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# Before the brink: considering sublethal impacts of climate change on stingless bee flight performance

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## ABSTRACT

Vulnerability to climate change is often predicted using species critical thermal limits ($CT_{MAX}$), the temperature at which an organism experiences a loss of physiological function. However, climate change will impact species physiological traits, behaviour, reproduction, and phenology before their critical thermal limits are reached. Thermal performance curves (TPCs) are one way to evaluate how temperature impacts ecologically relevant traits before species reach their upper thermal limits. Comparing species TPCs to the climatic conditions they experience through their geographic ranges can provide insights into how vulnerable species are to further climate change and how their ranges might be altered. We assessed how flight performance – an important trait for escaping predators, dispersing, and finding resources and mates – is affected by temperature in two agriculturally important species of native stingless bees, *Austroplebeia australis* and *Tetragonula carbonaria*. *A. australis* has a broad arid/tropical geographic range and *T. carbonaria* has a narrower coastal subtropical range. We tested the thermal flight performance of both species at seven distinct temperatures between 18 and 42 °C. *A. australis* had a broader TPC and higher thermal optima than *T. carbonaria* reflecting the broader range of environmental temperatures and the hotter average environmental conditions they experience across their range. However, while *A. australis* could maintain flight performance at hotter temperatures, a larger proportion of their range is hotter than their thermal optima, suggesting their geographic range might constrict prior to the range of *T. carbonaria*.

## 1. Introduction

The capacity to tolerate further anthropogenic climate change is often evaluated by using measures such as upper critical thermal limits, the temperature at which an organism loses physiological function (Dunlap, 1968; Bennett et al., 2021; da Silva et al., 2021; Hoffmann and Sgro, 2018; Kellermann et al., 2009). Upper thermal limits can be helpful for ranking species vulnerability to climate change by calculating metrics such as warming margins or thermal safety margins (da Silva et al., 2023; Sunday et al., 2014). However, climate change will have impacts on species performance and fitness well before they reach their upper thermal limits and drive species towards local extinction (da Silva et al., 2020; van Heerwaarden and Sgrò, 2021). For example, species might have a reduced ability to obtain food at warmer temperatures, or their physiological capacity for growth and reproduction could be impacted. These impacts are likely to have knock-on effects on species geographic ranges, and ability to provide functional roles in ecosystems at lower temperatures than predicted from metrics such as $CT_{MAX}$ (maximum critical thermal tolerance) (Buckley et al., 2022; Carlo et al., 2018; White and Dillon, 2023). Thus, examining sublethal exposure to elevated temperatures is key for understanding how climate change will influence organismal performance, fitness, and ecosystem function in the future.

Estimating the shape of species thermal performance curves (TPC) (i.e. examining the relationship between performance and temperature) for traits with clear ecological relevance (such as locomotion, metabolic rate, and fertility), can provide crucial information on the range of thermal conditions species can perform optimally, as well as how further climate warming will impact species life history traits (Angilletta, 2009; Jayatilaka et al., 2011; Kenna et al., 2021; van Heerwaarden and Sgrò,

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2021) (Fig. 1). Generally, once a species thermal performance optima is reached (Fig. 1; the temperature at which they perform best), performance rapidly declines with further increases in temperature (Angilletta, 2009). Understanding how quickly performance declines with temperatures above species thermal optima is thus crucial for understanding sublethal effects of climate change on performance and fitness (Buckley et al., 2022).

The slope of the relationship between performance and temperature at temperatures above a species' thermal optima depends on whether the species have narrow or broad thermal performance breadths (Fig. 1). Thermal performance breadth is the range of temperatures where performance exceeds an arbitrary threshold, where 80 % of maximal performance is commonly used (Angilletta, 2009; Angilletta et al., 2010). Performance breadth is hypothesised to depend on evolutionary history and geographic ranges (Calosi et al., 2010; Gaston and Spicer, 2001; Gilchrist, 1995). Species with broad geographic ranges (which tend to experience a great deal of thermal variability) are expected to have broad TPCs, and those with narrower geographic ranges (that likely experience less thermal variability throughout their range) are expected to have narrower TPCs (Fig. 1) (Calosi et al., 2010; Clusella-Trullas et al., 2011; Gaston and Spicer, 2001); however, support for these generalisations is mixed (da Silva et al., 2019). Optimal performance is also expected to be impacted by thermal performance breadth, whereby thermal specialists with narrow thermal performance curves have greater optimal performance than thermal generalists with broad thermal performance curves (Angilletta, 2009). This is known as the 'jack-of-all-trades master of none' hypothesis, where thermal generalists have lower thermal performance optima than specialists due to energy allocation trade-offs, potentially due to biochemical constraints in enzyme structure at different temperatures (Levins, 1968; Somero, 1978; Angilletta, 2009). However, this hypothesis also has equivocal support, where the jack-of-all-trades is also known to be a master of all (i.e. thermal generalists perform better at all temperatures) (Huey and Hertz, 1984). By estimating how quickly species performance will decline at temperatures over their thermal optima we can begin to predict how sublethal/near-term changes in climate will impact species behaviour, fitness, and how they might shift their ranges with further climate change.

