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RESEARCH ARTICLE

Experimental heatwaves disrupt bumblebee foraging through direct heat effects and reduced nectar production

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Abstract

1. Heatwaves are an increasingly common extreme weather event across the globe and are projected to surge in frequency and severity in the coming decades. Plant-pollinator mutualisms are vulnerable due to interacting effects of extreme heat on insect pollinator foraging behaviour and their forage plants.
2. We designed an experiment to parse the impact of extreme heat on bumblebee foraging mediated directly through air temperature and indirectly through changes in plant rewards.
3. Temperatures simulating a moderate heatwave negatively impacted foraging bumblebees reducing the proportion of successful foraging bouts, foraging bout duration and plant and flower visitation and indirect stress through reduced nectar production that limited foraging bout duration.
4. Our experimental results provide a mechanistic link between climate, plants and pollinators and suggest in situ conditions from heatwaves could have profound negative consequences for bumblebee colony persistence and maintenance of pollination services.

KEYWORDS
bumblebee, climate change, extreme heat, foraging, global change, heatwave, plant–pollinator interaction

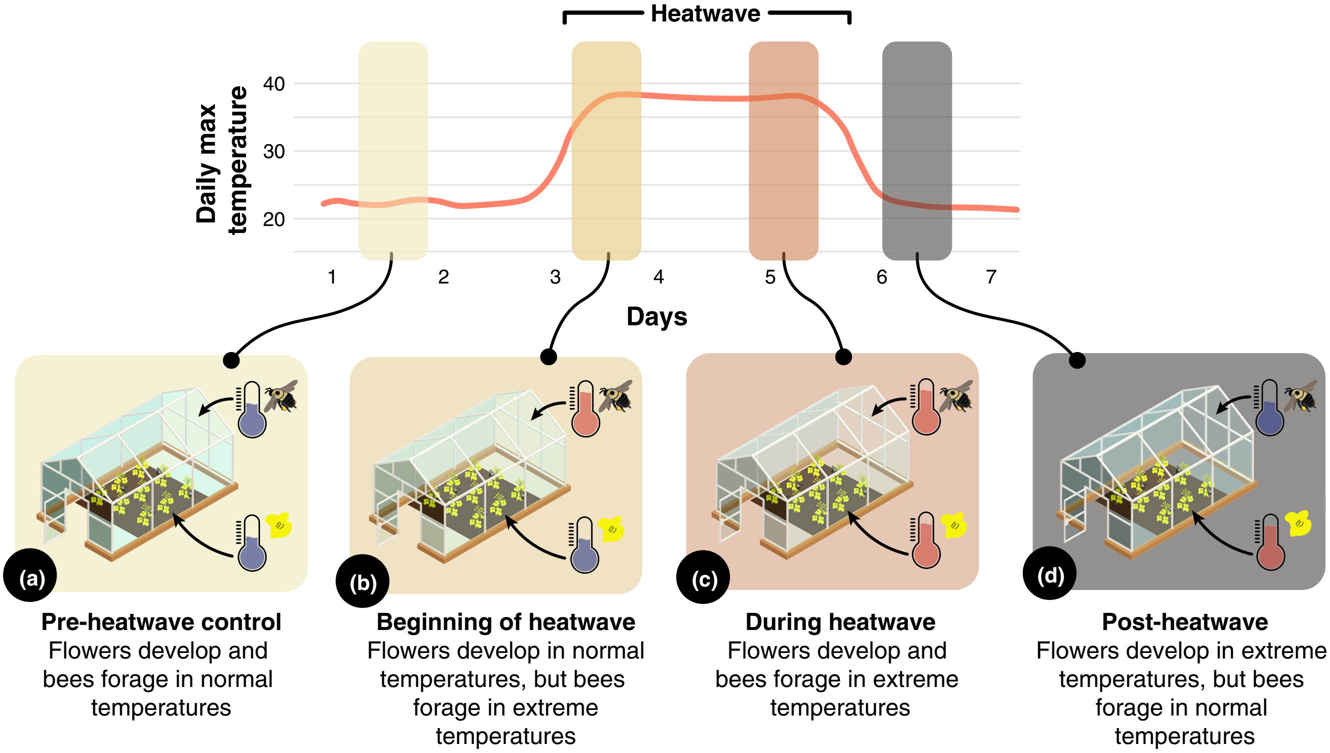
1 | INTRODUCTION

Global climate change is a contributing factor in the decline of insect populations including insect pollinators (Halsch et al., 2021; Kerr et al., 2015; Wagner et al., 2021). Of the major global change drivers, a changing climate threatens pollinators through rising average temperature (Kerr et al., 2015) and through more frequent extreme weather events, including transient periods of extreme heat known as heatwaves (Rasmont & Iserbyt, 2013). Over the last several decades, heatwaves have become more common and are projected to significantly increase in frequency and magnitude over the next century (Meehl & Tebaldi, 2004; Stillman, 2019; Thiery et al., 2021). In addition to disrupting plant–pollinator interactions by potentially directly killing insects (Martinet et al., 2015; Rasmont & Iserbyt, 2013), or limiting bee reproduction (Martinet et al., 2021), heatwaves may also change the timing of pollinator activity (Heinrich, 1974; Rader et al., 2013) and reduce floral rewards through direct stress on plants (i.e. pollen and nectar Borghi et al., 2019, increased water loss, Marchin et al., 2022). Despite a growing understanding of heatwave effects on plant performance and pollinator mortality, our understanding of their impact on pollinator behaviours relevant to plant–pollinator interactions remains limited (Pincebourde et al., 2017).

