

Evaluating Critical Thermal Tolerances of Solitary Bees

Laura Naslund, Michael Stemkovski, Rebecca Irwin

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Abstract

Climate change is predicted to impact pollinators through both direct and indirect mechanisms: by altering physiological stress through warming temperatures and by changing species interactions through the altered phenology and abundance of food sources and competitors. While research has been done to evaluate the indirect mechanism of climate change on bees, less is known about the direct mechanism of thermal stress. To fill this gap, we measured the critical maxima (CT_{max}) of 20 distinct solitary bee taxa to 1) evaluate differences in CT_{max} among taxa, 2) identify the life history-traits that influence thermal tolerance, 3) determine how well CT_{max} predicts success in hotter-than-average years, as a proxy for conditions under long-term warming, and 4) evaluate if there is local adaptation of CT_{max} at different elevations within the same species. We found significant differences among taxa in average CT_{max} , driven primarily by *Lasioglossum inconditum*, *Halictus virgatellus*, *Sphecodes* sp., and *Habropoda* sp. which had significantly lower CT_{max} and *Pseudopanurgus bakeri*, *Halictus rubicundus*, *Osmia* spp. and *Megachile* spp. which had significantly higher CT_{max} than all additional species tested. In evaluating the traits related to differences in thermal tolerance, we found that only mass significantly predicted CT_{max} , with larger bees demonstrating higher CT_{max} . We found that CT_{max} predicted responses to a hotter-than-average year, indicating a relationship between thermal tolerance and fecundity effects. Finally, we found evidence for local adaptation in CT_{max} to elevation only in *Hylaeus* spp. and *Megachile* spp. Taken together, these results indicate a direct mechanism of climate change impact beyond alterations in the phenology and abundance of interacting species and indicate a species-specific response to warming based on both the breadth of thermal tolerance and local adaptation of populations.

Introduction

Global temperatures are projected to rise at least 1.5°C by 2100 (Collins *et al.* 2013). Accompanying this temperature increase is a predicted alteration of ecosystem services (Nelson *et al.* 2013) such as water supply (Janus 2010), wildfire regulation (Stephens *et al.* 2013), and fishery production (Cohen *et al.* 2016). One ecosystem service of particular concern and vulnerable to climate change is pollination (Settele *et al.* 2016). Climate change can impact pollinators both directly by creating a physiologically stressful environment (Pörtner & Farrell 2008) and indirectly by altering the phenology of pollinators' food sources and their competitors (Ogilvie & Forrest 2017). While the indirect consequences of climate change on bees have been investigated (Roulston & Goodell 2011; Ogilvie & Forrest 2017), the role of direct physiological stress on bee pollinators is less clear (Hamblin *et al.* 2017).

To evaluate the potential physiological stress of increased temperature on pollinators, it is helpful to consider the classic 1969 paper by Porter and Gates which introduced the idea of a climate space: a physiological niche accounting for radiation, air temperature, wind, and humidity in which an animal can survive (Porter & Gates 1969). While the impact of climate change on the other climate space variables (radiation, wind, and humidity) may be unclear or greatly variable (Wright *et al.* 2010; Pryor *et al.* 2012; Colman 2013), most climate models predict extreme temperatures, including extreme high and low temperatures, to be an essential

component of climate change (Collins *et al.* 2013). If these extreme temperatures lie outside of an organism's thermal tolerance, they may significantly impact the organism's success and by consequence the ecosystem service to which that organism contributes. Previous research has demonstrated that ectotherms, including many insect pollinators, are particularly vulnerable to experiencing temperatures outside of their physiological niche because of the temperature dependence of their basic functions (Huang *et al.* 2006; Deutsch *et al.* 2008). The negative impacts of thermal stress on an individual ectotherm may scale up to population level impacts through population declines and range shifts (Doak & Morris 2010). Thus, investigating how thermal tolerance relates to pollinators' responses to climate change is an important step towards understanding the direct impact of climate change on pollinators.

To test the thermal component of the climate space in which an organism can exist, measures of critical thermal maxima have emerged as useful indicators. The critical thermal maximum (CT_{max}) is described as the upper nonlethal temperature at which an organism would be incapable of escaping a threat (Diamond *et al.* 2012). While CT_{max} defines the extreme of an organism's thermal tolerance range, organisms may experience sublethal fitness consequences near these limits, thus CT_{max} may be useful in predicting responses even to less extreme temperatures (Lutterschmidt & Hutchison 1997). Critical thermal limits have not been assessed for the majority of solitary bees (but see Hamblin *et al.* 2017 for an exemplar study in southeastern US urban habitats) and not at the Rocky Mountain Biological Laboratory (RMBL) where much work has been done to evaluate the indirect impacts of climate change (Forrest & Chisholm 2017; Ogilvie *et al.* 2017). Pairing this previous work with thermal tolerance data may allow for a more complete understanding of the interactions of the direct and indirect impacts of climate change.