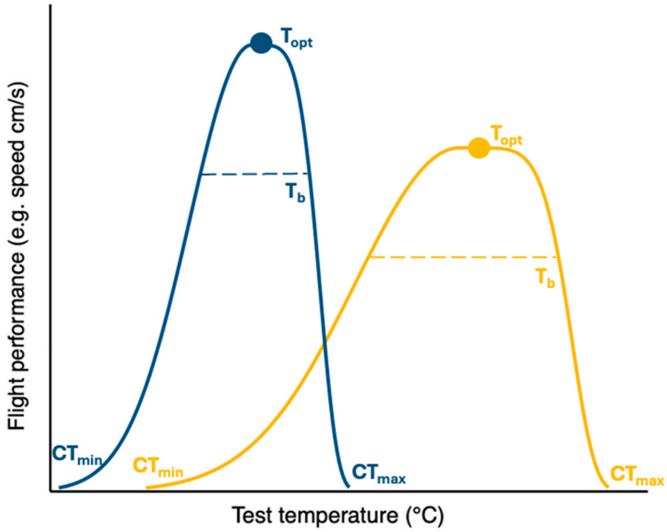

**Fig. 1.** Conceptual illustration of the thermal performance curves of a species with a narrow geographic range that experiences a moderate amount of thermal variation (blue), and a species with a broad geographic distribution that experiences a large degree of thermal variability (yellow). $T_{opt}$ = optimal performance temperature, $T_b$ = thermal performance breadth, $CT_{min}$ = thermal minimum, $CT_{max}$ = thermal maximum. Thermal performance curve illustration inspired by Huey and Stevenson (1979) and Angilletta (2009).

The effect of temperature on ecologically important performance traits, such as flight, can provide insights into species evolutionary histories and how further climate change will influence species functional ecology (Clusella-Trullas et al., 2011). For most insects, flight is a key trait that facilitates escape from predators, finding mates, locating resources, and for small- and large-scale movement (Kenna et al., 2021). For pollinating insects, such as bees, which are the most important animal pollinators on earth (Michener, 2000), changes in temperature can influence their thermal foraging windows (Jaboor et al., 2022), and therefore pollination capabilities, which could have a range of negative cascading effects.

We examined the flight TPCs of two species of native Australian stingless bees, *Austroplebeia australis* and *Tetragonula carbonaria*. Stingless bees are generalist foragers that make important contributions to pollination of a wide range of native flora throughout the world's tropics and subtropics (Bueno et al., 2023). *A. australis* has a broad arid/tropical geographic range where they likely experience more climatic variability across their range (Fig. 2) (Dollin et al., 2015; Halcroft et al., 2013), than *T. carbonaria* which has a narrower subtropical/temperate distribution (Fig. 2). *A. australis* are also likely to experience hotter maximum environmental temperatures (with their tropical/arid range) than *T. carbonaria*, which is reflected by their higher critical thermal maxima (Nacko et al., 2023). Thus, we expect the thermal performance curve of *A. australis* to look similar to the broad (yellow) thermal performance curve in Fig. 1, and the *T. carbonaria's* thermal performance curve to look more similar to the specialist (blue) thermal performance curve in Fig. 1.

In this study, we had two main aims. First, to predict the impact of sublethal increases in temperature on important pollinator performance by assessing each species thermal flight performance curve. Second, to determine the vulnerability of each species to climate change across their geographic ranges by estimating the proportion of each species range where temperature exceeds their thermal optima and upper edge of their thermal performance breadth (where performance drops below 80 % capacity). By examining how temperature impacts flight performance (speed and acceleration) we will gain an understanding on how sublethal increases in temperature are impacting ecologically relevant traits before species reach their upper thermal limits and go locally extinct from climate change.

## 2. Methods

### 2.1. Experimental protocol

*Tetragonula carbonaria* and *Austroplebeia australis* workers were collected from nest boxes (5 and 3 boxes respectively) on the Macquarie University main campus. All nests have been located on campus for multiple years, and thus all bees were locally acclimatized to the same environmental conditions. Two of the *A. australis* nests were sourced from https://zabel.com.au/in 2003 (one black and one orange abdomen phenotype), and the third nest was a black phenotype sourced from southeast Queensland in 2008. The black phenotype is more common in central/northern Australia, and the orange phenotype is more common in eastern Australia, however, they co-occur in the northwest of their distribution and individuals with mixed characteristics are found throughout the distribution (Dollin et al., 2015). The *T. carbonaria* nests were sourced from the Ku-ring-gai council stingless bee program. Bees were collected from nest entrances using an aspirator (in batches of 3 individuals per nest multiple times per day) and placed into plastic collection vials with a foam lid to allow airflow. Bees were collected between 9am–12pm roughly 10 min before they were placed into an acclimation chamber set at the same temperature as the daily test temperature for 1 h prior to testing their flight performance at different acute test temperatures. We tested flight performance at seven acute temperatures (18, 22, 26, 30, 34, 38, 42 °C) (one test temperature per day) in a randomized order (test day in Supplementary data). We tested

