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Research

Field Observations of Body Temperature for the Wolf Spider, *Rabidosa rabida* (Araneae: Lycosidae), Differ From Reported Laboratory Temperature Preference Suggesting Thermoconforming Behavior

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Abstract

Temperature affects all aspects of ectotherm ecology, behavior, and physiology. Descriptions of thermal ecology are important for understanding ecology in changing thermal environments. Both laboratory and field estimates are important for understanding thermal ecology. *Rabidosa rabida* (Walckenaer 1837) (Araneae: Lycosidae) is a large wolf spider with some natural history, including laboratory estimates of thermal preference, tolerance, and performance, reported in the scientific literature. Laboratory tests suggest the active choice of temperature environment. To test published estimates of thermal ecology from the laboratory, we took body temperature measurements of mature spiders in the field nocturnally and diurnally using a FLIR camera in July 2019. We made comparisons between sexes and activity periods using field observations. We compared these measurements with the published values for thermal preferences and thermal maximum and with mean weather station data. Observed field temperatures differed significantly from published preference, but not from mean temperature from a local weather station. This suggests that this species is thermoconforming rather than actively thermoregulating. Reported thermal preference fell between the diurnal and nocturnal mean measurements closer to the diurnal than nocturnal temperatures. These field observations show how important it is to make field observations for physiology and thermal ecology. Maximum observed diurnal temperatures closely approached the published critical thermal maximum. We observed spiders performing behaviors such as hunting and feeding in conditions well above published thermal preference and near-critical high temperature. These observations suggest that *R. rabida* is thermoconforming in this limited period but does not rule out that they might thermoregulate in certain situations.

Key words: thermal ecology, thermoregulation

Temperature affects animals by altering the physical structure of the body, its internal environment, and by influencing chemical reactions that allow movement, survival, growth, and reproduction (Cossins 1987, Johnston and Bennett 1996, Angilletta et al. 2002). Because of the many influences of temperature, we need to learn more about the thermal biology of ectotherms to understand their ecology, behavior, and evolution. Understanding the influences of temperature on diverse life forms has never been more important as the climate changes around us (IPCC 2013; Barnett and Facey 2016). More than ever, we need a baseline understanding of the thermal ecology of ecologically important organisms. Many studies of thermal ecology, physiology, and behavior have been conducted in the laboratory due to the difficulty and technological challenges of making field observations (Geiser et al. 2007). Past studies have shown the value of testing if laboratory observations can be applied to animals in the field (Irschick et al. 2005, Huho et al. 2007).

Spiders are ectothermic and ecologically important organisms (Foelix 1996; Nyffeler and Birkhofer 2017). *Rabidosa rabida* (Walckeanaer 1837) (Araneae: Lycosidae) is a large wolf spider, a generalist predator, and abundant across the Eastern half of North America (Brady and Mckinley 1994). Numerous studies have demonstrated that *R. rabida* influences herbivorous arthropod populations and the vegetation on which many arthropods go about their lives (Reichert 1974, Sokol-Hessner and Schmitz 2002, Hlivko and Rypstra 2003). Unlike many Lycosids, *R. rabida* spends much of its time above ground roaming the vegetation. This spider is also one of the few cursorial spiders with published laboratory estimates of thermal preference, maximum and minimum tolerance, and thermal performance (Stork 2012). An active choice of temperature environment in the laboratory suggests that this spider is at least in some situations thermoregulating despite having many characteristics and behaviors that would make us predict thermoconforming (Stork 2012). These characters make *R. rabida* an interesting species for studies in thermal ecology.

Thermal preference, in a thermoregulating organism, should predict body temperature in the field. Unfortunately, this is rarely the case as many variables that are controlled in the laboratory, such as hunger, thirst, and community interactions often show measurable influences on thermal ecology. It can be expected that critical thermal values, above and below which the animal is no longer able to function, should be avoided in the field so long as acclimatization is accounted for. The connection between body temperature and thermal preference does assume some level of thermoregulation. It has been suggested that this species is a thermal generalist, which may not have to actively thermoregulate, but it has also been shown to actively choose a temperature in a laboratory setting (Stork 2012).

