

# Thermal flight performance reveals impact of warming on bumblebee foraging potential

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## Abstract

1. The effects of environmental temperature on components of insect flight determine life-history traits, fitness, adaptability and, ultimately, organism ecosystem functional roles. Despite the crucial role of flying insects across landscapes, our understanding of how temperature affects insect flight performance remains limited.
2. Many insect pollinators are considered under threat from climatic warming. Quantifying the relationship between temperature and behavioural performance traits allows us to understand where species are operating in respect to their thermal limits, helping predict responses to projected temperature increases and/or erratic weather events.
3. Using a tethered flight mill, we quantify how flight performance of a widespread bumblebee, *Bombus terrestris*, varies over a temperature range (12–30°C). Given that body mass constrains insect mobility and behaviour, bumblebees represent a useful system to study temperature-mediated size dependence of flight performance owing to the large intra-colony variation in worker body size they exhibit.
4. Workers struggled to fly over a few hundred metres at the lowest tested temperature of 12°C; however, flight endurance increased as temperatures rose, peaking around 25°C after which it declined. Our findings further revealed variation in flight capacity across the workforce, with larger workers flying further, longer, and faster than their smaller nestmates. Body mass was also positively related with the likelihood of flight, although importantly this relationship became stronger as temperatures cooled, such that at 12°C only the largest workers were successful fliers. Our study thus highlights that colony foraging success under variable thermal environments can be dependent on the body mass distribution of constituent workers, and more broadly suggests smaller-bodied insects may benefit disproportionately more from warming than larger-bodied ones in terms of flight performance.
5. By incorporating both flight endurance and likelihood of flight, we calculated a simple metric termed 'temperature-mediated foraging potential' to gain a clearer understanding of how temperature may constrain colony foraging. Of our tested

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temperatures, 27°C supported the highest potential, indicating that for much of the range of this species, higher mean daily temperatures as forecasted under climate warming will push colonies closer to their thermal optimum for flight. Subsequently, warming may have positive implications for bumblebee foraging returns and pollination provision.

#### KEYWORDS

alloethism, climate change, foraging range, insect pollinator, temperature, tethered flight mill, thermal performance curve, worker size dependence

## 1 | INTRODUCTION

For the majority of insect species, flight is critical in facilitating important life-history traits including dispersal and resource exploitation (Zera & Denno, 1997). The influence that the dynamic surrounding environment has on flight behaviour and performance can therefore be a primary determinant of organism fitness and ecosystem functional roles (Greenop et al., 2020; Kenna et al., 2019; Kremen et al., 2007; Niitepõld et al., 2009). Understanding how temperature mediates insect flight performance, for example, can reveal species success across different geographical regions. Indeed, with regional temperature increases associated with insect population range shifts (e.g. Herrera et al., 2014; Jacobson et al., 2018; Kerr et al., 2015; Powney et al., 2019) and localised extinction risk (e.g. Soroye et al., 2020), there is a need to understand the thermal limits of insect flight. Furthermore, such studies will help us predict spatial movement of key insect functional groups under different scenarios of climate change and the subsequent impacts on ecosystem service provision (Rader et al., 2013). For insect pollinators, sensitivity of flight to temperature fluctuations could affect foraging and subsequent reproductive success while affecting pollination of flowering wild plants and crops with major ecological and economic implications (Duchenne et al., 2020; Gill et al., 2016; Potts et al., 2016). To date, however, we lack quantification of the degree to which flight performance changes over a thermal gradient for insect pollinators, or even insects in general (but see Niitepõld et al., 2009; Spiewok & Schmolz, 2006).

The shapes of the relationships between temperature and an organism's performance traits—thermal performance curves (TPC)—are crucial for understanding the functional responses of populations and communities to climatic fluctuations (Angilletta, 2006; Dell et al., 2011; Huey & Stevenson, 1979). By quantifying the TPC of flight performance, we can determine where insect pollinators are operating in respect to their thermal limits, and better understand flight responses to projected temperature change (IPCC, 2014). Understanding how individual mobility traits such as flight motivation, endurance and velocity respond to temperature can highlight the capabilities of foraging individuals to reach increasingly patchy floral resources under projected climate change (Jha & Kremen, 2013; Senapathi et al., 2017). This is particularly relevant

to eusocial bees such as bumblebees, which as central place foragers (have a fixed nest site), are unable to adaptively move to track within-season floral resource turnover and variation in microclimatic conditions (Bladon et al., 2020; Raine & Gill, 2015).

Bumblebees are keystone species in many terrestrial ecosystems (Goulson et al., 2011) and represent a group of insects that are critical for the pollination of many wild and cultivated plants (Breeze et al., 2011; Goulson, 2003; Velthuis & Van Doorn, 2006). It is thus concerning that recent research indicates them to be under threat from rising temperatures and frequent extreme heat events associated with climate change, pushing species more regularly towards their critical thermal (CT) limits (Sirois-Delisle & Kerr, 2018; Soroye et al., 2020; Vanderplanck et al., 2019). At present, these thermal limits are often determined by measures of tolerance or mortality (e.g.  $CT_{max}/CT_{min}$ ), where studies identify temperatures at which individuals enter unresponsive states or die (Hamblin et al., 2017; Oyen & Dillon, 2018; Pimsler et al., 2020; Zambra et al., 2020). However, the extent to which temperature constrains behavioural functions such as foraging, that likely operate within narrower thermal limits, is not well documented (Rader et al., 2013). This is despite us knowing that changes to flight performance alter the amount of food brought back for colony growth and hence fitness (e.g. Gill et al., 2012). To predict colony success under warming, we must therefore understand how individual flight across the collective foraging workforce is impacted by temperature.

As for most flying insects, bee flight muscle activity rates are a direct function of muscle temperature (Coelho, 1991; Heinrich, 1975; Woods, 2005). Bumblebees are heterothermic, meaning they can transition between ectothermic and endothermic states. Through endogenous heat production, individuals can raise their thoracic temperature to facilitate the required muscle temperatures for flight (Heinrich, 1975). The temperature of the surrounding environment will determine the energy expenditure of this thermogenic process, and thus ambient temperature should place constraints on bumblebee flight performance (Bishop & Armbruster, 1999; Dudley, 2000; Harrison & Roberts, 2000; Woods, 2005). This is supported by observations of bumblebee foraging activity changing in response to daily and/or seasonal variation in ambient temperature (Arce et al., 2017; Kwon & Saeed, 2003; Rader et al., 2013). What remains unclear, however, is which components of physical flight are

being affected by temperature to produce such effects. Moreover, when investigating these questions in social bumblebees, we need to consider that workers exhibit large intra-colony variation in body size, thought to be important for task partitioning (Couvillon, Fitzpatrick, et al., 2010; Goulson et al., 2002). Flight performance across the colony workforce is therefore unlikely to be uniform because key flight determinants, such as morphology and wing loading, are dependent on body mass (Billardon & Darveau, 2019; Bishop & Armbruster, 1999; Skandalis & Darveau, 2012). Indeed, worker body size has been reported to positively correlate with both foraging rates and range (Goulson et al., 2002; Greenleaf et al., 2007; Kapustjanskij et al., 2007; Spaethe & Weidenmuller, 2002; Worden et al., 2005). Size-dependent traits, such as thermogenic capacity, may also influence the thermal sensitivity of foraging workers. For example, the large body mass of alpine bumblebees is believed to allow individuals to forage in temperatures down to 5°C (Bishop & Armbruster, 1999; Corbet et al., 1993; Lundberg, 1980). To reveal colony-level foraging potential, therefore, we must elucidate the size dependence of flight performance.