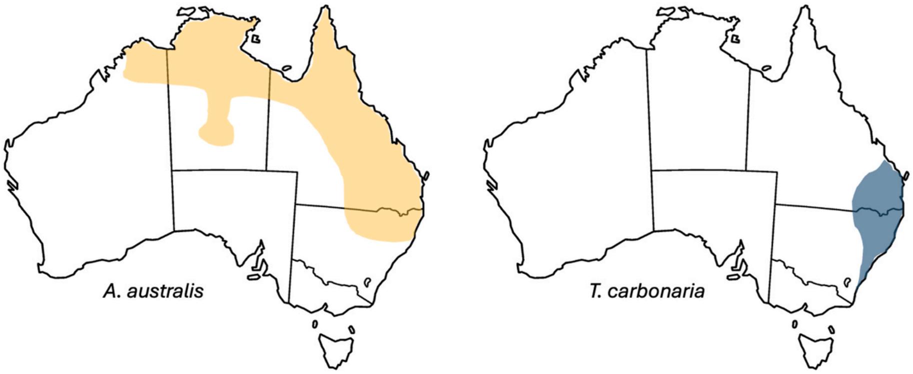

**Fig. 2.** Geographic range of *Austroplebeia australis* (left) based on observed records from (Dollin et al., 2015) and *Tetragonula carbonaria* (right) distribution adapted from (Heard, 2016; Vlasich-Brennan, 2023).

approximately 30 individuals in each species at each test temperature, which resulted in 195 records of *A. australis* and 210 records of *T. carbonaria* (sample sizes for each test temperature provided in Supplementary Table 1). Individuals were tested once and then released at the end of the day. Because worker numbers in each hive are high (~4000 & 10,000 for *A. australis* and *T. carbonaria* respectively), it is unlikely we re-sampled the same individuals at different test temperatures.

To measure flight performance (speed and acceleration), individual bees were placed at the entrance of a transparent temperature-controlled flight tunnel (1m in length, 10 cm in diameter). The flight tunnel was installed within a 46L cooler box which was fitted with a TE Technology Inc., USA, AC-027 air cooler/heater (Fig. 3). The temperature of the cooler box and flight tunnel was set and maintained with a TE Technology TC-720 temperature controller. Temperature was monitored inside the flight tunnel with a TE Technology MP-3193 thermistor, which communicates with the temperature controller on how to adjust the temperature to maintain the set test temperature. The flight tunnel had many small holes drilled into it so that the test temperature would permeate homogeneously throughout the tunnel. The tunnel entrance was fitted with a styrofoam plug to maintain tunnel temperature, which was opened to place bees into the chamber. A thick (6 mm) perspex sheet replaced the lid of the cooler box so that flights could be filmed at 100 frames per second using a Chronos 2.1 high speed camera (Kron Technologies, Canada) that was set up on a tripod with a direct dorsal view of the transparent flight tunnel.

The end of the flight tunnel was positioned so that bees had the view of the sky as an escape stimulus. A clear cap (top of a large Petri dish) was placed at the end of the tunnel so that bees could not escape (and to keep tunnel temperature constant), but could still see the outside escape route. The inner walls of the cooler box were lined with vertical black and white gratings to provide optic flow information. Immediately upon release into the flight chamber bees flew towards the end of the tunnel to attempt escape. Bees were then collected and placed into individual vials. In batches of ~20, bees were then placed in a refrigerator so that they would slow down enough to allow a body mass measurement to be taken. Individual bee body mass was measured on a microbalance (Sartorius Entris II, BCA224I-1S). Bees were released back at their nest boxes once all bees were tested for the day so that the same bee was not tested twice throughout the day, and to avoid killing bees after the experiment.

### 2.2. *Flight performance extraction from video footage*

We carried out a frame-by-frame analysis and tracked head position of each bee using the DLTdv8 app (Hedrick, 2008) within Matlab version R2023b (Mathworks, Natick, Massachusetts). We extracted x,y coordinates, converted pixels into centimetres and smoothed flight paths using a smoothing function. Flight speed was extracted by calculating the distance between each consecutive point within the flight path and then using eq. (1) to calculate speed for each consecutive point comparison.

$$\text{Flight speed } (\text{cm}/\text{s}) = \text{displacement of head position between frames x 100 fps} / \text{scale (pixel to cm conversion)} \tag{Eq 1}$$

Flight acceleration was calculated using eq. (2).

$$\text{Flight acceleration } (\text{cm}/\text{s}^2) = \text{rate of change of flight speed} \ / \ \text{time (s) between frames} \tag{Eq 2}$$

We then extracted the maximum flight speed and acceleration for each individual at each test temperature.

