



Research

Thermal Tolerance in the Millipede *Euryurus leachii* Gray (Polydesmida: Euryuridae)

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Abstract

Temperature extremes often limit animal distributions. Whereas some poikilotherms (e.g., winged insects) can escape local thermal extremes, many less vagile organisms (e.g., insect larvae and arthropods with limited dispersal ability) are at the mercy of local microenvironmental conditions. Here, we quantified the thermal tolerance of an abundant, endemic, Nearctic millipede (*Euryurus leachii*), and explored the effects of seasonality, mass, and sex on its critical thermal maxima (CT_{max}). We also measured the thermal microenvironments of dead wood representing different decay classes. Overall, the mean CT_{max} for this species was ca. 40.5°C. Mass and sex had no effect on millipede CT_{max} . However, the mean CT_{max} for millipedes collected in the fall was 0.6°C higher than for individuals collected in the spring. An exposed dry log representing one common microhabitat for *E. leachii* readily warmed to temperatures exceeding its CT_{max} . The results suggest that CT_{max} is a seasonally plastic trait in *E. leachii* and that microclimatic conditions potentially limit the local distribution of this species. With habitat fragmentation and climate change contributing to warmer temperatures in forested systems, understanding the responses of detritivores like *E. leachii* can help predict potential shifts in community composition and ecosystem processes.

Key words: critical thermal maximum, Diplopoda, seasonality, thermal physiology, wood

Temperature is a key abiotic constraint on the distribution of organisms. At higher latitudes, cold extremes generally limit the geographic ranges of poikilotherms (Ungerer et al. 1999, Bale 2002). However, extremely high temperatures also can influence small-scale activity patterns and microhabitat occupancy by temperate species. For example, leaf-dwelling spider mites exhibit behavioral thermoregulation by avoiding microhabitats on single-leaf surfaces that exceed their optimal performance temperatures (Caillon et al. 2014). The high temperature threshold for motor control (i.e., the critical thermal maximum, or CT_{max} ; Huey 1991) varies among and within species (Kellermann et al. 2012, Kaspari et al. 2015, Verble-Pearson et al. 2015, Klockmann et al. 2017, Franken et al. 2018). Understanding how this variation affects the behavior and local distribution of arthropods is essential for predicting the effects of climate change, especially higher summer temperatures (Hoffmann et al. 2013, Boggs 2016, Truebano et al. 2018), on the abundance and diversity of temperate species.

Larval insects and other flightless arthropods that occupy patchy habitats are especially vulnerable to thermal extremes. For example,

African chironomid midges inhabiting ephemeral rock pools must withstand both extreme heat and dehydration during the dry season (Hinton 1960, Gusev et al. 2014). Coarse woody debris in forests (fallen tree branches and trunks; CWD) is a key patchy resource for many saproxylic arthropods (Ulyshen and Hanula 2009, Schowalter 2017, Grodsky et al. 2018, Myers and Marshall 2021). As with rock pool midges, many invertebrate inhabitants of CWD cannot easily relocate to a new patch if local conditions become unfavorable. Because many CWD inhabitants are sensitive to thermal extremes (Romo et al. 2019) and cannot relocate to more favorable conditions, we expect hotter environments (e.g., forest gaps, habitat edges) to influence species occupancy.

Millipedes (Diplopoda) are common invertebrate detritivores that inhabit leaf litter and CWD. They perform a variety of ecosystem services (e.g., wood decomposition, nutrient cycling) that facilitate the success of primary producers (Cárcamo et al. 2000, Stašiov et al. 2012, Taylor and Victorsson 2016, Ulyshen 2016, Schowalter 2017, Seibold et al. 2021). Like other flightless arthropods, millipedes exhibit limited dispersal ability (David and Handa 2010, Gilgado et al.

