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Critical thermal maxima differ between groups of insect pollinators and their foraging times: Implications for their responses to climate change

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Abstract. Insects perform essential roles within ecosystems and can be vulnerable to climate change because of their small body size and limited capacity to regulate body temperature. Several groups of insects, such as bees and flies, are important pollinators of wild and cultivated plants. However, aspects of their thermal biology remain poorly studied, which limits predictions of their responses to climate change. We assessed the critical thermal maximum (CT_{Max}) of bees and flies visiting flowers in urban and periurban areas in tropical and subtropical regions of the Americas. We also assessed the effect of the foraging time of the day on CT_{Max}. Overall, we found that bees displayed higher CT_{Max} than flies. Flies foraging in the morning and afternoon displayed similar CT_{Max} while bees in the morning displayed a higher CT_{Max} than in the afternoon. The results of this study suggest differences in the vulnerability to climate change between these two major groups of pollinators, with flies being more at risk.

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INTRODUCTION

Insect pollinators provide critical ecological roles in natural areas and ecosystem services to agroecosystems through the facilitation of plant reproduction via pollination (Klein *et al*., 2007; Ollerton *et al*., 2011). Increasing evidence suggests that insect pollinators are in decline at local and global scales (Zattara & Aizen, 2021; Turley *et al*., 2022). Declines in pollinators have been linked to habitat loss, pesticide exposure, and increased pathogen and parasite pressure (McArt *et al*., 2017), but the negative effects of all these stressors are likely exacerbated by high ambient temperatures (Harvey *et al*., 2023).

Insect pollinators are particularly susceptible to atmospheric warming because of their small size, high mobility, limited capacity to regulate body temperature, and high energetic metabolic demands of flight (Angilletta & Angilletta, 2009; Harrison *et al.*, 2012). Thus, assessing the range of temperatures across which individuals can survive and perform key ecological functions (also known as thermal tolerance range) is essential to understanding a species' ability to survive global changes and continue to function as an effective pollinator (Diamond & Yilmaz, 2018).

Critical thermal limits (CTL), the minimum and maximum temperatures at which motor function is lost, are a common metric used to estimate an organism's thermal tolerance (Angilletta & Angilletta, 2009). Such thermal limits have been associated with variations in precipitation and temperature, which determine species' distribution at both geographic and temporal gradients (Kellermann *et al*., 2012; García-Robledo *et al*., 2018; Nascimento *et al*., 2022). Critical thermal limits are also predictors of organisms' responses to land and climate change (Hamblin *et al*., 2017). Unfortunately, information on the CTL of insect pollinators is still limited (Oyen *et al*., 2016; Gonzalez *et al*., 2020).

In this study, which was conducted during the COVID-19 pandemic and coordinated virtually as part of a National Science Foundation (NSF) International Research Experience for Students (López-Uribe *et al*., 2022), we evaluated the critical thermal maxima (CT_{Max}) of bee and fly pollinators collected during foraging trips in the morning and afternoon across sites in tropical and subtropical regions to answer the following questions: (1) does CT_{Max} vary between bees and flies? and (2) does CT_{Max} vary among individuals foraging at different periods of the day when the ambient air temperature is different? Available information on bees' average estimates of CT_{Max} indicates values well above 40 °C (*e.g*., Hamblin *et al*., 2017) while those for flies are near or below 40 °C (Kellermann *et al*., 2012; Leclerc *et al*., 2022). Thus, we hypothesize that foraging bees would display higher values of CT_{Max} than flies. Because CT_{Max} values are associated with ambient temperatures during foraging (Roeder *et al*., 2022), we further hypothesize that individuals foraging in the afternoon, when ambient air temperatures are high, would tolerate higher values of CT_{Max} than those foraging in the morning.

