



Thermal ecology and physiology of an elongate and semi-fossorial arthropod, the bark centipede

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ABSTRACT

Organismal performance is strongly linked to temperature because of the fundamental thermal dependence of chemical reaction rates. However, the relationship between the environment and body temperature can be altered by morphology and ecology. In particular, body size and body shape can impact thermal inertia, as high surface area to volume ratios will possess low thermal mass. Habitat type can also influence thermal physiology by altering the opportunity for thermoregulation. We studied the thermal ecology and physiology of an elongate invertebrate, the bark centipede (*Scolopocryptops sexspinosus*). We characterized field body temperature and environmental temperature distributions, measured thermal tolerance limits, and constructed thermal performance curves for a population in southern Georgia. We found evidence that bark centipedes behaviorally thermoregulate, despite living in sheltered microhabitats, and that performance was maintained over a broad range of temperatures (over 20 °C). However, both the thermal optimum for performance and upper thermal tolerance were much higher than mean body temperature in the field. Together, these results suggest that centipedes can thermoregulate and maintain performance over a broad range of temperatures but are sensitive to extreme temperatures. More broadly, our results suggest that wide performance breadth could be an adaptation to thermal heterogeneity in space and time for a species with low thermal inertia.

1. Introduction

Organismal performance is strongly linked to temperature because of the fundamental thermal dependency of enzyme activity (Shapley, 1924; Angilletta Jr et al., 2010b; Dell et al., 2011). At the organismal level, these relationships between temperature and activity of individual enzymes combine to drive a similar relationship between temperature and whole animal performance (Huey and Kingsolver, 1989; Secor et al., 2007; Streicher et al., 2012; DeLong et al., 2017). However, organismal traits (behavioral, morphological, and physiological) can alter the relationship between temperature and performance (Novarro et al., 2018; Bodensteiner et al., 2019; Fey et al., 2019). Thermoregulation, either behavioral or physiological, can allow animals to regulate body temperature to become thermal specialists, optimizing performance within a narrow temperature range (Angilletta Jr et al., 2002, 2010a;

Logan et al., 2019; Neel et al., 2020). Morphology can also affect the body temperatures of organisms, with integumental boundaries impeding heat transfer with the environment (Best, 1982; Cena et al., 1986; Dawson and Maloney, 2004), body size altering thermal inertia (Stevenson, 1985; Paladino et al., 1990), and the surface area to volume ratio regulating rates of core temperature flux (Bell, 1980; Phillips and Heath, 1995). For obligate ectotherms, loss of endogenously generated heat is not an issue, and so they have evolved sizes and shapes (elongate, flattened) that are not possible for endotherms (Pough, 1980). Indeed, shapes and sizes that allow rapid equilibration to environmental temperature can be beneficial in the context of thermoregulation (Carrascal et al., 1992). However, microhabitat characteristics can structure the thermal environment to constrain the relationship between habitat, temperature, and performance.

Habitat structure can alter the thermal landscape to impact the

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thermal biology of organisms (McEnitre and Maerz, 2019). Spatially heterogeneous or patchy environments might offer thermal heterogeneity, which could facilitate thermoregulation (Sears and Angilletta Jr, 2015; Sears et al., 2016), while spatially homogeneous environments limit the potential for thermoregulation (Deutsch et al., 2008). Even in spatially heterogeneous environments, microhabitats can be thermally buffered from ambient air temperatures, which could conceivably facilitate or constrain thermoregulation (Huey et al., 1989; Cox et al., 2018; Logan, 2019). However, the relationship between temperature, performance, and habitat remain unknown for many organisms, especially small, secretive ones like centipedes.

