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Hydric effects on thermal tolerances influence climate vulnerability in a high-latitude beetle

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Abstract

Species' thermal tolerances are used to estimate climate vulnerability, but few studies consider the role of the hydric environment in shaping thermal tolerances. As environments become hotter and drier, organisms often respond by limiting water loss to lower the risk of desiccation; however, reducing water loss may produce trade-offs that lower thermal tolerances if respiration becomes inhibited. Here, we measured the sensitivity of water loss rate and critical thermal maximum (CT_{max}) to precipitation in nature and laboratory experiments that exposed click beetles (Coleoptera: Elateridae) to acute- and long-term humidity treatments. We also took advantage of their unique clicking behavior to characterize subcritical thermal tolerances. We found higher water loss rates in the dry acclimation treatment compared to the humid, and water loss rates were 3.2-fold higher for individuals that had experienced a recent precipitation event compared to individuals that had not. Acute humidity treatments did not affect CT_{max}, but precipitation indirectly affected CT_{max} through its effect on water loss rates. Contrary to our prediction, we found that CT_{max} was negatively associated with water loss rate, such that individuals with high water loss rate exhibited a lower CT_{max}. We then incorporated the observed variation of CT_{max} into a mechanistic niche model that coupled leaf and click beetle temperatures to predict climate vulnerability. The simulations indicated that indices of climate vulnerability can be sensitive to the effects of water loss physiology on thermal tolerances; moreover, exposure to temperatures above subcritical thermal thresholds is expected to increase by as much as 3.3-fold under future warming scenarios. The correlation between water loss rate and CT_{max} identifies the need to study thermal tolerances from a "whole-organism" perspective that considers relationships between physiological traits, and the population-level variation in CT_{max} driven by water loss rate complicates using this metric as a straightforward proxy of climate vulnerability.

KEYWORDS
climate change, climate vulnerability, mechanistic niche model, precipitation, thermal tolerance, water loss rates

1 | INTRODUCTION

Rapid climate change coupled with species declines have motivated the development of several metrics of vulnerability to environmental change with the goal of identifying which species are likely to persist or decline (Somero, 2010; Stillman, 2003). Thermal tolerances are one of the most common metrics used to assess vulnerability to environmental change across a variety of terrestrial and aquatic ectotherms (Deutsch et al., 2008; Pinsky et al., 2019; Sunday et al., 2011, 2019). These indices are often determined by heating or cooling an organism until a behavioral threshold is observed (such as spasms or the loss of a righting response in the case of the critical thermal maximum [CT_{max}]) or if the metric is lethal, when a proportion of individuals experience mortality from extreme temperatures (Huey et al., 1992; Lutterschmidt & Hutchison, 1997). CT_{max} is one of the most common nonlethal indices and has provided insight into the relative vulnerability of marine and terrestrial species to climate warming, the mechanisms underlying macroecological patterns, and geographic range shifts (Gunderson & Stillman, 2015; Pinsky et al., 2019; Sunday et al., 2019, 2012). Due to the importance of CT_{max}, many studies have sought to understand the causes and consequences of variation in CT_{max} either at the individual or genotypic level (i.e., phenotypic plasticity) or at the population level (Cicchino et al., 2023; Gunderson & Stillman, 2015; Healy et al., 2019). While methodological approaches such as ramping rates and duration of temperature exposure are known to generate variation in CT_{max} (Sunday et al., 2019; Terblanche et al., 2007), few studies have assessed the sensitivity of CT_{max} to other linked physiological traits (Bujan et al., 2016; Johnson & Stahlschmidt, 2020).

Understanding the mechanisms that shape organismal performance often requires an integrated, whole-organism perspective due to interactions between underlying physiological processes (Pörtner, 2010; Pörtner et al., 2006). For instance, upper critical thermal limits may be shaped by the oxygen demands of an organism exceeding their capacity to deliver oxygen at extreme temperatures (Pörtner, 2001). Most of the evidence supporting oxygen limitation comes from aquatic species (Pörtner & Farrell, 2008; Sommer et al., 1997; Zielinski & Pörtner, 1996); while, experiments in terrestrial species have found mixed support for the oxygen limitation hypothesis (Boardman & Terblanche, 2015; Klok et al., 2004; Stevens et al., 2010). Thus, oxygen limitation is likely not a unifying principle underlying thermal tolerances (Verberk et al., 2016). Alternatively, upper critical limits may be more related to the disruption of protein function, ion homeostasis, and membrane integrity in response to high temperatures (Schulte, 2015). Variation in upper critical limits has also been attributed to variation in diet (Bujan & Kaspari, 2017) and exposure to seasonal variation in photoperiod (Healy & Schulte, 2012). Together, these studies emphasize the importance of a more holistic, "whole organism" perspective on traits that might influence upper critical limits. This is particularly true for traits that directly influence thermal performance, like water loss physiology.

Maintaining water balance is critical for whole organism performance and fitness-related activities, like foraging (Anderson & Andrade, 2017; Chaplin, 2006; Lighton et al., 1994). Yet, water loss is required for respiration in terrestrial taxa because oxygen must dissolve into an aqueous solution before diffusing across a respiratory surface (Maina, 2002). As a consequence, organisms must lose water in order to breathe in oxygen. Due to this fundamental linkage, water loss rates and gas exchange are closely associated across a wide variety of terrestrial taxa, including insects (Woods & Smith, 2010). In insects, water loss occurs across the cuticle and when spiracles (i.e., the regulatory valves separating the trachea and air) are open for gas exchange (Quinlan & Gibbs, 2006). The lipid composition of the cuticle or waxy secretions on the cuticle as well as spiracular regulation have the potential to contribute to total evaporative water loss rates (Benoit, 2010; Chown et al., 2011; Gibbs, 1998). In response to dry conditions, many arthropods have the capacity to reduce water loss rates (Baumgart et al., 2022; Elnitsky et al., 2008; Fischer & Kirste, 2018; Holmstrup et al., 2002; Terblanche et al., 2006), and spiracular regulation appears to play a clear role in limiting water loss and balancing water budgets (Chown & Davis, 2003; Edney, 2012; Quinlan & Gibbs, 2006). Moreover, humidifying anoxic air ameliorates reductions in CT_{max} caused by dry anoxic air, suggesting the need to balance water budgets contributes to thermal tolerances and is potentially shaped by oxygen limitations (Boardman & Terblanche, 2015). By limiting spiracular water loss in response to dry conditions or dehydration, insects might also impede their ability to acquire oxygen, lowering CT_{max}. Thus, understanding how insects respond to humidity or water availability can reveal critical insights into mechanisms driving variation in thermal tolerances.