The aims of this study were as follows:

1) To measure the CT_{max} of native, solitary bees and to determine if there are differences among taxa

The focus of this study was solitary bees, which constitute the majority of bee biodiversity at a global scale and RMBL (Michener 2007). In addition to their importance due to numeric abundance, solitary bees may also be important agricultural pollinators in the face of declining honeybee populations (Winfree *et al.* 2007; Garibaldi *et al.* 2014).

2) To determine the degree to which bee life-history traits are related to differences in CT_{max}

We paired traits we measured including mass, intertegular span, and sex in bees we resolved to species with a trait dataset compiled by Gabriella Pardee (2018) to begin to tease apart the traits that may drive differences in CT_{max} , including nesting location, nesting substrate, nesting habit, lecticity, and phenology. In assessing the life-history traits which are related to differences in CT_{max} , we may be better able to predict bee responses to climate warming.

3) To assess how well CT_{max} predicts bee success in response to a hotter-than-average year

We paired the measured critical thermal limits with data from a long-term bee phenology

study described in Gezon *et al.* 2015 and Ogilvie *et al.* 2017. Because the long-term phenology study encompasses only nine years of data, natural climatic stochasticity may overwhelm the warming trend over the study period. Thus, we used a hotter-than-average year as a proxy for conditions under climate warming. Because the solitary bees at RMBL are likely univoltine, we would expect the impact of elevated temperatures through fecundity effects to only become apparent in the year following a hot year (Bewick *et al.* 2016, Pardee 2018); thus, we used the difference between the catch rate in the hotter-than-average year and the following year as the metric of bee success in response to a hotter-than-average year.

4) To assess if there is local adaptation in bee critical thermal tolerance among the same species sampled at different elevations

The finding of differences in critical thermal tolerance at different elevations may suggest the ability of bees to adapt to warming temperatures. These data may also provide insight into which species are likely to experience population declines and range shifts in response to climate change. Previous research in ants has demonstrated that species occupying environments closer to their upper thermal limits negatively responded to experimental warming while species occupying areas farther from their upper limits did not strongly respond to experimental warming (Diamond *et al.* 2012). If a species is regularly experiencing temperatures close to its thermal limits and does not exhibit differences in thermal tolerance—which may be suggestive of a lack of phenotypic plasticity—, it may be predicted that this species will experience a population decline and/or a range contraction in response to warming. If a species is not living close to its thermal limits or does exhibit plasticity, it may be predicted that this species will not experience population decline or a range contraction and may even experience a range expansion as the ranges of their less thermally tolerant competitors' contract. We predicted that for species that did exhibit differences in CT_{max} by elevation, individuals living at higher elevations would have higher CT_{max} . Previous work that has demonstrated such a relationship has suggested that higher elevation individuals exhibit higher thermal tolerance as they are exposed to more frequent and larger thermal fluctuations and thus experience a greater selective pressure to maintain a wide thermal tolerance range (Huang *et al.* 2006; Oyen *et al.* 2016).

Methods

Sites and collection procedures

From June 29, 2018 to July 25, 2018, we netted solitary bees for CT_{max} testing at nine sites (Figure 1), encompassing an elevation range of 2877-3069m, chosen for their proximity to the Rocky Mountain Biological Laboratory (2886 m elevation, 38°570 N, 106°590 W) (Gezon *et al.* 2015). Eight of the sites were adjacent to sites included in a long-term bee monitoring effort, described in Gezon *et al.* 2015. Upon capturing the bees, we placed them in 1.5mL microcentrifuge tubes with holes punctured in the caps to allow the bees to breathe during the trial and filled with approximately 0.75mL of hardened plaster of Paris to create a flat surface from which the bees could be observed during the thermal trials. We limited netting time at each

site such that netting time and transit time back to the lab for thermal maximum testing together summed to one hour. We implemented this measure to reduce the handling time of the bees outside of the CT_{max} trials, as the handling time itself may induce a stress response in the bees which may impact CT_{max} measurements.