Centipedes are ectotherms with extremely high surface area to volume ratios and are both voracious predators and frequent prey (Lewis, 1981; Shelley, 2002; Yang et al., 2012; Luo et al., 2018). As such, the thermal dependence of traits like locomotor performance should be tightly linked to fitness in this group (Culler et al., 2014). Because of centipede body size and shape, they should rapidly equilibrate to environmental temperature which could facilitate behavioral thermoregulation to their preferred temperatures when optimal thermal microclimates are available. However, rapid equilibration rates could be costly, as any sudden shift in temperature to a non-optimal range could cause a swift drop in performance, or even death. Additionally, centipedes are often nocturnal and found under thermally buffered cover objects that could restrict movement (Shelley, 2002), which might limit the potential for thermoregulation. Finally, the ecology and thermal biology of centipedes is poorly known, with studies concentrated on only a few species (Lewis, 1981; Fusco and Minelli, 2000). To our knowledge, the thermal characteristics of microhabitats, thermoregulatory behavior, and the relationship between temperature and performance has not been previously studied for centipedes.

We characterized the diurnal thermal ecology and physiology of the bark centipede (*Scolopocryptops sexspinosus*). This relatively large centipede is distributed throughout the eastern United States under surface objects and in leaf litter. We conducted several experiments to 1) characterize diurnal body temperature and environmental temperature distributions in nature, 2) determine thermal tolerance limits and assess thermal inertia, and 3) measure the relationship between temperature and locomotor performance.

2. Materials and methods

2.1. Study system

The bark centipede (*Scolopocryptops sexspinosus*) is a medium sized (maximum length 69 mm) scolopendramorph centipede (Shelley, 2002). Scolopendramorph centipedes are distinguished by their large, muscular forcipules (front limbs that are modified into venom-delivering appendages) and are powerful and voracious predators. Bark centipedes are also relatively heavy-bodied, averaging 0.75 g and ranging from 0.26 to 1.46 g in our study. This species has a broad geographic range and is found in most habitats of the eastern United States, although recent research has suggested that this widespread taxon may in fact be a complex made of six distinct species (Garrick et al., 2018). Our study location was a relatively open-canopy mixture of pine and hardwood trees in Bulloch County, southeastern Georgia. At our study site, we almost exclusively found bark centipedes under the bark and logs of fallen longleaf (*Pinus palustris*), loblolly (*Pinus taeda*), and slash (*Pinus elliottii*) pine trees. These partially decayed logs had loosened bark and were honeycombed with holes and cracks that provided a complex matrix of potential habitat for centipedes. Underneath the logs was a layer of leaf litter and pine duff over the soil surface that was dotted with burrows and cracks. Indeed, when uncovered, the centipedes would often escape into the interior of the log or into the soil. Meanwhile, the ground surface adjacent to the logs was covered in pine duff (from the three primary pine species) and leaf litter from common deciduous trees

such as water oak (*Quercus nigra*), sweetgum (*Liquidambar styraciflua*), and tulip poplar (*Liriodendron tulipifera*). We occasionally found other centipedes (*Theatops posticus*, *Hemiscolopendra marginata*) in these habitats as well, but bark centipedes were the most abundant chilopod.

2.2. Field collection and housing

We collected bark centipedes during the beginning of their active season from February through May of 2018. We collected centipedes both under logs and under the loose bark on those same logs. Upon discovery, centipedes were grasped with long forceps, and transported in 50 ml conical vials to the Georgia Southern University Insectary. Centipedes were maintained at 20 °C with a 12L: 12D photoperiod in 1 L plastic containers with soil and a cover object (bark) from their habitat for 3–7 days. We did not feed centipedes prior to measuring physiological traits to ensure that they were postabsorptive to minimize measurement variation (Secor et al., 2007; Cox and Secor, 2010). We were not able to determine sex, as the only way to accurately ascertain sex for most scolopendramorph centipedes while they are alive is to anaesthetize them for detailed morphological examination (DeLong et al., 2017), which would have been impractical given our study goals. We measured body mass using a digital scale (Ohaus Scout Pro, Ohaus Corporation, Parsippany, NJ, USA). We did not measure body length because stretching the centipedes could cause limb autotomy or otherwise injure the animal. Animals were not fed during the study, and cages were misted to provide water. Centipedes were released at the site of capture at the end of the study.