Studying the physical flight of small mobile insects, however, has proved challenging. When examining flight behaviour under field or semi-field setups, it is difficult to isolate the effects of temperature from other confounding/covarying factors (Henry et al., 2014). Additionally, current tracking technologies typically cannot record a full foraging bout, with RFID tagging limited to recording bees moving past a fixed location, providing little information on what occurs during the flight trip (e.g. Gill & Raine, 2014). Harmonic Radar can track a bee over a foraging bout, but only in uncluttered landscapes and heavy tags likely confine potential foraging ranges, which would have a disproportionate effect on smaller bees (O'Neal et al., 2004; Osborne et al., 1999). To help address this challenge, we here use the benefits of a tethered flight mill under controlled environment conditions (Kenna et al., 2019; Minter et al., 2018; Tosi et al., 2017). We quantify how different components of flight for individual bumblebees (*Bombus terrestris*) respond over a thermal gradient and determine how these relate with worker body mass. We report how motivation to fly, flight 'endurance' (distance and duration) and flight velocity dynamics vary over a 12–30°C range. Finally, we use these individual-level flight performance results to develop a simple yet novel measure of 'temperature-mediated foraging potential'. We discuss how our findings reveal the ways that future changes in ambient temperature could affect the foraging potential and pollination service of bumblebee colonies, and the implications of our body-mass-specific performance findings for understanding responses of small- versus large-bodied insects.

## 2 | MATERIALS AND METHODS

### 2.1 | Bumblebee husbandry and tagging

Eight *Bombus terrestris audax* colonies, each containing 80–100 workers, were supplied by Biobest (distributed by Agralan Ltd). On

arrival, colonies were kept under red light in a controlled environment (CE) 'holding' room at 60% relative humidity (RH) and 21°C (mid-point temperature of tested thermal gradient). Colonies were fed 40% w/w sucrose solution ad libitum and 3 g of honey bee collected pollen daily (Agralan Ltd). During the 5 days after arrival, we applied the tagging protocol described in Kenna et al. (2019) to 60 workers per colony. This involved placing individuals on ice to cool and immobilise (Okubo et al., 2020) while a small circular galvanised iron tag was attached to the thorax using superglue (allowing later attachment to the flight mill magnet). Care was taken to ensure tag attachment would not interfere with wing movement, with the small tag size (diameter = 2 mm) easily fitting between the wing joints of even the smallest tested worker with no obstruction. For any substandard tag placement, the respective bee was removed from the experiment (<5% of bees per colony). Tagged workers were then placed in separate plastic pots for 60 min to rest, after which they were returned to the natal colony.

### 2.2 | Experimental design

We assessed individual flight performance at seven evenly distributed temperatures (12, 15, 18, 21, 24, 27 and 30°C; all at 60% RH) representing a realistic temperature gradient experienced by workers of temperate bumblebee spp. during the typical flight period months of April to September (Figure S1 for UK data; also see Fick & Hijmans, 2017; Hooker et al., 2018). The experiment was split into two blocks ( $n = 4$  colonies per block), which allowed an adequate number of workers to be tested while limiting potential differences in age and development. Per block, each temperature was tested on a single day. To try and account for any impacts of age or disturbance on normal behaviour caused by the tagging process, we swapped the order of testing between blocks. For block-1, temperatures were tested sequentially in ascending order over a 7-day period (i.e. 12°C on day 1, 15°C on day 2 and so forth), whereas block-2 was tested in a descending temperature order starting at 30°C. Per temperature, a cohort of 48 workers were tested ( $n = 24$  workers per block), consisting of six workers per colony.

We selected workers for testing such that the distribution of worker body mass within each temperature cohort was symmetric about a similar mean, as bumblebee colonies tend to produce workers with normally distributed body sizes throughout the colony life cycle under standard conditions (Couvillon, Jandt, et al., 2010). This was achieved by assigning workers to cohorts based on their wet mass directly following removal from the natal colony.

### 2.3 | Flight mill setup

The flight mill apparatus was adopted from Kenna et al. (2019), with each full rotation of the mill arm (from here-on termed 'circuit') recorded by an attached Raspberry Pi 3 computer (Model B). A magnet hanging from one end of the mill arm allows a metal tagged worker

to be attached through magnetic attraction, allowing the suspended bee to fly without carrying the load of the tag and subsequent flight circuits recorded (see Figure S2 for visual overview of feeding and flight mill setup). Wet mass of each tested bee was measured again directly preceding the flight trial, and subsequently a respective small (150 mg), medium (225 mg) or large (300 mg) counterweight (made of modelling clay) was attached to the end of the opposing arm of the mill based on which was closest to the worker's mass. The mills were setup in a separate CE 'testing' room set at the experimental ambient temperature (Table S1) and with the option of being under red (Philips TLD 58W Red 1SL/25; mean 660 nm) or white (Philips TLD 58W 840) light. Each mill was placed on non-glare green card, and providing a gap of 60 mm from the end of the mill arm (mill radius = 135 mm), we encircled each mill with a vertical border (border radius = 195 mm) of alternating black and white vertical stripes (Tosi et al., 2017; diameter of each stripe = 35 mm). The border (a) prevented potential interfering air currents, as wind speed has been shown to affect the hesitancy for worker flight take-off (Hennessy et al., 2020); (b) allowed relative isolation from neighbouring mills and (c) presented an identical visual stimulus to each tested worker, which can be a contributing factor in determining flight velocity (Baird et al., 2005).

## 2.4 | Flight trials

On each day of testing, four flight performance 'bouts' were run, with each bout consisting of six flight mills running simultaneously. The six workers per bout were removed from colonies (one worker from two colonies, and two workers from the remaining two colonies; Table S2) and placed in feeding tubes setup in the same 21°C holding room. In the tubes, each bee was presented with a droplet (minimum 90 mg) of 40% w/w sucrose solution placed on a microscope coverslip and allowed to feed for a 5-min period while being observed under red light. Each worker was allowed to feed multiple times within this period to increase the likelihood that workers had fed to satiation (please see Supplementary Methods for support), with the aim of limiting any proportional differences in endogenous energy stores between workers prior to flight trials (N.B. no worker consumed the entire droplet). Feeding tubes consisted of a Perspex tube (length = 100 mm, internal diameter = 19 mm) with a rubber bung at one end, which was then placed inside a queen marking cage such that the open end of the Perspex tube was placed against the mesh end of the marking cage, allowing the worker to feed through the mesh. Direct feeding was identified as the proboscis extending into the sucrose droplet, with the length of time that each worker fed recorded through direct observation. We weighed the coverslip with the droplet before and after feeding to calculate the mass of sucrose solution consumed. With workers varying in the volume of sucrose consumed over the 5-min period, we produced a 'mass-specific consumption' value per worker, calculated as the total mass of sucrose consumed (mg) per unit of body mass (mg of dry mass). Any bees observed not to

feed within the 5-min feeding period were removed from further testing.

