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Physiological Ecology

Thermal profiles of *Cicindelidia haemorrhagica* (Coleoptera: Cicindelidae) activity in hot springs in Yellowstone National Park

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The wetsalts tiger beetle, *Cicindelidia haemorrhagica* (LeConte) (Coleoptera: Cicindelidae), is found in several active thermal hot spring areas in Yellowstone National Park (YNP) where substrate surface temperatures can exceed 50 °C. However, relationships between surface temperatures and the time adults spend on them remain poorly understood. Therefore, we characterized thermal profiles of Dragon Spring and Rabbit Creek, 2 thermally active research sites containing *C. haemorrhagica* in YNP, to quantify the time adults spend at different surface temperatures. We took 58 thermal video recordings of adults over 6 total days of observation ranging from 10 to 15 min for each adult. Thermal video analysis results indicated a positive relationship between the total time adult beetles spent on surface temperatures from Dragon Spring and Rabbit Creek as temperatures increased from 20 °C. Once surface temperatures exceeded 40 °C, the total time spent at those surface temperatures declined. Adults were recorded on substrates exceeding 50 °C at one of the 2 research locations. Rabbit Creek had substantially more instances of adults present with surface temperatures exceeding 40 °C, including one individual on a surface temperature of 61.5 °C. There were 3 instances of beetles spending more than 4 min at a particular surface temperature, all within the preferred range of 30–40 °C. Our thermal profile results and previous behavioral observations suggest that adults may be resistant to the heat produced from the thermal waters that influence the substrate temperatures but may not be subject to high surface temperatures as previously reported.

Key words: Cicindelidae, rocky mountain, extremophile, thermophile, temperature tolerance

Introduction

The wetsalts tiger beetle, *Cicindelidia haemorrhagica* (LeConte), has been observed actively hunting and scavenging in the hot springs of Yellowstone National Park (YNP) for more than 100 years (Hubbard 1891, Bertholf 1979). Although Hubbard (1891) noted that the environments these beetles inhabited likely exceeded the upper thermal limits for most known insect species, his paper was only an ecological survey for species identification within YNP and he did not study their thermal tolerances.

Outside of YNP, *C. haemorrhagica* is rarely found in environments other than saline flats and sandy, wet substrate. However, in YNP this species thrives in environments with thermal waters, high concentrations of heavy metals, and alkaline or acidic pH that most vertebrates and invertebrates in YNP actively avoid (Inskeep and McDermott 2005, Boyd et al. 2009, Fouke 2011). *Cicindelidia haemorrhagica* is only found associated with thermal areas in YNP (Willemssens 2019, Peterson 2022, Willemssens et al. 2023).

As ectotherms, insects often behaviorally thermoregulate to adjust their internal body temperatures. Tiger beetles, including species in environments like those of *C. haemorrhagica*, behaviorally thermoregulate in warm conditions by stilting, shading, and dipping their abdomens in water to evaporatively cool themselves (Dreisig

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1981, 1990, Morgan 1985, Pearson and Lederhouse 1987, Knisley et al. 1990, Brosius and Higley 2013, Willemssens 2019, Willemssens et al. 2023).

Willemssens (2019), Adams et al. (2024), and Willemssens et al. (2023) studied several aspects of the ecology of adult *C. haemorrhagica* in YNP. Adults were observed for several minutes on shallow water and soil surfaces where temperatures exceeded 50 °C. In addition, adults seemed to engage infrequently in cooling behaviors on the hot surfaces. Willemssens (2019) also compared behaviors between YNP *C. haemorrhagica* and a population of the same species at an Idaho salt flat without hot springs. She observed that YNP populations behaved differently than the Idaho population. This was especially apparent with thermoregulatory behavior. The YNP beetles spent significantly more time warming and significantly less time cooling than the Idaho beetles. Specifically, there were lower frequencies of shading, posture adjustment (i.e., stilting), and abdomen dipping in water for evaporative cooling (Willemssens 2019) for the YNP beetles.

Although Willemssens (2019) observed *C. haemorrhagica* on heated substrates, the accuracy of her surface-temperature measurements was limited by the available equipment. She used readings from an infrared (IR) gun during or immediately after behavioral observations. Consequently, our objective in this study was to characterize more accurate and precise thermal profiles and timespans that individual adult *C. haemorrhagica* spends at different surface temperatures using thermal videography and direct temperature measurement.

