of *D. crocata*. Also, this time range of low temperatures coincides with the time when the experiments were performed. It has been reported that this species feeds on the isopods with which they coexist (Cooke 1965, Bradley 2013). In Chile, it is common to find *D. crocata* sharing its habitat with the common woodlouse *Porcellio laevis*, which would be its usual prey. A study of preferred temperatures of this isopod demonstrated that it is variable at different locations in Chile and according to the time spent in the measurement system (Castañeda et al. 2004). Interestingly, the preferred temperature for specimens of *P. laevis* in Santiago was $9.4^{\circ} \pm 1.1$ °C using a measurement period similar to the time that we ran our experiments, and varied between $9.4^{\circ} \pm 1.1$ °C and $12.2^{\circ} \pm 1.1$ °C in the total experimental range of this study, which is fully consistent with our results. Thus two species that share a habitat in the field, one a predator and the other its prey, have similar preferred temperatures. A similar result was reported for the spider *Loxosceles laeta* (Nicolet 1849) and its predator *Scytodes globula* Nicolet 1849 (Canals 2004; Canals & Solis 2013), in which the preferred temperatures, the critical temperatures and desiccation tolerances have a large overlap (Alfaro et al. 2013; Canals et al. 2013). The body temperature of *D. crocata* varied from an initial temperature of $15.6^{\circ} \pm 5.6$ °C to $9.6^{\circ} \pm 4.6$ °C in 5 minutes, and afterwards remained close to their preferred temperature (Fig. 3), with an average displacement

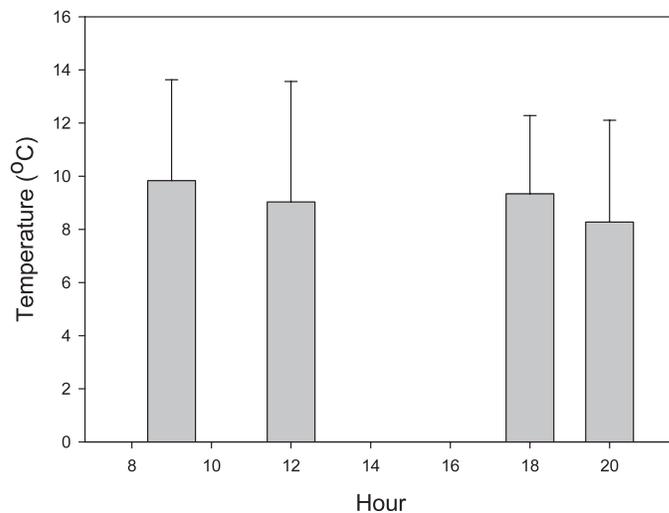


Figure 4.—Preferred temperatures of *Dysdera crocata* at different times of the day (mean and standard deviation).

of about 6 cm in 5 min suggesting that spiders actively sought their preferred temperature.

D. crocata did not present hourly variations in preferred temperature throughout the experimental hours, contrasting with those reported in other arthropods (Canals et al. 1997), mygalomorph spiders with crepuscular and nocturnal activity (Alfaro et al. 2012), and other nocturnal araneomorph spiders (Alfaro et al. 2013).

Regarding thermal preferences, *D. crocata* had a standard deviation of ± 5.12 °C, a value that is nearly 1 °C low than other spiders such as *L. laeta* and *S. globula*, suggesting a more narrow range of thermal microenvironment preference than these species. The election of low temperatures and a relatively narrow range may be explained by phenotypic plasticity as an adaptation to the particular environmental conditions present in Chile. This plasticity in preferred temperatures has been reported in *Paraphysa parvula* Pocock 1903 and *Grammostola rosea* (Walckenaer 1837), two mygalomorph spiders of central Chile (Alfaro et al. 2013). Species from different environments typically also have different thermal preferences (Pulz 1987; Schmalhofer 1999) and these may vary seasonally (Schmalhofer 1999), with the breeding season (Hanna & Cobb 2007; Veloso et al. 2012) or during the day, as in other ectotherms (Canals et al. 1997; Alfaro et al. 2013).

The woodlouse spider, *Dysdera crocata*, originated from the Mediterranean and eastern European region (Cooke 1965) but has spread throughout the world; it is considered to be a cosmopolitan spider. Its distribution is mainly in the holartic region and it is more common near the coast. It is a common spider in regions with cold temperatures and winter snow cover (e.g., Illinois, Ohio, Great Britain, Tasmania) as well as in regions with the hot, dry summers and mild winters of a Mediterranean climate (e.g., southern California, Greece) (Southcott 1976; Roberts 1995; Bradley 2004; Bosmans & Chatzaki 2005; Vetter & Isbister 2006). The projection of our results from the micro scale to the temperature conditions associated with its world distribution would be not correct because preferred temperatures indicate the suitable environments for *D. crocata*. These preferred temperatures may be

different in hotter environments (phenotypic or physiologic plasticity), or this spider has a great ability to find its preferred microenvironments, probably associated with its prey: isopod populations.

