RESEARCH ARTICLE

Impact of empty flowers on foraging choice and movement within floral patches by the honey bee, *Apis mellifera*

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Abstract
Floral displays often signal the presence of nectar, but nectar may not always be present due to previous visits by nectarivores or temporal changes in nectar availability. But how does the presence of empty flowers impact the preferences of foraging honey bees for the available flowers? We aimed to test if previously rewarding flowers changed the preference relationship between neighboring flowers, and if empty flowers impacted overall visitation, in the honey bee *Apis mellifera*. Using artificial flowers, we showed that although empty flowers did not influence foraging choices in *A. mellifera* workers, empty flowers did increase movement between flowers in the patch. The presence of empty flowers also resulted in increased rates of patch abandonment. Our results suggest that while empty flowers may not directly impact foraging preferences in bees, they can have an impact on visitation within patches and in the surrounding area, with possible knock-on effects for the pollination of both the emptied flower and neighboring plants.

Keywords Bee · *Apis* · Artificial flowers · Empty flowers · Pollination · Honeybee

Introduction

When foraging, bees choose flowers in a landscape based on attributes associated with both the patch and individual flowers. For example, floral attributes, such as nectar quality (Roubik and Buchmann 1984), ease of access to nectar (Zung et al. 2015), and landscape attributes such as the spatial arrangement of flowering plants (Bruninga-Socolar et al. 2022) may all influence the choices of foraging bees. Many individual bees also have innate preferences for floral attributes including floral color (Giurfa et al. 1995), shape (Lehrer et al. 1995), and symmetry (Rodríguez et al. 2004). Finally, flower choice can be influenced by neighboring plants in an environment, such that preferences depend not only on the traits of each flower in isolation but their spatial context within a patch.

One way in which flower visitation may be influenced by other plants in the area is if some plants in a patch are significantly more attractive to bees than others. Such highly

rewarding 'magnet' plants can encourage bee visitation to the broader patch and can lead to spillover effects where other plants in the vicinity of magnet plants gain pollination benefits (Johnson et al. 2003; Peter and Johnson 2008). As bees can learn to associate the color of highly rewarding plants with nectar (Johnson et al. 2003), magnet plants may particularly increase visitation to other plants that have visually similar flowers (Gigord et al. 2002; Johnson et al. 2003; Peter and Johnson 2008).

Flowers do not always contain nectar, however, and the presence of 'empty flowers' can also impact bee foraging behavior. Flowers can be empty of nectar due to nectar removal by other insects, temporal or physiological changes, or due to environmental conditions. Some 'deceptive' flowers contain minimal nectar or are always empty and never offer nectar as a reward (Gaskett 2011). Empty flowers often occur in reasonably high ratios on plants, as an energy-saving strategy, as the plant can maintain a large visual display while investing less in nectar production (Smithson and Gigord, 2003). Flowers also generally produce less nectar with age (Gilbert et al. 1991).

The impacts of empty flowers on bee foraging choice may vary depending on how often nectar is unavailable, and how many flowers in an inflorescence are empty. Increased frequencies of permanently empty flowers can

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result in floral visitors foraging on flowers that are morphologically dissimilar to the empty flowers (Smithson and Gigord 2003). Smithson and Macnair (1997) found that bumble bees, *Bombus terrestris*, that had encountered an unrewarding flower (which was never previously rewarding) were more likely to visit flowers that were dissimilar in color to the unrewarding flower. In this case, contact with the unrewarding flower may have driven learned avoidance of that flower type. In contrast, when a previously rewarding flower is no longer available, *B. terrestris* were more likely to seek out similar colored flowers (Gigord et al. 2002). Similarly, encounters with recently empty flowers can result in bees preferentially visiting flowers with more similar attributes to the unavailable flower (Tan et al. 2015).

The presence of empty flowers can influence whether or not bees will return to flowers. For example, plants can contain multiple inflorescences, and bumble bees will abandon an inflorescence if they visit too many empty flowers (Smithson and Gigord 2003). Unrewarding flowers can also cause foragers to abandon patches altogether if they occur at high enough frequencies (Biernaskie et al. 2002; Smithson and Gigord 2003). Patch abandonment can have knock-on effects on neighboring flowers in the patch, which may no longer receive insect visits and may therefore incur decreased pollination.