Insect behavioural patterns are particularly sensitive to changes in both long-term average temperatures (Marshall et al., 2020) and daily fluctuations and extremes (Polgar et al., 2015). Heatwaves may result in temperatures that exceed thermal optima and, thus, impact flight activity periods, flight performance and foraging behaviour and, in some cases, cause some pollinator species to reach their critical thermal limit (CTmax), particularly those that are relatively large (Willmer & Stone, 1997) or adapted to cool conditions (Oyen & Dillon, 2018). Here, we focus on bumblebees which are large-bodied insects historically adapted to the relatively cool Holarctic climates (Woodard, 2017), with declining species associated with more limited thermal niches (Williams et al., 2009). Such evolutionary history makes them particularly vulnerable to the increasing frequency and magnitude of extreme heat events forecast across the Northern Hemisphere.

Bumblebee foraging capacity depends greatly on temperature (Heinrich, 2004). Individuals must reach a threshold internal temperature of 30°C for flight muscle function and have a series of unique adaptations to generate (i.e. facultative endothermy) as well as sustain and shed internal body heat in accordance with ambient air temperature (Heinrich, 2004). At high ambient air temperatures (>35°C), bumblebees struggle to adequately shed heat from their bodies, impeding flight capacity and eventually leading to heat stupor at CTmax (Hamblin et al., 2017; Martinet et al., 2015; Oyen & Dillon, 2018). Published values of CTmax for bumblebees suggest tolerance up to 40–55°C, but current measurements, which are made under laboratory conditions, do not account for heat generation through foraging flight, the primary mechanism by which bumblebees generate internal heat. Under free-foraging conditions, the maximal ambient temperature threshold of bumblebees may be considerably lower (Heinrich, 1974), with reductions in foraging efficiency or changes in foraging behaviour occurring even lower yet (Kenna et al., 2021). For example, bumblebees may forage for less time or over a smaller distance, visit fewer plants or exhibit modified flower handling behaviours. Each of these changes in behaviour may negatively impact plant reproductive success.

Thermal stress from heatwaves also can impact the production of floral rewards in ways that affect bee foraging. For example, pollen and nectar production can be reduced due to heat and water stress (Descamps et al., 2018, 2021; Scaven & Rafferty, 2013). The combined direct and indirect impact of heat stress on bee physiology and nectar production, respectively, are likely to exacerbate the strain on bumblebee foraging and reduce resource acquisition. However, the absolute and relative magnitudes of these different impacts likely depend on the timing and duration of the heatwave relative to bee flower interactions. To give a hypothetical example, before a heatwave, flower development and bee foraging occur under normal temperatures (Figure 1a). During the beginning of a heatwave or one of short duration, pollen and nectar rewards may be less impacted because flower development has occurred prior



Pre-heatwave control Flowers develop and bees forage in normal temperatures

Beginning of heatwave Flowers develop in normal temperatures, but bees forage in extreme temperatures

During heatwave Flowers develop and bees forage in extreme temperatures

Post-heatwave Flowers develop in extreme temperatures, but bees forage in normal temperatures

FIGURE 1 Heatwaves are transient periods of extreme temperatures with impacts on plant–pollinator interactions likely to depend on the temporal extent (exposure) to heat. Four likely scenarios exist: (a) pollinators and plants forage and develop under normal conditions, respectively; (b) in the beginning of a heatwave, plant flowers have developed under normal conditions; however, pollinators are exposed to extreme temperatures when foraging; (c) during prolonged heatwaves, new flowers complete development during extreme temperatures, and pollinators are exposed to extreme temperatures when foraging; (d) post heatwave, lower temperatures allow pollinators to forage under normal conditions, however flowers may suffer persistent negative effects from development during the heatwave. The experiment was conducted in heat chambers within a greenhouse, see Figure S1 for an illustration of the setup.

to extreme heat, whereas bumblebees are forced to forage under extreme temperatures (Figure 1b). For extended heatwaves, both flower development (e.g. pollen and nectar production, changes in sugar content and/or microbial community) and bumblebee foraging occur during extreme temperatures outlining a worst-case scenario of extreme temperature exposure (Figure 1c). The impacts of extended heatwaves are also likely to have lagged impacts because flowers opening post-heatwaves were impacted during development and may exhibit reduced rewards for bees that are now foraging under normal temperatures (Figure 1d). Exploring these different scenarios experimentally would allow more accurate predictions of the consequences of increased heatwaves on plant–pollinator interactions.

We used a factorial experiment to partition the impact of heat stress on bumblebee foraging through direct heat effects on bee activity and flight performance and indirect heat effects through changes to floral reward production. We exposed rapid-cycling canola (*Brassica napus*), an economically important oil-seed crop, and one of its primary wild pollinators, the common eastern bumblebee (*Bombus impatiens* Cresson), to simulated heatwave treatments. Each treatment explored a biologically realistic scenario of impacts on bumblebees and their interaction with flower resources prior to, during and after a heatwave (Figure 1). We expected that simulated heatwaves would reduce flower nectar reward production (Figure 1c,d) and bumblebee foraging efficiency and effectiveness (Figure 1b,c), with the greatest reductions occurring when both bees and plants were exposed to simulated heatwaves (Figure 1c).

2 | MATERIALS AND METHODS

2.1 | Experimental design

To test the impact of simulated heatwaves on flower nectar production and bumblebee foraging behaviour, we designed a 2×2 factorial experiment manipulating flower development and bumblebee foraging temperatures. Each treatment combination represented a biologically relevant stage of a heatwave and allowed us to partition whether flower development temperature, foraging temperature or an interaction thereof best predicted aspects of bumblebee foraging behaviour. Treatment levels included as follows: (1) before heatwave temperatures (25°C for both flower development and bumblebee foraging temperatures); (2) beginning of a heatwave (25°C for flower development and 35°C bumblebee foraging temperatures); (3) end of an prolonged heatwave (35°C for both flower development and bumblebee foraging temperatures) and (4) post heatwave (35°C for flower development and 25°C bumblebee foraging temperatures, respectively). This design allowed us to parse apart the individual and interactive effects of temperature stress on flower development and reward production as well as bumblebee foraging behaviour. We replicated each plant/bee treatment combination (i.e. trial) 10 times for a total of 40 foraging trials.