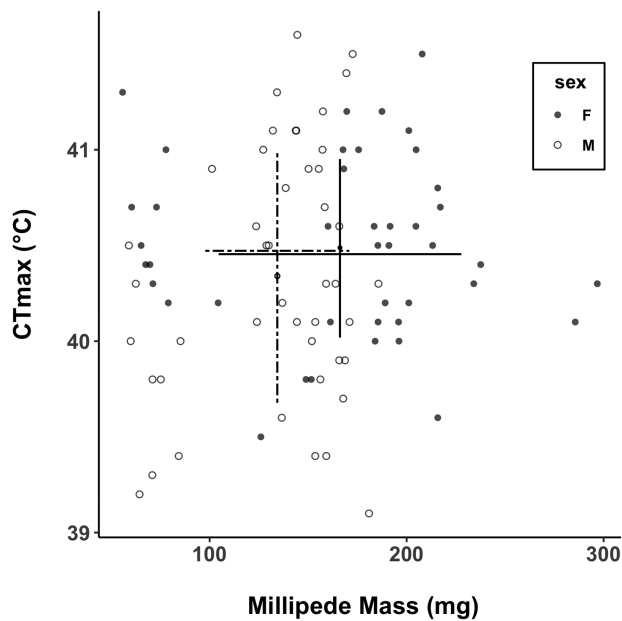


Fig. 1. Scatterplot of CT_{max} vs. *Euryurus leachii* mass (mg). Open points represent males ($n = 45$) and closed points represent females ($n = 42$). Mean \pm SD CT_{max} and mass are represented by dashed lines for males and solid lines for females.

2021). Despite their abundance and ecological importance in terrestrial ecosystems (Enghoff et al. 2015), the thermal biology of millipedes remains largely unexplored.

The principal goal of this study was to determine the thermal tolerance limits of a common CWD-inhabiting millipede in the east-central United States, *Euryurus leachii* Gray (Polydesmida: Euryuridae). This species commonly occupies CWD in earlier stages of decay (intact heartwood, structurally sound; decay classes 1–3; Woodall and Monleon 2008), and is usually absent from CWD in later stages of decay (rotten heartwood, spongy structure; decay classes 4 and 5; K.A.L., personal observation). We focused on three questions related to the CT_{max} of *E. leachii*: 1) Does CT_{max} vary predictably with sex and body size?, 2) Does the CT_{max} of this species differ between spring and fall?, and 3) How does their CT_{max} compare to the temperature profiles of CWD exposed to full sun conditions? We expected smaller individuals to have lower CT_{max} than larger individuals due to greater surface area to volume ratios (Bujan et al. 2016). We predicted that millipedes collected in the warmer fall months will have higher CT_{max} than those collected in the cooler spring months due to seasonal acclimation. Finally, we predicted that temperatures in CWD exposed to full sun (representing millipede habitats in gaps and forest edges) would exceed the CT_{max} of *E. leachii*, potentially explaining why millipedes were never found in these habitats in the field.

Materials and Methods

Study Site

Field work was conducted at the Horner Bird and Wildlife Sanctuary, a 85-hectare secondary oak-hickory forest (ca. 60-yr old) near Crestwood, Kentucky, USA (38.344°N, 85.529°W). The forest understory at this site is relatively open with abundant CWD and snags, both of which are primary microhabitats for *E. leachii*.

Euryurus leachii Collection

We collected a total of 87 millipedes from CWD at Horner in Fall 2020 (September–November) and Spring 2021 (April–May).

Millipedes were collected by hand through active searching, and immediately transferred to mesh-top plastic boxes containing humus and fragments of rotting wood from which individuals were collected. Millipedes were housed in laboratory growth chambers (70% RH, 23°C, 12:12 light:dark cycle) for at least 24 h (up to a maximum of 7 d) before heating trials were conducted. The sex of each millipede was determined by the presence or absence of male gonopods.

CT_{max} Determination

We constructed a simple dry bath consisting of an aluminum pot containing 1 liter of tap water and placed on a variable-temperature hot plate with a magnetic stirrer (model Isotemp; Fisher Scientific, Dubuque, IA, USA; Supplementary Fig. S1). Each millipede was brushed clean, weighed to the nearest 0.1 mg on an electronic balance, and placed into a glass vial (17 x 60 mm). Millipedes were not fasted prior to being weighed. Two vials were secured to the edge of the pot and submerged halfway into the water bath open-end-up such that the vial was orientated ca. 45° relative to horizontal. This setup was duplicated with a second pot and hotplate so that up to four millipedes could be tested at the same time (Supplementary Fig. S1). The hot plates were set to generate a temperature ramp rate of 0.5–0.9°C min⁻¹ with an initial water bath temperature of 22.0°C, which is within the range of temperatures experienced by millipedes in both the fall and spring at the study site. Preliminary trials with empty vials indicated that the temperatures of the water bath and the interior environment of the vial were similar (Supplementary Fig. S2). Whereas multiple dry bath techniques can be used to determine CT_{max} (Roeder et al. 2021), this setup specifically allowed for the continuous monitoring of millipede behavior without disturbing the test subjects.