Materials and Methods

Site Description

Dragon Spring is a relatively well-studied acid-sulfate-chloride spring located in the Norris Geyser Basin that has high levels of As (III) and $MeHg^{+}$ levels in the source waters and contains Hydrogenobaculum and thermophilic chemolithotroph species (D'Imperio et al. 2007, Boyd et al. 2009, Fouke 2011, Inskeep 2013). Between the numerous highly active thermal water sources for this spring is a peninsula primarily comprised of sulfate and calcium-based sediment that has been the primary research site for *C. haemorrhagica* since ecological research began in 2017 (Willemssens 2019, Willemssens et al. 2023, Adams et al. 2024). Here the beetles actively burrow, hunt, scavenge, mate, and oviposit while being continuously surrounded by thermal waters that directly influence surface temperatures. Dragon Spring has an average measured pH of approximately 2.88 and running water with sufficiently low temperatures in some areas to allow for the development of acid-loving *Zygogonium* spp. mats that can accommodate stratiomyid and ephydrid populations (D'Imperio et al. 2007, Boyd et al. 2009, Willemssens 2019, Willemssens et al. 2023, Adams et al. 2024). The fly larvae that reside in these mats also provide a reliable food source for *C. haemorrhagica* adults in the summer months. In addition to these fly populations, the tiger beetles at Dragon Spring also feed on a variety of small insects, including shore bugs and ephydrid adults, but will also scavenge and feed on anything that falls into the shallow thermal waters. Most water sources cool sufficiently within a few meters from the source to allow the growth of bacterial and archaea microbial communities, which produce a mat color that is indicative of water temperature and in some cases, pH (Inskeep and McDermott 2005). This mat color further indicates that a variety of temperatures may be experienced by insects, both convectively and conductively when traversing the terrain directly adjacent to the variable temperature thermal waters.

Rabbit Creek is the other hydrothermally active field research site we selected. Unlike Dragon Spring, this thermal area contains multiple alkaline water sources located in the Midway Geyser Basin. This field research site has an average pH of 9.2. Because this area is a constantly flowing water source that moves from east to west, it produces a wide range of water temperatures that in turn accommodate several different communities with Acidobacteria and Cyanobacterial mats (Weltzer and Miller 2013). Rabbit Creek is the larger of the 2 sites and contains a steep thermal gradient throughout the waterway, with estimated changes in water temperature of up to 7.5 °C for every 100 m of continuous waterway. The Cyanobacterial mats present in the waterways directly adjacent to thermal water injections stimulate the growth and development of numerous microbial and arthropod species, including thermophilic ephydrids. These ephydrid populations serve as a primary food source for *C. haemorrhagica* at Rabbit Creek.

Thermal Video

Previous infrared thermography studies conducted on insects established protocols for analyzing thermally induced stress in insects and are typically used when recording lower thermal limits (Palmer et al. 2004, Gallego et al. 2016). We recorded thermal video at each of the 2 YNP sites 15–21 July 2020. Recordings were taken using a FLIR T1020 thermal camcorder (FLIR, Wilsonville, OR, USA) with a stock 28° lens while mounted on a carbon fiber tripod (Swarovski, Cranston, RI, USA). Video files were stored on two 32GB SDHC memory cards.

Recordings occurred over 3 days at each research site. Each recording focused on one beetle at a time to capture its interaction with its environment (Fig. 1). The primary observer with the FLIR recorded from a minimum distance of 5 m from any observed beetle to avoid influencing its behavior during the observation period (Fig. 2). The number of individuals observed per recording varied because there were individuals that flew or ran away and were lost by the primary observer. Beetle thermal recordings were taken twice per hour from 10:00 to 15:00 for a 10- to 15-min period of observation for each beetle. A total of 28 beetles were observed from Dragon Spring and 30 beetles from Rabbit Creek over the 3-day period at each research site. After each day in the field, stored recordings were transferred to a BarraCuda 1TB solid state storage drive (Seagate, Cupertino, CA, USA) and the files on the memory cards were erased after each trip to the field to make room for the proceeding day of recording.

