Empty flowers have no impact on foraging choice in bumble bees (*Bombus impatiens*) in a social foraging context

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Abstract

Plants offer rewards such as nectar and pollen to entice flower-visiting insects. Flowers containing nectar may occasionally become empty due to climatic conditions, the time of day, or previous floral visitations. When flowers become empty, flower visitors must decide whether to abandon the flower or the patch. If the forager decides to remain in the patch, it must decide which flowers to visit next. Previously, *Apis cerana* and *Bombus terrestris* have shown evidence of similarity effects, where the bees were more likely to visit flowers more similar in colour, temperature, or nectar quality to the empty flower. Here, we examine the response of bumble bees, *B. impatiens,* when they encounter previously high-quality, now empty artificial flowers. We predicted that the presence of an empty, but previously rewarding flower changes bumble bee preferences for neighbouring flowers in the same patch. Furthermore, since bumble bees are social foragers, we also counted the nestmates present on flowers whenever a bee landed on a flower to feed. We found that for the most part, empty flowers did not affect bumble bees' preference relationships between the remaining flowers in a patch. Rather, their floral choice was influenced predominantly by social information, bumble bees were more likely to forage on a flower where other bumble bees were physically present. We conclude that while high-quality, yet unavailable options can affect the foraging preferences of individual bees, information from conspecifics is a more important driver of decisions in bumble bees.

Introduction

Animals make many choices in their lifetime, from what to eat, where to live and who to mate with. Sometimes, the preferred choice might become unavailable. For example, a perfect nest site that is occupied, or a food item that has been consumed by competitors. Optimal foraging theory assumes that animals make foraging choices by trading off between the likely losses and gains of each option. It implies an animal will assess all possible options before applying absolute valuation, where value of an item will not change, irrespective of outside factors (Rapoport, 1998). However, there is evidence that not all decisions are made using absolute valuations, with unavailable items sometimes changing preferences for other available items in a choice set. This is called the 'phantom decoy effect'.

In humans and other animals, phantom decoys most often increase preference to similar items in the choice set. This is called 'the similarity effect'. For example, when picking job applicants, if the 'best' candidate becomes unavailable, people are more likely to choose an available candidate most similar to the preferred unavailable one (Highhouse, 1996). While few non-human animals have been tested for the effects of phantom decoys, domestic cats and Asian honeybees (*Apis cerana)* have been shown to shift preferences in the presence of a phantom decoy (Scarpi 2011; Tan et al. 2015).

Phantom decoys may be particularly relevant to flower-visiting insects. While many flowers entice pollinators with floral rewards, such as pollen and nectar, not all flowers produce nectar and many flowers have peak times for nectar availability, or may run out of nectar following frequent visitations throughout the day (Chalcoff et al. 2006). It is already known that empty flowers can result in reduced visitation by bees (Smithson and Gigord 2003, Forster et al. 2023). When empty flowers are abundant, bumble bees tend to avoid flowers of similar colour to the empty flower, even

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when those flowers belong to different plant species (Smithson and Gigord 2003).

For social foragers such as bees, response to an empty flower could also be influenced by the social environment and by individual experience. Social behaviour can impact the choices insects make. Nest choice preferences in *Temnothorax* ants, for example, changes when individuals or groups of nestmates are choosing (Edwards and Pratt 2009). This effect breaks down, however, when searching in groups. In a real-world foraging context, it is likely, however, that individual bees will not be foraging independently, and may forage based on social information from nestmates and other foraging bees.

When foraging, bees often rely on social information to make effective decisions. Less experienced bumble bees are more likely to copy the floral choices of conspecifics (Kawaguchi et al. 2006; Jones et al. 2015). For example, bees with less foraging experience, spent more time following the choices of 'demonstrator bees' that shared similar innate colour preferences to the less experienced individuals (Jones et al. 2015). Scent marks from previous visitors can also be used to help individuals know if a flower is empty. Bumble bees, for example, will less likely visit a flower containing scent marks as they can be a sign of a depleted flower (Witjes and Eltz 2007).

In this study, we tested the impact of empty flowers on the foraging choice of bumble bees, *B. impatiens*. Since we were interested in the potential ecological consequences of the phantom decoy effect, our experiment aimed to answer two key questions. First, we tested if social information and foraging experience impact the effects of empty flowers on bumble bees. We predicted that experienced bumble bees would be more susceptible to the effects of empty flowers on choice in comparison to less experienced bumble bees, picking the flowers more similar to the empty flower. We then tested if social information and foraging experience impact the effects of empty flowers on bumble bees. We predicted that bumble bees would be more likely to visit flowers where more individuals were feeding.