2.3. Field body temperatures

It was not practical to measure body temperature while capturing centipedes for laboratory studies because they would rapidly escape into logs or underground. Thus, we separately surveyed field body temperatures of centipedes during April of 2018. We searched for centipedes by turning logs and bark in the appropriate habitat (same as environmental temperature data, see below) between 9 a.m. and 6 p.m. When we located a bark centipede, we quickly (prior to escape) measured their body temperature from a distance of ca. 12 cm using an infrared thermometer (Table S1). Because these centipedes are relatively small and elongate, the temperature of their integument should closely match their internal body temperature. We measured temperature using an infrared thermometer (IRT207, General Tools and Instruments, Secaucus, NJ, USA) with an 8:1 distance to spot ratio. We verified the accuracy of this thermometer by comparing measurements to those of temperature-controlled incubators. The spot size at 12 cm would be 1.5 cm, such that centipedes would generally fill close to 100% (minimum of 50%) of the spot size, depending on distance to the centipede and body size of the centipede. It is worth noting that centipedes have low thermal inertia, and ambient temperature should closely match body temperature.

2.4. Environmental temperature distributions

We measured environmental temperature distributions in bark centipede habitat by sealing 45 Thermochron iButton data loggers (Embedded Data Systems, Lawrenceburg, KY, USA) in watertight plastic bags and placing them in relevant habitat for bark centipedes. Environmental temperature distributions were characterized from early April to early May of 2018. We placed a third of the data loggers on the ground surface adjacent to logs that were likely habitat for bark centipedes, based on our previous field experience. While bark centipedes are rarely on the surface, one of the authors (CLC) has witnessed them on the ground surface adjacent to fallen logs. Surface data loggers may have been exposed to direct sunlight. We also placed a third of the data loggers under bark on logs and the final third underneath logs, both of which are where the vast majority of bark centipedes were encountered. We set iButton loggers to record temperature and time every 15 min and

recovered them after one month of deployment in the field. These loggers recorded a total of 90,112 temperatures, which we trimmed to 34,142 temperatures by removing all temperatures outside of the hours between 9 a.m. and 6 p.m. (Tables S2 and S3). This corresponds to the time frame when we sampled field body temperatures of bark centipedes.

2.5. Thermal tolerance

We measured the critical thermal minimum (CT_{min}) and the voluntary thermal maximum (VT_{max}) of centipedes ($n = 18$) as estimates of lower and upper thermal tolerances, respectively (Table S4). Because high temperatures can be more stressful than cool temperatures, we measured CT_{min} first, followed by VT_{max} . The prior measurement of CT_{min} thus could have influenced estimates of VT_{max} , although the impact would have been consistent among individuals. To measure CT_{min} , we placed centipedes in an empty plastic container, and placed that container in a cooler with ice. As the centipede cooled and began to move sluggishly, we then periodically (every few seconds) used forceps to turn the centipedes onto their dorsum and assessed their ability to turn back on their venter. When this righting response was lost, we measured their body temperature (“lost” CT_{min}) from a distance of ca. 12 cm using an infrared thermometer. We then removed the plastic container from the cooler to ambient room temperature (ca. 20 °C) and allowed the centipede to warm towards a temperature where they could once again right themselves. When the righting response was regained, we measured their body temperature (“regained” CT_{min}) from a distance of ca. 12 cm using the infrared thermometer. We measured VT_{max} rather than critical thermal maximum because early trials indicated that we could not estimate critical thermal maximum without substantial mortality. To measure VT_{max} , we placed centipedes in an open enclosure with a heat lamp. We identified VT_{max} by taking the external temperature of the centipede using an infrared thermometer (General Tools and Instruments, IRT207) when they vigorously attempted to escape the enclosure (Cowles and Bogert, 1944; Cox et al., 2018). Between individuals, the enclosure was returned to ambient temperature (20 °C).