Here, we conducted a laboratory experiment on click beetles (Coleoptera: Elateridae) to evaluate the relationship between water loss physiology and thermal tolerances and then used these results to inform a mechanistic niche model. Click beetles are geographically widespread and named for their remarkable ability to perform a bending maneuver to produce an ultrafast click, causing the individual to rapidly accelerate from the surface to right themselves, move, or escape from predators (Bolmin et al., 2021). In addition, the larvae of click beetles (called wireworms) are also well known as agricultural pests, causing extensive crop damage globally (Traugott et al., 2015). Therefore, further understanding of click beetle physiology will facilitate physiological discovery of thermal tolerances in general, but also potentially help understand the physiological responses of a global pest to environmental change. We collected click beetles from the field near Oulu, Finland (Figure 1) and conducted a laboratory experiment that evaluated the effect of short (acute) and longer term (24 h) exposure to different humidity treatments and recent exposure to precipitation in the field on CT_{max}. We also studied subcritical thermal tolerances (stT_{max}) because animals experience the negative effects of temperature far before critical limits (Sunday et al., 2014). Thus, stT_{max} can provide a more relevant metric of vulnerability

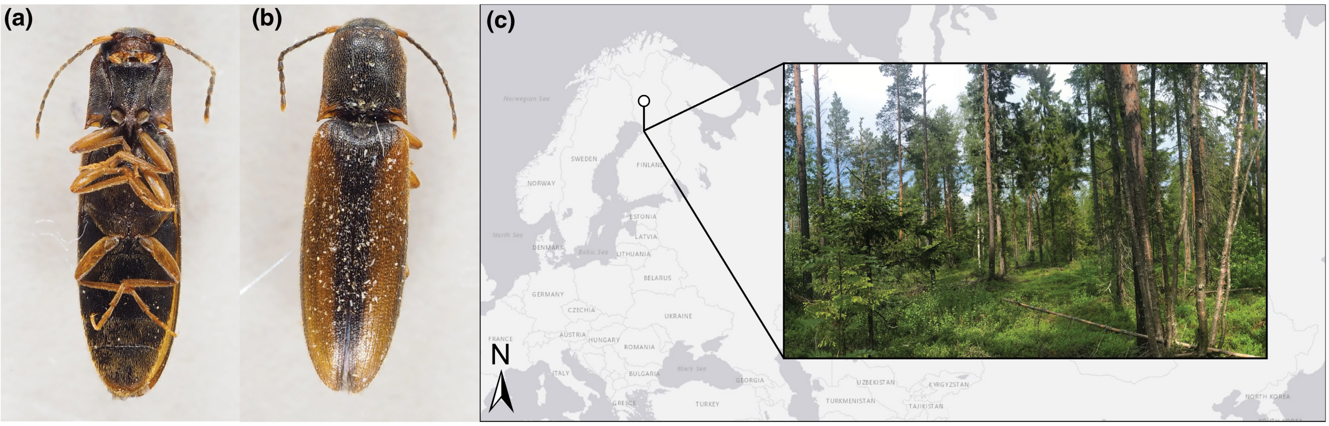

FIGURE 1 (a) Ventral and (b) dorsal detail photographs of the most abundant click beetle species in our study (*Athous subfuscus*). (c) A map of Europe with our study location (Oulu, Finland) with an inset image of a typical habitat in which we captured click beetles.

to environmental change (Braschler et al., 2021). We specifically measured the thermal sensitivity of the beetles clicking behavior as a proxy for subcritical thermal tolerances. We hypothesized that individuals exposed to desiccating conditions and more dehydrated individuals would exhibit a lower thermal tolerance due to efforts to reduce water loss rates (and thus oxygen delivery) via spiracular regulation. In other words, we expected a positive correlation between water loss rates and CT_{max}. Finally, to predict the impact of climate change on click beetle performance under future warming scenarios, we integrated click beetle thermal tolerances into a mechanistic niche model that links plant biophysical and physiological properties with insect heat flux. The model allows us to predict warming scenarios will impact activity and exposure to temperatures above physiological tolerances.

2 | MATERIALS AND METHODS

2.1 | Field sampling

We surveyed for Elateridae in the understory of mixed hardwood forests consisting of birch (*Betula* spp.), mountain-ash (*Sorbus* spp.), and conifers near Oulu, Finland, in early June of 2019. We primarily sampled birch saplings using the beating net method, which consisted of lightly shaking or tapping the sapling with the beating tray held underneath the branches to collect falling insects. We collected Elaterid beetles at two sites between 09:00 and 11:00 in the morning, and for each site, we sampled immediately after rain (less than 1 h since rain) and after several days since rain (at least 4 days). We collected 70 individuals, which included *Athous subfuscus* (87.1%), *Dalopius marginatus* (11.4%), *Sericus brunneus* (2.9%), and *Ampedus nigrinus* (2.9%). The click beetles were placed in collection tubes and immediately returned to the laboratory at the University of Oulu. We determined ecological relevance of laboratory conditions by measuring field temperature and humidity prior to beginning of the experiments. Conditions were recorded using the EL-USB-2-LCD+ (Measurement Computing™) placed roughly 1.5 m from the ground in deeply shaded habitat to limit any influence of radiation.

2.2 | Laboratory acclimation and water loss

In the laboratory, we recorded baseline mass for each beetle after returning from the field and randomly assigned individuals to an overnight acclimation treatment. The mass of each individual was recorded to the nearest 0.1 mg, and we ensured that individuals were healthy by ensuring they responded to stimulus prior to treatment assignment. For a few individuals, we recorded multiple measurements of mass on the same individual for estimates of repeatability, which were within the error of our scale (±0.1 mg). We then assigned individuals to overnight acclimation treatments using a custom sorting program written in Python. We attempted to generate a randomized, fully balanced experimental design; however, the different species were not evenly dispersed across treatments. We programmed two environmental chambers to regulate humidity at 30% and 50% relative humidity under the same temperature cycle (range 15–21°C). These temperatures and hydric conditions are conditions that beetles regularly experience during this time of year (Figure S1). After recording the mass and time of measurement (to the nearest minute), we placed the beetles in individually labelled containers (diameter = 5 cm, height = 3 cm) in their respective acclimation treatments. Each container contained dozens of holes which allowed the circulation of ambient conditions into each container.

After the overnight acclimation exposure, we recorded the mass of each individual and the time of measurement. We used these measurements to estimate water loss rates gravimetrically, assuming that the mass lost was primarily due to evaporative water loss. This assumption is likely true because the frass were exceedingly small (less than the error of the scale) and individuals generated little frass without access to any food. Thus, water loss likely occurred primarily through respiratory, transcuticular, or urinary pathways. We calculated water loss rate ($mg\,h^{-1}$) by dividing the change in mass during the overnight acclimation period by the total time exposed to the treatment. By doing so, we were also able to account for the variable time in the overnight acclimation treatment (19–27 h). After recording the mass, we immediately performed a thermal tolerance experiment.

2.3 | Thermal tolerance experiments

We measured CT_{max} of Elaterid beetles the day after the overnight acclimation exposure. We used a temperature-controlled water bath with eight glass chambers (volume = 0.29 L) submerged in the bath. The bath was created using an insulated container (Coleman 25 qt Stacker Cooler, 56 × 34 × 21 cm) with an aquarium water heater and two aquarium water pumps that continuously circulated the warming water. Within each chamber, the beetles were individually confined within a suspended petri dish (diameter = 34 mm, height = 10 mm) which were modified with a hardwire cloth base to promote air flow into the petri dish. The petri dish cover was required to prevent the beetles from escaping. During the experiment, the beetles were able to walk across the hardwire cloth base without restricted movement. We continuously monitored the temperature of the eight chambers using a type-T thermocouple (ThermoWorks, PT-6) embedded into the hardwire mesh base and connected to an eight-channel thermocouple data logger (Pico Technology; TC-08).

We exposed beetles to one of two acute humidity treatments during the CT_{max} trials. We manipulated the humidity in the petri dishes by placing water (~20 mL) in the bottom of the glass containers. Without water, the humidity in the chamber remained close to 30% during the experiment, whereas in chambers with water, relative humidity increased to 70% during the experiment, both representing ecologically relevant vapor pressures (Figure S1). These treatments (hereby referred to as dry and wet acute treatments) were designed to evaluate acute responses to humidity that might influence thermal tolerance. We used a balanced design across the four different treatments by randomly assigning an acute treatment and acclimation exposure to every individual. Together, the overnight acclimation and acute treatments evaluated the importance of long- and short-term exposure to humidity on thermal tolerances.