Of the 336 workers tested, 24 were removed from testing as five were visibly unhealthy or possessed damaged wings and 19 did not initiate feeding (Table S3). Considering all 312 workers that successfully fed, there was no difference in dry mass mean (ANOVA,  $p > 0.1$  for all pairwise comparisons) or variance (Bartlett's  $K^2 = 5.95$ ,  $df = 6$ ,  $p = 0.43$ ) between temperature cohorts. Once the feeding trial had ended, successfully fed workers were removed from their respective feeding tubes, placed into separate plastic holding pots (120 ml) and transported to the neighbouring testing room. Still under red light, workers were left to rest inside the pots for 5 min and immediately after were removed and magnetically attached to each respective flight mill. Once all were attached and following the same procedures in Kenna et al. (2019), the room was switched to white light and a support stand was used to hold workers to rest for a 10-min acclimatisation period deemed necessary to allow workers to settle while being held on the mill. Immediately after, the bee was manoeuvred (if required) to a forward-facing orientation and the support stand was quickly removed to stimulate loss of tarsal contact and initiate flight. If removal of the stand did not stimulate flight, then either (a) the tarsi would be gently tapped with the stand if all legs were hanging down or (b) plastic tweezers would be used to gently flick the legs off the tether if workers had their front or middle legs touching the tag attachment. This would be attempted twice per method, and if no flight response was exhibited this was considered a 'strike' and the stand would be placed back under to support the bee. Workers that successfully flew on this first flight attempt were monitored for any subsequent stoppages in flight. Following a stoppage, the stand was placed under the worker and this was again considered a 'strike'. For both these 'strike' scenarios, after 30 s of the worker resting the stand would again be removed and the process repeated.

Workers were not capped in terms of how long they could fly for, but were only allowed three 'strikes' in total, with their flight trial terminated on the third strike. Providing multiple flight opportunities allows workers to acclimatise to the flight mill setup while representing more realistic foraging conditions where workers will periodically stop to rest and feed (Woodgate et al., 2016). The decision to allow three 'strikes' was supported by Kenna et al. (2019), who showed that the majority of flight periods after a third stoppage were short-lived, indicating flight motivation or capacity had reached a limit by this point. After the third strike, workers were removed from the mill and frozen at  $-20^{\circ}\text{C}$ , followed by a measure of dry mass by weighing the worker after oven warming at  $80^{\circ}\text{C}$  for 48 hr. Workers were weighed with their metal tag attached, which did not bias any of our body mass measurements as tags were of standardised mass ( $18 \pm 0.1$  mg).

## 2.5 | Data and statistical analyses

When examining worker flight endurance for all tested workers, frequency distribution plots revealed a right skew to the data, with many

workers terminating flight before completing 100 m (Figure S3). As highlighted in Kenna et al. (2019), bees that fly under approximately 100 m appear to exhibit a distinctly different behaviour from those flying over this distance, with flight bouts <100 m consisting of short and intermittent flight periods with no periods of sustained flight, indicating low motivation to fly or lack of physical ability to initiate and sustain flight. As such, we only considered 'successful fliers' as those flying  $\geq 100$  m. This threshold served the dual purpose of allowing (a) investigation into drivers of flight motivation/success and (b) analysis of workers that are seemingly motivated to fly and to use normalised data to measure flight endurance allowing parametric linear models to be run.

For successful fliers, we measured (a) total distance flown during the flight test, calculated as the total number of circuits flown multiplied by the circuit circumference (0.848 m); (b) total duration of the flight test, calculated by summing all circuit interval times; (c) velocity of each circuit flown, calculated by taking circuit circumference and dividing by the respective circuit interval time; (d) mean velocity, calculated as the total distance flown divided by the total duration flown; and (e) maximum velocity, by taking the highest velocity circuit that was recorded. These calculations were carried out on cleaned data (please see Supplementary Methods for cleaning steps).

Statistical analyses were conducted using the 'lme4' (Bates et al., 2015) package in R v3.6.2 (R Core Team, 2019), with results reported using the package 'lmerTest' (Kuznetsova et al., 2017). For all analyses, the effect of body mass was examined using log-transformed dry mass (mg).

Bartlett's test was used to compare the distribution of body mass between temperature cohorts, while ANOVA with post-hoc Tukey tests (implemented using the 'TukeyHSD' function in base R 'stats' package) was used for pairwise comparisons of mean mass between temperature cohorts. Linear regression was used to examine the relationships between body mass and both the total sucrose consumption (mg consumed by end of the 5-min feeding trial) and rate of sucrose consumption (mg/s during observed feeding), with the latter response variable being log-transformed to meet model assumptions (see Supplementary Results; Figure S4).

For all analyses of the likelihood of successful flight (flight  $\geq 100$  m), flight distance (m), flight duration (s), mean velocity (m/s) and maximum velocity (m/s), we fitted linear mixed-effects models including colony as a random intercept to account for inherent colony-level differences. However, when examining the likelihood of successful flight, the random effect variance estimate was close to zero, and so colony was removed to avoid model overfitting and non-convergence. In all cases, the Gaussian distribution was used, except for when examining likelihood of successful flight, which was modelled as a binomial family distribution (flight <100 m = 0, flight  $\geq 100$  m = 1). Analyses examining both flight distance and duration were carried out on log-transformed data so that distributions met model assumptions. All models were initially constructed considering the main effects of temperature, body mass, mass-specific consumption and the interactions temperature  $\times$  body mass and

temperature  $\times$  mass-specific consumption, with all main effects modelled as continuous variables. Models were then simplified through stepwise removal of non-significant terms, checking after each removal that the simplified model had not significantly decreased explanatory power.

Visualisation of the relationship between both flight distance and duration with temperature revealed a unimodal curve (see Section 3), which was best explained by fitting a second-order polynomial relationship between temperature and distance or duration while assuming both body mass and mass-specific consumption to be linear predictors of the response variables. Thermal performance curves were constructed using these model predictions.

Assigning a mean velocity value calculated across the whole flight period may not fully encapsulate what occurred during the flight trial and could overlook the dynamics of flight. From visualising velocity flown by workers per temperature cohort over time (see Section 3), workers appeared to fly at comparatively high velocities immediately following the start of the flight mill test ('Immediate'), which is likely a stimulatory response to the withdrawal of the support stand. Following this, workers rapidly declined in speed ('Initial'); a response that appeared standard across all temperature cohorts after which flight velocity levelled-off and remained relatively steady over the remainder of the trial ('Steady'). Focussing on these characteristic periods of flight, and using linear mixed-effects models as previously described, we additionally examined mean velocity flown by workers per cohort for (a) immediate flight, encompassing the first 30 s of flight; (b) initial flight, encompassing flight >30 to  $\leq 300$  s post-flight initiation; and (c) steady flight, encompassing flight >300 to  $\leq 600$  s post-flight initiation. We capped steady flight at 600 s to ensure we could analyse a sufficient number of workers within each cohort to allow statistically suitable comparisons (Figure S5).

For all analyses examining flight metrics, additional linear mixed models were fitted in which temperature was modelled as a fixed factor, allowing pairwise comparison in flight metric means between temperature cohorts through Tukey contrasts. For this analysis, we report adjusted *p*-values which corrected for multiple testing through the single-step implementation in the 'MULTCOMP' R package (Hothorn et al., 2008).