### 2.3. *Statistics*

To determine how temperature impacts stingless bee flight performance and evaluate how species geographic ranges shape their thermal performance curves, we ran linear mixed effect models using the nlme package (Pinheiro et al., 2017) in the statistical program R (R Development Core Team, 2019). We ran two models, one with maximum flight speed and another with maximum acceleration as the response variable. Predictor variables were the same in both models and included body mass, test temperature (as a second degree polynomial), and

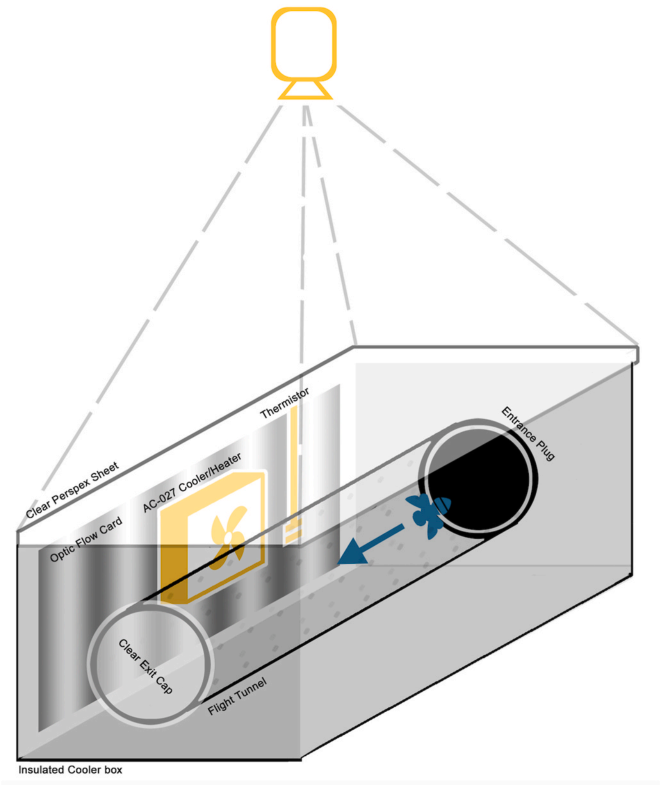

**Fig. 3.** Diagram of temperature-controlled flight tunnel experimental setup.

species. Colony number was included as a random factor within all models. We used model reduction and comparison using model Akaike Information Criterion (AIC) to arrive at a model that explained the most variation in flight speed and acceleration. Significance of predictor variables were tested using likelihood ratio tests.

### 2.4. *Thermal performance optima and breadth*

We calculated the thermal optima and maximum flight performance by estimating the quadratic equation associated with each species thermal performance curve. We then calculated the temperature at which performance was highest (thermal optima) by calculating the x-axis vertex of the quadratic equation using eq. (3),

$$\text{x vertex} = -\,b/2a. \qquad \text{(Eq 3)}$$

To determine the maximum flight performance at the thermal optima, we calculated the y-axis vertex using eq. (4),

$$\text{y vertex} = a * \text{x vertex}^2 + b * \text{x vertex} + c. \qquad \text{(Eq 4)}$$

To determine the thermal performance breadths of each species we calculated the range of test temperatures where performance was within 80 % of the thermal performance optima.

### 2.5. *Climatic variability throughout species geographic ranges*

To quantify the amount of climatic variability within each species geographic range, we extracted their observed GPS coordinates from GBIF (doi: https://doi.org/10.15468/dl.6refur & doi: https://doi.org/10.15468/dl.gmfphe). *T. carbonaria* is known to have isolated allopatric populations in Queensland, apparently restricted to higher altitude ranges of Australia's Great Dividing Range. It also has a morphologically cryptic cogeneration (*T. hockingsi*) which occurs in many lower altitude regions throughout Queensland, making it challenging to precisely map the distribution in some areas. For our models, we therefore chose a conservation estimate of *T. carbonaria* distribution by restricting only to (i) southern populations and (ii) regions with more than one datapoint. From these coordinates we extracted the maximum temperature of the hottest month (BIO5) and minimum temperature of the coldest month (BIO6), and mean annual precipitation (BIO12) at each occurrence record for each species from Worldclim2.1 at 2.5 min resolution (Fick and Hijmans, 2017).

### 2.6. *Predict how climate change is already impacting species performance*

To determine the overall rate at which performance will decline in each species as environmental temperatures surpass their thermal optima, we estimated the linear slopes between each species' thermal optima and their performance at 42 °C (hottest experimental temperature).

To understand how climate change is already impacting flight performance, we calculated the proportion of each species range where the hottest temperatures of the hottest month (BIO5) is higher than the thermal optima and upper thermal breadth for each species. For this, we constructed simple generalised linear species distribution models following the online tutorial by Jeff Oliver (https://jcoliver.github.io/learn-r/011-species-distribution-models.html), which included creating pseudo absence data, training our distribution models, and predicting species ranges based off a likelihood threshold.

## 3. Results

### 3.1. *Flight speed and acceleration*

For both the flight speed and acceleration models, we found that TPCs differed between the two species, where the best fitting models included a significant interaction between test temperature and species (flight speed: $F = 14.0$, $df = 2/390$, $p < 0.001$; acceleration: $F = 15.62$, $df = 2/390$, $p < 0.001$) (Tables 1 and 2). *A. australis* had a higher optimal performance temperature, a broader thermal performance curve, and greater optimal flight performance for both maximum speed and acceleration compared to *T. carbonaria* (Table 3; Fig. 4). Flight performance (speed and acceleration) 95 % confidence intervals around the modelled means overlapped at temperatures below 30 °C suggesting no difference in flight performance at colder test temperatures, however, from 30 °C onwards, *A. australis* flew faster and accelerated faster than *T. carbonaria* on average.