Empty flowers could also influence their neighbor's pollination success by altering preference relationships between other flowers in the patch. Although poorly studied in bees, the preferences of humans and some non-human animals can be influenced by unavailable options in choice sets, referred to as 'phantom decoys' (Scarpi 2011; Tan et al. 2015). When an individual's preference among two options changes with the addition of a third, unavailable, option, they are said to have been susceptible to the 'phantom decoy effect' (Trueblood and Pettibone 2017). For example, *Apis cerana* were tested for their preference between flowers that differed in sugar concentration and sugar temperature. Bees generally preferred higher concentrations of sugar in nectar and warmer nectar, so bees were presented with two flowers of 'equal value', one with high nectar concentration but lower nectar temperature, and another with lower nectar concentration, but at a higher temperature. If bees were also presented with a phantom decoy flower (a flower they had previously experienced as having high-quality, warm nectar but that was now empty) alongside the other two nectar-filled flowers, they preferred flowers that were more similar to the phantom decoy flower. For example, the flower more similar in temperature to the phantom decoy was preferred (Tan et al. 2015). If bees make consistent choices in the presence of a phantom decoy, it is possible that empty flowers could have an impact on pollination of nearby flowers in predictable ways that could be utilized in pollination systems.

Phantom decoys can cause a decision-maker to shift preferences based on multiple attributes that are being considered. They can act in two ways: the presence of a phantom decoy can result in the decision-maker picking options more similar to the decoy (similarity effect), or less similar to the decoy (dissimilarity effect). In tests of decoy effects, there will typically be two attributes under control, and the two available options will be of equal value in preference space. Attractive phantom decoys will be better than both options in the choice set but will be more similar in attribute space to one of the available options (typically the 'target' option). It is usually predicted that individuals will select the available option which is most similar in attribute space to the unavailable option (Highhouse 1996; Tan et al. 2015; Park and Jang 2018).

Here, we investigated how empty flowers impacted floral preference, movement between flowers, and abandonment of patches, in the honey bee *A. mellifera*. We hypothesized that:

(1) The preference relationships between two flowers would change in the presence of an empty, previously rewarding flower,
(2) The presence of an empty flower would increase movement between flowers, and
(3) The presence of empty flowers would result in faster abandonment of the patch.

Methods

Honey bees

We used the Western honey bee, *A. mellifera*, as a model pollinator for our floral choice experiment. Western honey bees are native to Africa, Europe, and the Middle East (Han et al. 2012), and were introduced to Australia in 1822. They are widespread across Australia and are used as crop pollinators due to their generalist foraging diet. Our bees came from six established Langstroth hives, containing between 2 and 3 boxes. Colonies were kept at the University of Sydney Camperdown campus, in New South Wales, Australia. Experiments were conducted between April and June 2021.

General methods

To investigate the impact of empty flowers on bee behavior, we compared bee visitation rates on the two focal options (herein, flowers A and B) in a binary test where only the two options were available, and in an 'empty flower' treatment, where a third, unavailable option was added to the choice set.

We used artificial flowers in all treatments. Artificial flowers consisted of a 50 mm diameter matte-laminated

paper shaped like a daisy. The flowers had a central Eppendorf tube containing sugar solution, with the tube length of the Eppendorf extended using a plastic tube. The flowers were colored blue, white, and yellow. To ensure the colors were suitably distinct, we quantified the reflectance of blue, white, and yellow papers using an OceanInsight JAZ reflectance spectrometer with pulsed PX-2 Xenon light, calibrated against a 99% diffuse white and 0% dark standard (Labsphere, New Hampshire). We then modeled the location of each sample in the hexagon color space using the visual phenotype of the honey bee, *A. mellifera* and selected shades that were separated by a Euclidean distance of at least 0.11; the absolute discrimination threshold for honey bees (Chittka 1992; Maia et al. 2019; Supplementary Fig. 1). Flowers were held by a 3D-printed triangular base that held the flowers 10 cm apart from each other. Each flower contained 5 ml of sucrose solution.

Artificial flowers differed in two attributes that we predicted would influence bee choice (sugar concentration and accessibility) and one neutral attribute (color) that ensured bees could learn which flower they preferred. We used attributes that have previously been used in decoy experiments testing *A. mellifera* by Shafir et al. (2002). We used nectar concentration as one attribute because honey bees can discriminate between different nectar concentrations, and tend to pick higher concentrations over lower concentrations (up to a threshold of 50% after which preference declines; Waller 1972). The second flower attribute was the accessibility of the reward as determined by tube length, where bees needed to crawl down a short tube (45 mm) or a long tube (100 mm) to access the nectar. Previous research suggests that honey bees prefer short tubes over longer tubes (Shafir et al. 2002).

We developed two flowers that were similarly preferred by bees (flowers A and B) and one flower that was the most preferred (Flower C). Flower A had a long (less preferred) tube containing the more preferred 50% sucrose (v/v) and flower B had a short tube (most preferred) containing 15% sucrose solution (less preferred). Our highly preferred option (flower C) contained 50% sucrose solution with a short tube (45 mm) (Fig. 1).