Published estimates of thermal physiology and performance present several questions about this spider's behavior, physiology, and thermal ecology. For example, the reported preferred temperature of 31.9°C is warmer than the temperatures that these spiders experience when hunting nocturnally. Nocturnal temperatures were assumed closer to the preferred temperature of this spider due to the vertical mobility seen during nocturnal hunting. Hunting behavior as the main factor driving the evolution of thermal physiology has not been tested, leaving the possibility that other fitness influencing traits may have a greater influence on body temperatures in the field. A difference in thermal sensitivity described between the sexes also brings up many questions about the behavior and reproductive physiology of this spider (Foster et al. 2009), such as how does temperature affect egg production (Watt 1992) and maturation (Marden 1995), and how does body size differences between the sexes (Maia-Carneiro and Rocha 2013) influence thermal ecology? Laboratory estimates are a starting point, but these estimates need to be compared with field observations to better understand how influences such as hunger, predation, and plasticity and acclimatization may influence thermal physiology and behavior (Culler et al. 2014, Gvoždík and Kristín 2017, Bennett et al. 2019).

In this project, we measured the body temperatures of *R. rabida* in the field under both nocturnal and diurnal conditions. We then compared these measurements with the published body temperature preference and maximum thermal limit from Stork (2012) and with local weather station mean temperatures (Wunderground.com). We hypothesize that the laboratory estimates would not differ significantly from field measurements. If this is confirmed, it would support the hypothesis of thermoregulation in this spider. We also hypothesized that nocturnal and diurnal body temperatures would differ significantly from each other. We hypothesized that there would be a difference in body temperature between the sexes due to previously reported thermal sensitivity differences (Stork 2012).

Materials and Methods

We collected *R. rabida* from the Harding University Gilliam Biological Research Station in White County, Arkansas, on 11 separate days between 5 and 31 July 2019. This species is differentiated from the other species of this genus found in Arkansas with a visual inspection of body size, dorsal patterning, and ventral markings (Brady and McKinley 1994). We used the spotlighting technique described by Wallace (1937) to locate spiders nocturnally. We started collecting at 10 p.m. CST to allow sufficient darkness for spotlighting. We walked the field for 2- to 3-h capturing, taking body temperatures, and marking all spiders of sufficient size to attach our RFID tags. We found that spiders with a body length of greater than 15-mm worked best for attaching tags as described below with minimum interference to behavior. We used visual searches and RFID trackers, described below, to located spiders diurnally. We started our daytime searches as 1 p.m. CST and continued until we had captured 10 previously marked spiders or until our equipment failed in the heat, which often took around three hours of midday heat. We captured most spiders in a field covered in low woody vegetation and grasses located just off the main entrance to the research station. We captured a few spiders in a power line right-of-way less than 0.5 km away, which also had a mixture of dense grasses and low woody vegetation. Due to the difficulty of accessing this area and difficulty in diurnal tracking of spiders in the power line right-of-way, we abandoned this location after the first week of the study. A comparison between locations showed no difference in body temperature measurements, and so we combined data from both locations for the tests described below.

To obtain body temperature measurements, we captured spiders in thin, plastic cups and used a FLIR I3 thermal camera to image the prosoma of each spider. No visible differences were observed between the temperatures of the prosoma and opisthosoma, but varying shapes and sizes of the opisthosoma made the prosoma a more consistent target to image. We took thermal photographs nocturnally with a warm handheld behind, but not touching, the cup to provide contrast to help aim the camera. During the day, we held a cold pack behind the cup to provide a thermal contrast for imaging. We took at least two images for each spider and only used images where the spider's body filled the targeting circle. For spiders of which we captured multiple good images, we took an average of the measurements. Following thermal imaging, we restrained spiders in a plastic, sandwich bag and cut a small hole in the bag over the opisthosoma. We placed a single drop of Gorilla Glue gel super glue (Cyanoacrylate) on the superior opisthosoma of each spider. We affixed a Biomark Inc. mini HPT8 RFID tag to the superglue. We allowed the superglue to dry for at least 30 min before we released spiders from their plastic bag, back to their capture location. We recorded the sex of the spider and placed a tape marker in the plant where we released the spider. The following day, we relocated as many spiders as we could, using the Biomark HPR Lite RFID reader and visual searching. Once we had recaptured a spider, we took body temperature measurements again using the same method described above, except that we used a cold pack instead of a warm hand as a contrasting background for aiming the thermal camera.