Thermal maximum testing

Upon return to the lab, we placed microcentrifuge tubes containing bees in a Boekel Tropicooler™ benchtop hot/cold block incubator along with two open microcentrifuge tubes containing water, to maintain consistent humidity throughout the thermal trial. At least one bee captured per site was left in a microcentrifuge tube on the benchtop to test the lethality of the handling methods other than the application of heat (Oyen *et al.* 2016). Throughout the trials, only one of twenty-three bees died on the benchtop without the application of heat, suggesting handling conditions did not have a strong effect on bee survival. We began the trials with a ten-minute application of 22°C to standardize the temperature the bees experience prior to the CT_{max} assay (Oyen *et al.* 2016). The temperature experienced by the bees was measured with a Fluke™ thermocouple thermometer 51II with a bead thermocouple probe (K-type) in a microcentrifuge tube containing plaster of Paris. After the initial ten-minute period, we increased the temperature at a rate of 0.5°C per minute. At the end of each temperature increment, we checked the bees for postural control, which was assessed primarily through visual inspection of wing position. Bees appearing to have lost postural control were flipped on their backs using featherweight forceps. The temperature experienced by the bee prior to the righting trial was recorded as CT_{max} if the bee was unable to right itself after thirty seconds (Oyen *et al.* 2016). Following the CT_{max} trial, the bees were sacrificed in the freezer, as identification to the species level is impossible in many genera without pinning and examining an individual under the microscope. The bees were then weighed to the nearest 0.1mg, pinned, measured for their intertegular span, sexed, and identified to the lowest possible taxonomic level (species for most genera).

Statistical analysis

Objective 1: detecting differences in CT_{max} among taxa

To determine if there were differences in critical thermal maxima among taxa, we ran a Kruskal-Wallis test. We chose not to test for differences in CT_{max} among taxa within a phylogenetic framework, and thereby implicitly assumed that each taxon was equally distant from every other taxa. This assumption was primarily made because the sequence data currently available would not generate the taxonomic resolution necessary to produce a tree with confidence. Constructing a tree based on assumed relationships—by taxonomic genera for example—, may have introduced more error than assuming equal distance between taxa. We further felt confident in making this assumption by observing that the spread of average CT_{max} among taxa did not appear to group by genus. The two species of *Halictus*, for example, had one of the highest and one of the lowest average CT_{max} observed. Additionally, a previous study on native bees did not find any relationship between phylogeny and CT_{max} (Hamblin *et al.* 2017).

Objective 2: relating traits to CT_{max}

To analyze if bee traits were related to CT_{max} , we included traits from a database compiled by Gabriella Pardee (2018), including nesting location, nesting substrate, nesting habit, lecticity, and phenology, to a full mixed model along with elevation, sex, mass, and IT span for all taxa that could be resolved to species. We determined inclusion of fixed effects variables using stepwise regression on a generalized linear model (glm) with both forward and backward elimination using Akaike's information criterion (AIC) as the selection criterion, using the stepAIC function in the MASS package in R (Venables & Ripley 2002). To account for potential population level differences in bees captured at different sites, we added site as a random effect to the fixed effects determined by the AIC model selection. We determined the fit of this linear mixed effects model by maximum likelihood (ML) estimation (Zuur *et al.* 2009) using the lme4 package (Bates *et al.* 2015). We calculated *p*-values for the coefficients of the glm by Satterthwaite's method using the lmerTest package (Kuznetsova *et al.* 2017).

Objective 3: predicting responses to hotter-than-average using CT_{max}

We calculated average maximum temperature across the study period using climate data recorded by RMBL resident, Billy Barr. Of the eight years contained in the long-term bee dataset with a complete sampling period corresponding to that of the CT_{max} trials, 2012 had the highest daily maximum temperature averaged across the study period, and thus we selected it as the focal hotter-than-average year.

To understand the impact of the higher temperature conditions in 2012, we defined the difference in catch rate (bees captured/hr) between 2013 and 2012 during the time period corresponding to our CT_{max} trials ($\Delta capture_{13-12}$) as the metric of bee success in response to hotter conditions. For this analysis, we only used data recorded from pan traps to control for variation in netting efficiencies between the two years. To reduce bias from potential stochastic variation at individual sites in the study years, we included all sites in the long-term data set: not just those we sampled for CT_{max} trials. We assessed potential influential points by calculating Cook's distances prior to analyzing the relationship between CT_{max} and $\Delta capture_{13-12}$ using a glm with a Gaussian distribution and weighted by the standard deviation of each species' CT_{max} measurements. The fit of the final model was assessed using McFadden's pseudo- R^2 .