Pre-training to artificial flowers and training bees to forage inside an experimental arena

Honey bees did not automatically recognize our artificial flowers as food sources. We therefore used a pre-training step designed to train groups of bees to forage on artificial flowers placed inside our experimental arena. To attract the interest of honey bees, they were trained en masse to gravity feeders containing 7% sugar water that was placed directly at the hive entrance. Gravity feeders consisted of a plastic plate covered in a paper towel. An inverted cup containing sugar water was set on top of the plastic plate,
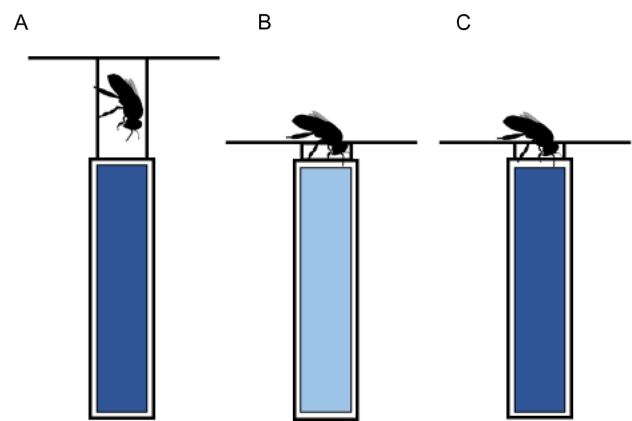
Fig. 1 Flowers in the choice set. Flower **A** consists of a 50% (v/v) sucrose solution (indicated by dark blue) and a 100 mm tube, Flower **B** consists of a 15% (v/v) sucrose solution (indicated by light blue) and a 45 mm tube length. Flower **C** consists of a 50% (v/v) sucrose and a 45 mm tube length. Image not to scale

allowing the sucrose solution to progressively leak out onto the paper towel. Individual bees were marked using paint when they arrived at the feeder.

Individuals that made at least five visits to the feeder were then trained to visit artificial flowers. To avoid creating potential experience biases, each artificial flower was colored 1/3 blue, 1/3 white, and 1/3 yellow. This color patterning was not used during the main training stage. We trained bees to visit artificial flowers by moving individuals from the feeder to the artificial flower using a cotton bud. At this stage, artificial flowers were located a short distance of approximately 5 cm from the feeder. Bees were moved while they were feeding, allowing honey bees to be moved with minimal stress.

Once individual bees were consistently visiting the artificial flowers (after approximately five returning visits) the flowers were moved incrementally into a wooden box (240 mm × 400 mm × 400 mm) with a door (140 mm × 130 mm) that could be closed upon entering. The box was clear from the top, as the box lid was covered in fly screen to allow for visibility by human observers and light to enter the box for the bees to identify flower colors once inside the box. Bees could only enter the box by flying through the door. Once bees finished foraging, the lid was lifted from the top of the box to allow bees to leave the box from the top.

Once honey bees were trained to enter the box, they were next trained to associate specific rewards with each of the three flower colors. Individual bees that entered the box were presented with one of the three flower types in a randomized order. Once the bee had fed on all three flowers five times, it was considered 'trained'.

Training bees to associate floral colors with floral attributes

The main training step was designed to train honey bees to associate specific colors with each flower type (A, B, and C). Once honey bees were trained to enter the box, they were shown each flower type in a randomized order by placing a single flower type in the box (three of these flowers were placed in the box at a time). When a marked individual entered the box, fed, left the box, and returned to the colony, it counted as a visit. To be considered 'fully trained', the honey bee had to feed on all three flower types during this training session at least five times. Some honey bees did not visit all three flower types during the training session; these bees were classified as 'untrained'. Trained or untrained was considered a binary variable in the models during analyses.

Testing

Flowers were randomly assigned a solid color each time the experiment ran. We chose blue, white, and yellow as colors for the flowers as bees have previously been tested on these, and blue, white, and yellow can be discriminated by bees (Giurfa 1991; Giurfa et al. 1997; Sanderson et al. 2006). Colors were used as associative cues and were randomized between experiments to minimize any influence of innate color preferences (Fig. 2).