We captured any additional spiders discovered during the day, and we took their body temperatures measured though we did not affix tags during the day because we had already determined that individual spiders were active both nocturnally and diurnally. Of the more than 200 captures of 134 spiders used in this study, only 23 were recaptures. In light of this, the tagging method was not continued for the entire project but was stopped 2 wk in allowing for more time to be spent visually searching for day-active spiders. We only used mature spiders in our analyses, as immatures were small enough and active enough to cause difficulty in getting images of them filling the thermal camera-aiming target. Maturity of spiders was determined due to the pigmentation of the epigynum in females and the darkly pigmented forelegs in males (Brady and McKinley 1994).

We tested the data for normality and skewness and determined that nonparametric tests were required. We ran Mann–Whitney *U* tests using the spider body temperature as the dependent variable and sex and diurnal/nocturnal activity period as the grouping variables. We calculated mean body temperature ± SE for all spiders, males, females, nocturnal spiders, nocturnal males, and nocturnal females. We graphed field-observed means with laboratory reports of critical thermal temperatures from Stork (2012) for visual comparison. We ran a χ^2 test for goodness of fit to compare field-collected body temperatures with the published laboratory estimates of body temperature from Stork (2012). We obtained ambient temperature data for July 2019 from the Searcy Airport via the Weather Underground website (Weather Underground 2020) for comparison with the observed spider body temperatures. A χ^2 test was run comparing individual body temperature measurements for all spiders, males, females, nocturnal, and diurnal groupings to the mean temperature for Searcy in July 2019.

We used 134 mature spiders in the analyses, with 102 females and 32 males. There were 84 nocturnal measures and 50 diurnal measures. During the night, we measured 70 females and 14 males, and during the day, we measured 32 females and 18 males. We ran all analyses following methods described by Sokal and Rohlf (1995). We obtained critical values from Statistical Tables by Rohlf and Sokal (1995). Statistical analysis used Microsoft EXCEL and MYSTAT software.

Results

The 134 spiders measured across all times showed a mean body temperature of 24.7 ± 0.85°C. The 50 spiders measured diurnally showed a mean body temperature of 36.5 ± 0.48°C and the 84 spiders measured nocturnally showed a mean body temperature of 17.7 ± 0.28°C. Female spiders showed a mean body temperature across all times of 23.4 ± 0.89°C with 70 nocturnal females showing a mean body temperature of 17.6 ± 0.29°C and 32 diurnal females showed a mean body temperature of 36 ± 0.64°C (Fig. 1). The 32 male spiders across all times showed a mean body temperature of 28.9 ± 1.79°C, with 14 nocturnal males showing a mean body temperature of 18.2 ± 0.91°C and 18 diurnal males showing a body temperature of 37.3 ± 0.67°C (Fig. 1). Previously reported thermal preference for females of this species is 32.9 ± 0.44°C (Stork 2012). Mean ambient temperature in Searcy, AR, for July 2019 was 29.06°C, with a reported maximum of 35°C and a minimum of 25.6°C.

A Mann–Whitney *U* test showed a significant difference in body temperature between sexes of mature spiders ($U = 1150$, df = 1, $P = 0.012$). A Mann–Whitney *U* test found a highly significant difference between diurnal body temperatures and nocturnal body temperatures with a ($U = 8.5$, df = 1, $P < 0.001$). We measured diurnal body temperatures averaging 4.2°C greater than the published thermal preference (Fig. 1). We measured nocturnal body temperatures at 15.2°C lower than the published thermal preference (Fig. 1). We found that diurnal female body temperatures were the closest to the published preference differing by only 3.1°C. Diurnal male body temperatures differed from the expected preference by 4.4°C, whereas both male and female nocturnal body temperatures differed from the expected preference by greater than 14°C (Fig. 1).