Objective 4: detecting the impact of elevation on CT_{max}

We analyzed a subset of the taxa collected to assess local adaptation in CT_{max} along an elevational gradient. To determine which taxa had sufficient representation across the different elevations, we first divided the nine sites into four groups, allowing for less than 25m difference among the elevations of the sites in each group. We included taxa in further analysis if they had greater than 1 individual captured in at least three out of four groups. The taxa selected for further analysis were *Andrena spp.*, *Colletes spp.*, *Dufourea harveyi*, *Hylaeus spp.*, *Lasioglossum spp.*, *Megachile spp.*, *Osmia spp.*, *Panurginus cressoniellus*, and *Panurginus ineptus*. To detect differences in CT_{max} across an elevational gradient, we ran mixed models with sex, mass, IT span, and elevation as fixed effects and site as a random effect for each taxa.

We performed all analyses in R version 3.3.3 (R Core Team 2017). R code and raw data can be found in the public git repository https://gitlab.oit.duke.edu/lcn12/RMBL_Bee_2018.

Results

Over the course of the sampling period, we netted 281 solitary bees, representing 15 genera, 20 distinct taxa, and 11 resolved species, and tested their CT_{max} (Table 1). The range of CT_{max} was 27.5°C to 51.5°C (Figure 2), with statistically significant variation among taxa from the global mean (Kruskal-Wallis $\chi^2 = 47.21$, $df = 19$, $p = 0.0003$) (Figure 3). Most of the taxa had similar average CT_{max} around 36°C, with the notable exception of *Lasioglossum inconditum*, *Halictus virgatellus*, *Sphecodes* sp., and *Habropoda* sp. which had lower CT_{max} and *Pseudopanurgus bakeri*, *Halictus rubicundus*, *Osmia* spp. and *Megachile* spp. which had higher CT_{max} .

The final model used to determine which traits are related to CT_{max} included mass, lecticity, elevation, and phenology (Table 2), with site as a random effect. Of these fixed effects, only mass significantly predicted CT_{max} (t-test Satterthwaite's method, $t=3.90$, $df=126.2$, $p=0.000157$), with larger bees displaying a higher CT_{max} .

To determine how well CT_{max} predicted responses to a hotter-than-average year as a proxy for climate warming, we first determined which of the resolved species in the CT_{max} dataset were also present in both the long-term bee abundance data in 2012 and 2013. Of the 11 resolved species, 10 were captured in both 2012 and 2013. *Lasioglossum inconditum* was found to be an influential point [based on an analysis of Cook's Distance](#) and was excluded from the analysis, leaving 9 species to assess the relationship between CT_{max} and $\Delta capture_{13-12}$. CT_{max} was found to be a weakly significant predictor in the difference between catch rates in 2013 and 2012 (glm, coefficient=0.1211, $t=2.117$, $p=0.0786$) that explained 43% of the variation in the differences in catch rate between the two years.

Of the nine taxa with sufficient representation across elevations, elevation was only found to be a significant predictor of CT_{max} in two taxa: *Hylaeus* spp. (linear mixed model, coefficient=0.03072, $t=2.870$, $p=0.0069$) and *Megachile* spp. (linear mixed model, coefficient, 0.06234, $t=5.705$, $p=0.00467$).

Discussion

While much work has been done to assess the thermal tolerances of other ectotherms (Sinclair *et al.* 2016; Rohr *et al.* 2018), few previous studies have measured thermal limits in solitary bees (Hamblin *et al.* 2017), which are an important assemblage both for their numerical dominance in certain areas as well as the pollination services they provide (Michener 2007). We aimed to fill this gap by measuring the critical thermal maxima of solitary bees captured around the Rocky Mountain Biological Laboratory. We found that different taxa do exhibit differences in critical thermal maxima. This finding must be qualified, however, with the observation that the majority of taxa exhibited CT_{max} that were statistically indistinguishable from one another. The overall differences from the global mean observed, therefore, were largely driven by the few taxa exhibiting CT_{max} both above and below this CT_{max} mode.

This finding of many similar CT_{max} may be understood in an evolutionary context whereby the maintenance of a thermal range larger than necessary may be costly (Miller *et al.* 2012), and thus the bees occupying these thermally similar habitats have evolved similar thermal

tolerances. While the fitness cost of maintaining a higher-than-necessary thermal maximum has yet to be demonstrated in bees, studies of *Drosophila* (Loeschcke & Hoffmann 2007) and copepods (Willett 2010) suggest such an evolutionary trade-off. The existence of CT_{max} both above and below this mode, however, suggest at least one factor other than evolutionary history driving CT_{max} .