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LITERATURE CITED

- Alfaro, C., D.P. Figueroa, H. Torres-Contreras, C. Veloso, F. Venegas & M. Canals. 2012. Effect of thermal acclimation on preferred temperatures in two mygalomorph spiders inhabiting contrasting habitats. *Physiological Entomology* 38:20–25.
- Alfaro, C., C. Veloso, H. Torres-Contreras, R. Solís & M. Canals. 2013. Thermal niche overlap of the brown recluse spider *Loxosceles laeta* (Araneae; Sicariidae) and its possible predator, the spitting spider *Scytodes globula* (Scytodidae). *Journal of Thermal Biology* 38:502–507.
- Almquist, S. 1970. Thermal tolerances and preferences of some dune-living spiders. *Oikos* 21:230–236.
- Angilletta, M.J.J. 2009. *Thermal Adaptation: a Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Angilletta, M.J.J., P.H. Niewiarowski & C.A. Navas. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27:249–268.
- Bosmans, R. & M. Chatzaki. 2005. A catalogue of the spiders of Greece. *Newsletter of the Belgian Arachnological Society* 20 (2, Suppl.):1–124.
- Bradley, R.A. 2004. *Ohio's Backyard: Spiders*. Ohio Biological Survey Backyard Series #4.
- Bradley, R.A. 2013. *Common Spiders of North America*. University of California Press, Berkeley.
- Canals, M. & R. Solís. 2013. Is the tiger spider *Scytodes globula* an effective predator of the brown recluse spider *Loxosceles laeta*? *Revista Médica de Chile* 141:805–807.
- Canals, M., C. Alfaro, C. Veloso, H. Torres-Contreras & R. Solís. 2013. Tolerancia a la desecación y sobreposición del nicho térmico entre la araña del rincón *Loxosceles laeta* y un posible control biológico, la araña tigre *Scytodes globula*. *Parasitología Ibero-Latinoamericana* 72:52–60.
- Canals, M., M.E. Casanueva & M. Aguilera. 2004. Cuales son las especies de arañas peligrosas en Chile? *Revista Médica de Chile* 132:773–776.
- Canals, M., R. Solís, J. Valderas, M. Ehrenfeld & P.E. Cattán. 1997. Preliminary studies on temperature selection and activity cycle of Chilean vectors of the Chagas disease. *Journal of Medical Entomology* 34:11–17.
- Castañeda, L.E., M.A. Lardies & F. Bozinovic. 2004. Adaptive latitudinal shifts in the thermal physiology of a terrestrial isopod. *Evolutionary Ecology Research* 6:1–15.
- Cooke, J.A. 1965. A contribution to the biology of the British spiders belonging to the genus *Dysdera*. *Oikos* 16:20–25.
- Hanna, C.H.J. & V.A. Cobb. 2007. Critical thermal maximum of the green lynx spider *Peucetia viridans* (Araneae, Oxyopidae). *Journal of Arachnology* 35:193–196.
- Hazell, S.P., C. Groutides, B.P. Neve, T.M. Blackburn & J.S. Bale. 2010. A comparison of low temperature tolerance traits between closely related aphids from the tropics, temperate zone, and arctic. *Journal of Insect Physiology* 56:115–122.
- Hertz, P., R. Huey & R. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *American Naturalist* 142:796–818.
- Humphreys, W.F. 1987. Behavioral temperature regulation. Pp. 56–65. *In Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer Verlag, Berlin.
- Jaksic, F. & L. Marone. 2007. *Ecología de Comunidades*. 2nd ed. Ediciones Universidad Católica de Chile, Santiago.
- Kearney, M. 2006. Habitat, environment and niche: what are we modeling? *Oikos* 115:186–191.
- Kearney, M. 2012. Metabolic theory, life history and the distribution of a terrestrial ectotherm. *Functional Ecology* 26:186–191.
- Kearney, M. & W.P. Porter. 2009. Mechanistic niche modeling: combining physiological and spatial data to predict species' range. *Ecology Letters* 12:334–350.
- Kearney, M., S.J. Simpson, D. Raubenheimer & B. Helmuth. 2010. Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society B* 365:3469–3483.
- Platnick, N.I. 2013. *The World Spider Catalog*. Version 14.0. American Museum of Natural History. Online at <http://research.amnh.org/entomology/spiders/catalog/>
- Portner, H.O., A.F. Bennett, F. Bozinovic, A. Clarke, M.A. Lardies & R.E. Lenski et al. 2006. Trade-offs in thermal adaptation: in need of a molecular to ecological integration. *Physiological and Biochemical Zoology* 79:295–313.
- Pulz, R. 1987. Thermal and Water Relations. Pp. 26–55. *In Ecophysiology of Spiders*, (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Roberts, M.J. 1995. *Spiders of Britain & Northern Europe*. Harper Collins Publishers, London.
- Schmalhofer, V.R. 1999. Thermal tolerances and preferences of the crab spiders *Misumenops asperatus* and *Misumenoides formosipes* (Araneae, Thomisidae). *Journal of Arachnology* 27:470–480.
- Sevacherian, V. & D. Lowrie. 1972. Preferred temperature of two species of lycosid spiders, *Pardosa sierra* and *P. ramulosa*. *Annals of the Entomological Society of America* 65:111–114.
- Southcott, R.V. 1976. Arachnidism and allied syndromes in the Australian region. *Records of the Adelaide Children's Hospital* 1:97–186.
- Taucare-Rios, A., A. Brescovit & M. Canals. 2013. Synanthropic spiders (Arachnida: Araneae) from Chile. *Revista Iberica de Aracnologia* 23:49–53.
- Veloso, C., D. Luhr, R. Marfull, H. Torres-Contreras, D. Figueroa & P. Sabat et al. 2012. Characterization of the thermal micro-environment of *Paraphysa parvula* Pocock 1903 (Araneae, Theraphosidae), a spider from Chilean Andes. *Journal of Arachnology* 40:34–38.
- Vetter, R.S. & G.K. Isbister. 2006. Verified bites by the woodlouse spider, *Dysdera crocata*. *Toxicon* 47:826–829.
- Villaseca, S. 1990. La temperatura del suelo. *Agricultura Técnica* 50:155–160.

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