Methods

Bumble bees (*Bombus impatiens*)

We tested the foraging preferences of the Eastern bumble bee (*B. impatiens)*. *B. impatiens* is a generalist, commercially available pollinator, used across North America and Mexico. They are naturally distributed across the eastern side of Canada. Colonies typically contain up to 300 individuals but are often purchased in quantities of as few as 50 individuals.

Colony setup

We conducted experiments using three commercially sourced, medium-sized colonies of *B. impatiens* (Natupol, Koppert Products, Canada), each containing approximately 70 individuals. We fed bees with pollen from a glass container lined with pipe cleaners, which were sprinkled with crushed honeybee pollen. We provided a 15% (w/w) sucrose solution ad libitum via white-coloured artificial flowers. We carried out all experiments in a portable plastic greenhouse, with dimensions of 1480 mm × 1460 mm × 1950 mm (Rona) situated near open fields at McMaster University, Ontario, Canada. Colonies were kept at ambient temperatures outside the greenhouses. We placed a tube at the colony entrance and connected it to the greenhouse, to allow bumble bees to enter during trials. We tested bees between temperatures of 25 and 35 °C, and under ambient daylight, albeit with little ultraviolet transmittance (which has minimal impact on our non-UV colour set). We conducted experiments between the 19th of July and the 20th of August 2019. All experiments occurred between 9 am and 5 pm EDT.

Artificial flowers

We were interested in investigating the effects of empty flowers on the choice of bumble bees in the context of phantom decoys. We followed the standard protocol for detecting phantom decoy effects (Trueblood and Pettibone 2017), whereby we compared the relative preference for one of two options (A and B) when the decoy (C) is absent versus when it is present. If animals are using absolute valuation strategies, then the presence of a phantom decoy will not have an impact on their relative preferences for the two non-decoy options (Table 1). A phantom decoy was represented by an artificial flower that once contained nectar, but was now empty. This is similar to humans experiencing an item that was advertised but now sold out.

We used artificial flowers to test if bumble bees showed a change in preference between two flowers when in a binary treatment, where a pair of flowers was present, or in an empty flower treatment, where three flowers were present, including one previously high-rewarding flower that is present but empty of nectar. Artificial flowers consisted of a laminated daisy-shaped flower with a 5 ml specimen tube in the centre to hold sucrose solution (Fig. 1). We glued specimen tubes to a dowel which was attached to a wooden block to hold flowers.

During experiments, we exposed bumble bees to a flower set consisting of three flowers, flowers (A, B and C) (Table 1), which varied in two attributes that were

Table 1 Flower attributes in different treatments used in the experiment

Treatment	Experimental phase	Flowers	Sugar concentration	Cotton ball
Ternary	Training	A	40% (w/w)	Present
		B	45% (w/w)	Absent
		High-quality flower	55% (w/w)	Present
Binary	Testing	A	40% (w/w)	Present
		B	45% (w/w)	Absent
Empty flower	Testing	A	40% (w/w)	Present
		B	45% (w/w)	Absent
		Empty flower	No sucrose solution	Present