We tested bees' preferences by letting a single individual honey bee enter a box that contained either the binary or the empty flower test. Bees were randomly assigned a treatment and only tested on one treatment. We recorded the identity of every flower the honey bees fed on, including the empty flower. We classified a feeding event as when a bee's mouthparts made contact with the nectar solution for at least 1 s. Bees were allowed to re-enter the box, and we tested their preferences until the honey bee made 20 visits to the box. Each honey bee was only used once for experiments and was frozen at the end of the day to prevent her from returning to the colony. Some honey bees did not return to the flowers before all twenty trials were completed. Honey bees that took more than an hour to return were considered to have 'given up'. They were removed from the colony when they returned to the feeder the next morning to prevent re-entry to the box.

Statistical analysis

We tested the hypothesis that the presence of an empty flower would change preference relationships between the two neighboring flowers by comparing relative flower preferences when the empty flower was present, to the binary trial when the empty flower was absent. We constructed a generalized linear mixed model (GLMM) using the lme4 package (Bates et al. 2015) with the first flower that each
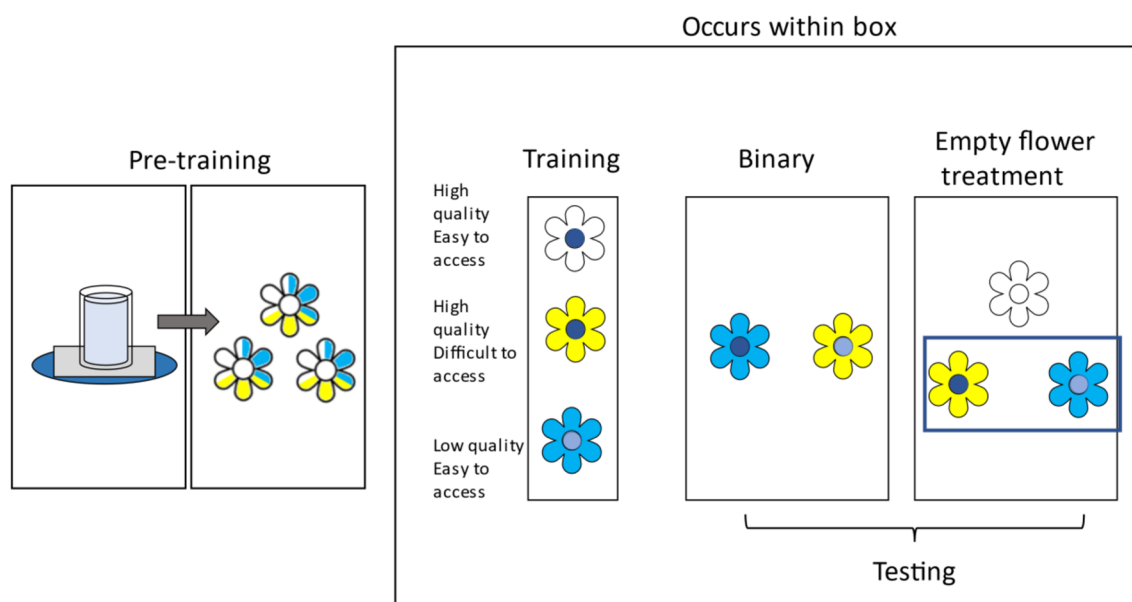
Fig. 2 Pre-training, training flowers, and treatments for experiments. Training flowers consist of three flowers: a high-quality, difficult-to-access flower (yellow), a low-quality easy-to-access flower (blue), as well as a high-quality, easy-to-access flower (white). The color in the center of the flower represents the concentration of sugar water, with darker blue being a higher concentration. The binary test consists of two flowers, one containing a high-quality, difficult-to-access flower, and a low-quality easy-to-access flower. The empty flower test consists of a high-quality, difficult-to-access flower, a low-quality easy-to-access flower, and a high-quality, easy-to-access flower with the nectar removed. Note, for experiments, colors associated with flowers were randomized each time an experiment was run

bee fed on (either A or B, not including the empty flower C) during each visit to the box as a binary response variable, and treatment ('binary' or 'empty flower') and training status ('trained' or 'untrained') as fixed effects. Honey bee identity was included as a random effect. The GLMM used a binomial distribution with a logit link function. Model assumptions were checked using the check_model function in the Performance package (Lüdecke et al. 2021).

We tested the impact of empty flowers on movement between flowers in individual honey bees using a GLMM with a binomial distribution and a link logit function, with the number of flower visits per bout as the response variable, and treatment (binary or empty flower test) as the predictor variable. Honey bee identity was included as a random effect. Model assumptions were checked using the check_model function in the Performance package (Lüdecke et al. 2021).