2.2 | Study organisms

Our experimental system consisted of a rapid cycling variety of oil seed rape *Brassica napus* (UW Madison Rapid Cycling Brassica Collection, RCBC) and one of its wild pollinators in the United States, the common eastern bumblebee *Bombus impatiens*. *Brassica napus* is an important insect pollinated oilseed crop that has previously shown sensitivity to extreme heat during flower development (Morrison, 1993; Nuttal et al., 1992; Young et al., 2004) and seed maturation (Aksouh-Harradj et al., 2006). Bumblebees respond to extreme heat via genetic and physiological mechanisms (Oyen & Dillon, 2018; Pimsler et al., 2020), but realistic tests of their thermal performance under free-foraging conditions are lacking (but see Kenna et al., 2021).

2.3 | Plant establishment and treatments

Brassica napus plants were grown from seed starting in February 2021. We sowed cohorts of 60 plants into 5 cm×5 cm square pots every 3 days to ensure a continuous and consistently aged supply of flowering plants during experimental trials. Plants were grown in standard potting soil mix (Vigoro All-Purpose Potting Mix) topped with vermiculite and provided nutrient supplementation every 3 days using a 1:1:1 N–P–K liquid fertilizer with micronutrients delivered at 200 ppm (Peter's Professional). We started the plants indoors under fluorescent grow lights and then transferred the seedling flats to the greenhouse when seedlings were 3–4 centimetres tall. Immediately following bud development, we transplanted the 5-cm pots into larger, 9-cm pots to assist in water management and provide greater stability for the growing plants. We controlled light to a 16-/8-h day/night light cycle throughout plant development.

Once plants had established branching racemes, we transferred a cohort of a single trial round ($n = 9$) into one of two treatment chambers to simulate heatwave conditions (Figure S1a). The first chamber was maintained under 'control' conditions with a daily max temperature of 25°C (20°C at night). The second chamber was warmed to heatwave conditions with a daily max temperature of 35°C (22°C at night), which exceeds the optimal temperature for developing oil seed rape flowers (Morrison, 1993; Nuttal et al., 1992; Young et al., 2004). Both chambers had large, full-spectrum LED grow lights (total of 3600 lumens) during the 3-day temperature treatment, and plants were watered daily to eliminate drought stress as a confounding stressor. At the end of the temperature treatments, we moved plants into an experimental foraging arena for trials. We trimmed branching racemes to equalize floral display size and removed 1 newly opened flower per plant ($n = 9$ per trial) to measure standing nectar using a 1 μl micro-capillary tube. This represented our estimate of nectar availability for each trial. Upon conclusion of a foraging trial, we extracted and measured nectar volume and concentration from three flowers per plant ($n = 27$ per trial) to determine the approximate nectar consumption by foraging bumblebees.

2.4 | Bumblebee establishment and treatments

We established microcolonies of the common eastern bumblebee *Bombus impatiens* to use in heatwave foraging trials. Microcolonies are small, queen-less colonies containing exclusively workers and are useful analogs of queen-right colonies for use in experimental settings where control of conditions is critical (Dance et al., 2017; Hemberger et al., 2020; Moerman et al., 2017; Tasei & Aupinel, 2008). We arbitrarily selected five workers from one of five queen-right feeder colonies from BioBest Biological and placed them into acrylic brood boxes containing a ~2-g pollen ball and ad-libitum nectar. We established two microcolonies daily beginning 10 days prior to experimental foraging trials, continuing establishment for 20 days to yield a total of 40 microcolonies, one for each trial. This sequential establishment allowed us to standardize the age of each microcolony so that they were all 12 days old upon foraging trials. During the establishment period, we fed microcolonies with fresh, ad-libitum pollen and nectar every 2 days. The purpose of this establishment period was to initiate egg laying and larval development to ensure that workers within the microcolony would behave (i.e. brood care, foraging) similarly to those under standard colony conditions. We kept microcolonies in a rearing room maintained at 25°C in darkness. Periods of prolonged darkness could have impacted bees circadian activity and foraging, however experimental evidence suggests that these rhythms are robust to shifts in light availability (Stelzer et al., 2010; Tasman et al., 2020). Two days prior to experimental foraging trials, we attached the microcolonies to a training chamber containing dwarf *B. napus* plants (RCBC no. 5-002) so that foragers could learn to handle and extract rewards prior to trials. This work did not require ethical committee approval.

We conducted experimental foraging trials within two, 120 × 120 × 120-centimetre foraging chambers constructed from rigid styrofoam insulation affixed to a metal frame (Figure S1b). One chamber was held at a constant, control temperature (25°C), and the other was held at heatwave temperature (35°C). Inside each of the foraging chambers, we placed nine plants from either the control or heatwave plant chambers that had undergone 3 days of treatment temperatures (Figure S1a). We then attached a trained bumblebee microcolony via an entrance tunnel equipped with an infrared gate sensor to allow monitoring bumblebee entrances and exits (AdaFruit Industries). Temperatures inside the foraging chamber and microcolony brood box were monitored using waterproof temperature probes monitoring unshielded air temperature. We allowed bumblebees to forage freely on treated plants for 6 h per trial, recording video of the trial using a 1080p Raspberry Pi wide-angle camera (Arducam OV5647; similar to Droissart et al., 2021). We selected a 6-h trial period to try and best navigate the tradeoff between maximizing the number of foraging trips captured on video and minimizing the impact of resource depletion on foraging behaviour/visitation. The video footage, temperature data and infrared entrance activity were all recorded using a Raspberry Pi 3b+ microcomputer. Bumblebee microcolonies were only used for a single trial to eliminate potential carry-over effects of heat stress between treatments.