Fig. 1 Examples of patterns of flowers used in experiments. Flowers consisted of a randomised colour and pattern combination
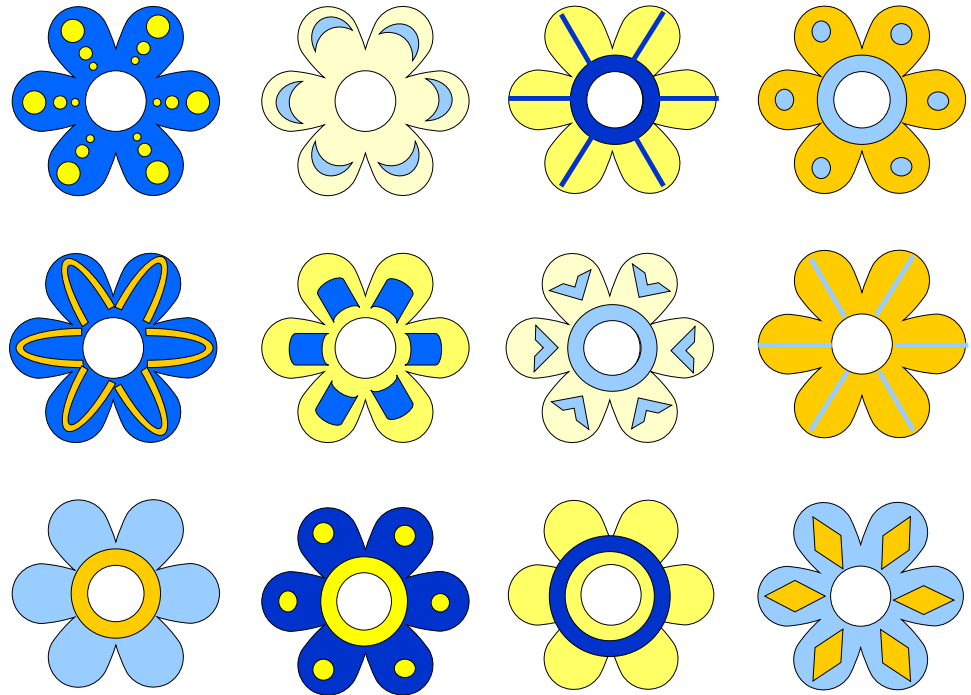
predicted to affect flower quality: sugar concentration and the accessibility of nectar. We used these attributes in combination as they could be traded off against each other; for example, low nectar quality may be worth feeding on if the flower is easy to access, but not when it is difficult to access. Decoy effects occur when the presence of an unavailable option affects the relative preferences for other items in the choices set. Trade-offs between item attributes are a common way of testing decoys, and decoy effects may be more prominent when attributes must be traded off. However, such trade-offs are not necessary for seeing decoy effects. For example, decoy effects have been found in hummingbirds when only nectar concentration was considered (Morgan et al., 2012).

To allow bees to learn which flowers had these attributes, we assigned flowers a unique colour and pattern which was randomised each time a trial was run. We randomised colours and patterns to prevent biases due to the effects of

innate preferences for particular patterns and colours on preferences made by bumble bees (Lunau and Maier 1995; Gumbert 2000).

In pilot trials, we found that bumble bees preferred flowers with a cotton ball on top, likely because they made nectar more accessible by soaking up sucrose solution. Based on pilot data, we designed flowers A and B to be similar in attractiveness to foraging bumble bees. flower A contained a lower sugar concentration (40% w/w) but had a cotton ball to make the sucrose solution more accessible, while flower B contained a higher concentration (45%) of sucrose solution but had no cotton ball. Flower C, which was used as the empty flower, had both a high sugar concentration (55% sucrose solution) and a cotton ball present and thus was expected to be the most preferred flower type when all three flowers contained nectar (Table 1). Bees were originally trained on flower C which only contained nectar at this stage but was empty of nectar during testing.

This empty flower had the same pattern and colour as the high-quality flower, but had no nectar on the cotton ball. The flowers' colour and pattern should have acted as a visual signal of its previous high quality. We chose to use a dry cotton ball rather than a cotton ball containing water as it may have received visitation purely for hydration purposes, whereas the dry cotton ball provided no nutrients or water, similar to what would occur in an empty flower in nature. We predicted that by removing the nectar from the highest quality flower (flower C), bumble bees would shift their preferences towards flower A as the accessibility of nectar (presence of a cotton ball) is the same as the high-quality flower C, making it more visually similar to the empty flower (Table 1).

We confirmed the discriminability of our floral colours, which included three shades of blue, and three shades of yellow, and white paper to bumble bees via reflectance spectrometry and visual modelling. This entailed first quantifying the reflectance of blue 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, USA). We then modelled the location of each sample in the hexagon colour space using the visual phenotype of the bumble bee (*B. Terrestris*) under an assumed D65 standard daylight illuminant and neutral background, and selected shades that were separated by a Euclidean distance of at least 0.11; the absolute discrimination threshold (albeit for honeybees; (Chittka 1992; Dyer and Chittka 2004; Maia et al. 2019; Supplementary Fig. 1; Supplementary Table 1), which should thus be readily separable by our focal bees.

Pre-training and training to flower types

We trained individuals to recognise artificial flowers and their associated attributes by placing flowers in a greenhouse, approximately 1.5 m above the ground, in patches of four. Each flower type (A, B or C) was associated with a different shade of either blue or yellow. To ensure colour preference did not skew preferences for flower types, a single trial consisted of a randomised selection of either three shades of yellow flowers, or three shades of blue flowers.