As a final analysis, we took individual flight performance across workers to produce a comparative metric of how ambient temperature determined 'temperature-mediated foraging potential'. To better understand a colony's potential foraging range and capability to exploit resources across a given landscape, we must incorporate not only flight endurance per worker but also the number of successful fliers constituting the colony workforce. With no significant difference in worker mass distributions between temperature cohorts, for each cohort we took the mean distance flown (m) and multiplied by the proportion of successful fliers (relative to those that initiated flight) to provide a relative value for temperature comparisons. We used mean flight distance as our measure of flight endurance in the calculation as it directly incorporates both flight velocity and duration.



### 3 | RESULTS

#### 3.1 | Likelihood of flight

Ninety-seven percent of workers ( $n = 304$ ) initiated flight, with all eight workers that did not fly coming from the 12°C cohort (Table S3; Fisher's Exact Test:  $p < 0.01$ ).

Across all temperature cohorts, 54% of workers ( $n = 164$ ) were classified as successful fliers (flew  $\geq 100$  m; Table S3), with the likelihood of successful flight showing an overall positive correlation with ambient temperature (GLM:  $z_{299} = 2.18$ ,  $p = 0.029$ ; Figure 1A, Table S4). The probability of a worker being a successful flier significantly increased with body mass (GLM:  $z_{299} = 3.40$ ,  $p < 0.001$ ; Figure 2A), but this relationship was influenced by ambient temperature (GLM: 'Temp  $\times$  Body Mass':  $z_{299} = -2.01$ ,  $p = 0.044$ ). Specifically, the negative estimate from the interaction term (est =  $-0.34$ ) indicated that as temperatures increased there was a reduction in the slope gradient. The reduced flight success at lower temperatures was therefore more severe for smaller workers (Figure 2A). Considering the 164 workers classed as successful fliers, there was an even variance in dry mass values between temperature cohorts (Bartlett's  $K^2 = 4.51$ ,  $df = 6$ ,  $p = 0.61$ ). However, successful fliers in the 12°C cohort had a significantly higher mean dry mass compared to successful fliers in the 24, 27 and 30°C cohorts ( $t_{157} \geq -2.40$ ,  $p \leq 0.02$  in all cases; Figure 2B).

Mass-specific consumption showed a positive association with the probability of being classed as a successful flier, but this parameter was not detected as significant (GLM:  $z_{298} = 1.84$ ,  $p = 0.07$ ; Figure S6).

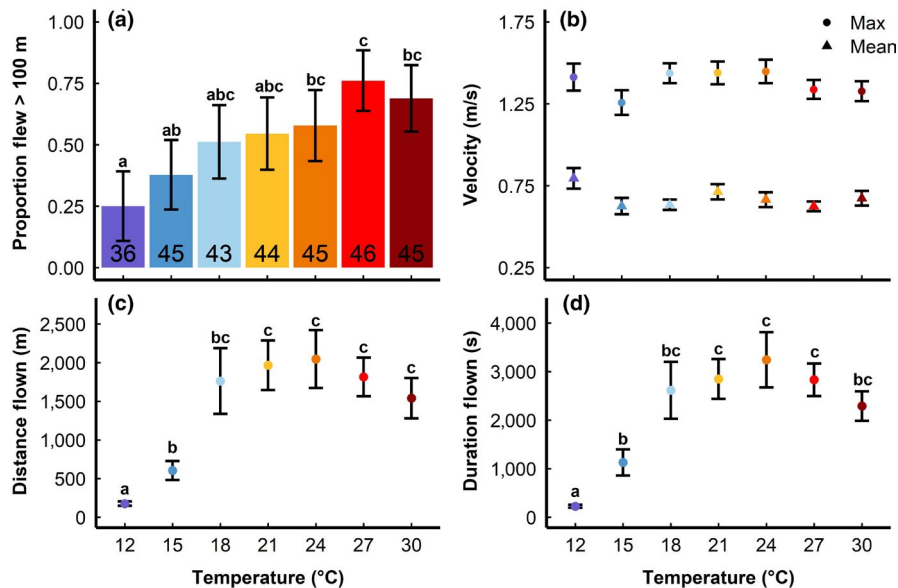
Pairwise comparisons between temperature cohorts revealed that at 12°C, workers showed a significantly lower likelihood of being

a successful flier relative to 24, 27 and 30°C ( $p \leq 0.029$  in all cases; Figure 1A; Table S5). Additionally, the 15°C cohort was less likely to be a successful flier relative to 27°C ( $p = 0.004$ ; Figure 1A).

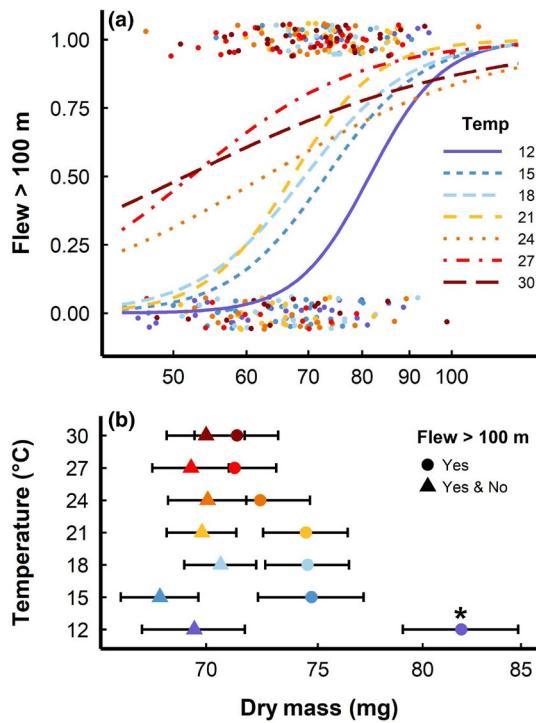
#### 3.2 | Flight endurance

Flight endurance showed a unimodal trend over the temperature gradient (Figure 1C,D). Mean ( $\pm$ SEM) flight distance at first increased from a minimum of  $176.8 \pm 27.3$  m at 12°C to a maximum of  $2,046.4 \pm 374.1$  m at 24°C, with a significant positive relationship between temperature and flight distance across the entire temperature gradient (LMM: 'Temp',  $t_{158} = 5.16$ ,  $p < 0.001$ ; Figure 1C, Table S6). As ambient temperature increased above 24°C, mean distance started to decrease falling to a mean of  $1,816.0 \pm 249.5$  m at 27°C and then  $1,540.1 \pm 261.9$  m at 30°C; a pattern best described by fitting a quadratic relationship (LMM: 'Temp<sup>2</sup>',  $t_{158} = -4.92$ ,  $p < 0.001$ ; Figure 1C). This unimodal trend was mirrored in the relationship between temperature and flight duration (see Supplementary Results and Figure 1D for details).