We began the thermal tolerance trials by placing beetles in their individual chambers at 20°C (mean ± standard error: 20.5 ± 0.2°C), near the peak temperature of the thermal cycle during the overnight acclimation period. Due to the design of the warming apparatus, we could perform thermal tolerance experiments on eight individuals per trial. We then began to increase the temperature using the aquarium water heater at a rate of 0.5°C per minute. We determined the CT_{max} based on a distinctive loss of locomotor capacity described as disorganized movement and spasms. We identified the CT_{max} by a lack of a righting response after they flipped onto their dorsum and unable to exhibit their characteristic clicking behavior to right themselves. We removed two individuals from the study that experienced mortality during the experiment.

We also recorded a subcritical metric (stT_{max}) of thermal tolerance during the experiment. The observer (C. K. Ghalambor) recorded the number of clicks and the temperature at which a click occurred across all individuals in a given thermal tolerance trial. We recorded these measurements as a proxy of escape behavior to understand subcritical thermal thresholds. A higher frequency of clicks indicates an increase in escape behavior because clicking occurs in an effort to flip onto their ventrum after turning over in an effort to escape the chamber. Based on this behavior, we used the temperature at which an increase in the frequency of clicks was observed to characterize the stT_{max}. After the thermal tolerance trial, we weighed each individual again to record the mass lost during the thermal tolerance trial. Finally, we recorded the dry mass for over half of the individuals ($n = 36$) by drying each individual in a drying oven for 24 h at 65°C. We then used these dry masses to estimate hydration state by (1) calculating the difference between body mass and dry mass to estimate the total water content, and then (2) we divided the water content by the total body mass to express hydration state as the proportion of mass due to water. We conducted this metric for two stages during the experiment (i.e., after capture and prior to the thermal tolerance experiment) and used each in the respective analysis on water loss rates or thermal tolerances, respectively.

2.4 | Mechanistic niche model

We built upon existing biophysical simulations (*Ectoscape*; www.github/com/ecophysiology/Ectoscape) to predict temperatures that click beetles experience under current conditions and future warming scenarios. Our simulations use first principles to calculate operative temperature (T_e) of small insects in realistic forest microhabitats. We calculated operative temperature using:

$$T_e = T_a + \frac{R_{abs} - \varepsilon_s \sigma T_a^4}{c_p \left(g_r + g_{Ha} \right)} \tag{1}$$

where T_a is the air temperature at the height of the animal, R_{abs} is the radiation absorbed, ε_s is the emissivity of the click beetle (0.97), σ is the Stefan–Boltzmann constant ($5.67 \times 10^{-8}\,W m^{-2} K^{-4}$), c_p is the specific heat of air at constant pressure ($29.3\,J mol^{-1} C^{-1}$), g_r is the radiative conductance, and g_{Ha} is boundary layer conductance. To estimate absorptance to short-wave radiation from the sun, we used a solar absorptance of 0.926 based on the solar absorptance of similarly colored beetles (Henwood, 1975). To estimate reflected radiation from the ground, we used albedo measurements from summertime Nordic birch habitat (~0.16) (Ramtvedt et al., 2021). Further explanations of variables can be found in a recently published study that used the same underlying code for a vertebrate ectotherm (Gunderson et al., 2022).

Air temperature is likely not a relevant temperature for insects that spend much of their time on the surface of leaves due to the solar and evaporative dynamics that determine leaf temperatures (Woods et al., 2022). Therefore, we replaced T_a in Equation (1) with an estimate of leaf temperature, which we calculated using humid operative temperature (T_{eh}). We calculated humid operative temperature using:

$$T_{\mathrm{eh}} = T_{\mathrm{a}} + \frac{\gamma^*}{s+\gamma^*}\left(\frac{R_{\mathrm{abs}} - \varepsilon_{\mathrm{s}}\sigma T_{\mathrm{a}}^4}{c_{\mathrm{p}}\left(g_{\mathrm{r}} + g_{\mathrm{Ha}}\right)} - \frac{D}{\gamma^* p_{\mathrm{a}}}\right) \tag{2}$$

where T_{a} is air temperature, s is the slope of saturation mole fraction function, R_{abs} is the absorbed short- and long-wave radiation, γ^* is the apparent psychrometer constant, ε_{s} is the emissivity of a leaf (0.95), sigma is the Stefan–Boltzmann constant, c_{p} is the specific heat of air at constant pressure, g_{Hr} is the sum of boundary layer and radiative conductance, D is the vapor pressure deficit of the air, and p_{a} is the atmospheric air pressure (Campbell & Norman, 1998). The estimate of T_{eh} incorporates dynamics related to evaporating cooling and solar radiation, which are both known to have important effects on leaf surface temperature (Pincebourde et al., 2021). Further explanations of variables can be found in a recently published study that used the same underlying code for an amphibian (Newman et al., 2022). We parameterized our leaf simulations based on the characteristics of birch leaves or similar deciduous leaves. We used a solar absorptance of 0.5 based on the typical range for deciduous leaves (Campbell & Norman, 1998), and for conductance to water vapor, we used a range of values associated with deciduous leaves, either 0.40 $\mathrm{mol\,m^{-2}\,s^{-1}}$ for open stomata or 0.005 for closed (see below for exact use of these values) (Campbell & Norman, 1998). To estimate the boundary layer, we assumed a leaf width of 3.8 cm and assumed a wind speed between 0.1 and 0.25 $\mathrm{m\,s^{-1}}$ due to the buffering impact of the forest on convective conditions on individual leaves (Campbell & Norman, 1998). We provide all code and supporting information for these simulations (called *Ectoscape*), and we will continue to grow these simulations on open access repositories (www.github.com/ecophysiology/Ectoscape). We also provide a process diagram to understand the flow of the various steps of the model and how they work together (Figure S2).

2.5 | Validation

We conducted analyses to validate estimates of leaf and click beetle operative temperatures. For the leaf temperatures (T_{leaf}), we compared estimates from our T_{eh} simulations with empirical data collected on the correlation between leaf temperature and air temperature (Woods et al., 2022). We downloaded the dataset from Data Dryad and parameterized our leaf temperature model with the day of year, latitude, longitude, and elevation of their site. To generate air temperatures from this dataset, we calculated the average air temperatures and standard deviation of air temperature for each hour that data were collected. We then sampled a normal distribution from the hour-specific mean air temperature and the respective standard deviation using the *random.normal*() function in the NumPy library. Woods et al. (2022) did not measure the amount of shade cover, wind speed, or relative humidity for each T_{leaf} measurement. Thus for each hour, we estimated realistic values of wind speed between 0.1 and 0.25 $\mathrm{m\,s^{-1}}$ and shade cover between full shade and full sun using the *random.uniform*() function in the NumPy library to randomly sample between these bounds. For relative humidity, we used the *random.normal*() function using 50% relative humidity as the mean with a 20% standard deviation to produce a range of realistic values for humidity. For conductance to water vapor, we randomly sampled values between 0.4 and 0.005 $\mathrm{mol\,m^{-2}\,s^{-1}}$ across a uniform distribution to capture a range of realistic values associated with open and closed stomata (Campbell & Norman, 1998). We then ran the simulations for 42:00 h to produce a similar sample size as the study. In a separate validation analysis, we assumed higher levels of shade in the morning to approximate the greater shading effects in a forest when the sun would be low on the horizon. For this simulation, we used the *random.uniform*() function to sample between full shade and 20% shade when hour of day was less than 09:00. For the statistical analysis, we used linear regression analyses with T_{air} as the independent variable and T_{leaf} as the response variable. We then reported the slopes with standard errors to compare regressions between empirical and theoretical datasets.

