

SHORT COMMUNICATION

CRITICAL THERMAL MAXIMUM OF THE GREEN LYNX SPIDER, *PEUCETIA VIRIDANS* (ARANEAE, OXYOPIDAE)

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ABSTRACT. The critical thermal maximum (CTMax) of *Peucetia viridans* Hentz 1832 adult spiders was determined in the laboratory. Mean temperature at death was higher for gravid spiders (49.4° C) than for postparturient females (47.2° C) and males (46.9° C). Painted copper spider models placed in the environment to examine available temperatures predicted that spider body temperatures would rarely exceed 40° C thus making it unlikely for *P. viridans* to naturally reach CTMax, at least in the climate of central Tennessee.

Keywords: Temperature, thermal tolerance

The range of thermal tolerances in ectothermic animals is important for better understanding the limitations of an animal's thermal ecology and behavior. An organism's upper and lower thermal limits can influence many aspects of life, including foraging, habitat selection, mating, and development (Angilletta et al. 2002). More specifically in spiders, those thermal limits could be useful in evaluating the suitability of foraging and nest-site habitats, especially in those species where the female remains at her nest guarding her egg sac. As organisms approach their thermal limits, negative physiological affects are typically observed, potentially culminating in death. The critical thermal maximum (CTMax) is a standard measure to evaluate the thermal requirements and physiology in organisms because the behavioral and physiological responses are the same across a wide diversity of taxa (Lutterschmidt & Hutchison 1997a). The commonly used dynamic method gradually increases the temperature until an end-point is reached (Lutterschmidt & Hutchison 1997b). Cowles & Bogert (1944) first introduced this method and the CTMax was defined as "the thermal point at which locomotor activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death."

The temperature change in the dynamic method must be gradual enough to allow the core temperature of individuals to equilibrate to the test tem-

perature without a significant time lag (Hutchison 1961), with heating rates of 0.5 to 1.5° C per min often being used (Lutterschmidt & Hutchison 1997b). Although various measuring points (e.g., loss of the righting response, sudden onset of muscular spasms, and death (Lutterschmidt & Hutchison 1997a, 1997b)) have been used to describe the CTMax, Lutterschmidt & Hutchison (1997a) support the use of onset of muscular spasms as the CTMax. However, the studies they reviewed primarily used ectothermic vertebrates. Muscular spasms in small invertebrates may be difficult to observe, thus other means (e.g., temperature at the point of thermal discomfort or temperature at death) may be necessary to determine the thermal limits.

The thermal biology of few spider species have thus far been studied (Humphreys 1987; Schmalhofer 1999), which has limited our knowledge of thermal tolerances and preferences associated with differing microhabitats. The CTMax has been described in a few species including *Loxosceles intermedia* Mello-Leitão 1934 and *L. laeta* Nicolet 1849 in Brazil (Fischer & Vasconcellos-Neto 2003), a number of dune-living spiders in Sweden (Almquist 1970), a riparian spider (Devito & Formanowicz 2003), an orb-weaving spider (Tolbert 1979), and two crab spiders (Schmalhofer 1999). In Schmalhofer's study *Misumenops asperatus* Hentz 1847 matured in the spring and *Misumenoides formosipes* Walckenaer 1837 in the summer. As predicted, the summer maturing spider experiencing higher temperatures was found to have a higher CTMax (Schmalhofer 1999). Also, crab spiders hunting on flowers exposed to warm temperatures had a higher CTMax, which presumably allowed them to forage

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Table 1.—CTMax determination temperatures (mean \pm SD) and range for *P. viridans*.

Adult Category	Thermal Discomfort Point ($^{\circ}$ C)	Onset of Muscular Spasms ($^{\circ}$ C)	Temperature at Death ($^{\circ}$ C)
Male ($n = 3$)	40.3 \pm 3.1 (38.3–43.9)	43.0 \pm 2.9 (39.8–45.5)	46.9 \pm 0.2 (46.8–47.1)
Gravid Female ($n = 3$)	41.0 \pm 1.4 (39.5–42.1)	43.1 \pm 1.2 (42.1–42.8)	49.4 \pm 0.9 (48.6–50.3)
Postparturient Female ($n = 4$)	40.0 \pm 2.3 (38.5–43.4)	42.4 \pm 1.6 (40.6–44.0)	47.2 \pm 0.4 (46.8–47.8)

more freely on pollinating insects (Schmalhofer 1999).