Data Analysis

Recordings were analyzed using the FLIR Video Analysis software provided with the T1020 camcorder. Video files were analyzed frame-by-frame using the point temperature-reading tool in the software to follow the individual throughout the entirety of the observation period. Surface temperature values directly below the beetle, with an accompanying timestamp from the video files, were recorded in an Excel spreadsheet each time the beetle moved to a new area with different surface temperatures. The point directly below the beetle gave us the most accurate temperature unobstructed by any solar reflection (Fig. 1). Excel spreadsheets were analyzed to obtain the total time spent at any given temperature throughout the video file using duplicate temperature values and the timestamps that provided aggregate temperature data.

An Excel Masterfile was then transferred to RStudio version 4.0.2 for further analysis (RStudio Team 2021). Once the data were condensed into a single data set that could be analyzed using RStudio,

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diagnostic visualizations of the data assessing statistical assumptions of normality and residual equal variance were performed to determine the shape of the data and assess the presence of influential points using Cook's distance. Any observation with a Cook's distance >0.5 was considered an influential point to the data set and would have been removed from the analysis to aid in creating a more accurate predictive model of beetle presence at any given temperature throughout the day. However, no observations surpassed this value, so all data points were included in the analysis. The data were initially separated and analyzed by research site before determining the possibility of a day effect.

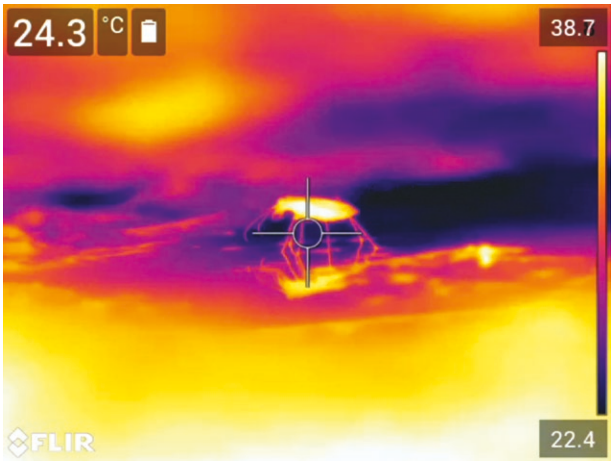

Fig. 1. A still image from the thermal video recording. The reflection of the beetle on the substrate is the more accurate surface temperature of the substrate not influenced by solar reflection and was the target area for measurement when analyzing the temperature-time relationship data in the recordings. Video still by JL Bowley.

Fig. 2. Thermal recording equipment on-site at Dragon Spring. The thermocouple reader/recorder can be seen in the background recording substrate and water temperatures while adult *Cicindelidia haemorrhagica* traverse the area. Photo by JL Bowley.

Using RStudio with the ggplot, lmer, ggthemes, and sjPlot packages, we produced data visualizations of each day of observational data, compiled data from each site, temperature regression curves from each site to characterize a relationship between temperature and time for an average summer day in July and compared temperature measurement figures to determine the accuracy of the FLIR camcorder.

To accompany these data, we recorded surface soil and water temperatures using an SD-947 4-channel thermometer/SD card data logger (REED, Wilmington, NC, USA). These temperature data were used as a standard for comparison with the thermal video to gauge the accuracy of the temperatures recorded with the FLIR camcorder. Two of the 4 thermocouples were placed on the water's surface near the most beetle-rich area at each field research site. The remaining 2 were placed on the soil's surface near the water's edge. The logger was set to record 4 temperatures, one from each thermocouple, every 5 min from 10:00 to 15:00 for 2 of the 3 days at both Rabbit Creek and Dragon Spring. Additional temperature recordings were also taken with an IR gun (Fluke, Everett, WA, USA) in a grid pattern across both research sites every other hour to obtain temperature readings from a third source. These measurements were used to produce a regression curve for the temperature at the warmest time of day at each site while exposed to direct sunlight in the thermal environment.

Results

Compiling the individual observations using time stamps with accompanying temperatures resulted in the total time spent at each surface temperature for each of the 3 days of observation at each research site. There were 3,414 observations of temperature total time change instances recorded across the 58 total beetle thermal recordings (Table 1). We found that *C. haemorrhagica* spent an average of 1.41 min at a mean surface temperature value of 36.4 °C. The mean value differed between research sites ($P < 0.001$). Beetles spent a mean of 1.45 min at a mean surface temperature of 38.9 °C at Rabbit Creek compared to 1.38 min at 33.1 °C at Dragon Spring (Table 1).