Lastly, we determined if the presence of an empty flower increased the rate of abandonment of the floral patch. We compared the number of completed trials in the empty flower and binary tests using a Kruskal–Wallis test (function: ruskal.test()), with the number of trials completed as the dependent variable, and the treatment as the independent variable. Kruskal–Wallis test was used due to a lack of normality in data, which can increase the chances of Type I errors when using single-factor ANOVA tests (McKight and Najab 2010).

All analyses were conducted using R version 4.1.2 (R Core Team 2021).

Results

Twenty individual honey bees experienced the binary test, and 25 experienced the empty flower test.

There was no evidence of a difference preferences between the two available flowers in the presence or the absence of an empty flower compared to those foraging in the absence of an empty flower ($p = 0.234$, Table 1). In the binary trials, individual bees visited the long high-quality flower (flower A) in 41% of the visits, compared to 35% of visits during empty flower trials. The level of training (trained or untrained) also had no impact on honey bee neighboring flower preferences ($p = 0.750$, Table 1) (Fig. 3).

Individual honey bees moved back and forth between available flowers more frequently if the empty flower was present ($p = 0.036$, significance level of 0.05; Table 2) (a mean of 0.8 ($\pm$ 0.05) flower visits per bout in the binary treatment, and a mean 1.21 ($\pm$ 0.06) flower visits per bout in the empty flower treatment; Fig. 4A). However, most between-flower movements were between the empty flower and one of the other two options (when empty flower visits are removed from the GLMM the moves between flowers is no longer significant, $p = 0.444$, Table 3, as opposed to 0.036 (where significance occurs when $p < 0.05$), Table 2; There was a mean of 0.8 ($\pm$ 0.05) visits per bout in the binary treatment and a mean 0.72 ($\pm$0.04) visits per bout in the empty flower treatment; Fig. 4B).

Honey bees were less likely to finish all 20 foraging visits if they were in the empty flower test: $\chi^2(1) = 6.767$, $p = 0.009$. On average, honey bees completed 17.9 ($\pm$ 4.12) visits to the arena in the binary test and 13.88 ($\pm$ 5.67) in the presence of the empty flower.

Discussion

We tested if foragers of the honey bee *A. mellifera* shifted their floral preferences between flower types in the presence of an empty flower. Overall, we saw no change in floral preferences in the presence of an empty flower. We did, however, see an increase in movement between flowers within the patch in the presence of an empty flower, and increased abandonment of the patch in the presence of an empty flower.

Table 1 GLMM outputs for preferences by individual honey bees

First Floral Choice				
Predictors		Odds ratios	CI	*p*
(Intercept)		1.40	0.87–2.25	0.166
Treatment [Empty flower]		1.32	0.84–2.08	0.234
Trained		1.08	0.67–1.75	0.750
Random effects				
σ^2	3.29			
τ_{00} bee identity	0.28			
ICC	0.08			
N bee identity	45			
Observations	705			
Marginal R^2/Conditional R^2	0.005/0.083			