In assessing which traits are related to differences in CT_{max} , we found that only mass was a significant predictor of thermal tolerance. In general, larger bees were able to withstand higher air temperatures. The interpretation of this result is complicated by the role that thermal inertia—the degree of resistance of an object to assume the temperature of its surroundings—may have played during the CT_{max} trials (Oyen *et al.* 2016). Put simply, the larger bees may have been able to withstand higher temperatures simply because they heated more slowly. In an environment with consistently higher temperatures, as is predicted in the face of climate change, the role of thermal inertia in driving differences among different-sized bees would be diminished and thus it is possible that the impact of mass would also be diminished. It is possible, however, that larger bees have higher thermal tolerances and are therefore better suited than smaller bees to adapt to a warming climate. A previous study of orchard bees found that larger bees not only had higher CT_{max} but also had higher internal temperatures immediately following death (Beans *et al.* 2017), indicating that the observed higher CT_{max} in larger bees may be attributable to higher thermal tolerance and not simply thermal inertia.

In contrast to a previous study on the traits impacting critical thermal limits in native bee assemblages, nest substrate did not significantly predict CT_{max} . One possible explanation for this lack of an observed relationship is that only one of the taxa resolved to species nests in stems. While it is possible that in the community from which we sampled, nest substrate does not significantly influence CT_{max} , with such an uneven distribution of nest substrate among the taxa evaluated, we likely lacked the power to observe this relationship if it does exist.

CT_{max} did significantly predict the change in bee abundance between 2012—a hotter-than-average year—and 2013—the following year in which the fecundity effects of the hotter-than-average year in these univoltine bees could be observed. This finding must be qualified by the observation that *Halictus virgatellus*, the species with the lowest measured CT_{max} included in the regression, is largely driving the fit of the model. While Cook's D was run to exclude influential points prior to running the model, one species, *Lasioglossum inconditum*, was so influential as to dwarf the impact of the *Halictus virgatellus* on the relationship. If Cook's D is run again following the exclusion of *Lasioglossum inconditum*, *Halictus virgatellus* becomes an influential point. For the purposes of this analysis, *Halictus virgatellus* was not excluded as exclusion would narrow the range of CT_{max} in the regression from (33.5°C, 38.6°C) to (35.5°C, 38.6°C). From these data it is difficult to extrapolate a causal relationship between higher CT_{max} and lower fecundity effects following hotter-than-average years; however, the addition of more intermediate points by resolving more taxa could make the correlation more robust. The relationship implied by the regression confirms the findings of a previous study which demonstrated that CT_{max} significantly predicted solitary bee responses to urban warming (Hamblin *et al.* 2017). These findings taken together indicate that the relationship between CT_{max} and abundance responses should be investigated further under natural warming conditions.

One possible explanation for the positive relationship we find between CT_{max} and declines in fecundity following hotter-than-average conditions is that the physiological stress of the heat directly lowers fecundity. Alternatively, it is possible that the relationship we observed may be explained by the heat's alteration of bee foraging time. If the additional heat narrowed the amount of time that a bee could forage (Burrill & Dietz 1981), the fecundity effects observed may not be attributable to the physiological stress of heat, but to a narrowing foraging time. Thus, the change in fecundity we observed would be a consequence of a decline in nutrition rather than an increase in heat stress. To distinguish between these two mechanisms, further research should aim to investigate the temperature dependence of foraging time in this solitary bee assemblage.

We also examined if there was a detectable relationship between elevation and CT_{max} within the same taxa. Using linear mixed models, we determined that elevation was only a significant predictor of CT_{max} in *Megachile spp.* and *Hylaeus spp.*, with bees found at higher elevations having higher CT_{max} , congruent with previous work (Huang *et al.* 2006; Oyen *et al.* 2016). It is worth noting that these are two of the taxa for which we have some of the best elevational representation and the largest sample size. For most of the bee taxa we captured, we did not capture the number of bees in each elevational category we had predicted would be necessary ($n=17$) through a power analysis assuming a small effect size. As such it is possible the other species have local adaptations in thermal tolerance and we simply lack the power to observe it. It should also be noted, however, that *Megachile* and *Hylaeus* were two of the taxa we were not able to resolve to species, so it is possible that the elevational differences we observed are artifacts of phylogenetic differences and not true differences by elevation.

Although it is difficult to predict responses to warming given the sample size we achieved in most taxa, from this analysis it is possible to predict that *Megachile spp.* and *Hylaeus spp.* will be relatively successful in the face of warming both because they exhibit CT_{max} higher than the mode CT_{max} and because they exhibit differences in CT_{max} across elevation which may indicate phenotypic plasticity in thermal tolerance traits.