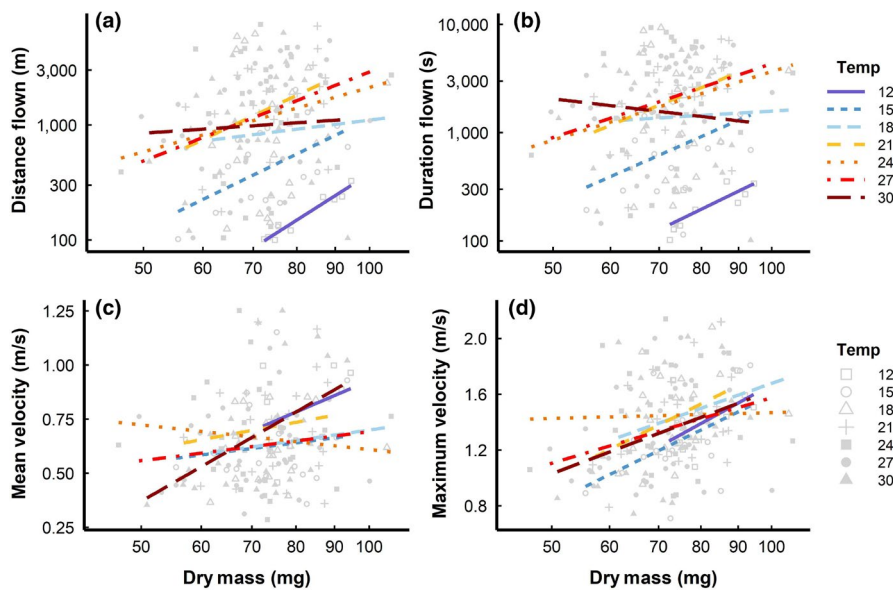
Body mass had a significant positive relationship with flight distance and duration (LMM:  $t_{158} \geq 2.73$ ,  $p \leq 0.006$ ). We found no significant change in the relationship between either flight distance or duration and body mass across the temperature gradient, although slope estimates were lowest for the 30°C cohort and greatest for 12 and 15°C cohorts (Figure 3A,B). In fact, 30°C was the only temperature that flight duration showed a negative relationship with body mass (Figure 3B). Mass-specific consumption was found to have no significant effect on either flight distance or duration (LMM:  $t_{157} \leq 1.38$ ,  $p \geq 0.17$ ; Figure S7).



**FIGURE 1** Effect of temperature on a selection of flight metrics. (A) Proportion of successful fliers (flight  $\geq 100$  m) relative to the number of workers that physically initiated flight (bottom of each bar); (B) mean (triangle) and maximum (circle) velocity (m/s) flown per worker over the whole flight trial; (C) total distance (m) flown per worker and (D) total duration (s) flown per worker. In panel (A), each bar is plotted with associated 95% confidence intervals calculated using the 'Wald' method. Panels (B), (C) and (D) only consider successful fliers, where points represent mean values plotted with associated standard error bars and treatment pairs displaying the same letter are not significantly different ( $\alpha = 0.05$ )



**FIGURE 2** Relationships between worker dry body mass and successful flight for each temperature cohort. (A) Effect of dry mass on the likelihood of successful flight ( $\geq 100$  m) shown in a logistic regression plot (unsuccessful flight = 0, successful flight = 1) and (B) comparison of worker mean ( $\pm$ SEM) dry mass per temperature cohort when considering all workers tested on the flight mills ( $n = 312$ , triangles) or just successful fliers ( $n = 164$ , circles); In both panels, dry mass has been plotted on a  $\log_{10}$  scale. In panel (A), jitter has been added in the y-plane and confidence intervals have not been plotted around model lines to aid visualisation. In panel (B), the asterisk (\*) indicates that worker dry mass of successful workers in the 12°C cohort significantly differed from the 24, 27 and 30°C cohorts ( $p < 0.05$ )

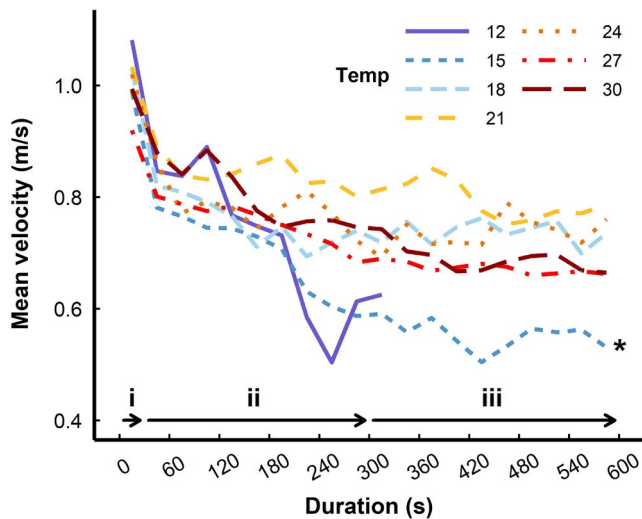


**FIGURE 3** Relationships between worker dry body mass and a selection of tested flight metrics for each temperature cohort. Scatter plots with linear best fit lines for each temperature cohort show the relationship between dry mass and (A) flight distance (m); (B) flight duration (s); (C) mean velocity (m/s) flown over the whole flight trial and (D) maximum velocity (m/s) flown over the whole flight trial. In all panels, dry mass has been plotted on a  $\log_{10}$  scale and confidence intervals have not been plotted around model lines to aid visualisation. In panels (A) and (B), respectively, distance and duration flown have been plotted on a  $\log_{10}$  scale, as these variables were log-transformed in the data analysis

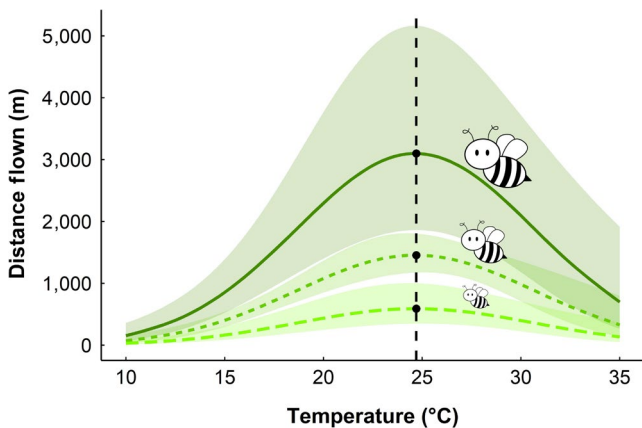
Pairwise comparisons highlighted that the 12°C cohort flew a significantly shorter distance and duration relative to all other temperatures ( $p \leq 0.045$  in all cases; Table S7). The 15°C cohort flew significantly less distance relative to 21, 24, 27 and 30°C ( $p \leq 0.038$  in all cases), and a significantly shorter duration relative to 21, 24 and 27°C cohorts ( $p \leq 0.034$  in all cases).