Body mass was not included within the model with the lowest AIC and it did not have a significant effect on flight speed or acceleration so it was removed as a predictor variable so that flight speed of all individuals (including those that escaped after the flight speed testing and could not be weighed) could be included within the analysis. We also assessed whether body mass impacts thermal flight performance within each species using linear models, but found that body mass did not play an important role in flight speed (Supplementary Table 2).

To understand the current impact of climate change on each species,

**Table 1**
AIC model comparison for maximum flight speed and maximum acceleration.

| Model | df | AIC | ΔAIC |
|---|---|---|---|
| *Maximum flight speed* | | | |
| poly(Test temp,2) * species | 8 | 2406.19 | 0 |
| poly(Test temp,2) + species | 6 | 2429.39 | 23.2 |
| Mass + poly(Test temp, 2) * species | 44 | 2446.76 | 40.57 |
| Mass + poly(Test temp, 2) + species | 42 | 2467.68 | 61.49 |
| Mass + Test temp * species | 42 | 2558.12 | 151.93 |
| *Maximum acceleration* | | | |
| poly(Test temp,2) * species | 8 | 4292.02 | 0 |
| poly(Test temp,2) + species | 6 | 4318.54 | 26.52 |
| Mass + poly(Test temp, 2) * species | 44 | 4334.71 | 42.69 |
| Mass + poly(Test temp, 2) + species | 42 | 4355.94 | 63.92 |
| Mass + Test temp * species | 42 | 4432.61 | 140.59 |

**Table 2**
Model summary of the effect of test temperature (modelled as a second-degree polynomial) on maximum flight speed for each species.

| Coefficient | Estimate ±SE | df | t-value | p-value |
|---|---|---|---|---|
| *Maximum flight speed* | | | | |
| Intercept | 12.13 ± 0.38 | 390 | 32.03 | <0.001 |
| poly(test temp, 2) 1 | 43.07 ± 7.03 | 390 | 6.12 | <0.001 |
| poly(test temp, 2) 2 | −43.54 ± 6.94 | 390 | −6.27 | <0.001 |
| Species (*T. carbonaria*) | −2.98 ± 0.52 | 9 | −5.77 | <0.001 |
| poly(test temp, 2) 1 x species (*T. carbonaria*) (slope) | −46.85 ± 9.54 | 390 | −4.96 | <0.001 |
| poly(test temp, 2) 2 x species (*T. carbonaria*) (quadratic curvature) | −18.64 ± 9.42 | 390 | −1.98 | 0.046 |
| *Maximum acceleration* | | | | |
| Intercept | 124.74 ± 3.46 | 390 | 36.08 | <0.001 |
| poly(test temp, 2) 1 | 434.43 ± 72.25 | 390 | 6.01 | <0.001 |
| poly(test temp, 2) 2 | −395.71 ± 71.19 | 390 | −5.56 | <0.001 |
| Species (*T. carbonaria*) | −22.97 ± 4.79 | 9 | −4.79 | <0.001 |
| poly(test temp, 2) 1 x species (*T. carbonaria*) (slope) | −497.78 ± 97.12 | 390 | −5.13 | <0.001 |
| poly(test temp, 2) 2 x species (*T. carbonaria*) (quadratic curvature) | −22.74 ± 96.67 | 390 | −2.36 | 0.019 |

we estimated the rate at which flight performance declines once each species reached its thermal optima. We found that flight speed performance declines almost twice as rapidly with each degree increase in environmental temperature in *T. carbonaria* than *A. australis* (Table 3). We also quantified the climatic conditions (environmental temperature (minimum, maximum, thermal variability) and mean precipitation) each species experiences at their occurrence records. *A. australis* is exposed to higher maximum temperatures, greater thermal variability, and drier habitats than *T. carbonaria* (Table 3). However, differences in the thermal variability throughout their ranges was not as great as expected (*A. australis* experiences an additional 4 °C of thermal variability throughout their habitat on average).

To evaluate how warming climates are impacting species performance, we estimated the proportion of their ranges where environmental temperatures already exceed their thermal optima and the upper edge of their thermal breadths (Table 4). We found that BIO5 temperatures (mean hottest temperature of the hottest month) do not exceed the upper edge of species thermal breadths, meaning that flight performance does not drop below 80 % of their maximum flight capacity throughout their entire range at present (Fig. 5). However, very large proportions of species ranges are already experiencing environmental temperatures (BIO5) above their thermal optima (74.15, and 59.39 % for *A. australis* and *T. carbonaria* respectively), where flight performance will decline with further increases in environmental temperature, where the rate of decline will be more rapid in *T. carbonaria* than *A. australis* (Tables 3 and 4).

## 4. Discussion

Using a custom-made flight tunnel, we investigated how escape flight performance (speed and acceleration) varied with ecologically relevant test temperatures in two species of stingless bees, *A. australis* and *T. carbonaria*. We found that both species have broad thermal breadths where they can maintain flight speed within 80 % of their capacity across thermal ranges of 13 °C (23.09–36.42 °C) and 17 °C (24.79–42 °C), respectively. These thermal flight performance breadths are quite broad compared to other insect species, such as 11 species of broadly distributed *Drosophila* which only have thermal flight performance breadths between ~3 and 7 °C (De Araujo et al., 2019). The broad thermal flight performance breadths of Australian stingless bees are likely to facilitate pollination across broad climatic conditions, and potentially buffer pollination services for the plants they pollinate in the near-term as climates continue to change.