2.6. Thermal performance curve

We measured sprint speeds of centipedes ($n = 18$) at seven different temperatures (10, 15, 20, 25, 30, 32, 35 °C). The order of temperatures was randomized on blocks of six animals. Sprint speed was measured by placing centipedes in the center of a plastic arena (40 × 28 cm) that was lined with graph paper. We then encouraged centipedes to crawl by gently touching the posterior of the body with forceps. When the centipede reached the edge of the arena, we used forceps to place them into the center and induced crawling again. We repeated this for a total of three trials per individual per temperature. Trials were recorded using a Casio Exilim HS® (Casio USAA, Dover, NJ, USA) camera at a frame rate of 40 fps, which was an adequate frame rate for capturing variation in centipede sprint speed. Videos were analyzed using Eagle Eye Pro-Viewer® (Eagle Eye Digital Video LLC, Saint Paul, MN, USA) motion-analysis software. We selected sections of the videos where the centipede moved in a linear fashion for at least one body length, and measured that velocity in cm/s. We then repeated this process for each independent trial for a total of three measurements of sprint speed at each temperature per individual. We then selected the maximum sprint speed among the three trials (Angilletta et al., 2002; Careau et al., 2014) for further analysis (Table S5).

2.7. Thermal performance curves and thermoregulatory efficiency

We used maximum sprint speed across temperatures to construct a thermal performance curve. We fit the full set of asymmetrical parabolic equations (both intercept and zero-intercept versions) that are built into the program TableCurve 2D (Systat Software Inc, San Jose, CA, USA) to

the performance data for the population. We then used corrected Akaike Information Criterion (AICc) to determine the best-fit function with optimized parameter values (Angilletta Jr, 2006; Logan et al., 2020; Neel et al., 2020). We chose asymmetrical parabolic equations because the shapes of thermal performance curves are constrained by biomechanics to be left-skewed (Hochachka and Somero, 2002; Angilletta Jr, 2009). We extracted the thermal optimum for performance (T_{opt}), maximum performance (P_{max}), and thermal performance breadth (T_{br} ; the range of body temperatures at which the population can achieve at least 80% P_{max}) by solving the best-fit function for every 0.1 °C. We then used T_{opt} to calculate thermoregulatory accuracy (d_b ; the deviation of mean field body temperature from T_{opt}), thermal quality of the environment (d_e ; the deviation of T_{opt} from mean environmental temperature), and thermoregulatory efficiency E using equations in Hertz et al. (1993).

2.8. Statistical analyses

We used full-factorial mixed-model repeated-measures ANOVA to account for autocorrelation within individuals and compared mean CT_{min} estimates and mean sprint speeds across temperatures (with body mass as a covariate, individual as a random factor, and temperature as a fixed factor). We compared mean sprint speeds in a pairwise fashion among temperatures using Wilcoxon sign rank tests and corrected for multiple comparisons using the Bonferroni method. We compared environmental and body temperature distributions using non-parametric Kolmogorov-Smirnov two-sample tests and Kruskal Wallis tests. In all cases, we confirmed that our data conformed to the assumptions of the statistical tests by examining frequency distributions of the raw data and residual plots. Data are presented as means ± SEM. All analyses were completed in JMP v 12.0 (SAS Institute, Cary, NC).

3. Results

3.1. Environmental temperature distributions

Environmental temperature distributions from the ground surface, under bark, and under logs all differed significantly from one another (Kolmogorov-Smirnov two-sample test, all $P_s < 0.0001$). Environmental temperature distributions on the ground surface were relatively warm (20.81 ± 0.043 °C) and leptokurtic (kurtosis, 1.09) with 1.49% of temperatures below CT_{min} or above VT_{max} (Fig. 1). Environmental temperature distributions under bark were relatively warm (21.08 ± 0.047 °C) and platykurtic (kurtosis, 0.52) with 1.13% of values below CT_{min} or above VT_{max} (Fig. 1). The environmental temperature distribution under logs was leptokurtic (kurtosis, 1.42) and cool (17.74 ± 0.025 °C), with no temperatures below CT_{min} or above VT_{max} (Fig. 1). Mean hourly temperatures were highest for the ground surface or under bark, with temperatures under logs up to ~5 °C cooler than other microhabitats (Fig. 1).