### 3.3 | Flight velocity and dynamics

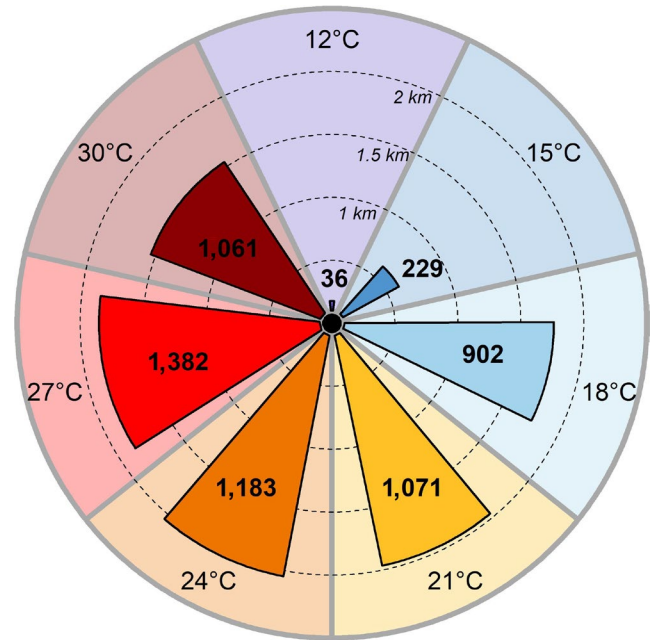
We found no clear relationship between ambient temperature and velocity when measured over the whole flight trial (LMM: mean:  $t_{158} = -0.61$ ,  $p = 0.54$  & maximum:  $t_{158} = 0.43$ ,  $p = 0.67$ ; Figure 1B; Table S8), with pairwise comparisons between temperature cohorts



**FIGURE 4** Mean velocity (m/s) flown by each temperature cohort over the first 600 s of flight. The mean velocity for each temperature cohort was calculated for each 30 s period from 0 until 600 s, with values then plotted on the mid-point of the period (e.g. mean velocity for period of 0–30 s plotted on  $x = 15$  s), and standard error bars have been omitted for visualisation purposes. Arrows indicate three time periods representing different velocity signatures: (i) Immediate Flight, encompassing the first 30 s, characterised by comparatively high velocities; (ii) Initial Flight, >30 to  $\leq 300$  s, characterised by decreasing velocities; (iii) Steady Flight, >300 to  $\leq 600$  s, characterised by more steady velocities. \*Examining all three time periods, the 15°C cohort significantly differed from the 18, 21 and 24°C cohorts ( $p < 0.05$ ) in steady flight mean velocity, but there were no other detected differences



**FIGURE 5** Thermal performance curves (TPCs) for workers spanning a range of body size. Three TPCs corresponding to mean (73.3 mg; middle line, short dashes), minimum (46.7 mg; bottom line, long dashes) and maximum (106.9 mg; top line, no dashes) dry body mass of all successful fliers. Black circles indicate the thermal optimum for each individual and dashed black line indicates the corresponding temperature (24.7°C). The curves are formed from predictions of our final linear mixed model (Table S6), each plotted with 95% confidence intervals



**FIGURE 6** Temperature-mediated foraging potential for each tested temperature. The black central spot indicates a hypothetical colony and dashed lines represent potential flight ranges from this fixed nest site. For each temperature cohort, there is a bordered darker coloured segment in which the length is determined by the mean distance flown (m) by successful fliers from that respective cohort, the angle and subsequent area is determined by the proportion of successful fliers relative to those that initiated flight in that cohort, and the number in bold depicts the relative temperature-mediated foraging potential value (calculated as the mean flight distance multiplied by the proportion of successful fliers; see Table S10 for full results). For each temperature cohort, the angle of the lighter shaded segment represents the maximum area available to the cohort if all tested workers were successful fliers

showing no significant differences (Table S9). Body mass had a significant positive effect on both mean and maximum velocity when considering flight across the whole trial (LMM:  $t_{158} \geq 2.63$ ,  $p \leq 0.009$  in both cases; Figure 3C,D), with no clear change in the slopes of these relationships across the temperature gradient (LMM: 'Temp  $\times$  Body Mass':  $t_{155} \leq 1.23$ ,  $p \geq 0.22$  in both cases). We found mass-specific consumption showed no relationship with maximum velocity (LMM:  $t_{158} = -0.42$ ,  $p = 0.67$ ); however, it was negatively related with mean velocity (LMM:  $t_{158} = -2.48$ ,  $p = 0.013$ ), indicating workers that fed more relative to their body mass flew slower on average (Figure S7).

We found no difference in mean velocity between temperature cohorts when considering both 'Immediate' (0–30 s) and 'Initial' (>30 to  $\leq 300$  s) flight ( $p > 0.05$  in all cases). However, when considering 'Steady' (>300 to  $\leq 600$  s) flight, we found that the 15°C cohort had a significantly lower mean velocity compared to 18°C (LMM:  $t_{117} = 2.05$ ,  $p = 0.043$ ), 21°C (LMM:  $t_{117} = 2.70$ ,  $p = 0.008$ ) and 24°C (LMM:  $t_{117} = 2.22$ ,  $p = 0.028$ ; Figure 4; Figure S8).



### 3.4 | Thermal performance curve

From the final fitted regression model used for analysing distance flown (Table S6; flight duration results mirror these outputs), we plotted model predictions of flight distance over the temperature gradient 10–35°C (Figure 5). This regression model was used to find the temperature at which distance was at its maximum, with the thermal optimum determined to be 24.7°C (Figure 5). As dry body mass was significantly positively related with flight distance (Figure 3A), the peak distance flown predicted by the thermal performance curve increased with body mass (Figure 5). However, since we detected no change in the slope of this relationship across the temperature gradient (Figure 3A), the predicted thermal optimum presented here was the same across the workforce (Figure 5).

### 3.5 | Temperature-mediated foraging potential

Incorporating both the mean distance flown and the proportion of successful fliers (Table S10), our calculated metric of temperature-mediated foraging potential for each temperature cohort highlighted 27°C to show the highest potential (see Figure 6).

## 4 | DISCUSSION

Using a bespoke tethered flight mill, we investigated how the flight performance of bumblebees varied over a thermal gradient. Our study showed that bumblebee workers were capable of initiating and sustaining flight over a wide thermal range, illustrating the capability of this key insect pollinator group to exploit thermally dynamic foraging landscapes experienced within a daily cycle and across the season (Arce et al., 2017; Corbet et al., 1993; Couvillon, Fitzpatrick, et al., 2010; Peat & Goulson, 2005). Both flight distance and duration showed a concave unimodal trend over the 12–30°C range (Figure 1C,D), with our model estimating 24.7°C as optimal for distance flown (Figure 5). Mean flight velocity over the entire flight trial, however, was not affected by temperature (Figure 1B). The longer distances flown in our trials at more optimal temperatures were therefore a result of increased flight duration rather than increased flight speed. Our findings further revealed variation in flight capacity across the colony workforce. Larger workers not only flew further, longer and faster than their smaller nestmates but were also more likely to fly, with this latter finding particularly striking at low ambient temperatures.