Table 1. Summary statistics of the linear model describing temperature with respect to the research location and day of observation. Predicted values are provided using day one of observation at Dragon Spring as the base intercept for the linear model. *P*-values for each day and site are presented in addition to 95% CI for each predicted value of the model with an R^2 value of 0.5

	Temperature (°C)		
Predictors	Estimates	95% CI	*P*
Dragon Spring, Day 1 (Intercept)	30.61	30.33–30.88	<0.001
Day 2	2.32	1.98–2.66	<0.001
Day 3	3.39	3.07–3.71	<0.001
Site [Rabbit Creek]	7.88	7.60–8.15	<0.001
Total Observations	3,414		
R^2/R^2 adjusted	0.505/0.504		

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There were a few instances where beetles at Rabbit Creek were on surfaces exceeding 50 °C. The maximum surface temperature on which an adult beetle resided was 61.2 °C for 1.5 s (Figs. 3 and 4). The greatest amount of time an adult spent at a temperature greater than 50 °C was 28.2 s at 55.1 °C (Figs. 3 and 4). This single observation was the second-highest surface temperature recorded. In addition, there were 2 observations at 53.1 °C for a cumulative time of 28.1 s, a single observation at 51.7 °C for 17.6 s, and a single observation at 50.9 °C for 12 s (Figs. 3 and 4). All observations of adults on surfaces exceeding 50 °C were from Rabbit Creek. Beetles at Dragon Spring spent a maximum cumulative time of 7.43 min at 32.9 °C. Individuals at Rabbit Creek spent a maximum cumulative time of 6.32 min at 32.6 °C.

Dragon Spring surface temperatures below the beetles were, on average, lower than those of Rabbit Creek based on the FLIR camcorder measurements (Figs. 3 and 4). Variance in temperature data collected throughout each observational period may have been due to cloud cover, soil saturation, and camera angle throughout the recording. There is considerable overlap in the data, suggesting there may be no statistical difference between the 2 sites. However, our linear model using temperature as a dependent variable for day of observation and research site suggests that there was a substantial statistical difference between research site within YNP ($P < 0.001$).

A polynomial regression curve was fit to the data for each research location to describe the relationship between total time spent and surface temperature (Fig. 5). The temperature-total time relationship

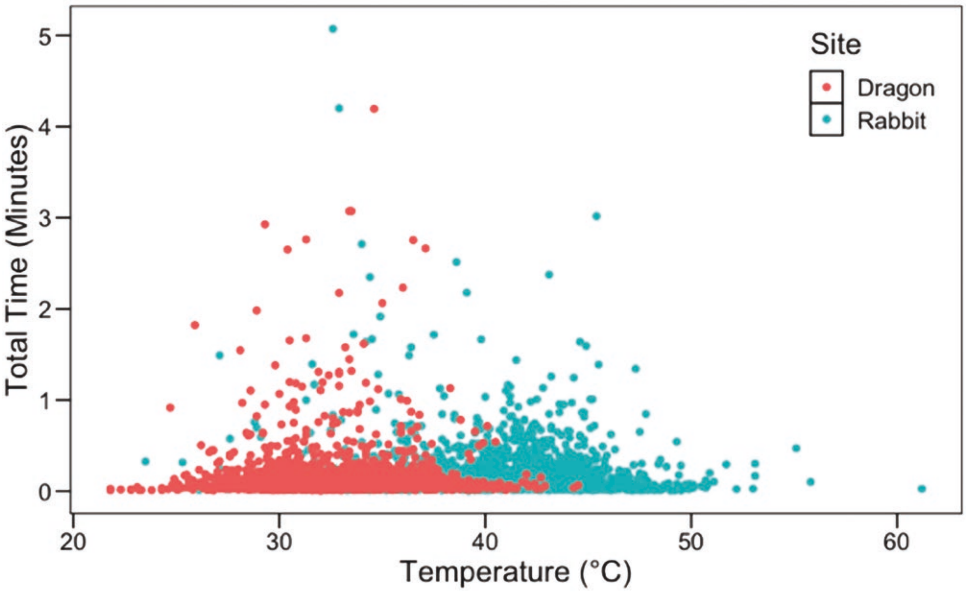

Fig. 3. Surface temperatures for each research site. Each point represents the time spent by one adult *Cicindelidia haemorrhagica* at a specific surface temperature.