The green lynx spider, *Peucetia viridans* Hentz 1832, is an ambush predator that hunts near the top of flowering herbaceous plants and feeds on pollinating insects in the southern United States and Mexico (Turner 1979; Willey & Adler 1989; Arango et al. 2000). Males and gravid females can be found on flowering vegetation in field habitats during the summer and early autumn. Males die soon after mating in early August and gravid females then lay an egg sac near the top of vegetation. Postparturient females remain with and protect their egg sac until spiderlings emerge and disperse (Fink 1987). Without females to protect the egg sac, ant predation and dislodgement commonly occur (Fink 1986, 1987; Hanna & Cobb 2006). Females attending egg sacs are exposed to the same ambient temperatures as their egg sacs (Hanna & Cobb 2006). These temperatures may be beneficial for egg development, but potentially could reach harmful levels for an adult spider. Understanding the CTMax of adult *P. viridans* could be useful in evaluating how suitable foraging and nest-site habitats are for guarding females.

The purpose of this study was to test whether gravid *P. viridans* have a higher thermal tolerance than postparturient female and male spiders. Because gravid females are generally located at more exposed sites on vegetation, we hypothesized that they may have a higher thermal tolerance. To obtain natural thermal conditions that spiders could be exposed to during the egg sac incubation period, we placed physical spider models in the field to measure potential spider temperatures.

Using the dynamic method, the CTMax was measured for three mature males, three gravid females, and four postparturient females. We collected postparturient females from the field within 48 h of producing an egg sac in September 2004. Spiders were collected from Rutherford County, Tennessee and voucher specimens have been deposited in the entomology collection at Middle Tennessee State University. Adult spiders were housed in a laboratory at 21.5 $^{\circ}$ C for 24 h prior to testing. For testing, we moved spiders to 5 \times 8 cm cylinders covered with cheese cloth and placed them in an environmental chamber (Percival I-36LL). Trials

initially started at 25 $^{\circ}$ C, increased at increments of 0.2 $^{\circ}$ C every 3 min, and could reach 50 $^{\circ}$ C. Three thermal end-points to the trials were measured. The first temperature recorded was the thermal discomfort point, or the point at which the spiders initiate rapid movement around their enclosure. The second temperature recorded was when the onset of spasms occurred. The third temperature recorded was the temperature at death, indicated by cessation of movement. To record these measurements, we positioned spiders within the chamber so that they could be video recorded via a chamber ventilation hole. One-way ANOVAs and Student-Newman-Keuls post hoc tests were used to compare the CTMax measurements.

For the test spiders, the thermal discomfort point, the temperature at the onset of spasms and the temperature at death were recorded (Table 1). No significant differences between males, gravid females, or postpartum females were observed for the thermal discomfort point ($F_{2,7} = 0.162$, $P = 0.854$) or the temperature at the onset of muscular spasms ($F_{2,7} = 0.137$, $P = 0.874$). However, gravid females did have a significantly higher temperature at death ($F_{2,7} = 19.34$, $P = 0.001$), than either males or postpartum females.

To determine potential temperatures that *P. viridans* may experience in the field, we placed physical spider models in typical locations where spiders were observed during the egg-laying season. We constructed spider models out of a hollow copper tube (2 mm diam., 20 mm long) for the body, and 20 ga copper wire for the legs. One end of the model was sealed with a waterproof sealant (i.e., caulk), and a 30 ga type T thermocouple wire was sealed inside the other end (Fig. 1). The thermocouple wire was measured with a multi-channel datalogger (Campbell Scientific, Inc. CR23x). Initially we placed the following models outdoors: models spray-painted black, neon green, jade, yellow, pebble, and white, along with two recently sacrificed gravid females and one male spider, on a 50 cm \times 50 cm white styrofoam tile (used to reduce convective heating from the ground). Body temperatures of sacrificed spiders were measured using a thermocouple wire inserted in their abdomen. We monitored both spiders and models for 80 min, and purposefully moved them into and out of bright sun

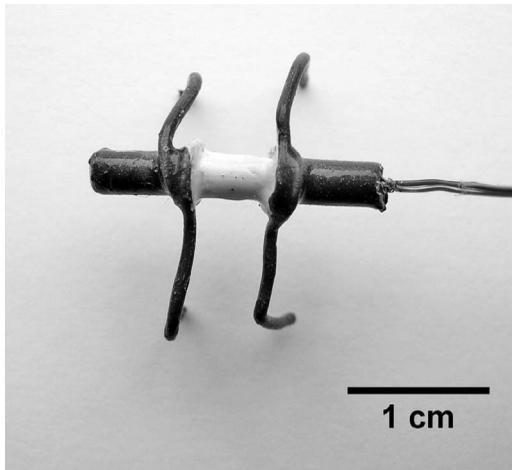


Figure 1.—A painted spider model with a thermocouple wire attached.

and full shade to determine which painted model was most thermally similar to real spiders.