MATERIAL AND METHODS

We collected specimens for CT_{Max} assays between June and November of 2021 at three locations in urban or periurban areas (Table S1): Cajicá (Cundinamarca, Colombia; 4°56'37''N, 74°00'34'' W), El Paso (Texas, USA; 31°55'35''N, 106°25'43'' W/ 31° 38' 34'' N, 106° 18' 21'' W) and Redondo Beach (California, USA; 33°84'92''N, -118°38'84''W). At each location, we captured bees and flies from plants flowering using an insect net during the morning (9:00 to 11:30 h) and afternoon (14:00 to 16:00 h). Taxon selection was based on the abundance of species visiting flowers at each site. We tracked ambient temperature during the days of the experiment using an AccuWeather (https://www.accuweather.com/) phone application. After collection, we kept the insects individually in vials covered with a net mesh inside a cooler (15–21°C) until fieldwork was completed. Once at the laboratory site, we determined the individuals' fresh body weight and acclimated them to 26 °C for 15 min before assessing their CT_{Max}. We tested insects within 1–3 h after capture. Because wild-caught individuals were used for this study, we were unable to control variations in thermal tolerance associated with the age of the individual.

To measure CT_{Max}, we placed insects individually in sealed glass vials (30 mL, 8 x 2.5 cm) that floated horizontally in a water bath. We used a portable and affordable device that consisted of a water heater (Proctor Silex 32oz Hot Pot, Model 45805; NACCO Industries, Cleveland, Ohio, USA) controlled by a light dimmer (TT-300H-WH; Lutron Electronics, Coopersburg, Pennsylvania, USA) (García-Robledo *et al.*, 2020). We tracked the temperature inside one of the vials by placing the probe of a digital thermometer (STC-1000; Lerway Tech, Shenzhen, China; accuracy ± 0.5 °C). We conducted several calibration trials before thermal assays to ensure that vials were heated up at a temperature change rate of ~1 °C min^{-1}. The water bath started with an initial temperature of 26 °C and increased at a rate of 1 °C min^{-1} with an accuracy of ± 0.3 °C. We recorded CT_{Max} as the temperature at which insects lost muscular control and began spasming (Lutterschmidt & Hutchison, 1997; García-Robledo *et al.*, 2016).

Specimens collected in Colombia were identified by Ruben Darío Martín and are in the insect collection of the Universidad Militar Nueva Granada, Cajicá, Cundinamarca (Colombia). Specimens collected in the United States were identified by Victor Hugo Gonzalez and are in the López-Uribe laboratory Insect Collection at Penn State University, University Park, Pennsylvania (USA) (Table S1). Male bees (*n* = 22) were removed from the dataset because they often show different CT_{Max} (Jones *et al.*, 2024) but did not have enough replicates to test the effect of sex on thermal limits.

We conducted all statistical analyses in R version 4.0.3 using the function lmer as implemented in the package 'lme4' (Bates *et al.*, 2015). Significance was assessed through the Anova function implemented in the package 'car' (Fox *et al.*, 2019). We tested the association between insect order and CT_{Max} fitting a mixed linear model with insect order, weight, and site as fixed effects, and species as a random effect. To investigate the association between foraging time and CT_{Max}, we subsetted the Diptera and Hymenoptera data and fitted a mixed linear model with time of day (morning/afternoon), site and weight as fixed effects, and species as a random effect.