3.2. Thermal tolerance and the temperature dependence of sprint speed

We found that the temperature when the righting response was lost during cooling (“lost” CT_{min} , 4.97 ± 0.08 °C) was significantly lower ($F_{1,17} = 13.12$, $P = 0.0021$) than the temperature where the righting response was regained (“regained” CT_{min} , 5.63 ± 0.17 °C) during rewarming after cold-immobilization, although the values were relatively similar. The voluntary thermal maximum (VT_{max}) was nearly 20 °C higher than CT_{min} (33.47 ± 0.18 °C). Sprint speed differed significantly ($F_{6,120} = 31.45$, $P < 0.0001$) among temperature treatments (Fig. 2), with sprint speed at the highest and lowest temperatures significantly lower than sprint speed at other temperatures (Wilcoxon sign rank test, $P_s < 0.05$).

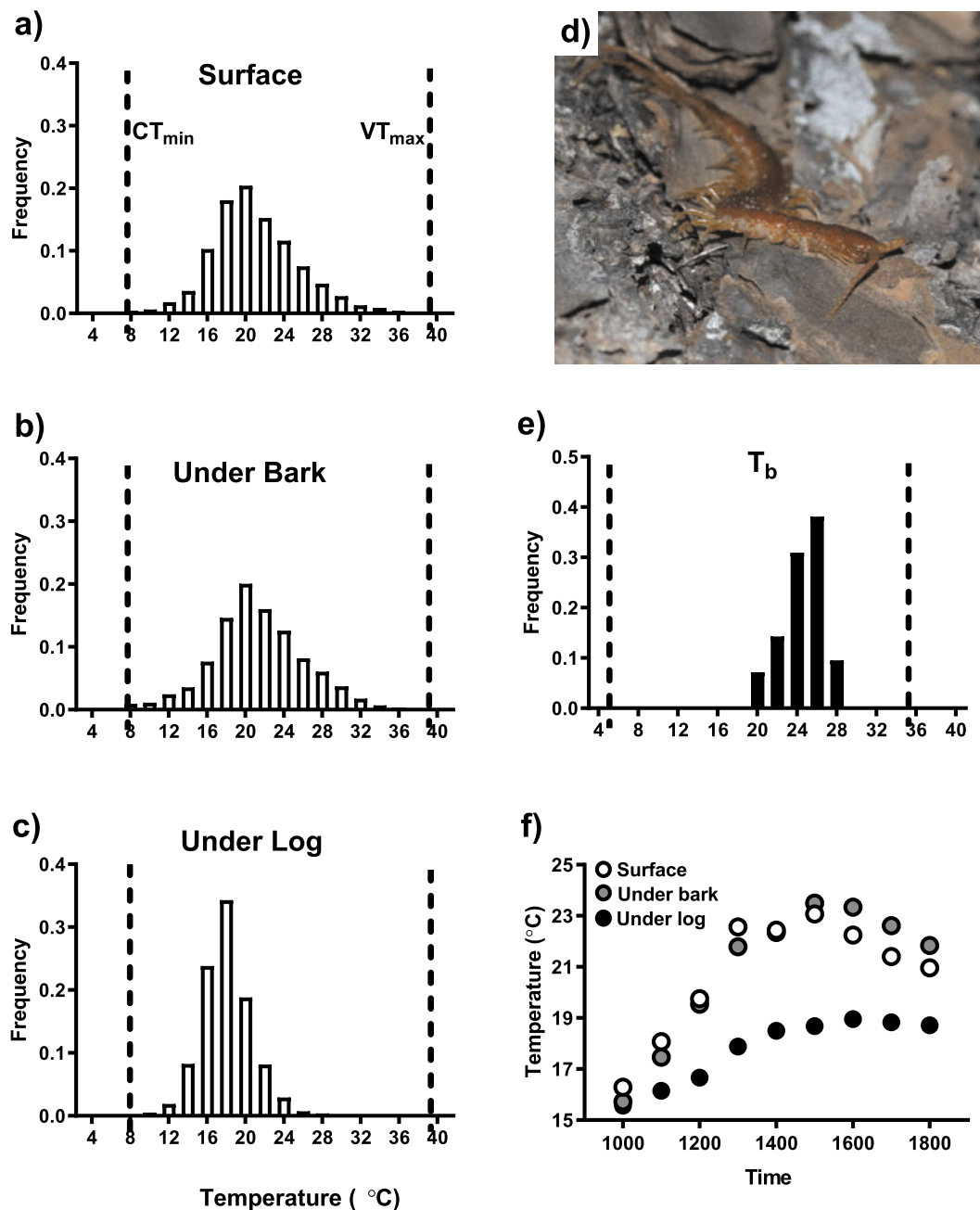


Fig. 1. Environmental temperature distributions and body temperatures of *Scolopocryptops sexspinosus*. Environmental temperature distributions (a) on the ground surface, (b) under bark, and (c) under logs. D) The bark centipede (*Scolopocryptops sexspinosus*). e) Field body temperatures (T_b) pooled across microhabitat types. f) Average hourly environmental temperatures of each microhabitat type, averaged across all dataloggers for a given hour of the day. Temporal temperature distributions were somewhat platykurtic and warm on the surface and under bark. By contrast, temporal temperature distributions under logs were relatively leptokurtic and cool. Centipede body temperatures were leptokurtic with a smaller range compared to environmental temperature distributions. Hourly environmental temperatures were highest on the ground surface and under bark and were up to 5 °C cooler under logs.

3.3. Thermal performance curves and thermoregulation

The function that best described the relationship between sprint speed and temperature had a broad plateau of high performance and a sharp decrease in thermal performance that corresponded closely to VT_{max} (Fig. 2). The optimal temperature for performance (T_{opt}) was 33.7 °C, slightly higher than VT_{max} . At T_{opt} , the predicted maximal performance (P_{max}) was 64.27 cm/s/g. Performance breadth (T_{br}) was substantial, with 80% of maximal performance capacity maintained over a 20.9 °C range.