Fig. 3 Proportion of visits by individual honey bees to each flower type In the binary test (**A**) and the empty flower test (**B**) ($n=45$)
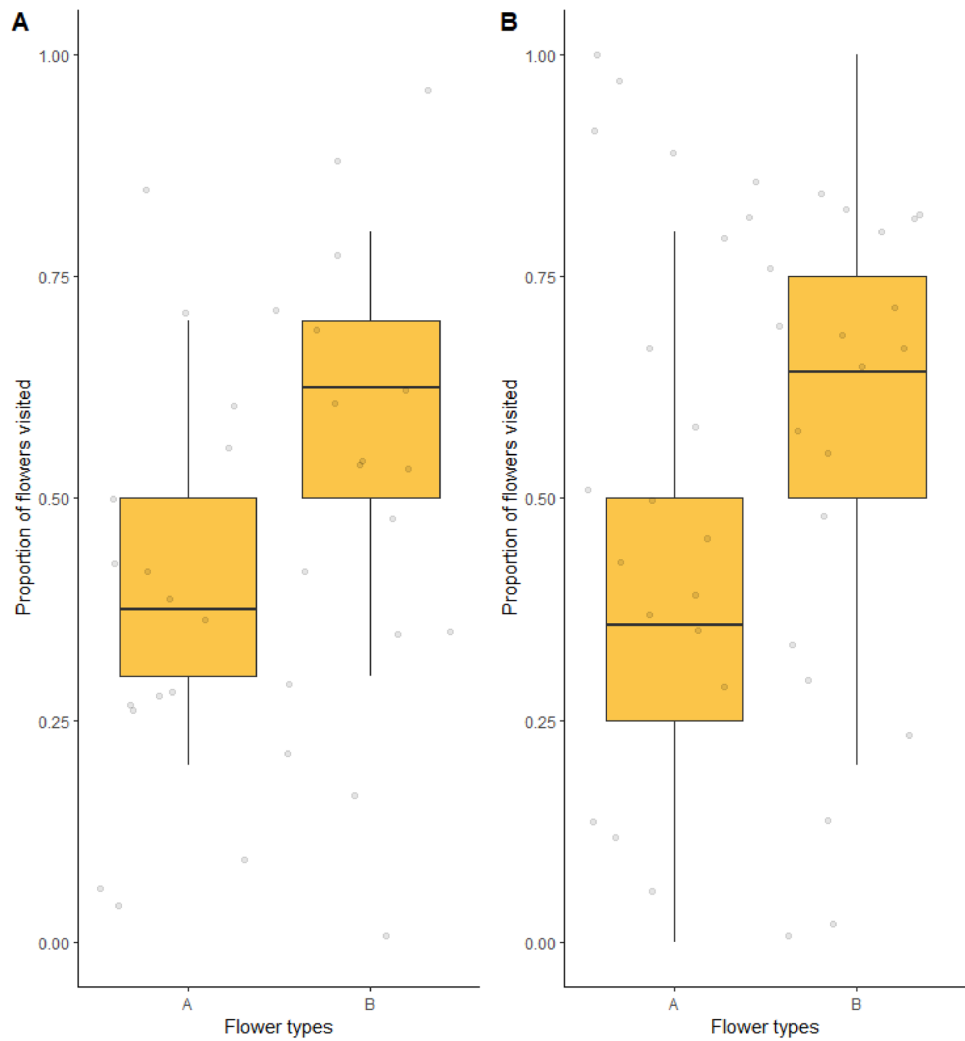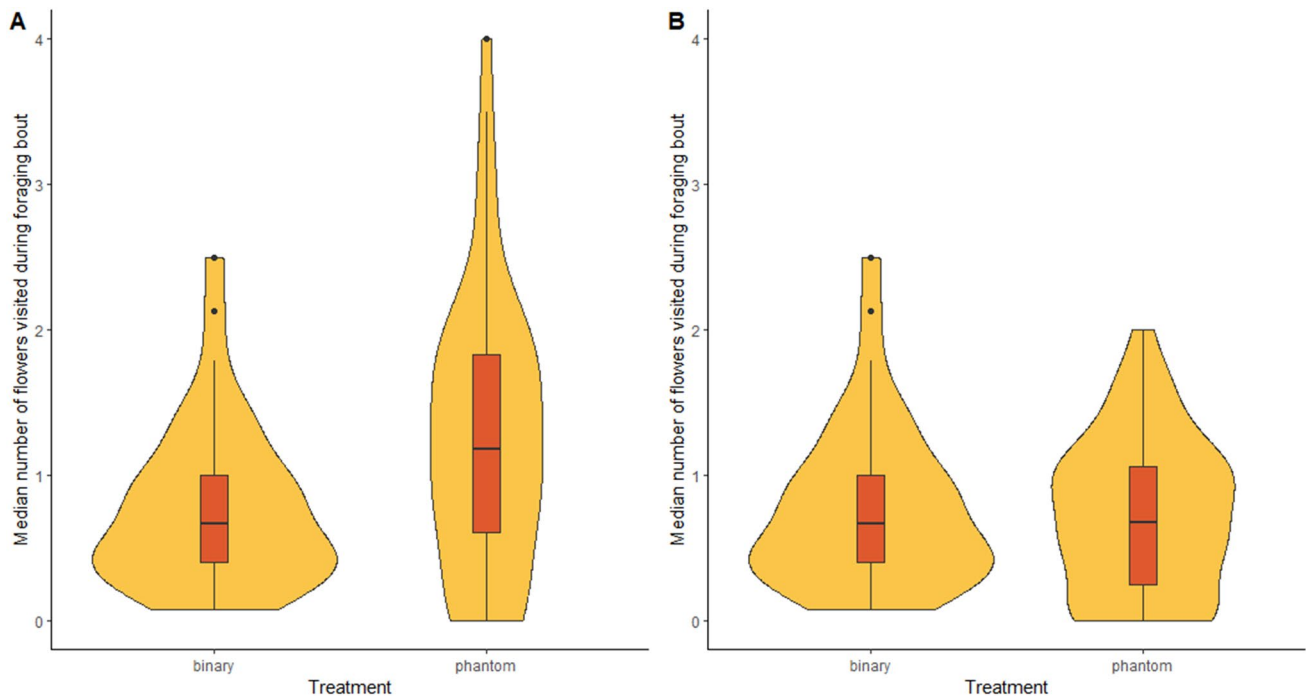