We found that *A. australis* which has an arid/tropical geographic range had a broader thermal performance breadth for both flight speed and acceleration than *T. carbonaria,* which has a narrower subtropical range. We also found that *A. australis* had a higher thermal performance optima (33.47 °C) than *T. carbonaria* (29.70 °C), reflecting the higher maximum environmental temperatures that they experience throughout their geographic range. However, speed and acceleration at cooler test temperatures (18 °C–26 °C) did not differ between the species (overlapping confidence intervals), even though *T. carbonaria* experiences cooler climates on average (Table 3). In contrast to our study, Kenna et al. (2021) did not find a TPC shape relationship between flight speed and test temperature. This could be due to differences in experimental

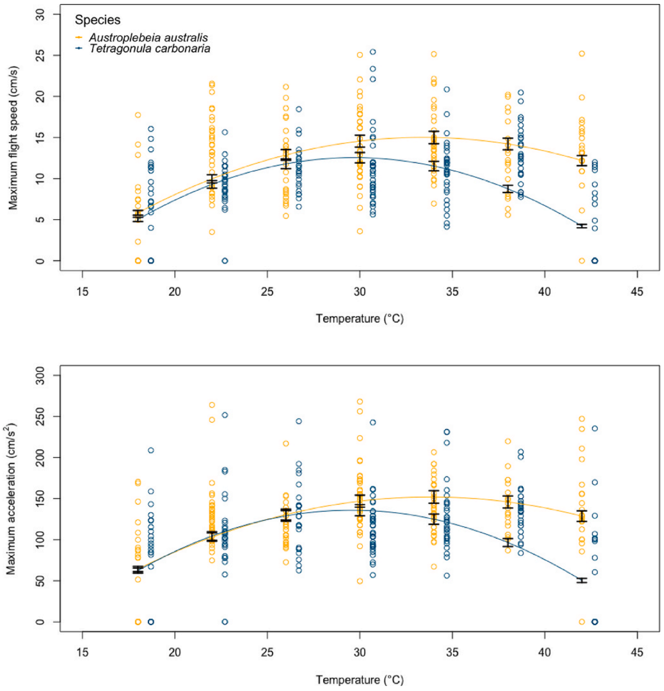

**Fig. 4.** Maximum flight speed (top) and acceleration (bottom) of *A. australis* (yellow) and *T. carbonaria* (blue) across the 7 experimental test temperatures. Lines go through the model means of each species' performance at each test temperature. Modelled 95 % confidence intervals are represented by error bars around the modelled mean performance for each species at each test temperature. Data at each temperature are offset only to improve visualisation.

**Table 3**
Summary table of species thermal flight speed performance curve metrics and climatic conditions each species experiences at their occurrence records.

| Species | Topt (°C) | Optimal flight speed (cm/s) | Thermal breadth (°C) | Rate of flight speed decline post $T_{opt}$ per deg warming | Max temp (°C) BIO5 | Min temp (°C) BIO6 | Climatic variability (°C) | Mean annual precip (mm) BIO12 |
|---|---|---|---|---|---|---|---|---|
| *Austroplebeia australis* | 33.47 | 15.06 | 17.21<br>(24.79–42) | −0.35 | 38.86 | 2.95 | 35.91 | 777.7 |
| *Tetragonula carbonaria* | 29.70 | 12.56 | 13.33<br>(23.09–36.42) | −0.69 | 31.46 | 0.19 | 31.27 | 1225.7 |

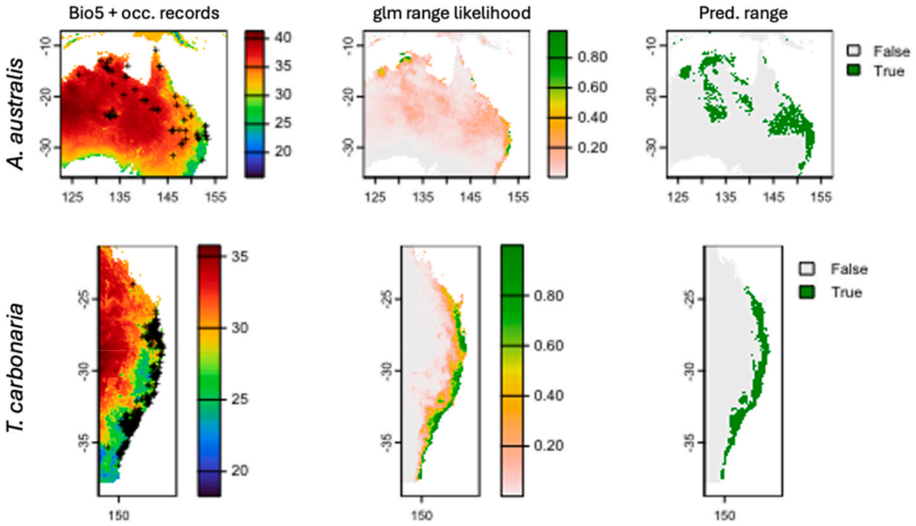

**Fig. 5.** Geographic distribution of *A. australis* and *T. carbonaria*. Left panel: Present day species occurrence records plotted over Worldclim variable BIO5 climate raster (hottest temperature of the hottest month) for *A. australis* (top row) and *T. carbonaria* (bottom row). Middle panel: generalised linear species distribution model predictions of species geographic range where colours indicate likelihood of occurrence. Right: predicted species geographic ranges above modelled likelihood threshold values (true (green) indicates where species are highly likely to occur, false (grey) areas indicate where species are unlikely to occur). BIO5 values within species predicted ranges were used to estimate the proportion of species ranges that exceed species $T_{opt}$ and upper edge of their thermal breadth.

protocol used between studies, they used a flight mill testing sustained flight speed, where the present study tested burst speed through a flight tunnel.