We also conducted an additional validation experiment to ensure the T_{e} calculations could approximate operative temperatures of click beetles. For this experiment, we inserted a type T thermocouple into the thorax of a specimen to record body temperatures in the field. The thermocouple was connected to a portable temperature logger (Measurement Computing; USB-TC Series), which recorded temperature measurements every 4 s. We placed one click beetle in an open area roughly 1.5 m from the ground, suspended roughly 10 cm above vegetation with the dorsal side of the beetle facing south to expose the dorsal surface to greatest degree of solar radiation. We placed the other click beetle inside the shade of a dense evergreen, approximately 3 m away from the specimen in sun. The purpose of the click beetle in the shade was to provide an estimate of T_{air} by minimizing the direct and reflected radiation as much as possible. We then used the measurements of the click beetle in the shade as our proxy of T_{air} to estimate the full range of T_{e} for a beetle in the sun. For the predicted values, we parameterized the simulation for Oulu, Finland, to incorporate the angle and strength of solar radiation on the day of the measurement (June 14, 2019). During the measurements, we also recorded when the sky was overcast and mostly sunny. We then used linear regression analyses to compare our observed estimates of T_{e} in full sun with our theoretical estimates of T_{e}.

2.6 | Environmental data

We downloaded hourly weather station data from the Finnish Meteorological Institute using their R package (*fmi2*). We downloaded hourly weather station data between January 1, 1996 to December 31, 2021 from the Siikajoki Ruukki weather station (64.68°, 25.08°), which was located 49.4 km from our field sites. To characterize the current climatic conditions for click beetles, we used air temperature and relative humidity from this dataset to calculate the T_{e} for click beetles and T_{leaf} of a deciduous leaf for each hour of the 25-year period. We then adjusted these conditions based on the Representative Concentration Pathway 6.0 (RCP 6.0) to generate future climatic conditions.

To estimate future climatic conditions, we used the CCSM climate projections from the RCP 6.0 warming scenario to determine the average increase in minimum and maximum temperatures for each month of the year by 2080 (Fick & Hijmans, 2017). Then, we calculated the average hourly temperature for each day of the year over 25 years from the weather station data. We also calculated the average variability in air temperature (using standard deviation; σ) for each day of year using the same dataset. We estimated the increase in daytime air temperature from the change in maximum monthly temperature and nighttime temperatures from the minimum monthly temperature (Figure S3). To incorporate variability under future warming scenarios, we included the daily site-specific standard deviation in temperature. We specifically used the normal distribution function in the NumPy library to generate an increase in air temperature based on the mean monthly change in temperature (from the RCP 6.0 scenario) and standard deviation in temperature (from the daily weather station data). Prior to generating this random increase in temperature, we used a uniform distribution to select a random percentage between −25% and 25% to augment the σ of the daily temperature, simulating the increased variability in temperature under the warming scenario for northern Finland (Bathiany et al., 2018). We then added this randomly generated increase in temperature (based on the average increase with site-specific and climate-driven variability) to each average hourly air temperature for that particular day to incorporate increased variability. This approach does not incorporate temporal autocorrelation in the variability of temperature (i.e., multi-day heat waves); however, by running the simulation for 25 years, we can capture the future climatic mean and variance in temperature, as well as generate a comparable dataset to the current climatic conditions. In general, relative humidity is not expected to change dramatically in Finland by the end of the century (roughly 0.5% per °K) (Byrne & O'Gorman, 2016); therefore, we assumed relative humidity remains stable under the future warming scenario by using the mean daily relative humidity from the 25 years of weather station data. Note, however, that the increase in temperature will result in higher rates of evaporation (and thus evaporative cooling for T_{leaf}) due to the rise in the vapor pressure deficit from the increase in saturation vapor pressure.

For each hour under each climate scenario (current and RCP 6.0), we determined whether T_e of the click beetle exceeded the thermal thresholds from our study. Hours above each of these thresholds were termed an "hour of restriction" and represent the amount of time an individual might experience lower performance or fitness (Sinervo et al., 2010). The thresholds included average critical thermal maximum associated with low water loss rates (CT_{LWLR}; 40°C), average critical thermal maximum associated with high water loss rates (CT_{HWLR}; 38°C), the pejus temperature associated with the thermal sensitivity of clicking behavior (T_{pejus}; 38°C), and the subcritical thermal limit (stT_{max}; 32°C). Note that CT_{HWLR} and T_{pejus} have the same temperature value. We also estimated a "thermal exposure index," which we define as the difference between T_e and a thermal threshold, like CT_{max}. In contrast to hours of restriction, the thermal exposure index indicates the magnitude by which T_e exceeds a certain threshold. Some studies refer to this value as the thermal safety margin (Pinsky et al., 2019), while other studies refer to this as warming tolerance (Deutsch et al., 2008). We specifically plotted the minimum thermal exposure index for each day over the 25-year period to illustrate the greatest exposure to hot temperatures. We also calculated these temperatures assuming the click beetle and leaf were in full shade, 50% shade, and full sun to assess the importance of microhabitat selection. Similar to the validation analyses, we randomly selected wind speeds between 0.1 and 0.25 $m\,s^{-1}$ and conductance to water vapor between 0.4 and 0.005 $mol\,m^{-2}\,s^{-1}$ for each simulation to incorporate realistic variation in environmental conditions. We also ran simulations that fixed stomatal conductance at 0.4 and 0.005 $mol\,m^{-2}\,s^{-1}$ to assess the sensitivity of overheating to plant leaf physiology.

We also ran an additional analyses in climates that were warmer than Oulu, Finland, based on the observation that most *A. subfuscus* live in regions 5.2°C warmer than our field site. First, we downloaded all coordinates of *A. subfuscus* from the Global Biodiversity Information Facility (GBIF). Then, we downloaded a global dataset of average annual temperature from Worldclim (Fick & Hijmans, 2017) and expressed the dataset relative to Oulu, Finland, such that zero represented the average annual temperature of our field site (Figure S4). Then, we used the point by sample tool in QGIS (v. 3.10) to extract the temperatures associated with each presence location (~20,000) and found that click beetle observations were concentrated in climates 5.2°C warmer than our field site (Figure S4). Thus, we ran an additional simulation under the RCP 6.0 scenario assuming air temperatures were 1–5.2°C warmer than our field site. The analysis evaluated how average temperature influenced the hours of restriction between our three different thermal tolerance limits, including the effect of water loss rates. The analysis assumes that thermal tolerances do not vary with annual temperature (which is generally true for many terrestrial animals; Sunday et al., 2019), but regardless, the simulation tests how small differences in thermal tolerance due to water loss physiology could impact climate vulnerability.

2.7 | Statistical analyses

We conducted all of our analyses in *R* (v. 4.0.2, "Taking off again") (R Core Team, 2017). We conducted two types of analyses: one that included all species and another that only included the most abundant species (*A. subfuscus*). We refer to the analyses with all species as the *multi-species* analysis and the analyses with *A. subfuscus* as the *single-species* analysis. For the multi-species analyses, we used mixed effects models from the *lme4* library to account for species-level differences and determined statistical significance using with Satterthwaite approximation for denominator degrees of freedom from the *lmerTest* library. We used mixed effects models to address the phylogenetic dependence among the four species within the random effects (Sunday et al., 2011). Since our analysis contained four species from four different genera within the same family (Elateridae), we included species as a random effect without the nested structure. Due to the uneven sample size with respect to species, we weighted measurements based on the proportion that each species composed of the total sample. For the single-species analyses, we analyzed the same predictors using an analysis of covariance on the species with the highest sample size, *A. subfuscus* which represented 87.1% of the sample size. For both analyses, we used Type II analysis of covariance due to uneven sample sizes (Langsrud, 2003).