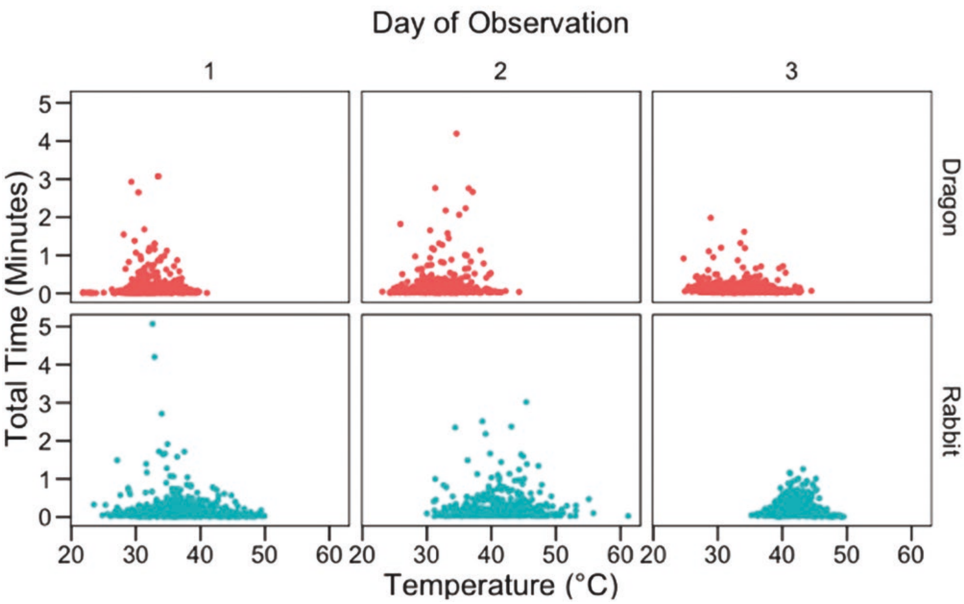

Fig. 4. Surface temperatures for each day of recording from Dragon Spring and Rabbit Creek. Each point represents the time spent by one adult *Cicindelidia haemorrhagica* at a specific surface temperature.

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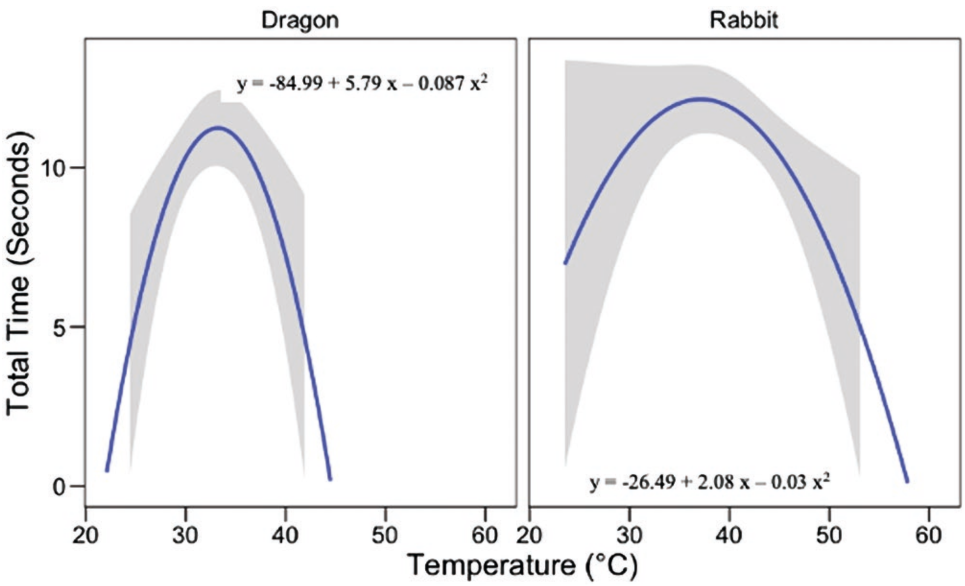

Fig. 5. Regressions of the relationship between substrate surface temperature from each research site and the time adult *Cicindelidia haemorrhagica* spent at those temperatures. The line is the fitted values using the total time averages from each research site. The gray shaded area represents the 95% CI for the average value.

regression curves for both research locations contain the estimated values with a 95% confidence interval for the true mean value for total time spent at the 20–60 °C temperature range. The apex of the relationship curve at approximately 38 °C at Rabbit Creek indicated a larger amount of time spent at higher temperatures than at apex of approximately 32 °C at Dragon Spring (Fig. 5).