The maximum body temperature recorded diurnally was 41.9°C, only 1°C from the reported critical thermal maximum of 42.9°C from Stork (2012). We recorded this body temperature in a male spider actively moving on the vegetation, off the ground, but in direct sunlight. We recorded the maximum body temperature for a female as 41.8°C. We also recorded the maximum female body temperature diurnally and in direct sunlight (Fig. 2). Nocturnal body temperatures never approached the reported critical thermal maximum, always staying below 27°C (Fig. 2).

A χ^2 test showed that field body temperatures across all times showed a highly significant difference from the laboratory-reported preferred temperature ($\chi^2 = 8{,}073.2$, df = 133, $P < 0.001$). A χ^2 test showed that both diurnal body temperatures and nocturnal body temperatures showed a highly significant difference from the laboratory-reported preferred temperature (diurnal $\chi^2 = 831.1$, df = 49, $P < 0.001$; nocturnal $\chi^2 = 7{,}242.1$, df = 32, $P < 0.001$). A χ^2 analysis did not show a significant difference between mean body temperature and observed mean spider body temperature for males ($\chi^2 = 3.82$, df = 31, $P > 0.9$), females ($\chi^2 = 9.75$, df = 101, $P > 0.9$), nocturnal ($\chi^2 = 26.44$, df = 83, $P > 0.9$), diurnal ($\chi^2 = 20.50$, df = 49, $P > 0.9$), or total body temperature measurements ($\chi^2 = 5.93$, df = 133, $P > 0.9$).

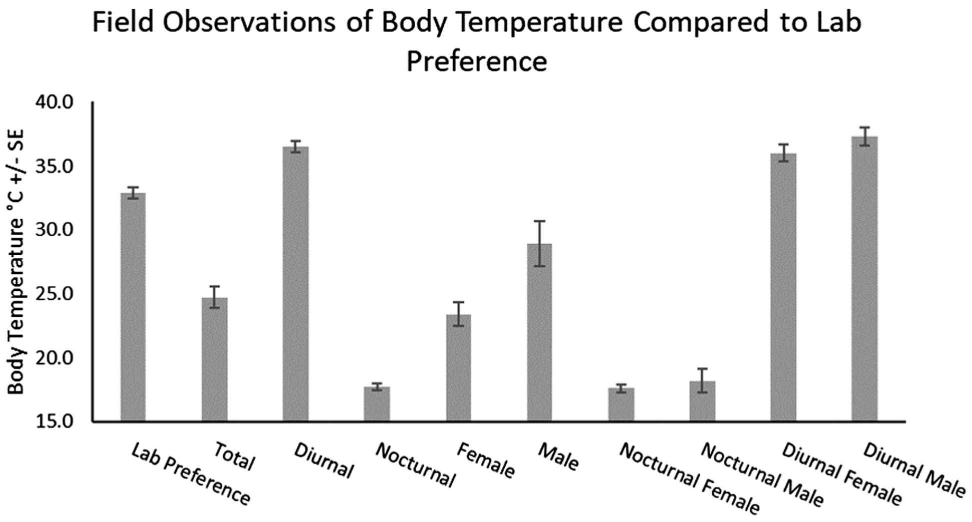

Fig. 1. A comparison of mean body temperature of *Rabidosa rabida* across time periods and sexes compared with laboratory thermal preference data from Stork (2012).