For our analysis on CT_{max}, we assessed the effect of body mass and water loss rate during overnight acclimation treatment (which we refer to as water loss rate) as covariates. Water loss rate during the thermal tolerance experiments was not included in the analysis because the amount of water lost was often indistinguishable from the measurement error in our scale due to the short duration of the trial. However, water loss rates prior to the experiments are likely correlated with rates during the experiment due to the high repeatability in water loss rates in insects (Rourke, 2000) and short duration of the experiment. Both covariates were scaled and centered to compare the relative strength of each effect (Schielzeth, 2010), and values were converted to untransformed values for the figures. We ensured that variance inflation factors were less than five for all analyses to avoid issues with collinearity (Craney & Surles, 2002). We included several factors, including (1) pre- or post-rain, (2) acclimation humidity treatments, (3) acute humidity treatment, and (4) an interaction between the acclimation humidity treatment and the acute humidity treatment. See Table S1 for descriptions of each variable. We included the interaction between acclimation and acute humidity treatments in case prior exposure to dry or humid treatments influenced physiological responses to acute humidity exposure during the experiment. We also assessed model performance without water loss rate (the reduced model) to evaluate whether CT_{max} varied with other variables related to hydric physiology. We then compared the full model with the reduced model using AIC model comparison. We did not conduct a similar analysis on stT_{max} because we were unable to assign clicks to specific individuals. Therefore, we focused on the group sensitivity of stT_{max} to temperature.

We also conducted separate analyses on the subset of individuals ($n=36$) that were dried to estimate hydration state throughout the experiment. We conducted two separate analyses on CT_{max} and water loss rates using the hydration state dataset. For the CT_{max} analysis, we included variables that significantly affected thermal tolerance in the full dataset as well as the hydration state immediately prior to beginning the thermal tolerance experiment. For the water loss analysis, we included variables that significantly affected water loss rates in the full dataset in addition to hydration state before entering the acclimation experiment. These hydration states were the most relevant to consider for each trait.

3 | RESULTS

3.1 | Water loss rates

Water loss rates were primarily influenced by the time of capture relative to when they experienced a precipitation event. Individuals collected post-rain exhibited significantly higher water loss rates than pre-rain individuals (Figure 2a, $F_{1,66.0}=157.29$, $p<.001$). The time of capture relative to precipitation also exhibited the greatest effect on variation in water loss rates ($\omega^2=0.70$), with water loss rates being 3.2-fold higher post-rain (Figure 2). Analyses on water loss rates also revealed an effect of body mass and acclimation humidity treatment. We found that larger click beetles exhibited higher water loss rates (Figure 2b, $F_{1,66}=16.53$, $p<.001$, $\omega^2=0.19$), and individuals in the 24-h humid acclimation treatment exhibited lower rates of water loss than in the dry treatment (Figure 2c, $F_{1,66}=4.58$, $p=.04$, $\omega^2=0.05$). These relationships were also similar for analyses conducted on *A. subfuscus*. In the single-species analysis, water loss rates were significantly higher after a rain event ($F_{1,54}=136.61$, $p<.001$, $\omega^2=0.67$) and with larger individuals ($F_{1,54}=12.91$, $p<.001$, $\omega^2=0.06$). We also found a marginal trend indicating that individuals in the humid acclimation treatment lost less water than in the dry treatment ($F_{1,54}=3.73$, $p=.06$, $\omega^2=0.01$).

We found similar results when accounting for hydration state, suggesting click beetles were actively regulating water loss rates. More hydrated individuals tended to have higher water loss rates than more dehydrated individuals (Figure 2d, $F_{1,30.7}=10.13$, $p=.003$, $\omega^2=0.22$); however, the effect of precipitation on water loss rates persisted even when accounting for hydration ($F_{1,30.7}=96.75$, $p<.001$, $\omega^2=0.75$). We also found the consistent positive effect of body mass on water loss rate ($F_{1,31.0}=16.02$, $p<.001$, $\omega^2=0.31$). We found a marginal effect of the humid acclimation treatment on water loss rates ($F_{1,30.6}=4.01$, $p=.05$, $\omega^2=0.09$), indicating water loss rates were lower in the humid acclimation treatment. For the single-species analysis, we found significant effects of time since precipitation ($F_{1,22}=105.20$, $p<.001$, $\omega^2=0.54$), body mass ($F_{1,22}=12.93$, $p<.002$, $\omega^2=0.05$), hydration state ($F_{1,22}=6.62$, $p=.02$, $\omega^2=0.27$), and humid acclimation treatment ($F_{1,22}=5.39$, $p=.03$, $\omega^2=0.04$) on water loss rates. The direction and magnitude of each effect were consistent between multi-species and single-species analyses.

3.2 | CT_{max}

We found a consistent negative relationship between water loss rate during acclimation and CT_{max}, indicating that, contrary to our prediction, individuals with higher water loss rates exhibited a lower CT_{max} (Figure 3, $F_{1,62.4}=9.00$, $p=.004$, $\omega^2=0.11$). Thermal tolerance was also positively associated with body mass such that larger individuals exhibited a higher CT_{max} (Figure 3, $F_{1,62.0}=10.09$, $p=.002$, $\omega^2=0.12$). We did not find an effect of time of collection relative to precipitation ($F_{1,62.9}=1.05$, $p=.31$, $\omega^2<0.01$), acclimation humidity treatment ($F_{1,61.8}=0.57$, $p=.45$, $\omega^2<0.01$), acute humidity treatment ($F_{1,61.7}=0.47$, $p=.49$, $\omega^2<0.01$), or the interaction between both treatments ($F_{1,61.7}=0.46$, $p=.50$, $\omega^2<0.01$). In the reduced model without water loss rate, only precipitation was associated with CT_{max} (Table S2); however, the full model far outperformed the reduced model (Table S3). These relationships were qualitatively similar in the single-species analysis on *A. subfuscus*. Specifically, we found a