The 'jack-of-all-trades, master-of-none' hypothesis predicts that species that have broader thermal performance curves should have reduced optimal performance compared to thermal specialists (Huey and Hertz, 1984). Despite the broader thermal performance breadth observed in *A. australis*, they had greater flight performance (speed and acceleration) at their thermal performance optima, and at all test temperatures higher than 26 °C (Fig. 4). This means that *A. australis* is not a 'jack-of-all-trades, master-of-none' but is in fact a 'jack-of-all-trades, master-of-all', supporting the hypothesis proposed by Huey and Hertz (1984), and reiterated by Gaston and Spicer (2001). A potential reason for why *A. australis* might have faster flight speeds than *T. carbonaria* could be due to differences in colony size, where *A. australis* are estimated to have a worker population of only 4000 individuals (Halcroft et al., 2011), but 10,000 for *T. carbonaria* (Heard, 2016). Perhaps there is stronger selection on traits, such as escape speed and acceleration, that facilitate survival from predators in species that live in smaller groups. When the number of workers bringing resources back to the nest are reduced, loss of workers could have a larger impact on colony fitness. Interestingly, *A. australis* have been reported to have the longest longevity compared to all other eusocial bees recorded (Halcroft et al., 2013), further indicating they have likely developed traits to facilitate survival over long durations compared to other species. Finally, species thermal performance breadths are directly linked to how rapidly their performance declines at temperatures above their thermal performance optima (Buckley et al., 2022), where those with narrow performance curves will have more rapid declines in performance than those with broad thermal breadths (see the next section).

### *4.1. Impacts of climate change on stingless bees*

Escape flights need to be fast and precise since the penalty for slow escape is usually severe. Reduced escape speed and acceleration at environmental temperatures above species thermal optima could make stingless bees more susceptible to predation as climates continue to warm. To quantify the vulnerability of these important pollinators to climate change, we estimated the rate at which flight performance will decline when environmental temperature surpasses their thermal optima. We found that flight speed and acceleration will drop at a faster rate in *T. carbonaria* than *A. australis*, owing to their narrower thermal performance curves. However, when assessing vulnerability to climate change it is also important to consider differences in the environmental conditions species experience within their ranges. Because *T. carbonaria* inhabit climatic conditions that are cooler than *A. australis* on average, neither species is exposed to (mean) maximum temperatures higher than the upper edge of their thermal performance breadth under current climate conditions, which means they can maintain flight performance within 80 % capacity throughout their entire geographic ranges. However, we also estimated the proportion of each species range that experiences environmental temperatures over each species thermal optima. These calculations show that a large proportion of each species range is already exposed to environmental conditions above their thermal optimum. However, even though *T. carbonaria* have a lower thermal optima to *A. australis*, a greater proportion of the geographic range of *A. australis* will be exposed to environmental temperatures above their thermal optima because they inhabit environments that are much hotter than *T. carbonaria* on average (Table 4; Fig. 5).

**Table 4**
Percentage of species' distribution ranges where BIO5 (hottest temperature of hottest month) is greater than each species upper thermal breadth (where performance dips below 80 % capacity), or is over $T_{opt}$ under present climatic conditions.

| Species | BIO5 > Topt | BIO5 > upper Tb |
|---|---|---|
| *Austroplebeia australis* | 74.15 % | 0 % |
| *Tetragonula carbonaria* | 59.39 % | 0 % |

We also estimated whether body mass explained differences in thermal flight performance between and within each species as body mass affects metabolic rate, which impacts thermal tolerance (Padfield et al., 2016; Peralta-Maraver and Rezende, 2021). However, in our study, body mass did not explain differences in flight speed between or within the two species (Supplementary Table 2). Previous research suggests that body mass is an important predictor for flight speed in beetle species (Farisenkov et al., 2020) and bumble bees (Kenna et al., 2021). Perhaps in very small insects such as stingless bees (which are about 10x smaller than bumble bees), other morphological traits such as wing area are better predictors of traits like flight speed. We aimed to conduct a non-lethal experiment (all bees were released after testing) so we were unable to collect wing area as accurate estimates require wings to be removed and photographed under a microscope. As variation in flight speed at each temperature within each species is not explained by body mass, it could potentially be explained by other factors such as age, worker role (e.g. forager or worker), or differences in individual motivation. These factors would be interesting to explore in further studies.