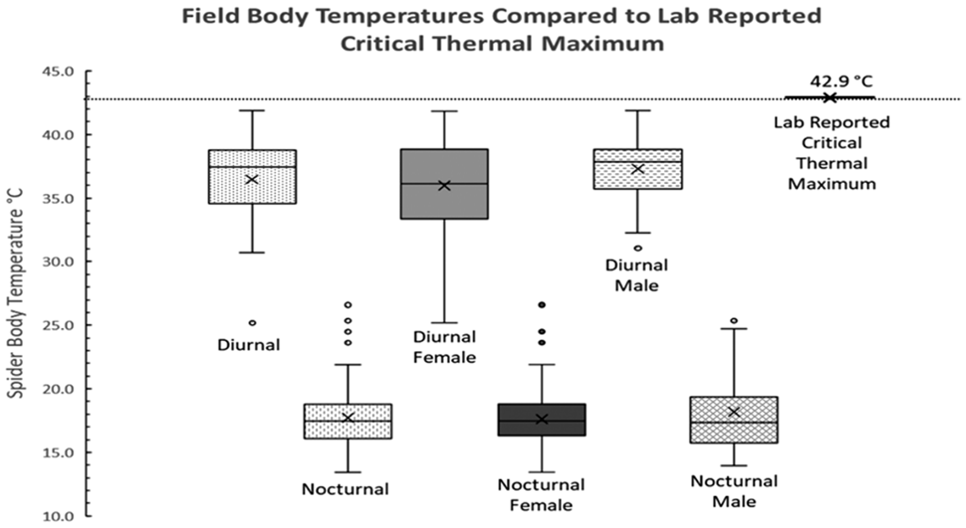

Fig. 2. A comparison of published critical thermal maximum for *Rabidosa rabida* from Stork (2012) compared with body temperatures measured between sexes and activity period.

Discussion

Field observations of the body temperatures of *R. rabida* did not match published estimates for thermal preference, causing us to reject our first hypothesis. Field observations did not significantly differ from ambient temperatures. This suggests that this spider is not actively thermoregulating during the observed period as previously hypothesized. This does not necessarily imply that these spiders are not capable of active thermoregulation. It does however suggest that they are not thermoregulating all the time. As a thermal generalist that is capable of locomotion across a wide range of temperatures (Stork 2012), this is not surprising. Spiders, both nocturnally and diurnally, were active off the ground in the vegetation and have a high surface area to volume ratio, both of which suggest a conforming thermal physiology (Alonso-Mejia and Arellano-Guillermo 1992, Pereboom and Biesmeijer 2003). Further investigation is needed to confirm whether this thermal generalist is thermoconforming at all times. The reported laboratory preference was lower than observed diurnal temperatures but higher than nocturnal temperatures. Diurnal temperatures did come closest to our expected preference value. Future tests need to look at differences across different times of day and different seasons to see whether there is a time that matches laboratory-reported preferred temperatures or one that best fits the optimum temperature for locomotor performance. Thermal performance is difficult to measure in the field but may provide a better view of the thermal physiology than thermal preference and tolerances do (Watson and Formanowicz 2012). We observed a range of behaviors and body temperatures. Despite diurnal temperatures above the reported thermal preference and even near to the critical thermal maximum, we observed spiders moving and feeding during both nocturnal and diurnal times (Stork et al. 2020). The only behavior not observed diurnally was mating. The absence of observed diurnal mating may be the result of the difficulty in finding spiders diurnally, or it could suggest that we need to further explore the thermal ecology of mating behaviors in this spider. We did observe significant differences in field body temperatures between times of day supporting our second hypotheses. This also supports our previous conclusion that in this situation *R. rabida* appears to be thermoconforming as there are significant temperature differences between day and night.

We did observe a difference between sexes; however, the unequal sample sizes between the sexes prevent us from concluding that there is a biological difference as there were nearly twice as many females measured during the night as the day, whereas males had nearly equal numbers between both times. Further work needs to test for sex differences in thermal ecology with better sample sizes and better controls for body size to test the trends observed in the laboratory.

One possible explanation for active choice of a thermal environment in the laboratory but not in the field is that the laboratory study was conducted a month later than when field observations were made. If reproductive physiology causes active thermoregulation in one sex but not the other that could explain this disconnect between laboratory and field observations. Another potential explanation for this mismatch is that laboratory estimates of thermal preference and tolerance used spiders of this species from a different location within Arkansas. We have previously suggested the potential for population level variation in this species (Stork 2012). Further work is needed to see how much of the differences between laboratory and field observations are explained by location.

Few estimates of thermal physiology and behavior have been made in the field for invertebrates and even fewer for arachnids. This study suggests that in temperate zones, both field and laboratory studies are needed to understand the behavioral and thermal ecology of invertebrates. Understanding the ecology of arthropods from all perspectives can provide numerous benefits to man. As global climate changes, many ecosystems with many ectothermic organisms will be greatly affected. We risk dramatically altering or losing benefits such as ecosystem services provided by arthropods if we do not gain a better understanding of the current and changing thermal ecology of these animals (Mooney et al. 2009; Palmer and Yahara 2009).

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