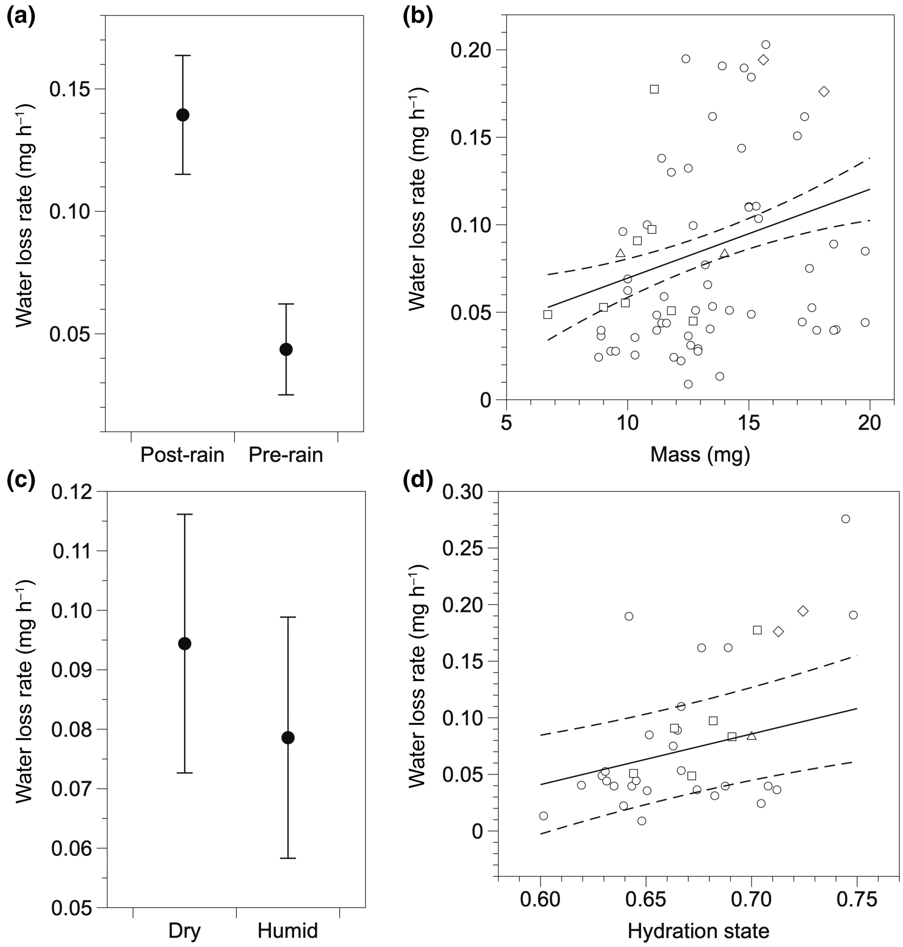

FIGURE 2 High water loss rates following precipitation. (a) Individuals exhibited water loss rates that were 3.2-fold higher after precipitation (post-rain) relative to several days since precipitation (pre-rain). (b) Larger individuals exhibited higher water loss rates compared to smaller individuals. Symbols represent different species (circles = *Athous subfuscus*, squares = *Dalopius marginatus*, diamonds = *Sericus brunneus*, triangles = *Ampedus nigrinus*). (c) Water loss rates were higher in the dry acclimation treatment relative to the wet acclimation treatment. (d) More hydrated individuals exhibited higher water loss rates, but hydration state still did not fully explain the high water loss. Hydration state is expressed as the proportion of body mass from water after drying samples. Linear mixed effect model is plotted with 95% confidence intervals.

similar negative relationship between water loss rate during the acclimation treatment and CT_{max} in *A. subfuscus* ($F_{1,51}=6.86$, $p=.01$, $\omega^2=0.11$), and CT_{max} was also positively associated with body mass ($F_{1,51}=8.89$, $p=.004$, $\omega^2=0.10$). We did not find an effect of time of collection relative to precipitation ($F_{1,51}=0.65$, $p=.42$, $\omega^2<0.01$), acclimation humidity treatment ($F_{1,51}=0.41$, $p=.52$, $\omega^2<0.01$), acute humidity treatment ($F_{1,51}=0.47$, $p=.47$, $\omega^2<0.01$), or the interaction between both treatments ($F_{1,51}=0.16$, $p=.69$, $\omega^2<0.01$).

For the multi-species analysis that included the subset of individuals with hydration state, we found a consistent relationship between water loss rates and thermal tolerance. We again found a significant negative relationship between CT_{max} and water loss rate ($F_{1,32}=5.38$, $p=.02$, $\omega^2=0.11$). Hydration state and body mass, however, were not significantly associated with thermal tolerance (hydration state: $F_{1,32}=0.01$, $p=.91$, $\omega^2<0.01$; body mass: $F_{1,32}=2.05$, $p=.16$, $\omega^2=0.03$). We found qualitatively similar results on the single-species analysis (water loss rate: $F_{1,23}=5.45$, $p=.03$, $\omega^2=0.10$; hydration state: $F_{1,23}=0.01$, $p=.92$, $\omega^2<0.01$; body mass: $F_{1,23}=2.74$, $p=.11$, $\omega^2=0.06$). These results indicate that hydration state did not affect thermal tolerances, despite water loss rate playing a consistent role. We also found similar results when analyzing the relationship between mass-specific water loss rate and thermal tolerance (Table S4).

3.3 | stT_{max}

Clicking behavior indicated a substantially lower subcritical thermal threshold relative to CT_{max}. The number of clicks began to increase above 32°C (Figure 4), which is approximately 6–8°C below the observed CT_{max}. The number of clicks increased dramatically until approximately 38°C—the pejus temperature (T_{pejus})—and then rapidly declined as individuals were unable to perform the clicking behavior to right themselves.

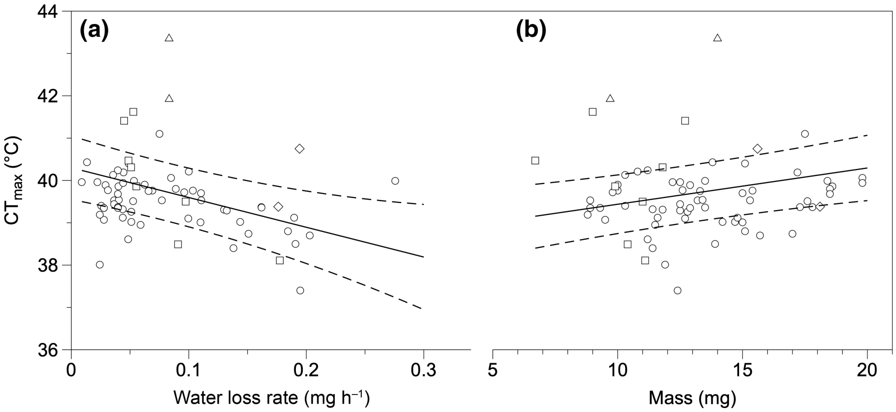

FIGURE 3 Water loss affects thermal tolerances. (a) Individuals with higher water loss rates during acclimation exhibited lower CT_{max} and (b) larger individuals exhibited higher CT_{max} compared to smaller individuals. Symbols represent different species (circles = *Athous subfuscus*, squares = *Dalopius marginatus*, diamonds = *Sericus brunneus*, triangles = *Ampedus nigrinus*). Regressions from linear mixed effects models are shown with 95% confidence intervals.

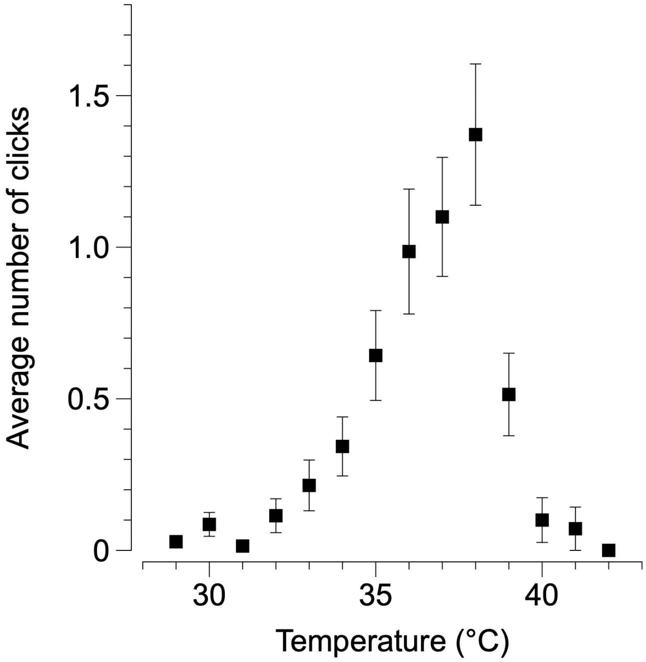

FIGURE 4 Thermal sensitivity of click behavior as a window into subcritical thermal thresholds. The average number of clicks per degree celsius indicates a definitive increase in clicking as a result of escape behavior near 33°C. Clicking behavior or equivalent behavioral markers are capable of identifying subcritical thresholds that drive responses to warming environments.