We found evidence that bark centipedes have body temperatures that

differ from their environment, with field body temperatures significantly higher (mean, 24.54 ± 0.31 °C) than any of the environmental temperature distributions we measured in various microhabitats (Kruskal Wallis, all $P_s < 0.0001$). At certain times of the day, average body temperature (T_b) was similar to mean hourly environmental temperatures on the ground surface and under bark, but not under logs. 47% and 44% percent of the daily environmental temperatures fell outside the T_b range on the surface and under bark, respectively, and over 75% of daily environmental temperatures were outside (mostly below) the T_b range under logs. While mean centipede body temperature was substantially lower than T_{opt} (mean d_b 9.16 °C, i.e., low thermoregulatory

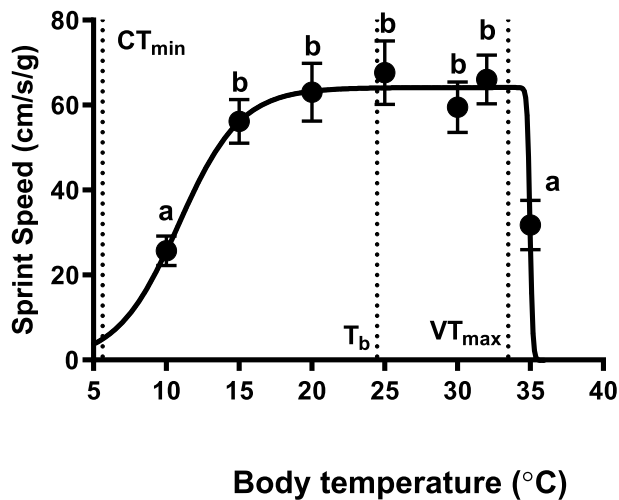


Fig. 2. The relationship between mass-corrected sprint speed and body temperature in the bark centipede. Symbols indicate means \pm S.E.M. Letters above symbols indicate significant pairwise differences between means ($a \neq b$) using the Wilcoxon sign rank test and a Bonferroni correction. The solid black line indicates the best-fit function that describes the thermal performance curve. The vertical dotted lines indicate CT_{min} (critical thermal minimum), T_b (average field active body temperature), and VT_{max} (voluntary thermal maximum). We found that high performance was maintained across a broad range of temperatures, and that performance declined rapidly at the temperature above VT_{max} .

accuracy), this was less than the mean deviation of environmental temperatures (d_e) from T_{opt} in all habitats, which suggests that centipedes are behaviorally thermoregulating to some extent. Correspondingly, effectiveness of thermoregulation (E) was relatively low (0.33).