In future analysis we hope to resolve more of the bees to species which will allow us to better tease apart the phylogenetic from the elevational impact on CT_{max} and perhaps allows us to identify general patterns in taxa that exhibit local adaptation of thermal tolerance at different elevations. In addition, resolving more taxa to species may allow us to add more intermediate points to our regression analyzing the relationship between CT_{max} and responses to a hotter-than-average year. In addition, we intend to add abundance data from 2018 and 2019, as 2018 has been a hotter-than-average year, further adding power to our analysis. Finally, we hope to combine our analysis of the direct physiological impact of warming with analyses of indirect impacts of climate change, in particular changes in floral resource abundance and in flowering phenology. In this effort, we hope to uncover a more complete understanding of climate change impacts from the level of individual pollinators to the scale of ecosystem services.

Acknowledgements

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Tables

Table 1. Differences in mass and critical thermal maxima (CT_{max}) of solitary bees captured from June 29, 2018 to July 25, 2018 around the Rocky Mountain Biological Laboratory, Crested Butte, CO, USA. Values are reported as the mean $\pm$ SD.

Taxa		Mass (mg)	CT_{max} ($^{\circ}C$)
<i>Andrena</i> spp.	♀ (38)	31.8 ± 7.9	36.4 ± 1.8
	♂ (2)	13.8 ± 3.7	34.5 ± 0.7
<i>Colletes</i> spp.	♀ (24)	25.0 ± 9.4	36.2 ± 2.4
	♂ (1)	16.2	31.5
<i>Dufourea harveyi</i>	♀ (17)	6.3 ± 0.6	36.4 ± 1.4
	♂ (1)	4.7	35
<i>Habropoda</i> spp.	♀ (1)	90	34
<i>Halictus rubicundus</i>	♂ (4)	12.9 ± 2.5	38.6 ± 3.8
<i>Halictus virgatellus</i>	♀ (1)	12.5	35.5
	♂ (1)	7.1	31.5
<i>Hoplitis robusta</i>	♀ (7)	10.0 ± 3.4	37 ± 4.1
<i>Hylaeus</i>	♀ (21)	8.7 ± 4.1	38.9 ± 5.1
	♂ (19)	4.8 ± 2.3	35.8 ± 2.5
<i>Lasioglossum</i> spp.	♂ (24)	6.2 ± 3.0	36.5 ± 2.0
<i>Lasioglossum inconditum</i>	♀ (2)	8.3 ± 0.4	30 ± 3.5
<i>Lasioglossum nigrum</i>	♀ (3)	10 ± 2.8	37.5 ± 1.3
<i>Lasioglossum ruidosense</i>	♀ (5)	4.9 ± 1.3	36.2 ± 2.9

<i>Lasioglossum tenax</i>	♀ (4)	4.8 ± 0.7	36.5 ± 3.0
<i>Megachile spp.</i>	♀ (3)	61.6 ± 24.4	42.5 ± 2.8
	♂ (6)	97.8 ± 72.3	40.4 ± 4.7
<i>Osmia spp.</i>	♀ (9)	32.8 ± 18.8	40.3 ± 3.5
<i>Panurginus cressoniellus</i>	♀ (63)	9.0 ± 1.3	35.9 ± 1.6
	♂ (9)	5.0 ± 0.7	33.9 ± 2.5
<i>Panurginus ineptus</i>	♀ (12)	6.4 ± 1.0	36.4 ± 2.5
	♂ (1)	4.4	33.5
<i>Pseudopanurgus bakeri</i>	♀ (1)	5.4	38.5
<i>Sphecodes sp.</i>	♂ (1)	2.4	33.5
<i>Stelis sp.</i>	♀ (1)	18.7	37

Table 2. Parameter estimates and t-test calculated by Satterthwaite's method for a mixed model of the relationship between CT_{max} and bee traits. Phenology describes the number of days from bare ground the bees were first observed in pan traps. Oligolecticity is the base condition for lecticity, thus the coefficient describes the impact of being polylectic

Model	Term	Coefficient	s.e.	t	p-value
CT _{max} ~ mass + lecticity + elevation + phenology + (1 site)	intercept	19.3	27.0	0.715	0.495
	mass	261.4	67.1	3.90	0.000157
	lecticity	-1.07	0.620	-1.73	0.0862
	elevation	0.00520	0.00909	0.572	0.582
	phenology	-0.00589	0.00206	-0.287	0.775

Figures

Figure 1.