3.4 | Mechanistic niche model

Our simulations accurately predicted leaf and click beetle temperatures. We found a similar relationship between T_{air} and T_{leaf} between the observed data and our predicted values, especially when incorporating the increased shade effect in the morning hours (Figure S5). Our click beetle simulations also produced accurate estimates of T_e by adequately simulating the effect of radiation on click beetle body temperature (Figure S6). These models were then coupled together to produce estimates of click beetle T_e in a deciduous forest in Oulu, Finland (Figure 1). Our simulations of future warming scenarios captured the increased variation and average air temperature (Figure 5a) and click beetle T_e (Figure 5b). Hours of restriction were very low for click beetles under current climatic conditions, including that click beetles have rarely experienced any body temperatures that exceed thermal thresholds even in the sun (Figure 5c). However, under the future warming scenario, our simulations predicted a substantial rise in hours of restriction for each thermal threshold, especially in the sun. For instance, click beetles are likely to experience a 3.3-fold increase in hours of restriction under climate warming based on the stT_{max} threshold. The impact of climate change on hours of restriction was also sensitive to the physiology of the plant leaf, with the hours declining by 37.1% when leaves exhibited high stomatal conductance (resulting in cooler leaf temperatures) whereas the hours of restriction increased by 2.9-fold when plants exhibited low stomatal conductance (resulting in warmer leaf temperatures). Click beetles can avoid exposure to temperatures above any of the thermal thresholds by seeking shaded microhabitats, with the exception of the stT_{max} threshold. Click beetles also experience a substantial reduction in the thermal exposure index, with operative temperatures exceeding the stT_{max} by nearly 10°C throughout the activity season (Figure 5d). In addition, simulations at warmer sites revealed that click beetles living in warmer environments experienced far higher hours of restriction relative to our field site (Figure S4), and hours of restriction were 2.2- to 4.0-fold lower for click beetles with a low water loss rate compared to beetles with a high water loss rate (Figure 6; Figure S4).

4 | DISCUSSION

The environment interacts with interconnected physiological traits to influence whole-organism performance and trade-offs that

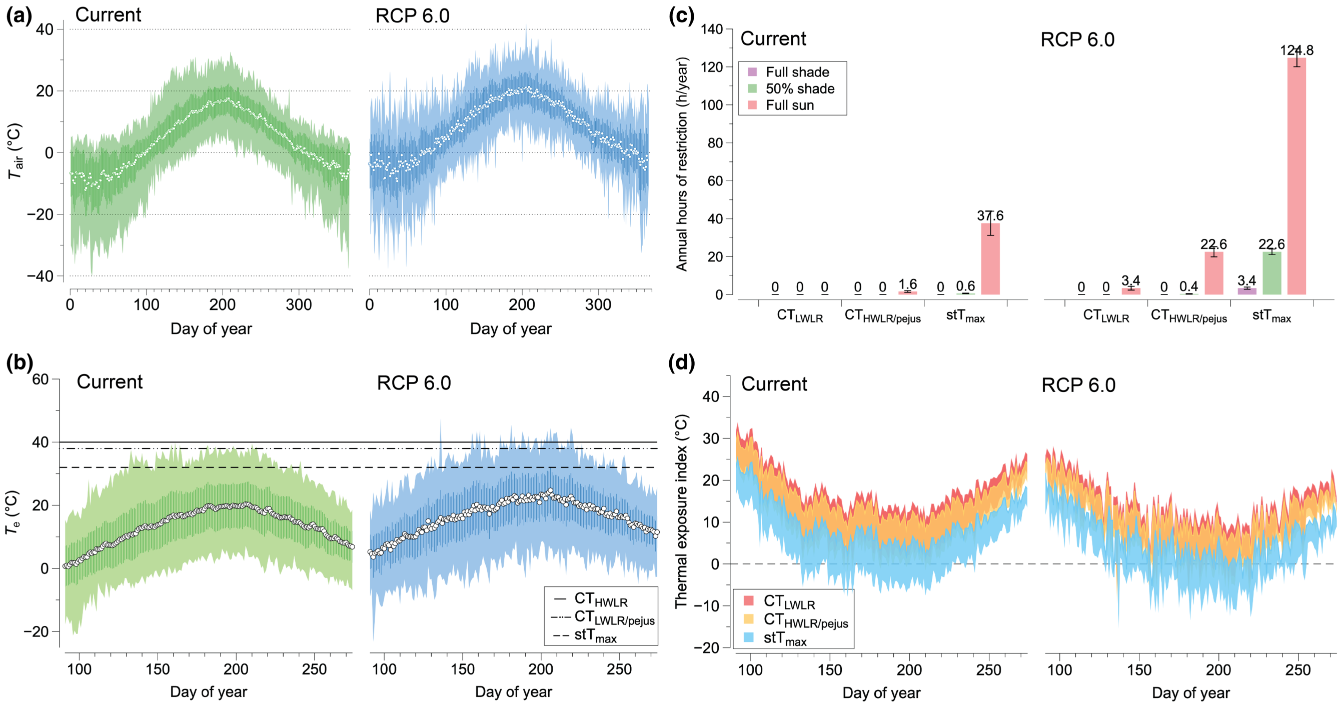

FIGURE 5 Exposure to climate warming depends on microhabitat conditions and thermal threshold. (a) Air temperatures (T_{air}) from weather station data over the last 25 years from the publicly available dataset (left) and the anticipated increased in air temperature under the RCP 6.0 climate warming scenario (right). (b) Estimates of operative temperatures (T_e) across the typical activity period of a click beetle with physiological thresholds superimposed over the T_e estimates. The thermal thresholds include the average critical thermal maximum (CT$_{max}$), the pejus temperature based on the thermal sensitivity of clicking (T_{pejus}), the critical thermal maximum associated with high water loss rates (CT$_{water}$), and the subcritical threshold (stT$_{max}$). Note that T_{pejus} and CT$_{water}$ have the same value (38°C). (c) The annual hours of restriction (h year^{-1}) for the thermal thresholds in full shade, 50% shade, and full sun for current and the RCP 6.0 warming scenario. Averages are shown with standard error. (d) The thermal exposure index for contemporary and future warming scenarios indicate the magnitude by which T_e exceeds each thermal threshold. Shaded region for each threshold indicates the minimum thermal exposure index for that day over the 25-year period in the full sun and full shade.

constrain organismal responses to environmental change (Cohen et al., 2012). In this study, we uncovered linkages between water loss physiology and CT$_{max}$ that were driven by recent exposure to precipitation. Water loss rates during the overnight acclimation treatment were very sensitive to recent exposure to precipitation, resulting in a 3.2-fold increase in water loss rates relative to click beetles that had not experienced precipitation recently. The subsequent thermal tolerance experiments then uncovered a relationship between the overnight water loss rates and CT$_{max}$. Thus, our experiment revealed interactions between precipitation, water loss physiology, and thermal tolerances. Further statistical analyses indicated that precipitation also affected CT$_{max}$, though indirectly through its effect on water loss rates (Tables S2 and S3). These results provide clear evidence that CT$_{max}$ can be sensitive to the hydric environment that organisms experience and resulting responses in water loss physiology. We also demonstrate that the effect of water loss physiology on thermal tolerances can have a large impact on climate vulnerability (Figure 6). Before understanding the connections between precipitation, water loss, and thermal tolerance, we explore the relationship between water loss and precipitation.