4. Discussion

Temperature can have a profound impact on the expression of fitness-associated traits, such as locomotor performance, and can be modulated by both morphology and ecology. Bark centipedes can be found in habitats ranging from moist deciduous forests on the Atlantic seaboard to dry oak savannahs in the eastern Great Plains across their broad geographic range (Shelley, 2002). Accompanying this habitat diversity is diversity in thermal landscapes. In one single population, we found evidence that bark centipedes thermoregulate within their microhabitats, but also maintained thermal performance over a broad range of temperatures. The combination of thermoregulation and broad thermal performance breadth could facilitate colonization of diverse habitats that differ in thermal characteristics and renders this species an ideal system for studying thermal ecology.

Bark centipedes are normally found under logs and bark, and their nocturnal habits would seem to preclude effective behavioral thermoregulation (Hoffman, 1995; Shelley, 2002). However, we found evidence consistent with thermoregulation by centipedes during the day, maintaining body temperatures that are higher than the environmental temperature of multiple microhabitats and that are closer to the thermal optimum for performance. Moreover, centipedes experience a narrower range of body temperatures than the range of environmental temperatures available in each microhabitat. However, centipedes might be selecting warmer and less variable microhabitats for some reason other than thermoregulation (e.g., proximity to a food source or potential mates), which cannot be determined by our study. Other nocturnal ectotherms, such as geckos and snakes, forage at night and thermoregulate within retreat sites during the day to optimize physiological functions such as digestion, growth, and reproduction (Bustard, 1967; Huey et al., 1989; Autumn and De Nardo, 1995; Kearney and Predavec, 2000; Rock et al., 2002; Cox et al., 2018). We found that daily environmental temperatures varied substantially among microhabitats within

centipede habitats, providing ample scope for spatial heterogeneity in temperature among and within retreat sites, which is a prerequisite for thermoregulation (Logan et al., 2013). Indeed, temperature distributions for the ground surface and under bark were relatively similar, suggesting that centipedes might use bark as protection from predators rather than to buffer against thermal extremes. By contrast, mean hourly temperatures underneath logs were cooler and more thermally stable than the other two microhabitats, which suggests that microhabitats under logs might function as thermal refuges from extreme temperatures. Indeed, we frequently found centipedes under logs, despite the fact that environmental temperatures in this microhabitat had the largest deviation from the optimal temperature for performance, implying that centipedes could be using these sub-optimally cool and thermally buffered habitats to avoid overheating. While relatively little is known about the ecology of bark centipedes, our data suggest that centipedes might move from cool (within and under logs) to warm (ground surface and under bark) microhabitats to thermoregulate and maintain physiological performance. Thermoregulation by centipedes might be important not only for performance traits associated with feeding and predator escape (sprint speed), but also for physiological functions like growth, reproduction, and digestion.