Four K-type thermocouples (model TP-01; Reed Instruments, Wilmington, NC, USA) attached to a four-channel data logger (model HH309A; Omega Engineering, Stamford, CT, USA) recorded water temperatures surrounding each vial once per second. The thermocouples were submerged to approximately the same depth as the millipedes and secured in place to avoid contact with the pot or vial.

We conducted pilot heating trials using the methods described above with 20 *E. leachii* that were closely observed until death. We used the resulting array of behaviors (Supplementary Table S1) as the basis for identifying a reliable premortem indicator of CT_{max} (°C). For this species, CT_{max} was clearly evident as the onset of muscle spasms and diminished motor control (Supplementary Table S1, Lutterschmidt and Hutchison 1997). Data from these pilot trials were excluded from analyses. All trials ultimately resulted in the death of the tested individual; thus determination of postthermal stress recovery was not possible.

CWD Temperatures

We measured the thermal properties of the two principal microhabitats occupied by *E. leachii* (dry standing dead wood and relatively wet downed wood). We collected two white ash (*Fraxinus americana*) logs of similar dimensions (30-cm diameter x 75-cm length) but differing in decomposition stage (Woodall and Monleon 2008). One log fell within decay class 3 (soft heartwood and missing bark) and the other was in decay class 1 (intact sapwood, heartwood, and bark). Only decay class 1 and 3 logs were tested because they represent the two extreme CWD conditions that millipedes occupy in the field (K.A.L., personal observation).

A 5-mm diameter hole was drilled to 1-cm depth below the bark on one side of each log. A thermocouple connected to a data logger (see above) was inserted into the hole in each log, and the gap surrounding each thermocouple was plugged with modeling clay.

The logs were placed near each other in an open grassy field with complete Sun exposure at the study site. A pair of thermocouples simultaneously recorded ambient air temperatures near each log. Temperatures were recorded every 5 min from 08:00 to 19:30 on a single clear day in July, which is the hottest month of the year in Kentucky and other north temperate regions (Andresen et al. 2012).

Seasonal Conditions

To evaluate seasonal differences at the study site, we calculated the average daily mean temperature for the dates millipedes were collected in the fall and in the spring using weather data archives for the Crestwood, Kentucky weather station (Weather Underground 2021). We also compiled average temperature data from the same ranges of dates over the last 10-yr (2012–2021) to characterize longer-term seasonal variation at the study site.

Statistical Analyses

We used a linear model to determine how the CT_{max} of the 87 millipedes varied with sex, mass, season, and all possible pair-wise interactions of these fixed effects. We used stepwise model reduction methods to determine which effects to include in the final model. We compared models using Akaike's Information Criterion (AIC)—a mathematical method for determining the fit of a model to the data. Effects and interactions were removed if AIC decreased by > 2.0 . The final model included mass, sex, and season as fixed effects along with sex:season and mass:sex as interaction terms. We used a Welch's *t*-test to compare millipede masses between males and females.

Temperature data for the ash logs representing decay classes 1 and 3 were collected on a single day, and thus lacked replication for statistical analysis. Consequently, we used summary statistics to compare their temperature profiles with ambient air temperature and *E. leachii* CT_{max} . Temperature data from the Crestwood weather station were compared between seasons with *t*-tests.

Results

The 87 millipedes used in this study included 45 males and 42 females. Male-to-female sex ratios were uneven between the fall (1.0:1.3; $n = 52$) and the spring (1.0:0.6; $n = 35$). Millipede mass ranged from 55.8 to 296.8 mg, and females (mean \pm SE; 166.14 ± 9.49) were significantly larger than males (134.36 ± 5.44 ; $t = 2.90$, $df = 65.8$, $p = 0.005$).