Table 2 GLMM outputs for the impact of the phantom decoy treatment on the number of floral visits per foraging bout

First floral choice				
Predictors		Odds ratios	CI	*P*
(Intercept)		0.80	0.56–1.16	0.238
Treatment [Empty flower]		1.45	1.03–2.04	**0.036**
Trained		0.86	0.60–1.24	0.430
Random effects				
σ^2	0.75			
$^{T}00$ bee identity	0.26			
ICC	0.26			
N bee identity	45			
Observations	705			
Marginal R^2/conditional R^2	0.041/0.288			

Bold represent significance at $\alpha < 0.05$

This study showed that there was not a clear change in preference for flowers in the presence of a previously highly rewarding, now empty flower. Asian honey bees *Apis cerana* show preference shifts when presented with empty flowers (Tan et al. 2015). *Tetragonula carbonaria*, in contrast, do not show similarity effects when an empty flower is present (Forster et al. 2023). It is likely that the effects of empty flowers on foraging preferences depend on floral traits being

Fig. 4 A Median number of floral visits by individual honey bees in the presence and absence of an empty flower; **B** Median number of floral visits by individual honey bees in the presence and absence of an empty flower, when visits to the empty flower were removed from the dataset. Note, that the first landing was not counted as a movement from a flower

Table 3 GLMM outputs for the impact of the empty flower treatment on the number of floral visits per foraging bout, when the empty flower was removed from the dataset

First floral choice			
Predictors	Odds Ratios	CI	p
(Intercept)	0.77	0.54–1.09	0.137
Treatment [Empty flower]	0.88	0.63–1.23	0.444
Trained	0.92	0.65–1.31	0.649
Random effects			
σ^2	0.91		
τ_{00} bee identity	0.21		
ICC	0.19		
N bee identity	45		
Observations	705		
Marginal R^2/conditional R^2	0.004/0.194		

considered by bees choosing alternative flowers. Tan et al. (2015) for example considered nectar quality and temperature, but only color was considered for *T. carbonaria* (Forster et al. 2023).

Honey bees were less likely to return to the floral patch in our experiments if the patch contained an empty flower. The abandonment of patches containing empty flowers may occur because bees attempt to mitigate the risk of frequently visiting unprofitable patches. Previous studies have also reported that encounters with empty flowers increase the probability that a bee will abandon a patch (Hodges 1985; Cresswell 1990; Kadmon and Shmida

1992; Smithson and Gigord 2003). While honey bees (*A. mellifera*) often return to unrewarding food sites if they have previously proven to be rewarding (Al Toufailia 2013), they may also display risk-averse behavior, and be less likely to visit patches that contain a high number of empty flowers (Cartar and Dill 1990; Shafir et al. 1999; Biernaskie et al. 2002; Nakamura and Kudo 2016). In the context of foraging, empty flowers may play an important role in determining when a bee leaves a patch. We only tested the effects of empty flowers on a small patch of three flowers. However, it would be beneficial to understand if larger patches of multiple species of plants get

abandoned in the presence of a previously rewarding, higher-quality flower.

Empty flowers could act as magnet plants. Magnet plants are highly attractive plants that benefit neighboring flowers by attracting floral visitors to the area (Thomson 1978). Over time, visitors like bees generalize floral cues associated with the magnet plant, which could include color, scent, or even the location of the magnet plant. Other plants in the area with similar traits then become attractive to these floral visitors (Johnson et al. 2003; Peter and Johnson 2008). In our study, in both treatments, bees continued foraging on the two lower-quality flowers even after the nectar from the high-quality flower was removed, albeit for a shorter time in the empty flower test. While magnet effects do not require a flower to be empty, our results suggest that the impact of magnet plants on their neighbors can continue even if the magnet does become unrewarding (Gilpin et al. 2019). It would be beneficial to study how long magnet effects persist when magnet plants experience a decrease in nectar quality.

We found that movement between flowers occurred more frequently in the presence of an empty flower. Movement usually involved movement between the empty high-quality flower and the lower-quality flowers, potentially suggesting bees were waiting for nectar replenishment. In previous experiments, movement between flowers in *B. terrestris*, *B. flavifrons*, and *Selasphorus rufus* decreased with increased rates of empty flowers (Biernaskie et al. 2002; Smithson and Gigord 2003). Movement between empty flowers also increases the distance bees travel for flowers, with unrewarding flowers resulting in increased flight distance to flowers by *Bombus terrestris* (Keasar et al. 1996). The impact of empty flowers on between-flower movements might depend on the probability that a flower will be empty, and also the quality of the nectar in the empty flower. Keasar (2000) found that if there is a 50% chance that visited flowers will be empty the next time a bee (*B. terrestris*) visits, bees will move between flowers more than if flowers consistently had nectar.