Small, elongate organisms that rapidly equilibrate to environmental temperature may be able to precisely regulate their body temperature at times, but they may also be exposed to sub-optimal temperatures during times of the day when thermoregulation is not possible (e.g., during the night). Indeed, some centipede species have evolved freeze tolerance, presumably as an adaptation to extreme cold (Tursman et al., 1994; Tursman and Duman, 1995). Given their lack of thermal inertia, it is likely that centipedes are occasionally exposed to extreme temperatures that they do not have time to escape (Tursman et al., 1994; Tursman and Duman, 1995), especially during the warmer months of the summer (outside of the time frame of this study). We found that the range of diurnal body temperatures in the field was substantial (nearly 10 °C). We also found that high performance was maintained across a broad range of temperatures (performance breadth of over 20 °C), and only performance at the highest and lowest temperatures was detectably diminished. Because centipedes may not be able to regulate temperature precisely and might experience suboptimal temperatures at night, selection should favor high performance over a broad range of temperatures. Studies have demonstrated that differences in biophysical characteristics of habitats can exert selection that can shape the evolution of physiological traits (Kingsolver and Gomulkiewicz, 2003; Logan et al., 2014; Cox and Cox, 2015; Gilbert and Miles, 2017), provided that the traits under selection are heritable (Gilchrist, 1996; Logan et al., 2018, 2020; Martins et al., 2019). Hence, the maintenance of high performance of sprint speed over a 20 °C range of temperatures could be an adaptation to the interplay between rapid thermal equilibration and heterogeneity in environmental temperature.

Because of the disproportionate risk of overheating relative to overcooling (thermal performance curves are left-skewed), ectotherms are expected to maintain body temperatures that are below the optimal temperature for performance. Indeed, many organisms actually maintain body temperatures below T_{opt} (Martin and Huey, 2008) despite the environmental temperatures and thermoregulatory ability to reach optimal temperatures. Likewise, we found that centipedes maintain body temperatures in the field that are more than 9 °C lower than T_{opt} , despite the fact that 20% and 24% of daily temperatures exceeded T_b on the ground surface and under bark, suggesting at least some opportunity to maintain higher body temperatures. We found that bark centipedes experience an extremely sharp decline in performance above 35 °C, which is perilously close to their T_{opt} of 33.7 °C. Moreover, centipedes seek to escape temperatures that are actually slightly below T_{opt} ($T_{opt} = 33.7$ °C, $VT_{max} = 33.47$ °C), suggesting that they actively avoid high temperatures that, despite providing higher performance, would increase their risk of injury from overheating. Although the centipedes used for performance and tolerance trials were collected over a several

month period, it is interesting to note that there was relatively low variation in thermal tolerance or sprint speed at a given temperature. Because the thermal performance breadth of centipedes is so broad, they can thermoregulate to body temperatures that are well below T_{opt} with only a minimal cost to performance. It is also possible that the thermal optima for other physiological processes (e.g., digestion) is lower than that for locomotor performance, and that bark centipedes are thermoregulating to achieve those alternative optima (Angilletta Jr, 2009). For organisms like centipedes that rapidly equilibrate to environmental temperatures, maintaining T_b well below the upper thermal limits may minimize the risk of damage and fitness lost from high environmental temperatures.

Our results also have implications for understanding how the scale of spatial heterogeneity in temperature will influence organisms differently based upon their body size and shape. Spatial heterogeneity is usually thought to favor narrow body temperature distributions and narrow thermal performance curves because spatial variation in temperature is a prerequisite for behavioral thermoregulation (Logan et al., 2013; Sears and Angilletta Jr, 2015; Sears et al., 2016). However, organisms with low thermal inertia (e.g., small or elongate organisms) might equilibrate to environmental temperatures so rapidly that any spatial variation generates correspondingly substantial variation in body temperature. For example, such an organism might move into a sun-exposed warm area and instantly equilibrate to a high temperature before moving into the shade and rapidly equilibrating to a cool temperature, thereby generating high variation in body temperature. The crucial relationship determining the shape of thermal performance curves is likely the grain size of environmental temperature distributions relative to organismal thermal inertia. Mismatches between the scale of spatial heterogeneity in temperature and thermal inertia should lead to different thermoregulatory strategies. For example, organisms with high thermal inertia that experience habitats with fine-grained spatial heterogeneity in temperature would be likely to exhibit mass homeothermy or gigantothermy (Stevenson, 1985; Paladino et al., 1990). On the other hand, organisms with low thermal inertia should evolve thermal generalization (wide thermal performance breadth; this study) even when thermal patch size is relatively fine-grained. The evolution of accurate behavioral thermoregulation is only likely to occur when there is a match between body size and the spatial scale of thermal heterogeneity.

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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.2020.102755>.

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