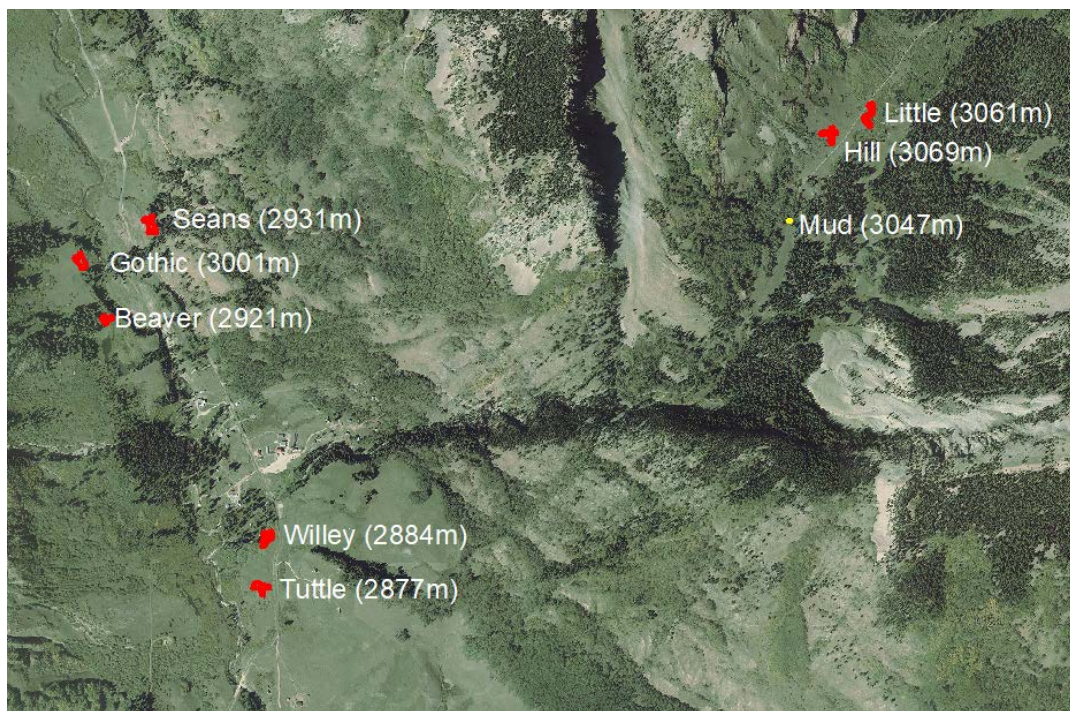


Figure 2.

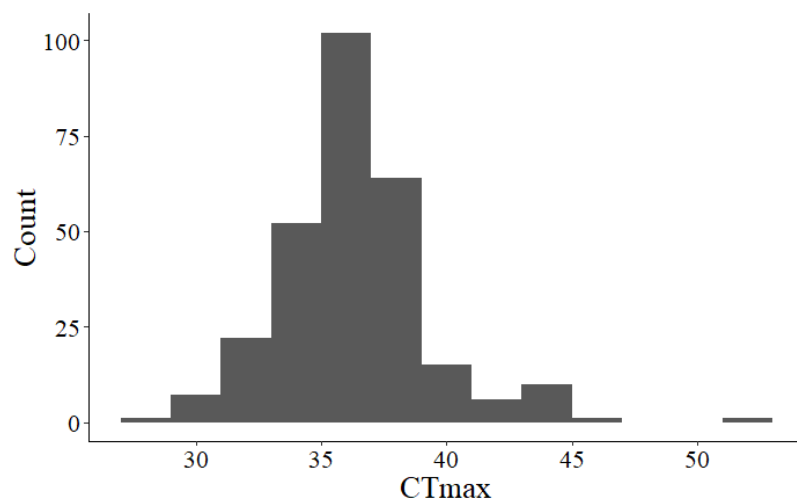


Figure 3.