### 4.1 | Individual-level flight performance

We saw little difference in mean flight velocity (for whole flight trial) across the tested temperature gradient—a finding that contrasts with Hrassnigg and Crailsheim (1999) when testing tethered honey bees in a similar flight mill setup. It seems unlikely this finding is due

to flight mill limitations on velocity potential, as mean flight velocity was around half the recorded maximum velocities, demonstrating scope for mean velocity to increase. A more plausible explanation centres around thermoregulation. For bees, flight muscle performance is positively associated with muscle temperature up to certain tipping points (Coelho, 1991; Heinrich, 1975; Woods, 2005). As a result, wingbeat frequency, and thus flight velocity, should be driven by the temperature of the thorax (Hrassnigg & Crailsheim, 1999; Tong et al., 2019). During flight, bumblebee workers are able to effectively regulate thorax temperature to optimise muscle performance and prevent overheating (Dudley, 2000), which may explain the similar mean flight velocities between temperature cohorts (Spiewok & Schmolz, 2006; Figure 1B). This constancy of muscle temperature during flight is achieved by a dynamic balance of heat gain and loss, with workers gaining heat from the environment or through endogenous heat production (Heinrich, 1975; Rubalcaba & Olalla-Tarraga, 2020), and losing heat through processes such as convective cooling and forced transfer of heat from thorax to abdomen (Harrison & Roberts, 2000; Heinrich & Esch, 1994). These processes provide an explanation for our observed concave curves with respect to flight endurance. For example, lower ambient temperatures may demand a greater energy expenditure as workers will need to generate more heat to maintain a sufficient thorax temperature for flight (Heinrich, 1975). Conversely, at higher ambient temperatures, workers may not be able to lose heat to the environment at a fast enough rate to prevent thorax overheating (Heinrich, 1975), which could explain the observed decrease in flight endurance past 24°C. This latter point could support why field studies have observed higher bumblebee activity on hot days occurring primarily in the early morning and late afternoon (Arce et al., 2017; Kwon & Saeed, 2003).

Although bumblebees demonstrate heterothermy, the majority of non-bee insect pollinators, such as most butterflies and *Dipterans*, are ectotherms. As such, they rely on solar radiation and other environmental heat sources to warm up flight muscles rather than endogenous heat production (Wickham, 2009), and consequently low ambient temperatures could be more limiting for these non-bee pollinating insects compared to bumblebees. Interestingly however, our thermal optimum estimate for flight distance aligns closely with the thermal optimum estimated for dispersal of a genotype of the Glanville fritillary butterfly (~24°C) using harmonic radar in the United Kingdom (Niitepõld et al., 2009), which to our knowledge is the only other study to look at insect flight TPCs.

Dependent on resource availability in the landscape, bumblebee foraging ranges are estimated to reach around 2 km from the nest (Osborne et al., 2008; Walther-Hellwig & Frankl, 2000), equating to a foraging round trip of 4 km. Although the tethered nature of the flight mill setup meant that workers had a limited requirement to generate lift (Riley et al., 1997), the vast majority of individual flight distances fell within the 4 km mark with only 6% of workers surpassing this distance. This demonstrates that 4 km was attainable, but that the mill setup was not allowing bees to fly longer than they would naturally. Although our results are primarily intended as

comparative estimates of flight performance across a temperature gradient, this highlights that our results are providing ecologically relevant insights into bumblebee flight endurance.

## 4.2 | Relationship between worker body mass and flight

Worker body mass was positively related with all measured flight metrics (Figure 3; body mass explained between 3.4% and 9.2% of the variation in the responses). For instance, for every twofold increase in bumblebee body mass, there was a predicted threefold increase in flight duration and a 0.2 m/s increase in mean flight velocity (across whole flight trial), supporting the theory that energy efficiency of insect flight increases with body mass (Billardon & Darveau, 2019; Darveau et al., 2005; Skandalis & Darveau, 2012). These positive relationships, which would be expected under metabolic scaling theory (Brown et al., 2004), may also be partially explained by differences in morphological traits and flight kinematics, as wingbeat frequency in insects directly relates to energy consumption and is inversely related to body mass and wing surface area (Billardon & Darveau, 2019; Darveau et al., 2005; Santoyo et al., 2016). Another important consideration here is the capacity of individuals to store food. Across insects, while the absolute energy demand of flight is generally greater in larger-bodied individuals, this can be more than compensated for by greater baseline endogenous energy stores, which results in flight endurance capacity increasing with body size (Kaufmann et al., 2013).

Foraging bumblebee workers are known to collect up to 60%–80% of their own body mass in nectar and pollen on a single foraging trip (Combes et al., 2020). Interestingly, we found that workers with higher mass-specific sucrose consumption flew slower on average, which could indicate that carrying a heavier load places constraint on flight velocity or could indicate a determined kinematic response to cope with the heavier load (Combes et al., 2020; Heinrich, 1975). Although we tried to ensure that each bee had fed to satiation prior to flight, there was no way to definitively control this, and therefore the variation in flight performance between workers of similar body mass (Figures 3 and 5) could stem from variable endogenous energy stores prior to flight (Kaufmann et al., 2013). This would seem plausible as flying insects are believed to have metabolic enzymes working close to maximum flux rates, and thus the only way for an individual to improve flight capacity is via increased energy consumption (Niitepöld et al., 2009; Suarez, 2000).

Ultimately, our controlled laboratory findings imply that larger individuals are able to reach flowering resources more quickly and over a greater distance than their smaller counterparts, supporting field observations of foraging scope and efficiency increasing with body size (Goulson et al., 2002; Greenleaf et al., 2007; Spaethe & Weidenmüller, 2002; Willmer & Finlayson, 2014) and providing a further mechanistic explanation for observed alloethism in bumblebees (Herrmann et al., 2018; Holland et al., 2020). Interestingly, agricultural intensification and associated declines in habitat quality and

quantity appear to be leading to shrinkages in bee body size, not just in *Bombus terrestris* but also across other social and solitary species (Oliveira et al., 2016; Renauld et al., 2016). Applying our findings on size-mediated flight performance across taxa therefore suggests this trend of declining bee body size could have negative consequences for pollination service delivery by contemporary bee communities.

Furthermore, we found that the effect of body mass on flight success (flight  $\geq 100$  m) became stronger as temperature decreased (Figure 2A). This can potentially be explained by considering how thermoregulatory capacity varies with body mass, with the lower surface area to volume ratio of larger individuals resulting in a slower rate of heat transfer to the environment, allowing them to more effectively retain heat (Bishop & Armbruster, 1999; Heinrich, 1975; Peat et al., 2005).

## 4.3 | Temperature-mediated foraging potential

When applying our individual flight performance results to the context of temperature-mediated foraging potential, we considered not only flight distance but also the proportion of tested workers motivated or physically able to fly at the respective temperatures. Subsequently, while mean distance was highest in the 24°C cohort, there were more successful fliers in the 27 and 30°C cohorts, meaning that foraging potential at the colony level may actually be maximised at temperatures closer to 27°C (Figure 6).