Many insects can rapidly adjust water loss rates in response to the hydric environment (Orchard & Lange, 2020), yet few studies have investigated responses of water loss physiology to precipitation. For instance, desiccation resistance increased in *Drosophila melanogaster* only after a few hours of exposure to low humidity (Hoffmann, 1990). Similar responses indicative of rapid, adaptive acclimation have also been found in butterflies, springtails, ants, and tsetse flies (Baumgart et al., 2022; Elnitsky et al., 2008; Fischer & Kirste, 2018; Holmstrup et al., 2002; Terblanche et al., 2006). These studies often focus on the adaptive benefits of reductions in water loss in response to dry conditions, but few studies have focused on the implications of higher water loss rates in wetter environments. For instance, higher water loss rates may be needed following fluid-filled meals, during the onset of flight, or to clear toxins (Orchard & Lange, 2020). Increased respiratory water loss might also improve aerobic scope and performance by increasing gas exchange (Woods & Smith, 2010). Alternatively, waterproofing hydrocarbons found in the cuticle may be costly to produce; therefore, producing less could save energy even at the cost of leakiness (Gefen et al., 2015). More explicit tests of these hypotheses will improve our understanding of the consequences of being "leaky" and the possible linkages with related physiological traits, such as thermal tolerances.

The relationship between water loss rates and CT$_{max}$ may be related to exposure to certain environmental conditions (Renault

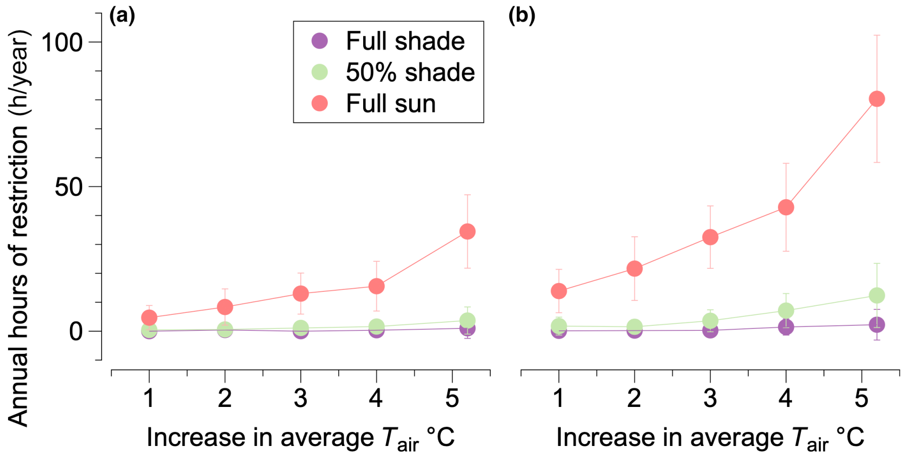

FIGURE 6 Click beetles with high water loss rate experience greater climate vulnerability in warmer climates compared to beetles with low water loss rates. Estimates of hours of restriction for click beetles with low water loss rates (a) and high water loss rates (b) under scenarios in which the mean air temperature was increased relative to Oulu, Finland. Simulations were run for each shade scenario (purple = full shade, green = 50% shade, and red = full sun). Means are plotted with standard deviation.

et al., 2005; Terblanche et al., 2005, 2006). Correlations between CT_{max} and metrics of water loss physiology support evaporative cooling as a mechanism allowing insects to tolerate warmer temperatures (Bujan et al., 2016; Mutamiswa et al., 2021; Nervo et al., 2021; Overgaard et al., 2012; Rezende et al., 2011). However, studies have also found negative correlations between water loss rates and CT_{max} and point to alternative mechanisms, such as pilosity or sculpturing of the cuticle (Buxton et al., 2021) or effects of dehydration (Johnson & Stahlschmidt, 2020). Contrary to our expectation, we found that water loss rates during the acclimation period immediately prior to the thermal tolerance experiments and CT_{max} were inversely related, with higher water loss rates coinciding with lower thermal tolerances (Figure 3a). Possible explanations may be related to exposure to desiccating conditions in the field. For instance, exposure to desiccation can raise thermal tolerances to heat, possibly due to the co-evolution of thermal and desiccation tolerances (Gotcha et al., 2018). Thus, exposure to desiccation might prompt insects to prepare for hot, dry conditions. Such a response might explain why the click beetles with the lowest water loss rate also exhibited the highest CT_{max}. Although some studies suggest that starvation or dehydration during thermal tolerance experiments may lower critical limits (Rezende et al., 2011), experiments indicate these effects are an unlikely explanation (Overgaard et al., 2012). Regardless, disentangling these relationships is likely to improve our ability to predict climate vulnerability from a more “whole-organism” perspective.

Traditional measurements of CT_{max} may be far less relevant for predicting the consequences of warming compared to subcritical thresholds. Our experiments revealed that subcritical thermal thresholds occur up to 8°C below the observed CT_{max}, similar to studies comparing critical and subcritical thermal thresholds in other insects (Braschler et al., 2021). Clearly, ectotherms respond to warming at much lower temperatures than the critical limits, and avoidance behaviors likely have important consequences for fitness by reducing opportunities for important behaviors, such as foraging and finding mates (Huey, 1991). For instance, insects often experience sublethal effects on growth and reproduction at warm temperatures far below their CT_{max} (Briscoe et al., 2012; Faske et al., 2019; Rukke et al., 2015), and some insects rarely experience temperatures above their CT_{max} due to buffering of temperatures provided by microhabitats in tree canopies (Woods et al., 2022). Consequently, studies in thermal ecology are increasingly emphasizing the importance of subcritical metrics of thermal tolerance, such as voluntary thermal maxima (Camacho et al., 2018; Lima et al., 2022; McTernan & Sears, 2021). We further underscore the importance of subcritical measures of thermal tolerance and assessing the thermal sensitivity of ecologically relevant escape behaviors, such as clicking.

Our simulations under future warming conditions suggest click beetles are likely to face an increase in exposure to challenging temperatures. Under contemporary climates, click beetles have faced little overheating risk at our high latitude field site in Oulu. However, climate change will expose click beetles to substantially higher frequency of body temperatures over subcritical thresholds. The climate simulations in Oulu also suggest that variation in CT_{max} driven by water loss physiology does not have a major impact on exposure to overheating risk, but the effect of water loss physiology on indices of climate vulnerability becomes much more pronounced in the southern range of the click beetle distribution where they experience warmer environments (Figure 6; Figure S4). Thus, our results suggest that the combined effect of water loss physiology and thermal tolerances could play a role in establishing the “fingerprint” of climate warming on insect population dynamics (Boggs, 2016). These results also underscore the importance of understanding the seemingly small effects of water loss physiology on thermal tolerances (~2°C) that can have relatively large effects on climate vulnerability.

Finally, our study identifies the multiple dimensions of organismal physiology that can improve predictions of performance under changing environmental conditions. First, any framework for predicting performance would benefit from taking an integrated organismal approach, particularly by incorporating trade-offs or linkages between linked physiological traits (Garland, 2014; Mykles et al., 2010). Few studies have explicitly incorporated these interactions among traits into estimates of performance under changing environmental conditions (Riddell et al., 2018; Riddell & Sears, 2020). Our study encourages further exploration into the relationship between water loss physiology and thermal tolerances. Second, we found that water loss physiology can be remarkably sensitive to precipitation, yet precipitation patterns are not often directly incorporated into estimates of performance, particularly for animals (Bartelt et al., 2022; Gustafson et al., 2015). Third, a greater emphasis on subcritical thermal tolerance may provide a more accurate predictions of performance, especially if they incorporate the effects of behavior and microhabitat buffering (Woods et al., 2022). Together, these aspects will help to substantially improve predictions on the effects of environmental change and performance of organisms in general.

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CONFLICT OF INTEREST STATEMENT

The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.8076157

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SUPPORTING INFORMATION

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