The CT_{max} of the millipedes did not vary predictably with mass ($F = 1.48$, $p = 0.23$) or sex ($F = 1.38$, $p = 0.24$; Supplementary Table S2). CT_{max} values for males (mean \pm SE; 40.34 ± 0.10) were nearly identical to those for females (40.48 ± 0.07 Fig. 1). By contrast, the CT_{max} of the millipedes collected in the fall ($n = 52$; 40.66 ± 0.06) averaged 0.6°C higher than values for millipedes collected in the spring ($n = 29$; 40.03 ± 0.09 ; $F = 42.37$, $p < 0.001$; Fig. 2). There was no interaction between sex and season ($F = 3.07$, $p = 0.08$) or between mass and sex ($F = 3.25$, $p = 0.08$).

Average (\pm SE) temperatures were ca. 10°C higher in the decay class 1 log ($41.70 \pm 0.73^\circ\text{C}$) than in the decay class 3 log ($30.81 \pm 0.32^\circ\text{C}$), and ambient air ($32.32 \pm 0.25^\circ\text{C}$; Fig. 3). Temperatures recorded in the decay class 1 log were more variable and reached a higher maximum (53.2°C) than those of the decay class 3 log (35.0°C). Temperatures of the decay class 3 log and the ambient air never exceeded 36°C during the measurement period (Fig. 3).

Mean (\pm SD) temperatures from the Crestwood weather station during the fall collection dates ($18.54 \pm 4.34^\circ\text{C}$) tended to be warmer than during the spring collection dates ($16.64 \pm 3.13^\circ\text{C}$). Despite this

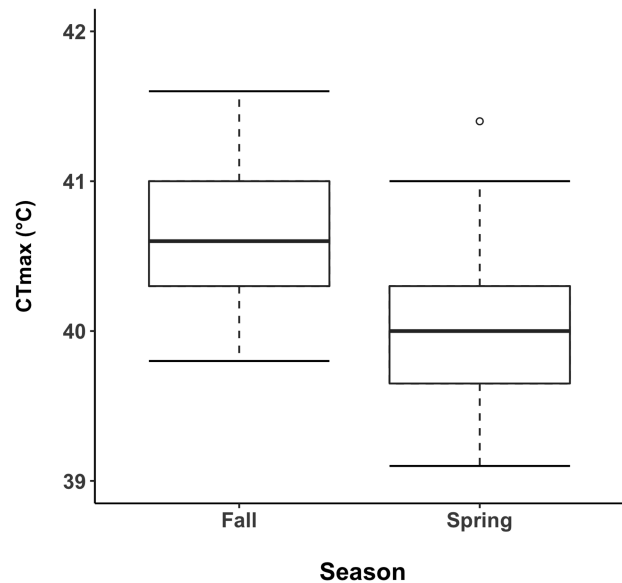


Fig. 2. Median, interquartile range, minimum, and maximum values of CT_{max} for *Euryurus leachii* individuals collected in fall ($n = 52$) versus spring ($n = 35$).

trend, the means did not differ statistically between seasons ($t = 0.32$, $df = 60$, $p = 0.75$) within the narrow time frames that millipede collections were conducted. However, data compiled from the last 10 yr showed that average fall temperatures at the study site were warmer ($19.69 \pm 1.30^\circ\text{C}$) than spring temperatures ($18.20 \pm 1.30^\circ\text{C}$; paired $t = 2.47$, $df = 9$, $p = 0.035$).

Discussion

Terrestrial organisms with limited mobility (e.g., flightless arthropods) are at the mercy of local environmental conditions. Drying habitats or superheated substrates can be lethal to organisms lacking heat-resistant traits (Hinton 1960, Gehring and Wehner 1995). Here, we quantified the CT_{max} of a common millipede that inhabits CWD in temperate forests, and compared its thermal tolerance limits to temperature extremes occurring in the field. Sex and specimen mass had no statistical effect on the CT_{max} of *E. leachii*; however, CT_{max} differed seasonally. Field measurements also indicated that some decay classes of logs reach temperatures exceeding the CT_{max} of *E. leachii* under highly exposed conditions.

The lack of a sex-based difference in thermal tolerance in *E. leachii* is consistent with other studies of saprophagous arthropods (Franken et al. 2018). Similar to other millipedes, *E. leachii* exhibits sexual size dimorphism with females averaging larger body mass (Adolph and Gerber 1995, Rowe 2010, Ilić et al. 2016). However, the lack of an effect of mass on CT_{max} differs from previous studies of invertebrate thermal physiology (Kaspari et al. 2015, Verble-Pearson et al. 2015, Franken et al. 2018), and from our expectations. Given that key components of the arthropod nervous system (the nerve cord and most major ganglia) are concentrated ventrally and not in the center of the insect, simple surface area to volume ratios may not be the best predictor of CT_{max} across a range of masses. Regardless, effects of body size on arthropod CT_{max} often are inconsistent due to multiple factors (e.g., Verble-Pearson et al. 2015, Franken et al. 2018) that require further study.