2.5 | Data extraction and analysis

After the conclusion of foraging trials, we reviewed bumblebee foraging video footage and recorded plant and flower visitation. For each foraging bee that entered the chamber (i.e. began a foraging bout), we recorded the following: (1) total foraging bout duration (from chamber entrance to exit), (2) number of plant visits (counting any plant where a flower was visited), (3) number of flower visits per plant, (4) time per flower visit, (5) time per plant visit and (6) order of plant visit. During video playback, we followed only one bee at a time to ensure we were not mixing foraging observations between multiple, co-occurring foragers. If another bee entered the chamber during the foraging trip of the bee we were following, we made note of the time and then went back to independently monitor and record data on that bees' foraging activity. We used infrared sensor data from the microcolony entrance tunnel as an approximate measure of foraging bout attempts as the sensor was located immediately before the exit into the foraging chamber.

We fitted a series of generalized linear mixed models to determine whether plant development temperature, bee foraging temperature or their interaction impacted various metrics of bumblebee foraging behaviour and nectar consumption (see Table S1 for full model list). Generally, our models were of two categories: plant level effects (i.e. impact of plant treatment temperature on plant nectar production/consumption) and bee level effects (i.e. impact of plant and bee treatment temperature on bee foraging behaviour). We used a priori information to choose an initial model error structure and then tested alternate models and additional error structures using likelihood ratio tests to determine the best model fit. Where appropriate, we included the beginning of trial nectar volume and its interaction with plant treatment temperature as a covariate to account for the effect of nectar availability on bumblebee foraging behaviour. Additionally, and where appropriate, we included random grouping factors of trial and bee foraging bout nested within trial. After selecting best fit models for each response (Table S2), we conducted post-hoc contrasts to determine whether estimated marginal treatment means were statistically different from one another, including both all pairwise and averaged treatment means for plant development and bee foraging treatments (Table S3).

We conducted all data cleaning, analysis and visualization in R version 4.0.1 (R Core Team, 2017) using the following packages: glmmTMB (Brooks et al., 2017), emmeans (Lenth, 2022), performance (Lüdecke et al., 2021), sjPlot (Lüdecke, 2021), janitor (Firke, 2021) and tidyverse (Wickham et al., 2019).

3 | RESULTS

3.1 | Extreme heat reduces nectar production

Plant treatment chambers maintained average temperatures within 5° of the target treatment temperatures. The average temperature of the treatment chamber under heatwave conditions was

30.55±3.91°C (mean±SD), slightly under the target temperature, while the control chamber was 24.98±2.20°C (Figure S3). Nectar production varied widely, with plants producing between 0 and 10 µl of nectar per flower (pooled mean = 0.83±1.23 µl). Flowers that developed under heatwave conditions exhibited a significant reduction in available nectar, producing on average 70% less than flowers developing at 25°C (Figure S3; control flower chamber = 1.00±0.17 µl, heatwave flower chamber = 0.30±0.06 µl; post-hoc plant treatment effect t_{351} = 5.376, $p < 0.001$). For models that revealed no significant interactions, we present the estimated main effects.

3.2 | Extreme heat reduces bee foraging time, plant and flower visitation

Foraging treatment chambers maintained average temperatures within 2° of the target temperatures. The average temperature of the treatment chamber under heatwave conditions was 33.29±3.57°C, while the control chamber was 23.92±2.43°C (Figure S4).

Over the 40 foraging trials, we recorded 234 bumblebee foraging bouts together amounting to 4018 plant and 9300 flower visits. On average, bumblebees completed an equivalent number of foraging bouts regardless of the plant and foraging treatment temperatures (Figure 2a,b). The infrared sensors at the entrance to the foraging chamber, however, recorded significantly more activity in the heatwave foraging chamber relative to the control foraging chamber (Figure 2c,d; control foraging chamber = 57.1±10.3 reads/trial, heatwave foraging chamber = 231.8±41.6 reads/trial; post-hoc foraging treatment effect t_{32} = 5.49, $p < 0.001$). We suspected this infrared activity may be an indication of attempted foraging bouts, as bees needed to traverse the entire entrance tube to the foraging chamber exit to trigger the infrared sensors. As such, we modelled whether the proportion of actual foraging bouts (with infrared reads representing a Bernoulli outcome of either an actual or false positive foraging bout) varied as a function of our treatment conditions. Heatwave temperatures significantly reduced the proportion of actual foraging bouts relative to control foraging chambers (Figure 2e,f; control foraging chamber proportion = 0.23±0.04, heatwave foraging chamber proportion = 0.04±0.01; post-hoc foraging treatment effect t_{33} = 6.46, $p < 0.001$).

Bumblebees spent significantly less time foraging both when flowers developed under heatwave temperatures (Figure 3a,b; control flower chamber = 8.22±1.18 min, heatwave flower chamber = 4.16±0.97 min; Post-hoc plant treatment effect t_{224} = 2.60, p = 0.01) and when bees foraged under heatwave temperatures (control foraging chamber = 8.04±1.34 min, heatwave foraging chamber = 4.25±0.69 min; post-hoc foraging treatment effect t_{224} = 3.88, $p < 0.001$). Visit durations on plants, and on flowers, however, were consistent regardless of the plant and foraging treatment temperatures (Figure 3c–f).