At the other end of the temperature scale, successful fliers in the 12 and 15°C cohorts exhibited a mean flight distance of just 177 and 605 m, respectively, with nearly two-thirds of the workers classed as unsuccessful fliers (not flying past 100 m; Figure 1A,C). On cold days, foraging bees can use direct solar radiation to assist in warming (Rubalcaba & Olalla-Tarraga, 2020; Stabentheiner & Kovac, 2014), which was not available to workers under our controlled flight mill setup. This should be noted when extrapolating our findings directly to real-world scenarios, as bumblebees are known to forage in temperatures of  $\leq 12^\circ\text{C}$  (Bishop & Armbruster, 1999; Corbet et al., 1993; EFSA, 2013). Additionally, the workers tested in this study were from commercial colonies with no prior flight experience. This allowed us to standardise flight comparisons between temperature cohorts, but should be considered when comparing flight distances on the mill with foraging distances in the field, as flight experience has been reported to influence aspects of foraging performance (Peat & Goulson, 2005). However, foraging *Bombus terrestris* workers often fly around 600 m from the nest to exploit floral resources (Darvill et al., 2004; Osborne et al., 1999), and have been noted to fly up to 2 km in agricultural landscapes (Osborne et al., 2008; Walther-Hellwig & Frankl, 2000), so our work suggests that temperatures down to 12 and 15°C may prevent colonies from reaching resources they would otherwise forage on under warmer conditions. In addition, when examining the dynamics of flight velocity over the flight trials, we did find that workers flew slower at 15°C compared to warmer temperatures once they had settled into a steady rhythm of flight (Figure 4; Figure S8). If such conditions translate to workers

taking longer to reach and move between flower patches, this may subsequently increase the energetic cost of foraging trips, exacerbating the challenge faced at the colony level.

Consistent temperatures of  $\leq 15^{\circ}\text{C}$  are only likely to affect colonies of temperate bumblebee species in their first stages of development (early spring months), when the predominant foragers will be larger-bodied queens that are capable of foraging in cooler conditions relative to workers (Bishop & Armbruster, 1999; Lundberg, 1980). Recent and projected extreme weather events, however, do suggest that erratic and longer-term cold spells may become more common within bumblebee ranges early in the year. As colonies tend to produce smaller workers earlier in the season (Hefetz & Grozinger, 2017), this could potentially lead to an unmotivated and ineffective workforce (Cohen et al., 2018; Francis et al., 2018; Kretschmer et al., 2018). These results highlight the need for ample flowering resources close to nests early in the year to allow shorter and less demanding foraging trips (Gervais et al., 2020; Westphal et al., 2006), which may be an issue with co-occurring increases in human-induced fragmentation of natural floral resources (Jha & Kremen, 2013; Osborne et al., 2008; Redhead et al., 2016). With bumblebees being central place foragers, this is of particular concern, as a fixed nest site prevents within-season relocation of the 'central place' to track floral resource turnover or more favourable thermal microclimates (Bladon et al., 2020; Raine & Gill, 2015).

Our temperature-mediated foraging potential values were calculated based on a colony with a normal distribution of worker body mass, but it would be useful to understand how colonies with different worker mass distributions determine variation in colony foraging potential. Our results suggest that a workforce consisting of a higher proportion of larger-bodied workers would benefit a colony under cold conditions. However, producing larger workers can come at a cost to a colony as they are more energetically expensive to rear and maintain, and larger workers have been reported to exhibit lower longevity and be less resistant to starvation than their smaller sisters (Couvillon & Dornhaus, 2010; Kerr et al., 2019). Furthermore, in hot conditions, large workers may be more at risk of overheating during flight (Dudley, 2000; Harrison & Roberts, 2000; Rubalcaba & Olalla-Tarraga, 2020). Therefore, large body mass may not confer such an advantage to a colony under hotter conditions, and it is interesting that a global decline in the body size of many ectothermic taxa has been associated with climate warming (Gardner et al., 2011). On this note, our observations showed that the correlation between flight distance and body mass was least positive at the highest tested temperature of  $30^{\circ}\text{C}$ , with flight duration correlating negatively with body mass at the same temperature (Figure 3A,B). In other words, smaller workers appeared to perform on average comparatively better than larger workers at the highest temperature studied. If workers of different mass are more suited to forage in different thermal conditions and thus at different times of the day, it may better allow bumblebee colonies to temporally exploit their foraging landscape (Couvillon, Fitzpatrick, et al., 2010; Peat & Goulson, 2005). Given that ambient temperatures throughout temperate bee species' ranges are predicted to more commonly rise above  $30^{\circ}\text{C}$  in the

coming years (IPCC, 2014), it would be useful to expand body mass versus flight performance relationships to higher temperatures to better predict how intraspecific worker size variation may mediate colony-level responses to climate warming. Additionally, by applying these findings across insect taxa with similar thermal mechanisms, we may be able to gain deeper insights into how the foraging capacity and pollination service delivery of whole insect pollinator assemblages will vary under future environmental temperature scenarios.

#### 4.4 | Impacts of climate change

When considering the geographical range of our study species *B. terrestris*, it is interesting that temperatures experienced throughout the foraging season mostly fall on the ascending slope of our predicted thermal performance curve (Figure 5; Figure S1). Species of terrestrial insects in higher latitudes have been shown to occupy areas with mean temperatures below their thermal optimum (Buckley et al., 2013; Kingsolver et al., 2013), and well below their thermal limits (Deutsch et al., 2008), which is seen as a mechanism to buffer against seasonal temperature variation and the fitness consequences associated with overheating (Buckley et al., 2013; Martin & Huey, 2008). Indeed, in Europe, the probability of bumblebee occurrence is greater when seasonal thermal variation is low (Ghisbain et al., 2020).

Given that mean daily temperatures are projected to increase across much of the temperate range of bumblebees (i.e. c.  $2\text{--}4^{\circ}\text{C}$  rise by 2100; IPCC, 2014), our findings suggest global warming may actually push bumblebee colonies closer to their flight thermal optimum, potentially improving foraging returns and pollination delivery (Deutsch et al., 2008; Herbertsson et al., 2021; Sánchez-Bayo & Wyckhuys, 2019). However, our results also suggest that if ambient temperatures more frequently pass  $30^{\circ}\text{C}$  from extreme climatic events such as extended heatwaves, this could start to have detrimental effects on key behaviours underpinning colony fitness (Meehl & Tebaldi, 2004). Further study on this could offer a potential explanation for reported bumblebee losses at southern range limits (Kerr et al., 2015; Sirois-Delisle & Kerr, 2018; Soroye et al., 2020). Conversely, although bumblebees are commonly considered an insect pollinator group that can cope well with cold conditions (Hines, 2008), our data further suggest that prolonged cold snaps, as more commonly predicted in the early months of the year under climate change, will be detrimental to the foraging capacity of developing bumblebee colonies which commonly do not store sufficient food to last for extended periods (Couvillon & Dornhaus, 2010).

## 5 | CONCLUSIONS

Our results suggest that climate warming may favour aspects of bumblebee flight performance, such as motivation and endurance, across large parts of their geographical range. However, sensitivity to climate change can vary widely both between bumblebee

species and across insect groups more generally (Arribas et al., 2012; Hamblin et al., 2017; Sunday et al., 2014; Zambra et al., 2020), and our results suggest that even within the same species, responses to temperature vary with body mass and thus likely affect smaller- and larger-bodied taxa differently. It is therefore important that we quantify and compare flight and other key behavioural thermal response curves for species across the insect phylogeny to understand spatiotemporal risks and identify conservation priorities of similar and different functional groups.

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## CONFLICT OF INTEREST

The authors declare no conflicting interests.

## AUTHORS' CONTRIBUTIONS

D.K. and R.J.G. conceived and designed the project; S.P. provided input on the theory behind thermal performance; D.K. undertook the experiments; D.K., S.P. and R.J.G. analysed the data; D.K. and R.J.G. wrote the manuscript; S.P. provided input on the later versions. All authors gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.18931zcxr> (Kenna et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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