### 4.2. *Study limitations*

While species thermal performance curve metrics did reflect the environmental conditions they experience throughout their geographic ranges on average, we did not assess how TPC shape might vary across populations within each species (Sinclair et al., 2016). Populations are expected to have different thermal performance breadths and optima due to local genetic adaptation and plastic responses to different climatic regimes experienced throughout a species range. Unfortunately, there are actually very few intraspecific examples that compare population TPCs across climatic gradients (rather than thermal limits) (but see (Bennett et al., 2019; Schmidt and Donelson, 2024). As thermal limits are often correlated with climatic gradients across populations (Castañeda et al., 2015; Healy et al., 2019; Pereira et al., 2017), it is likely that thermal optima will also shift with mean or extreme climates across species ranges. However, if intraspecific trait-climate relationships match interspecific correlations, we are likely to see an even closer association between thermal optima and environmental temperature than CTmax across populations, as thermal optima tends to increase more with environmental temperature (is more labile) than CTmax across species (Buckley et al., 2022). This means that species vulnerability is likely underestimated if the rate of performance decline is considered, rather than simply species upper thermal limits (Buckley et al., 2022). Finally, whether intraspecific variation in thermal breadths change predictably with changes in thermal variability across populations remains understudied. Thermal breadths depend on both population acclimation capacity and how predictable environmental fluctuations are within their environment making them difficult to estimate (da Silva et al., 2019). Thus, to characterise how warming climates will impact whole species across their geographic ranges, and to gain a clearer understanding on how TPC shape evolves in general, testing the TPCs of multiple populations across species ranges will be key.

In this study we did not account for variation in microclimate species' experience throughout their ranges nor did we account for their capacity to behaviourally thermoregulate. Many species have the capacity to buffer themselves from extreme thermal conditions by moving into the shade, underground, or into moist microhabitats (Kemppinen et al., 2024). For example, some insect species have the capacity to behaviourally thermoregulate by contracting wing muscles to warm up, and cooling down via convection and evaporative cooling (De Farias-Silva and Freitas, 2021). Eusocial bees are known to use a range of behaviours to moderate their nest temperatures such a fanning, nest evacuation, evaporative cooling, metabolic heat production and direct incubation (Ostwald et al., 2024). By moving into more optimal conditions, or altering the temperature around them, species can influence what environmental conditions they are exposed to and might therefore be able to avoid unfavourable environmental conditions and associated reductions in performance all together. However, changes in species behaviour due to unfavourable environmental conditions can also limit species interactions if changes in activity time are not synchronised, and can impede species growth and reproduction if the time for acquiring energetic resources or mates is reduced due to narrowing thermal activity windows (De Farias-Silva and Freitas, 2021; Jaboor et al., 2022).

## 5. Conclusion and path forward

We found that Australian stingless bees *A. australis* and *T. carbonaria* have broad thermal performance curves, but that large proportions of their ranges already experience environmental temperatures over their thermal flight performance optima. Flight performance drops more rapidly at temperatures over their thermal optima in *T. carbonaria* than *A. australis*, however, a larger proportion of the *A. australis* range is exposed to temperatures over their thermal optima suggesting their range could be more likely to become restricted with further climate warming.

Large global datasets, such as GlobTherm (Bennett et al., 2018) of species thermal tolerances exist for traits such as upper and lower thermal limits. These large databases are useful for understanding how species traits evolve across space and time, and also for ranking species vulnerabilities to climate change. But, no such databases exist for species TPCs that we are aware of. This is likely due to the wide variety of methods used to estimate species TPC across taxa and for the many different performance traits assessed. However, a broad range of methodologies are also employed and included within thermal tolerance databases (Allen et al., 2016; Clusella-Trullas et al., 2021; Diamond and Yilmaz, 2018; Terblanche et al., 2007). Despite these methodological differences, analyses have found that estimates of thermal limits using different methodologies can be standardised using conversion calculations (Jørgensen et al., 2019). If species thermal performance curves are tested across similar test temperatures, animals are brought to test temperatures at a similar rate, and comparable traits are tested (i.e. locomotion traits such as speed to understand climate change impacts on predator-prey dynamics), it is likely that we will be able to gain useful insights on the sublethal impacts of climate change on interacting species and ecosystems from large species TPC databases.

It is also worth noting that within species, different traits have distinctly shaped thermal performance curves (Kellermann et al., 2019; Schmidt and Donelson, 2024), which makes predicting overall species vulnerabilities to climate change tricky. Which traits should then be chosen to make inferences on climate change vulnerability? For traits like locomotion, it is easy to link predators and prey since traits like speed are easily comparable. When trying to understand the energetic demands of species and how they might change in warming environments, most studies use metabolic rate, which is also easily comparable across taxa (Seebacher et al., 2015; White et al., 2022). However, species are mosaics of traits, and understanding how key traits interact, and how and when different traits will be impacted by climate change is important. Better predictions of the impacts of warming on species performance before they reach their upper thermal limits will facilitate earlier and improved conservation action and mitigation strategies.

## CRediT authorship contribution statement

**Carmen Rose Burke da Silva:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lachlan David Macnaughtan:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Oliver William Griffith:** Writing – review & editing, Supervision. **Ajay Narendra:** Writing – review & editing, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis.

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## Declaration of competing interest

There are no competing interests.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2025.104286.

## Data availability

The raw data is available as a supplementary dataset.

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