Consistent with reduced foraging bout durations, bumblebees visited significantly fewer plants when foraging under heatwave conditions (Figure 4a,b; control foraging chamber = 11.43±1.77 plants/bout, heatwave foraging chamber = 4.79±0.59 plants/bout; post-hoc foraging treatment effect t_{225} = 5.56, $p < 0.001$). In accordance with fewer plant visits, bees foraging under heatwave conditions visited fewer total flowers per foraging bout (Figure 4c,d; control foraging chamber = 44.50±8.70 flowers/bout, heatwave foraging chamber = 25.80±5.11 plants/bout; post-hoc foraging treatment effect t_{219} = 2.55, p = 0.01) and were more likely to visit no flowers (zero-inflated model foraging treatment parameter estimate, z = −3.245, p = 0.001). On a per plant visit basis, however, bees visited an equivalent number of flowers regardless of plant or bee foraging treatment conditions (Figure 4e,f; control foraging chamber = 2.23±0.09 flowers/plant, heatwave foraging chamber = 2.18±0.11 flowers/plant).

The number of flowers visited per plant when accounting for the order of plant visit was explained by a three-way interaction between foraging treatment temperature, plant treatment temperature and the order of plant visit (Figure 5, Wald chi-square = 35.75, $p < 0.001$). As we would expect, the number of flowers visited per

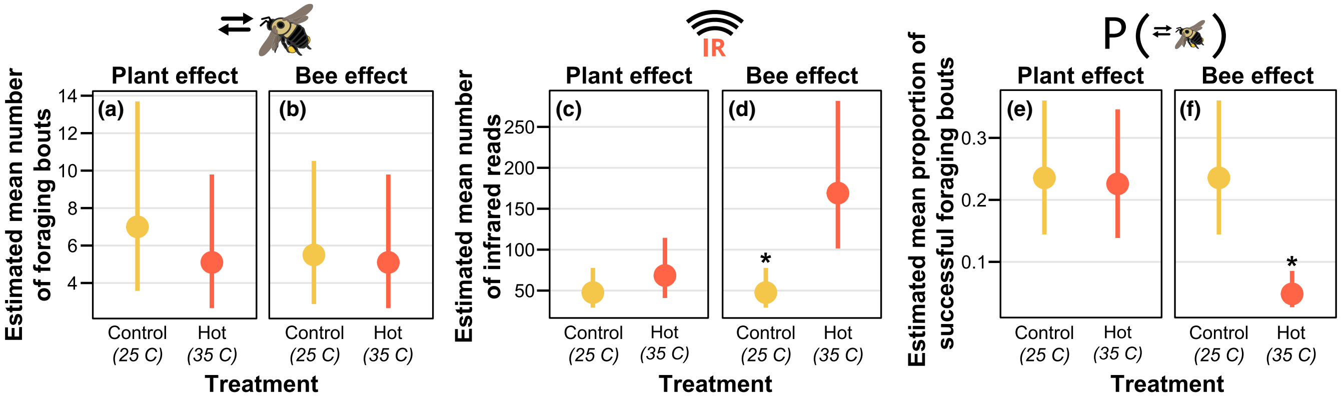


FIGURE 2 Treatment effect plots for response variables related to bumblebee foraging bouts, including (a and b) the number of foraging bouts, (c and d) the number of infrared reads at the foraging chamber entrance and (e and f) the probability of a successful foraging bout (i.e. bee exits microcolony and forages successfully; essentially a model of (a and b) divided by (c and d) per trial). As only main effects were significant, we present these rather than interaction plots. Asterisks represent significant effects ($p < 0.05$) from Tukey-corrected post-hoc comparison. Error bars are 95% confidence intervals.

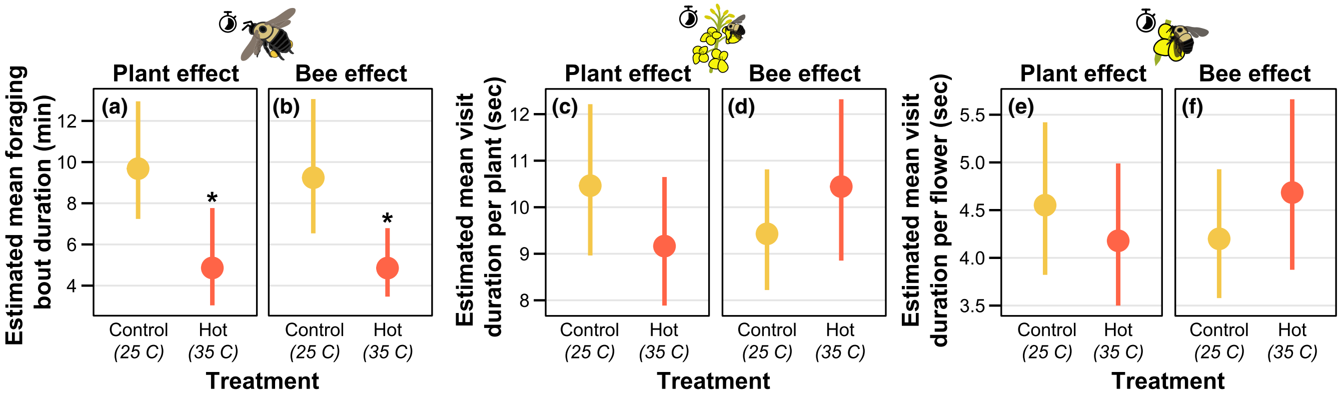


FIGURE 3 Treatment effect plots for response variables related to foraging duration, including (a and b) total foraging bout duration, (c and d) per plant visit duration and (e and f) per flower visit duration. Asterisks represent significant effects ($p < 0.05$) from Tukey-corrected post-hoc comparison. Error bars are 95% confidence intervals.