The majority of the FLIR data were like the temperature measurements we observed with the thermocouples (Fig. 6). Any differences were likely because the beetles were seeking out warmer surfaces, whereas the thermocouples were measuring background surface temperatures.

Discussion

Cicindelidia haemorrhagica adults spend a considerable amount of time on surfaces with increased surface temperatures in YNP relative to the environments where this species is typically found. Moreover, they spend much of their adult lives (4–8 wk) on these relatively high-temperature surfaces, seemingly without the need to behaviorally cool and therefore seem different from many other insects. Previous research suggested that YNP beetles are on surfaces exceeding 50 °C (Willemssens 2019). Our results reveal that beetles are on surfaces that exceed these temperatures, but they do not remain on these surfaces for long periods.

There are many tiger beetle species that survive in thermally extreme environments, but they typically prefer cooler areas where food items are more likely to be present (Pearson and Lederhouse 1987, Brosius and Higley 2013). These species primarily remain in areas between 30 °C and 40 °C, where they are more likely to mate and hunt without the risk of overheating (Dreisig 1979, 1981, Pearson and Lederhouse 1987). Therefore, we would expect *C. haemorrhagica* populations outside of YNP and other warm-adapted tiger beetle species to behaviorally thermoregulate by constantly shifting microhabitats, stilting, and basking to regulate their internal body temperatures in YNP conditions (Dreisig 1979, 1981, Pearson and Lederhouse 1987, Schultz and Hadley 1987, Brosius and Higley 2013).

These thermoregulatory behaviors in extreme conditions are not limited to tiger beetles. The Saharan silver ant, *Cataglyphis bombycina* (Hymenoptera: Formicidae), is currently the most heat-tolerant insect known. Workers of this species are on desert substrates that exceed 60 °C (Shi et al. 2015). However, when on these surfaces, workers behaviorally thermoregulate by stilting, basking, and climbing vegetation to avoid high surface temperatures. Body orientation and scaling vegetation are also important behaviors for thermoregulation in species such as *Melanoplus sanguinipes* (Orthoptera: Acrididae), which prefers temperature ranges between 37.4 °C and 40.5 °C and must behaviorally thermoregulate throughout the day to remain in this preferred temperate zone (O'Neill and Rolston 2007). Other beetle species continuously move with shaded areas throughout the day to reduce their direct exposure to the sun (Alves et al. 2018).

Much like *C. bombycina*, we predict that YNP *C. haemorrhagica* can resist high surface temperatures for extended periods. However, unlike *C. bombycina*, which possess lightly colored triangular setae that provide increased reflectance from the sun and black-body radiation from the sand on which it forages (Shi et al. 2015), we do not yet know the precise mechanism for *C. haemorrhagica* (Bowley 2021).

Because *C. haemorrhagica* spend little time behaviorally cooling themselves compared to another population of the same species in Idaho, there is likely some mechanism that is responsible for resistance to bottom-up heating from the geothermally heated surfaces. Willemssens (2019) showed that YNP *C. haemorrhagica* adults might have a slightly greater critical thermal limit than the adults of the Idaho population, but the explanation seems to be more physical than physiological. Exoskeletal structures may influence internal body temperatures, but isolating and identifying the mechanism responsible can be difficult (Amore et al. 2017). The mechanism might be a physical structure like that of *Rosalia alpina* (Coleoptera: Cerambycidae), which uses pyramid-shaped microstructures on its elytra to improve its radiative heat exchange with its environment (Pavlović et al. 2018). The mechanism may also contain multiple structures that work together to produce improved thermal tolerance or resistance, or both.