This increased movement between flowers can have impacts on the pollination of neighboring plants. In our experiment, flowers in close vicinity to the high-quality flower, albeit empty, meant visitation of lower-quality surrounding flowers was increased, which may increase visitation. However, a previous study using artificial flowers suggested that high-quality magnet plants may also result in more heterogeneous pollen movement (Thomson et al. 2019). The implications of hetero-specific pollen movement on pollination have mixed effects on the overall reproductive success of plants, so understanding specific-specific responses to magnet plants may be necessary, given the higher likelihood of interspecific pollen transfer when high-quality flowers become empty (Thomson et al. 2019; Lopes et al. 2022; Morales and Travaset 2008).

Our study involved empty flowers of a higher quality, which may have meant bees were more invested in returning to empty flowers to receive nectar rewards in comparison to situations where flowers were of equal value. Previously, experiments testing how often flowers were replenished involved testing flowers of the same reward quality (Keasar et al. 1996; Keasar 2000; Smithson and Gigord 2001, 2003; Biernaskie et al. 2002). Given we tested the effects of unavailable, but also previously highly rewarding flowers, returning bees may have been anticipating the replenishment of a high-quality flower. It would be beneficial to test the impact of reward schedules of high-quality flowers on neighboring flowers.

The increased movement we observed could be due to the presence of a third flower, rather than due to the presence of an empty flower. We did not incorporate a treatment that involved all three flowers (including a rewarding flower C) as we were principally interested in the effects of empty flowers on foraging behavior. Nevertheless, our results show that the presence of a previously rewarding flower can increase flower movements and patch abandonment rates compared to treatments where the empty flower is absent. Moreover, we have shown that an empty flower can impact movement rates even though it provides no reward. Future research could include a treatment where all three flowers are present. This would allow direct comparisons between a single pair of flowers, an empty flower test, and a trinary treatment where the high-quality flower is still available.

In previous unrewarding decoy experiments, social behavior has been shown to be an important factor in their effectiveness. Tests on individual eusocial bees have shown that foraging is impacted by decoys (Shafir et al. 2002; Tan et al. 2015). A previous experiment on *Tetragonula carbonaria* bees in groups showed that the removal of nectar from a high-quality flower did not impact floral choice on other available flowers (Forster et al. 2023).

Asymmetrically dominated decoys have also been tested in ants, showing similar results. while searching for new nests, individual *Temnothorax* ants were susceptible in the sense they picked nests similar to less rewarding decoy nest options presented to them (Edwards and Pratt 2009). However, if choosing nests on a group level, decoy nests did not impact nest choice. In a real-world foraging context, it is likely, however, that individual bees will forage based on social information from nest-mates and other foraging bees. Our study focused on the impact of empty flowers on *Apis mellifera* in a controlled environment that reduced some impacts of social choice in the experiment. Given the variable impacts of different decoy types on eusocial insects, it would be beneficial to test eusocial bees at both individual and group levels to really grasp how impactful empty flowers may be in a natural foraging context. As there are currently no studies on the impacts

of empty flowers on solitary bee species, future research could also investigate similar questions for the foraging ecology of solitary bees.

The current study focused on impact of empty flowers on the foraging choices of honey bees in isolation, within a close foraging distance to the hive. Because we did not know the colony to which foragers belonged, we were unable to detect behavioral impacts caused by within colony social interactions. However, honeybees can communicate the desirability of a resource using dance behavior (Frisch 1967; Seeley et al. 1991; Jack-McCollough and Nieh 2015). It is possible that testing the impacts of empty flowers could have knock-on effects on neighboring flowers, as dance behavior may encourage bees to forage elsewhere, and reduce overall visitation on a patch of differing flowers.

In summary, our study aimed to test the effects of empty flowers on foraging choices in honey bees. We found no evidence that empty flowers influenced the preference relationships between neighboring flowers. Instead, empty flowers appeared to increase between-flower movements and increased patch abandonment. Empty flowers have the potential to impact the reproductive success of neighboring flowers, by impacting both movement and abandonment rates of floral visitors. High-quality nectar-containing flowers can also gain pollination benefits when empty, as individuals may visit conspecific flowers after the empty high-quality flower is visited. Overall, our results suggest that the presence of empty flowers may not influence preference relationships between neighboring plants. However, more research is necessary to determine if different attribute combinations or degrees of similarity can influence the impact of empty flowers on neighboring flowers.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

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