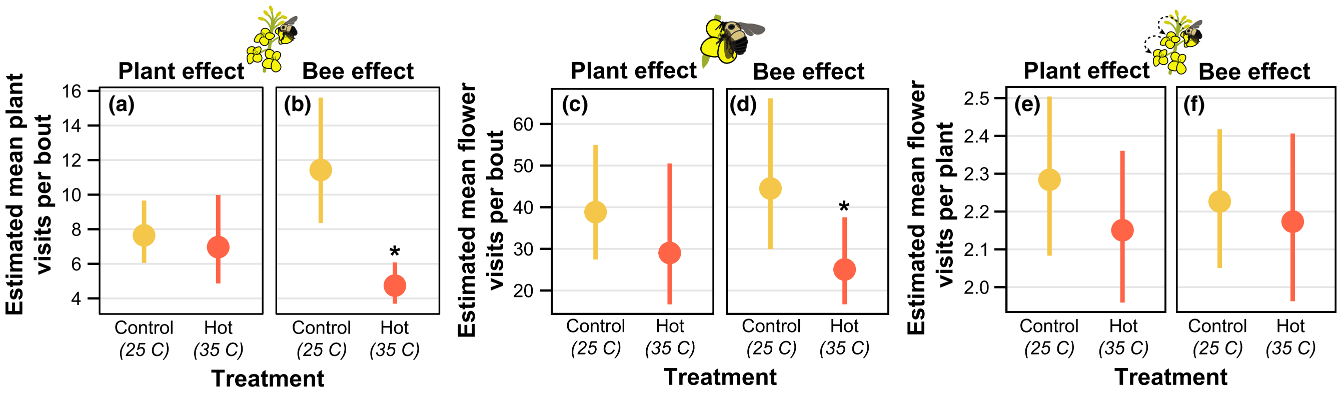


FIGURE 4 Treatment effect plots for response variables related to bumblebee plant visitation, including (a and b) plant visits per bout, (c and d) flower visits per bout and (e and f) flower visits per plant visit. Asterisks represent significant effects ($p < 0.05$) from Tukey-corrected post-hoc comparison. Error bars are 95% confidence intervals.

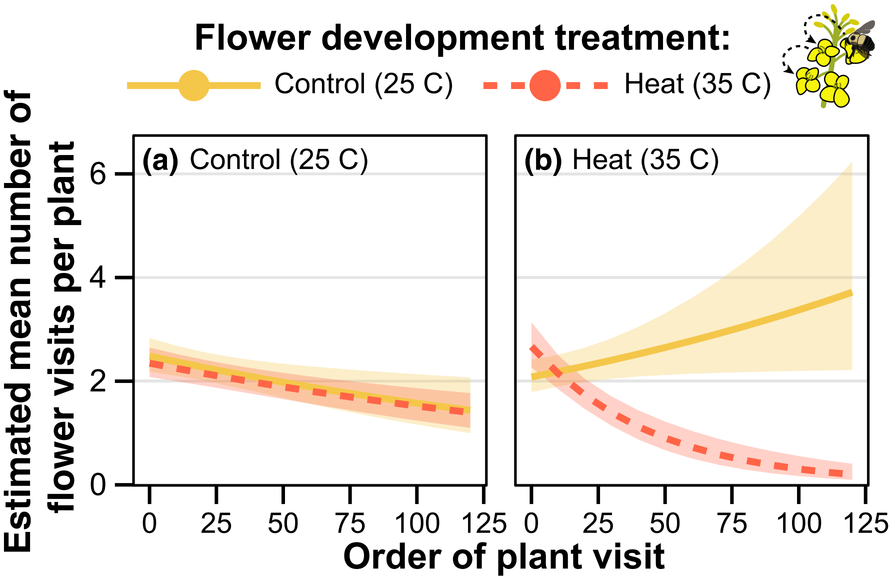


FIGURE 5 Interaction plot of the predicted number of flower visits per plant visit as a function of the order of plant visit during a foraging bout. Panels correspond to foraging treatment conditions: (a) control and (b) heatwave. Line colour and type corresponds to flower development treatment temperatures. Shaded regions are 95% confidence intervals around the predicted value.

plant decreased with successive plant visits within a foraging bout (Figure 5a). This relationship was especially strong when bees were foraging under heatwave temperatures on heatwave-treated plants (Figure 5b). However, when bees foraged under heatwave temperatures on control temperature plants, the number of flower visits increased as the number of plants visited increased.

4 | DISCUSSION

Using simulated heatwaves, we explored how the foraging patterns of an important, common bumblebee species and reward dynamics of their foraging resource are interactively affected by extreme heat conditions. Temperatures representing a moderately severe heatwave negatively impacted foraging bumblebees via direct stress that reduced the proportion of foraging bouts, foraging bout duration and plant and flower visitation, and indirectly through reduced nectar production that further reduced foraging bout duration. Our results provide a mechanistic link between climate, plants and their pollinators while also outlining the potential risks facing both wild and managed plant–pollinator interactions under future climate scenarios. The design also provides an experimental framework with which to evaluate additional plant–pollinator mutualisms in the face of increasingly frequent and severe heatwaves.