Graphical comparison of the painted spider models to actual spiders revealed the neon green model was 1–2° C warmer, while the pebble model was 1–2° C cooler. Therefore, we painted a model with the distal thirds neon green and the middle third pebble and again compared the model to two recently sacrificed female spiders. The banded model differed on average by 0.08° C from the real spiders (Fig. 2) ($r^2 = 0.981$, $P < 0.001$), with no significant differences between the spider and the model (paired $t = 0.705$, $P = 0.482$). Therefore, our model spiders accurately predicted the temperature of real spiders, including times of heating and cooling, which made it possible to predict spider body temperature without disturbing or harming real spiders.

We placed three banded model spiders in the field at positions where real spiders were typically observed and recorded temperatures at 10 min intervals for 50 days beginning 7 September 2004. All three models were 75 cm above the ground; one placed on a south-facing vertical stem, a second placed on top of a goldenrod (*Solidago nemoralis*) inflorescence, and a third placed under the inflorescence of *S. nemoralis* (common location of egg sacs).

In the field, the warmest spider model was on the south-facing stem at 75 cm, with the warmest temperature recorded being 39.3° C. The warmest temperature recorded for the other models was 35.2° C (under the goldenrod inflorescence) and 36.5° C (exposed on the inflorescence). The maximum difference in temperature between different models during the day was 10.8° C on 17 September, when the temperature on the south-facing stem was 39.2° C and the model below the inflorescence was 28.4°

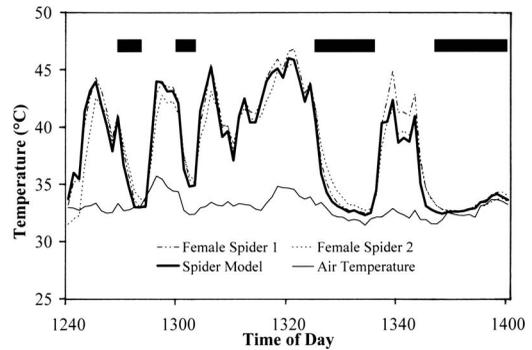


Figure 2.—Temperature comparisons for a painted spider model and two female green lynx spiders on 27 August 2004. Shaded air temperature was measured near the models. Bars indicate when spiders and models were moved into full shade.

C. While model placement greatly influenced predicted temperatures, differences potentially could be even larger if the spider selected plants with more vegetative growth and consequently more shade.

Gravid female *P. viridans* are often found in open field habitats on flowering vegetation foraging during the summer when air temperatures can be quite warm (i.e., August). Withstanding warmer temperatures is beneficial for gravid females that are foraging heavily before expending energy producing an egg sac. This provides gravid females the benefit of foraging in places or during times when it would potentially be too warm for males or non-gravid females. Male *P. viridans* die soon after mating, and are rarely observed in the field when females begin laying their egg sacs. Therefore, male *P. viridans* are generally not foraging during the warmest part of summer, but rather they spend more time seeking a mate, moving between different microclimates. Postparturient females occurred on or near their egg sacs and were infrequently found with prey. In addition, postparturient females are rarely found exposed on inflorescences. Notably, postparturient females have a lower CTMax than gravid females, but it is still 8° C higher than the warmest temperature recorded by a model spider in the field, meaning temperatures in central Tennessee should not harm or stress *P. viridans* while guarding their egg sacs.

Although the field temperatures in this study did not approach the maximal thermal limitations for *P. viridans*, it should be noted that the spider models were monitored during September and October when postparturient females are prevalent. In central Tennessee, temperatures occasionally become warm enough in late summer to reach CTMax, as indicated by our spider-model calibration in August (Fig. 2). These are the temperatures gravid females

would most likely be experiencing and may account for their higher temperature at death measurement (Table 1). It should also be noted that the summer of 2004 in central Tennessee was not unusually warm and *P. viridans* populations further south in their range would probably be exposed to higher temperatures.