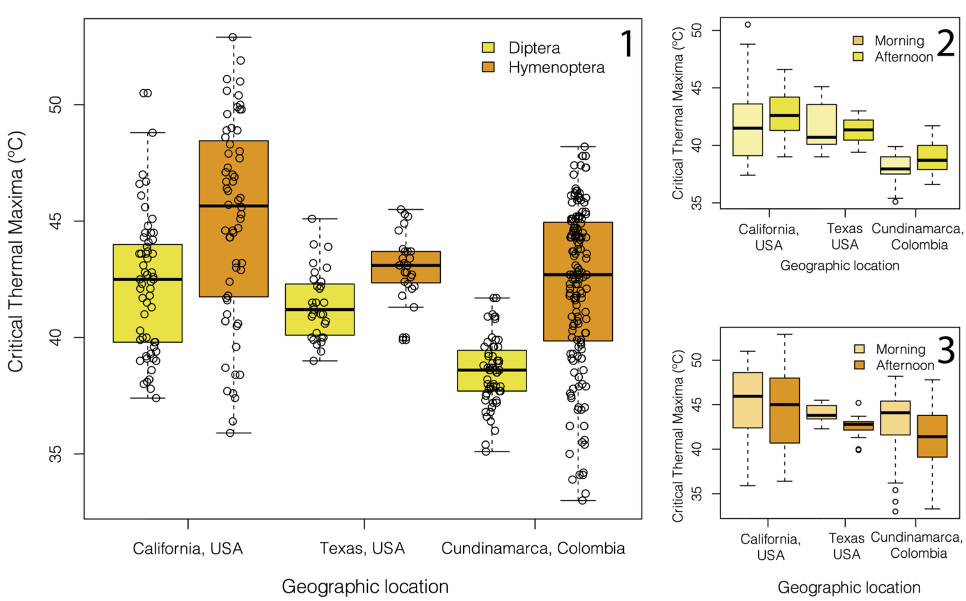
RESULTS AND DISCUSSION

We collected CT_{Max} data from 408 individuals representing 11 species of bees (Anthophila; *n* = 239) and 4 species of flies (Diptera; *n* = 150) from two subtropical (California, USA = 119; Texas, USA = 68) and one tropical site (Cundinamarca, Colombia = 221) (Table S1). The only species that was collected across the three sites was *Apis mellifera* Linnaeus (Table S2). All taxa were collected in the morning and afternoon except for two bee species: *Sphecodes* sp. (Halictidae) (collected in the morning) and *Bombus pauloensis* Friese (Apidae) (collected in the afternoon). Average ambient temperatures were consistently lower in the mornings (California: 26.54 °C, SD = 3.36; Texas: 26.33 °C, SD = 2.42; Cundinamarca: 16.97 °C, SD = 0.78) than in the afternoons (California: 32.82 °C, SD = 2.87; Texas: 31.92 °C, SD = 2.77; Cundinamarca: 18.87 °C, SD = 0.80) across all sites.

We found that bees and flies differ in CT_{Max} (Table 1). Specifically, bees displayed, on average, 2.3 °C higher CT_{Max} than flies ($\chi^2 = 3.6886$, $P = 0.05449$, Fig. 1). Geographic location explained most of the variation in CT_{Max} for both bees ($\chi^2 = 14.34$, $P < 0.001$) and flies ($\chi^2 = 90.03$, $P < 0.001$). Individuals in tropical regions (Cundinamarca, Colombia) showed lower CT_{Max} than individuals in temperate regions (post hoc test: $\chi^2 = 21.1$, $P <$ 0.001, Table 1; Fig. 1). The weight of the individual did not explain significant variation in the full model (Table 1). CT_{Max} also varied with foraging time for bees, with 1.3 °C higher values in the morning than in the afternoon ($\chi^2 = 16.41$, $P < 0.001$, Table 1; Fig. 3). For flies, CT_{Max} did not vary throughout the day ($\chi^2 = 1.832$, $P = 0.176$, Table 1; Fig. 2).

Table 1. Parameter estimates for the mixed linear models testing the relationship between order (flies vs bees) and geographic site (California, Texas, Cundinamarca) as predictors of critical thermal maximum (CT_{max}). The weight of the individuals was log-transformed and used as a fixed effect for each model. *P*-values lower than 0.05 are indicated in bold.

Model	Term	χ^2	df	*P*-value
CTmax ~ Order + Site + log(Weight) + (1 ǀ Species)	Order	3.68	1	*0.054*
	Site	21.325	2	**<0.001**
	log(Weight)	0.099	1	0.754
CTmax Flies ~ Time_Day + Site + log(Weight) + (1 ǀ Species)	Time_Day	1.073	1	0.3
	Site	90.033	2	**<0.001**
	log(Weight)	2.188	1	0.139
CTmax Bees ~ Time_Day + Site + log(Weight) + (1 ǀ Species)	Time_Day	16.205	1	**<0.001**
	Site	14.34	2	**<0.001**
	log(Weight)	0.0145	1	0.904



Figures 1–3. Summary of the effects of insect order and time of foraging on critical thermal maxima (CT_{Max}). **1.** Boxplots depict differences in CT_{Max} for flies (Diptera; yellow) and bees (Hymenoptera; orange) collected from three geographic regions: two subtropical (USA) and one tropical (Colombia). **2, 3.** Boxplots show differences in CT_{Max} for flies (2) and bees (3) foraging in the morning (light) and afternoon (dark).