4.1 | Direct heat effects on foraging bumblebees

Consistent with our expectations, heatwave conditions reduced bumblebee foraging efforts. On average, foraging bouts were less than half as long in heatwave chambers as control chambers. This reduction in time spent foraging was largely attributable to fewer total plant and flower visits. Like other animals, activity above thermal optimum results in reduced performance, including flight endurance in other bumblebee species (Kenna et al., 2021). The direct effects of heat on foraging behaviour suggest that B. impatiens were foraging well above their thermal optimum during heatwave treatments (Couvillon et al., 2010; Glass & Harrison, 2022). Above thermal optima, bumblebees use several strategies to shed heat, including active heat transfer by pumping hot hemolymph from the thorax to the abdomen (Heinrich & Esch, 1994). We saw several instances within the heatwave chambers where bumblebees ceased foraging to rest on plant stems for extended periods of time, ostensibly to cool down. These observations are consistent with our anecdotal observations of bumblebees stopping to cool during heatwaves in California. Future research aimed at measuring this response in situ to determine the physiological stress experienced by foraging bees during extreme heat is needed.

In addition to reductions in foraging endurance, bumblebees were less likely to exit the colony to forage during heatwave conditions. On average, we observed a 250% increase in attempted exits from the microcolony to the foraging chamber in heatwave treatments, however only ~2% resulted in recorded (or actual) foraging bouts (that is, bees that exited and were observed on recorded footage). In the control foraging chamber, almost 25% of exits led to recorded foraging bouts. Insects have evolved several mechanisms with which to detect and respond to heat (González-Tokman et al., 2020). It is likely that bumblebees in microcolonies connected to heatwave foraging chambers were stimulated by the significant increase in heat detected at the colony entrance, triggering reads from the infrared detector. Although this response could simply be an increase in activity due to slightly elevated in-colony temperatures (Figure S3), it may also be that the decreased proportion of successful foraging trips as a direct result of perceived potential heat stress leading foragers to decide to remain in the microcolony, and current evidence suggests that bumblebees do weigh trade-offs of heat exposure (Gibbons et al., 2022). Our experiment cannot fully confirm either explanation, however our results suggest an interesting avenue for future research.

4.2 | Indirect heat effects on foraging bumblebees

Plant stress also indirectly impacted bumblebee foraging behaviour; however, these results were independent from direct heat effects. Reduced nectar production in flowers that developed under heatwave temperatures was associated with a 50% reduction in bumblebee foraging bout duration, equivalent to the reduction due to direct heat effects experienced by bee foraging under high temperatures. Critically, this reduction in foraging bout duration was observed even when bees were foraging under control temperatures. Foraging is the metabolically most costly activity for bumblebees (Heinrich, 2004) and colonies had been deprived of ad-libitum nectar for 2 days prior to trials making adequate nectar rewards critical to foraging bees. In this experiment, foraging on previously heat-stressed flowers, regardless of the foraging temperatures, did not provide sufficient rewards to sustain continued foraging. Indeed, the number of flowers visited per plant quickly decayed with successive visits when bees foraged under heatwave conditions and on heat treated plants. This result suggests that heatwaves may have delayed effects on foraging bumblebees even after temperatures have returned to normal due to a heat-damaged resource landscape (Borghi et al., 2019; i.e. heat-induced reduction in nectar production by flowers Takkis et al., 2018).

Surprisingly, we did not find evidence for an interactive effect of plant and bee stress: bumblebees foraging on stressed plants under heatwave temperatures behaved similarly to those foraging on control plants under heatwave temperatures. That is, under our experimental concept, bumblebees would exhibit an identical response both at the beginning and late into heatwaves (Figure 1b,c), reducing their foraging duration in response to foraging temperatures. The exception to this was when we accounted for the order of plant visitation. Then, bees foraging in heatwave temperatures exhibited diverging foraging behaviours depending on the heat treatment of plants. This may represent an adaptive behaviour to heat stress whereby foraging bees visit either more or fewer flowers depending on the condition of plant rewards. Overall, our results indicate that heatwaves might have a prolonged impact on bumblebee foraging behaviour well after a heatwave ends (e.g. Figure 1d) and may contribute to the scarcity of bumblebees observed during and after extreme heat (Rasmont & Iserbyt, 2013). Our assessment of the negative impacts on bumblebee foraging, however, is likely conservative given that we could not test for any additive effects of prolonged exposure of colonies to extreme heat (that is, we only used microcolonies for a single trial). Future work should explore how single colonies or microcolonies respond to both direct and indirect prolonged extreme heat exposure.

4.3 | Implications for bumblebees and pollination

Reductions in foraging effort (e.g. foraging time) is likely to have detrimental effects on bumblebee colony growth and reproduction. Although we did not measure microcolony growth due to the temporal scope of each trial, reduced resource intake to bumblebee colonies limits growth Malfi et al. (2022). Most bumblebee colonies maintain only a few days of food reserves (Couvillon & Dornhaus, 2010) and an extended heatwave could exacerbate food limitation and create resource bottlenecks (Maron et al., 2015; Schellhorn et al., 2015), especially in landscapes with limited resources (Samuelson et al., 2018). Extended heatwaves may also negatively synergize with other stressors such as pesticide use (Goulson et al., 2015; Kenna et al., 2019; Rundlöf et al., 2022; Stuligross & Williams, 2020) and land-use change (Hemberger et al., 2021; Marshall et al., 2018). Alarmingly, the time of year when heatwaves are most likely to push temperatures above thermal optima corresponds with periods of reduced resource abundance, typically in early and late summer (Timberlake et al., 2019), although larger colonies may be more able to handle short-term reductions in foraging given food stores (Heinrich, 2004). Additionally, colony performance may be limited by a reduction in pollen and nectar diversity (i.e. micronutrients, Vaudo et al., 2016) if heatwaves limit flower reward production among forage plants in the surrounding landscape.