Because of the high surface to volume ratio in *P. viridans* body dimensions, low thermal inertia is expected giving *P. viridans* the ability to heat and cool quickly. Using data from the initial paint matching test, we calculated the heating and cooling rates for three sessions using one male and two female spiders. Heating rates did not differ from cooling rates and the mean rate of change for the male spider was 3.1° C per min ($n = 6$ sessions) and for females was 2.6° C per min ($n = 12$ sessions). Combined heating/cooling rate for all three spiders was 2.8° C per min.

Such a low thermal inertia makes it likely that microhabitat variation allows spiders to simply make short movements to a cooler location if CTMax is approached. Although geographic variation and plasticity of CTMax in spiders remains to be tested, this implies, in general, that the likelihood that small spiders would encounter lethal body temperatures is low and that only in extreme environments with little thermal microhabitat differences would a spider species be at risk of overheating. However, implications for species behaviorally limited by factors such as web or egg sac placement risks would remain.

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LITERATURE CITED

- Almquist, S. 1970. Thermal tolerances and preferences of some dune-living spiders. *Oikos* 21: 230–236.
- Angilletta, M.J., Jr., P.H. Niewiarowski & C.A. Navas. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27: 249–268.
- Arango, A.M., V. Rico-Gray & V. Parra-Tabla. 2000. Population structure, seasonality, and habitat use by the green lynx spider *Peucetia viridans* (Oxyopidae) inhabiting *Cnidioscolus aconitifolius* (Euphorbiaceae). *Journal of Arachnology* 28:185–194.
- Cowles, R.B. & C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* 83:261–296.
- DeVito, J. & D.R. Formanowicz, Jr. 2003. The effect of size, sex, and reproductive condition on thermal and desiccation stress in a riparian spider (*Pirata sedentarius*, Araneae, Lycosidae). *Journal of Arachnology* 31:278–284.
- Fink, L.S. 1986. Costs and benefits of maternal behaviour in the green lynx spider (Oxyopidae, *Peucetia viridans*). *Animal Behaviour* 34:1051–1060.
- Fink, L.S. 1987. Green lynx spider egg sacs: sources of mortality and the function of female guarding (Araneae, Oxyopidae). *Journal of Arachnology* 15:231–239.
- Fischer, M.L. & J. Vasconcellos-Neto. 2003. Determination of the maximum and minimum lethal temperatures (LT₅₀) for *Loxosceles intermedia* Mello-Leitao, 1934 and *L. laeta* (Nicolet, 1849) (Araneae, Sicariidae). *Journal of Thermal Biology* 28:563–570.
- Hanna, C.J. & V.A. Cobb. 2006. Effect of temperature on hatching and nest site selection in the green lynx spider, *Peucetia viridans* (Araneae: Oxyopidae). *Journal of Thermal Biology* 31: 262–267.
- Humphreys, W.F. 1987. Behavioral temperature regulation. Pp. 56–65. *In* *Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Hutchison, V.H. 1961. Critical thermal maximum in salamanders. *Physiological Zoology* 43:92–125.
- Lutterschmidt, W.I. & V.H. Hutchison. 1997a. The critical thermal maximum: data to support the onset of spasms as the definitive end point. *Canadian Journal of Zoology* 75:1553–1560.
- Lutterschmidt, W.I. & V.H. Hutchison. 1997b. The critical thermal maximum: history and critique. *Canadian Journal of Zoology* 75:1561–1574.
- Schmalhofer, V.R. 1999. Thermal tolerances and preferences of the crab spiders *Misumenops asperatus* and *Misumenops formosipes* (Araneae, Thomisidae). *Journal of Arachnology* 27:470–480.
- Tolbert, W.W. 1979. Thermal stress of the orb-weaving spider *Argiope trifasciata* (Araneae). *Oikos* 32:386–392.
- Turner, M. 1979. Diet and feeding phenology of the green lynx spider, *Peucetia viridans* (Araneae: Oxyopidae). *Journal of Arachnology* 7:149–154.
- Willey, M.B. & P.H. Adler. 1989. Biology of *Peucetia viridans* (Araneae, Oxyopidae) in South Carolina, with special reference to predation and maternal care. *Journal of Arachnology* 17:275–284.

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