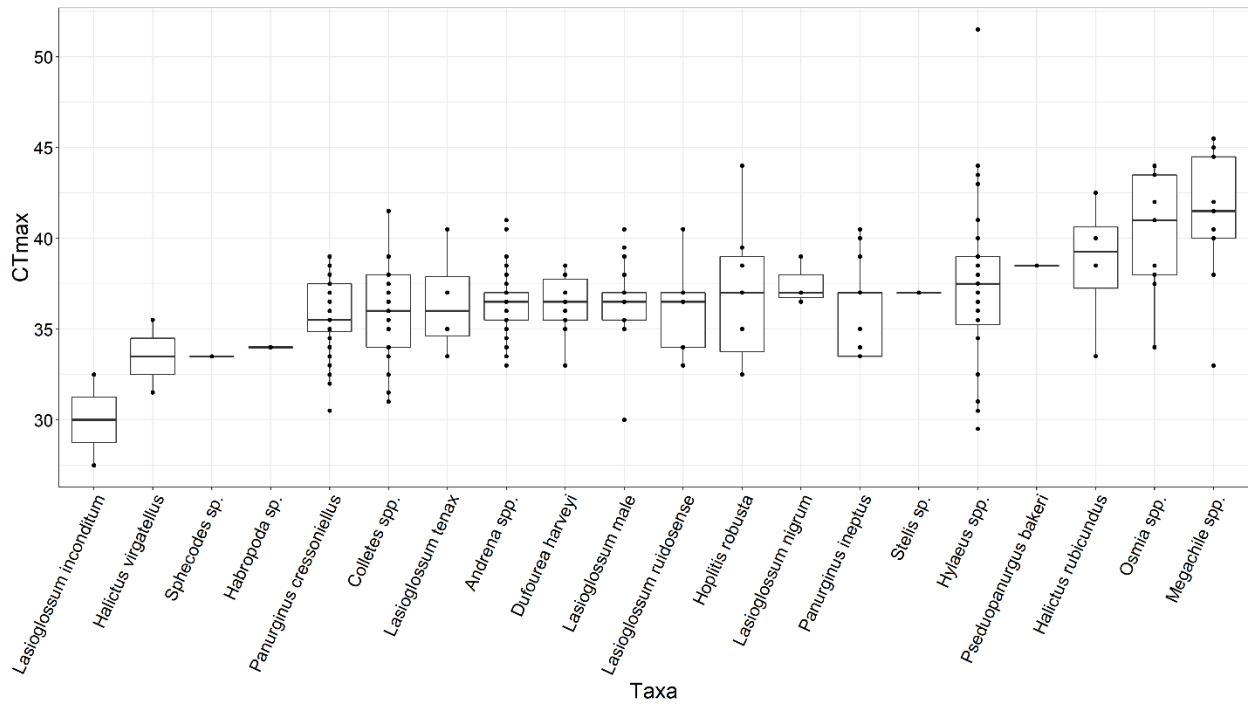


Figure 4.

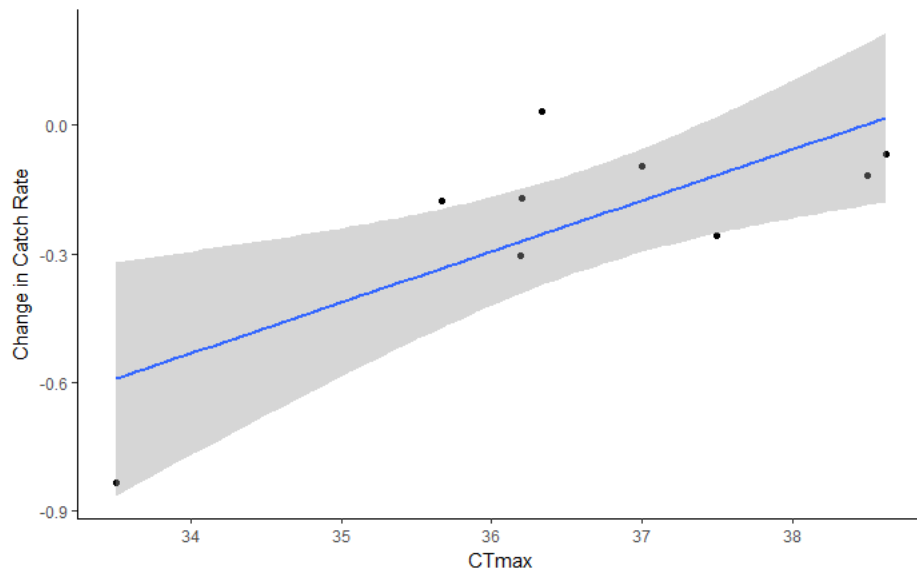


Figure Captions

Figure 1. Study sites near the Rocky Mountain Biological Laboratory Crested Butte, CO, USA. Sites mapped in red are those included as part of the long-term bee monitoring effort described in Gezon et al. 2015, while the site in yellow was unique to this sampling effort.

Figure 2. The distribution of critical thermal maxima (CT_{max}) measured in solitary bees collected from June 29, 2018 to July 25, 2018 near the Rocky Mountain Biological Laboratory, Crested Butte, CO, USA.

Figure 3. Boxplot of the measured CT_{max} for solitary bee taxa captured from June 29, 2018 to July 25, 2018 around the Rocky Mountain Biological Laboratory, Crested Butte, CO, USA.

Figure 4. Bee taxa with a higher CT_{max} performed significantly better in the year following a hotter-than-average year than those with a lower CT_{max} .

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