Taken together, these results suggest that flies will operate closer to their critical thermal limits as ambient temperatures continue to increase due to climate change. The dominance of fly pollinators in higher-elevation areas—where the average ambient temperature is lower than at lower elevations—has been previously documented and indicates that flies may be more vulnerable to ongoing increases in ambient temperature (McCabe & Cobb, 2021). In contrast, bees exhibited higher thermal tolerance than flies in agreement with the hypothesis that this group of insects originated in deserts where they experience extreme ambient temperatures during development and foraging (Orr *et al*., 2021).

Even though CT_{Max} is evolutionarily constrained and generally not determined by ambient temperature (Bennett *et al*., 2021), we observed significant variation in the maximum thermal limits of bees and flies between geographic locations that exhibit contrasting differences in ambient temperature (Fig. 1). The tropical site we sampled (Cajicá, Colombia) is in a high-elevation area where the average ambient temperature during the experiment was ~18 °C and maximum daily temperatures reach up to 20 °C. Both bees and flies exhibited the lowest CT_{Max} values at that site (bees CT_{Max} = 42.24 °C, flies CT_{Max} 38.53 °C). In contrast, the two sites in higher latitudes exhibited average ambient temperatures of ~29 °C, and bees and flies consistently showed higher CT_{Max} values (California: bees CT_{Max} = 45.03 °C, flies CT_{Max} 42.24 °C; Texas: bees CT_{Max} = 43.07 °C, flies CT_{Max} 41.67 °C). These results suggest that high-elevation tropical insects exhibit wider warming tolerance—defined as the difference between a measure of heat tolerance (*e.g*., CT_{Max}) and ambient temperature (Diamond & Yilmaz, 2018)—than insects in subtropical regions. Still, insect populations in the tropics generally show little variation in heat tolerance along altitudinal gradients (Gonzalez *et al*., 2022), suggesting that lowland tropical species may be more vulnerable to warming than their subtropical counterparts (Diamond *et al*., 2012).

The observed differences in CT_{Max} during different times of the day also highlight the variable nature of this physiological metric. We did not find support for the hypothesis that CT_{Max} varies in response to the ambient temperatures exhibited by individuals during foraging activities temperatures. In contrast, for bees, we found that during the cooler temperatures in the morning, individuals exhibit higher CT_{Max} (Fig. 3). The variation in CT_{Max} during the day may be due to differences in the nutritional and hydration status of the individual at the time of the assay. Insects with higher moisture content can exhibit lower thermal tolerance (Gonzalez *et al*., 2020). The observed variation in thermal tolerance values throughout the day reiterates that CT_{Max} measurements, while valuable in a comparative framework, can be impacted by variables not controlled for and that their absolute values should be interpreted with caution (Ørsted *et al*., 2022).

Bees and flies are among the most important pollinators worldwide and are vulnerable to fluctuating environmental thermal extremes. Our study empirically demonstrates that these insects are physiologically different in their thermal tolerance and it is likely these underlying differences will impact their vulnerability to climate change. Foraging flights can be limited by ambient temperature, and our results indicate that physiologically bees are better equipped to forage and tolerate higher ambient temperatures and may have a better chance of persisting during heat waves and the rising global ambient temperatures. Despite the importance of characterizing thermal tolerance in pollinating species, only a handful of field studies have investigated these traits in bees and flies (Kellermann *et al*., 2012; Hamblin *et al*., 2017; Gonzalez *et al*., 2020; da Silva *et al*., 2021; Jones *et al*., 2024). Studying thermal tolerance across these two groups of pollinators is critical and has important implications for understanding their vulnerability to climate change to our study and highlights the critical need to recognize the differences in thermal tolerance between different groups of bees and flies as pollinators.

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SUPPLEMENTAL MATERIAL

Table S1. Geographic coordinates, elevation, daily temperature, and plants used to capture bees and flies.
Table S2. List of species of flies (Diptera) and bees (Hymenoptera) used to quantify critical thermal maxima in pollinator insects.

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