Upper thermal limits in arthropod species often are assumed to be fixed traits (Sunday et al. 2012), but some species exhibit profound

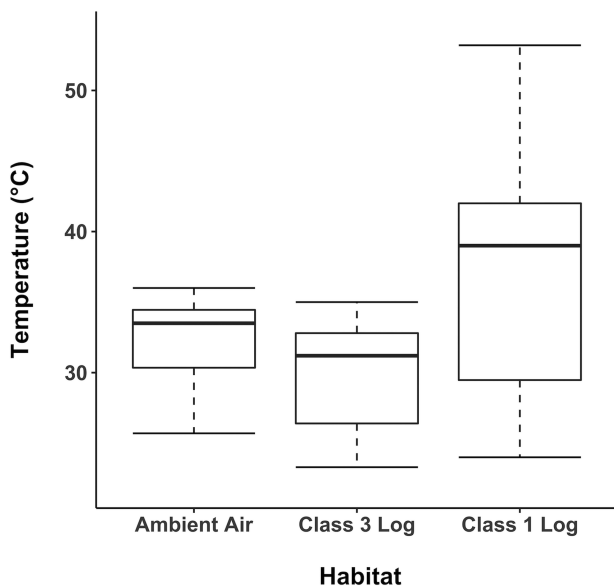


Fig. 3. Median, interquartile range, minimum, and maximum values of temperature data for ambient air and two ash logs representing decay classes 1 and 3.

differences in CT_{max} across seasons (Bujan et al. 2020, Sasaki and Dam 2020) and developmental conditions (Kellermann and Sgrò 2018). CT_{max} appears to be a seasonally plastic trait in *E. leachii*, with slightly higher thermal tolerance during the warmer months. Although some arthropods exhibit much greater seasonal differences in CT_{max} (Jensen et al. 2019, Bujan et al. 2020), the difference observed here (0.6°C) is likely to be biologically relevant given the fundamental importance of temperature to ectotherm metabolism (Neven 2000). Historical weather data for the study site suggest that the observed seasonal differences in CT_{max} reflect acclimation to consistently warmer temperatures in the fall (e.g., Somero 2010), although variation in wood moisture content, food quality, and multiple other factors could be driving this result. Thus, additional experimental data are needed to clarify the mechanisms for seasonal differences in the thermal tolerance of this species.

Results from the simple log exposure experiment suggest that thermal extremes exclude *E. leachii* from relatively dry CWD in exposed habitats. By contrast, the higher moisture content of decay class 3 logs presumably provides a buffer against thermal extremes until the wood eventually dries. We commonly found *E. leachii* in drier pieces of CWD in the forest interior. This suggests that shading from the forest canopy allows *E. leachii* to occupy drier CWD that would be uninhabitable in highly exposed settings such as canopy gaps created by treefalls (Krasny and DiGregorio 2001) and insect outbreaks (Gandhi et al. 2014), and forest edges associated with habitat fragmentation (Tuff et al. 2016, Arroyo-Rodríguez et al. 2017). Fragmentation and disturbance are increasing in forested systems (Seidl et al. 2017), thus understanding the effects of such changes on common detritivores such as millipedes is essential for predicting changes in trophic patterns and ecosystem function (Hoekman et al. 2009).

The results of this study suggest that *E. leachii* exhibits slight seasonal plasticity in CT_{max} , potentially providing a buffer to rising temperatures in the short term (Richard et al. 2019). However, plasticity in arthropod CT_{max} tends to be narrower than lower critical limits (Chown 2001, Hoffmann et al. 2013, Slatyer et al. 2016), suggesting limitations to plasticity as global temperatures continue to rise at unprecedented rates (Gunderson and Stillman 2015; Hoffmann

et al. 2013). With increasingly warmer climates (Wang et al. 2021) and reductions in global arthropod abundances (Didham et al. 2020, Wagner 2020), understanding the responses of common detritivorous species like *E. leachii* to thermal extremes is critical to predicting changes in ecosystem-level processes.

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