A reduction in foraging bout duration due to fewer plant and flower visits may impact bumblebees' ability to disperse pollen during heatwave events. Bumblebees under heatwave conditions made fewer total visits to fewer plants suggesting that there could be reductions in the quantity of pollen dispersed during heatwave events, when plants may be more dependent on pollinators (Bishop et al., 2016). Despite a reduction in between-plant movements during heatwave conditions, plant and flower visit durations and the number of flowers visited were equivalent regardless of temperature treatments, suggesting quantity and quality of pollen deposited might be maintained. Specific measurements of the response of plant reproduction to the conditions simulated in this study were beyond the scope of this paper, but critical to address in future research.

Although our method was laboratory-based, we would expect direct heat effects to be exacerbated during heatwaves in a field setting where foragers are forced to fly farther and for longer in search of patchily distributed resources, increasing exposure to extreme temperatures. Temperature variability due to microclimates may provide some refuge as is the case in other animals (e.g. bird; Kim et al., 2022), but this has yet to be explored with bumblebees. Moreover, our experiment only exposed foraging bees to 6 h of extreme heat, whereas heatwaves last several days. On the other hand, heterogeneity among plant species responses to extreme heat may alleviate indirect effects on foraging bumblebees by ensuring nectar availability. At high temperatures, however, even heat-adapted plant communities tend to exhibit significantly decreased nectar secretion, though the directionality of the response was species-specific (Takkis et al., 2018).

Our experimental design provided a successful test of the interactive effects of heat stress on bumblebees and their foraging resources. However, the design necessitated several choices that may have affected our results. For example, plants were exposed to prolonged periods of extreme temperatures, whereas bumblebees were only measured for an acute response to extreme heat. This difference, while biologically realistic in certain scenarios, may have allowed plants an opportunity to acclimate to conditions—an opportunity not afforded to bumblebees. Future research should explore the suite of different temperature conditions that could realistically be experienced by both plants and pollinators to provide more accurate predictions of plant–pollinator interactions during heatwaves.

4.4 | Consequences of climate change

Climate projections suggest that heatwaves will become more severe, frequent and longer over the next 100 years (Coumou & Robinson, 2013; Cowan et al., 2020; Meehl & Tebaldi, 2004). Indeed, over the past decade we have seen some of the most vivid examples of extreme heat brought forth by a changing climate, including record high temperatures both in historically warm (e.g. California, Hulley et al., 2020) and historically mild (e.g. 2021 ‘heat domes’ over the Pacific-Northwest and Canada, 2022 heatwaves in Western Europe) regions set just this past year. In the context of our work, canola growing regions are among regions with large, predicted increases in extreme heat. However, due to their relative temperature thresholds, early-season heatwaves (and climate warming, generally) may benefit many pollinator species as temperatures approach physiological optima of certain species (Rader et al., 2013). Those species active during mid- to late-summer extreme heatwaves, however, are likely to face multiple periods of prolonged heat stress each year. Such events may lead to local extinctions or rapidly advancing climate envelopes (Marshall et al., 2020) Whether insect benefits and detriments to a hotter climate will balance, however, is an open question (Lehmann et al., 2020; but also see Jackson et al., 2022).

The expected increases in heatwaves suggest several possible options for bumblebees. First, they could reduce foraging efforts during heatwaves, relying on existing food stores in the colony. For many species, minimal food stores may not bridge extended or back-to-back heatwaves resulting in resource shortfalls Malfi et al. (2022). Second, bumblebees might adjust daily foraging windows to early and later in the day when temperatures are more aligned to their physiological constraints. Bumblebees are capable of foraging during periods of low-light availability, suggesting an existing capacity to exploit cooler periods outside of the hottest portion of the day (Chapman et al., 2022; Stelzer & Chittka, 2010). This strategy moves bumblebees outside of physiological danger zones; however, plants may still offer reduced reward in accordance with heat stress (Takkis et al., 2018), and this may increase the temporal overlap and potential competition among formerly phenologically separated bee species. Lastly, bumblebees may acclimate to increasingly warm temperatures. However short-term, current evidence suggests that acclimation to short-term extreme heat is unlikely (Oyen & Dillon, 2018), and there is some evidence that a set of bumblebee species' occurrence have decreased where temperatures have warmed (Jackson et al., 2022; Soroye et al., 2020). Future experiments that address these outcomes in both laboratory and in situ field conditions will enable more accurate predictions of species susceptibility to heatwaves.

5 | CONCLUSIONS

Climate change poses a salient threat to insect pollinators and pollination services. Our results provide experimental evidence of the combined impact of heatwaves on free-foraging bumblebees and their resources and suggests that even moderate heatwaves can reduce bumblebee foraging effort through both direct (i.e. physiological stress) and indirect (i.e. reduced nectar production) pathways. Critically, we show that the relatively moderate heatwave conditions explored in our results have a large, negative impact on bee foraging behaviour. Heatwaves are expected to become more frequent and intense, and our results suggest that this may threaten both pollinator health and the stability of pollination services to wild and crop plants. Moving forward, we should assess species risks to extreme heat as well as develop conservation strategies such as microclimate refugia (e.g. Duffy et al., 2015) and begin supplementing landscapes with drought and heat adapted plants to ensure spatiotemporal resource continuity in the climates of tomorrow.

AUTHOR CONTRIBUTIONS

Jeremy A. Hemberger and Nick M. Rosenberger conceived, designed and carried out the experiment. Jeremy A. Hemberger analysed the data and wrote the initial draft of the manuscript. Jeremy A. Hemberger, Nick M. Rosenberger and Neal M. Williams contributed to revisions.

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CONFLICT OF INTEREST

Authors declare no conflicts.

DATA AVAILABILITY STATEMENT

All data and code needed to reproduce the analyses within this manuscript are available on FigShare (data: https://doi.org/10.6084/m9.figshare.20292549, code: https://doi.org/10.6084/m9.figshare.20292561).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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