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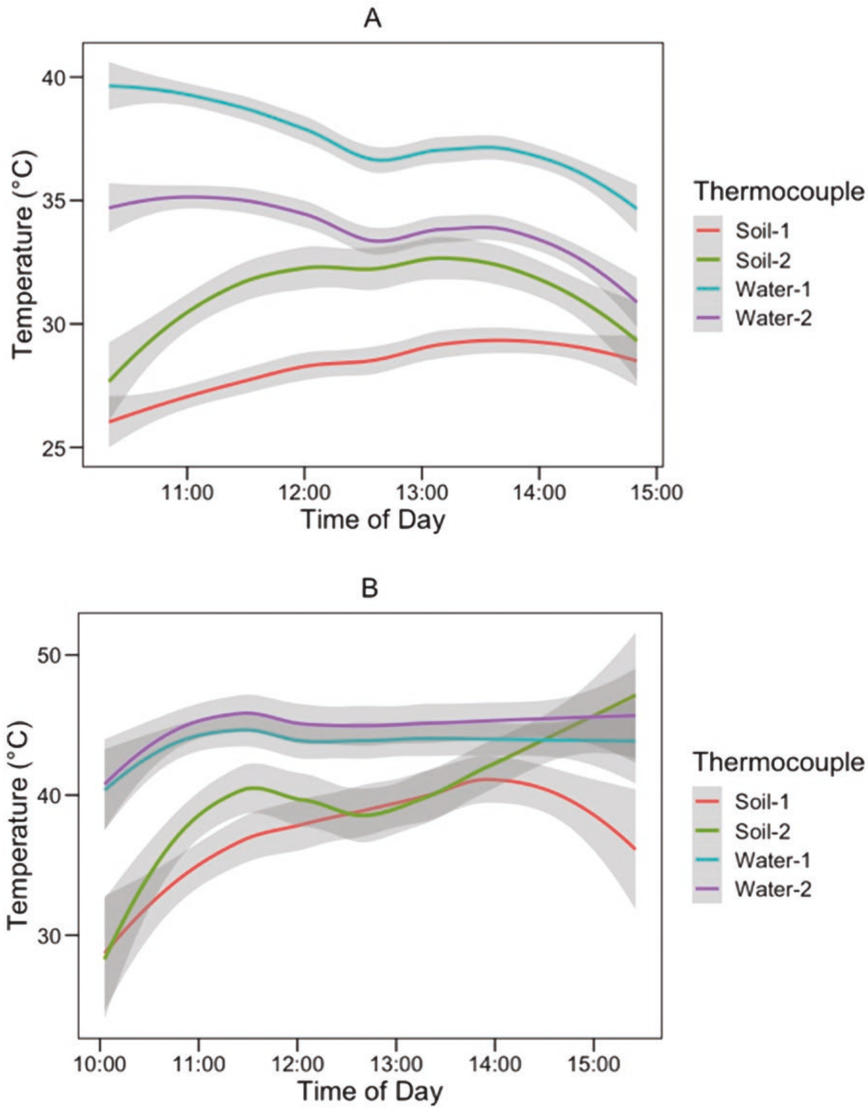

Fig. 6. A) Average temperatures during periods of observation at Dragon Spring recorded by thermocouples. B) Average temperatures during periods of observation at Rabbit Creek recorded by thermocouples.

For instance, *Neocerambyx gigas* (Coleoptera: Cerambycidae), possess reflective micro setae with corrugated facets on one side. Cross-sectional analysis of these setae revealed that the corrugated facets work with the 3-dimensional pyramidal shape of the setae to provide total internal reflection along the elytra, lowering the overall internal temperature of the beetle (Zhang et al. 2020). Structures working together to reduce temperature increases are also found in the multiple hollow cylindrical structures found on the elytra of *Goliathus goliatus* (Xie et al. 2019).

However, the structure of *C. haemorrhagica* in YNP is more likely to be present on the venter as opposed to the dorsal face of the beetle (Bowley 2021). *Cicindelidia haemorrhagica* experiences much of its environmental heat from conductively heated surfaces as opposed to the direct heat from the sun experienced by *N. gigas* and *G. goliatus*. Bowley (2021) demonstrated that the mechanism is most likely associated with the physical structure of the abdominal ventrites and is not directly associated with the cuticular wax structure or composition. This suggests the mechanism may lie within the structural layering of the cuticle in *C. haemorrhagica*, which has been known to play a role in heat transfer with other tiger beetle species (Schultz and Hadley 1987, Seago et al. 2009). However, to date, more refined structural explanations have not been elucidated.

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Data availability

Video and temperature data are available upon request to the corresponding author.

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