For all experiments, bees were allowed to forage as a group, directly from the colony. This provided bees with the opportunity to forage in an ecologically relevant setting where other bees are present during their decision-making process. This also allowed us to test the impact of social foraging behaviour on choice.

We started a training session by placing a set of nine flowers of a single type into the greenhouse on a shelf approximately 1.5 m from the ground. Bumble bees were then sequentially exposed to all three flower types (A, B, C) one at a time, plus a final training phase with all three flower types together (Fig. 2). The order in which bumble bees experienced flower types was randomised. We recorded and individually marked all bees that landed on each flower with coloured paint pens, the colour combinations of markings were used to identify individuals. Bumble bees were allowed to forage freely from the flowers until at least 10 individuals had visited each flower type at least 5 times. Some bees visited flower types more than the necessary five times to be considered trained in the process of other individual being trained. It usually took approximately 45 min for a sufficient number of bees to visit each flower type at least five times
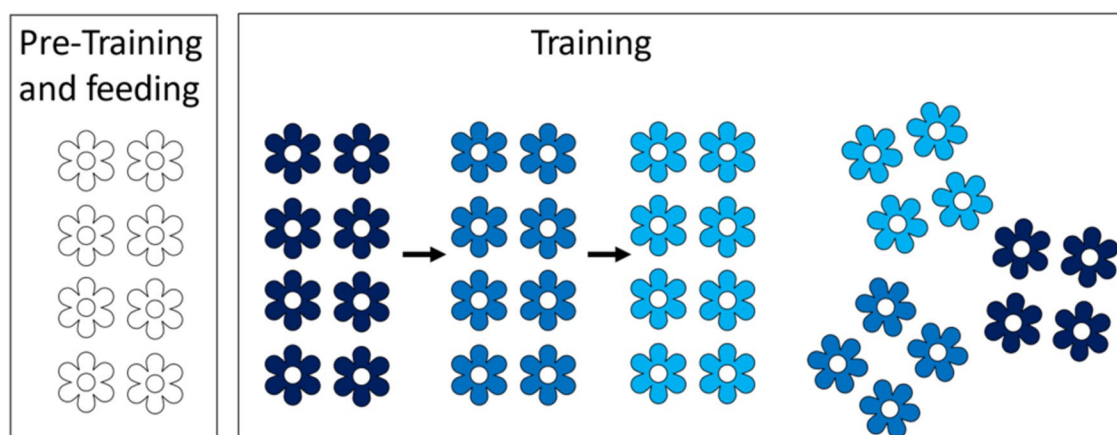

Fig. 2 Experimental setup for pre-training and training phase. Bees were originally fed on plain white flowers. During the training, bees were introduced to three different sets of flowers in a randomised order to train bees to visit a patch with the different flower types. Bees were considered trained after ten individuals had visited each flower type five times. Bees were then allowed to feed on all flowers together, offered in groups of four for half an hour. The number of visitors to each flower type was recorded. When experiments were conducted on a colony that had already been tested, we used a different colour and new pattern for the flower set. Colonies were given at least one day between each test

and, therefore, be considered trained. It usually took 2.5 h for bees to be trained to each individual flower type and complete the 45-min preference recording containing all three flowers. If training was not complete by 3 pm, training was stopped and resumed the next day. If experiments were conducted over 2 days, bees were given a 'refresher' at the beginning of the session where they were exposed to each flower type for 30 min. There were four occasions where a refresher was necessary.

Test phase: choice trials

In the choice trials, we either presented bumble bees with a binary set containing flowers A and flower B (Table 1) or an empty flower set containing flowers A, B and C, with C being empty of nectar and so acting as the empty flower. We randomised the order in which bees received the two treatments. All choice sets (binary, training and empty flower treatments) consisted of the same total number of flowers, with the binary set only containing flowers A and B, and the empty flower containing A, B, C (Fig. 3).

We started trials by placing all three flower types approximately 1 m away from the tube that allowed bumble bees to enter the greenhouse. The trial began once we had placed all flowers in the choice set. A visit was counted if a bumble bee landed and fed on the nectar available. When a bumble bee landed, we recorded its identity based on paint markings, the flower it landed on as well as the number of bees currently present on the flower at the time of visitation. Each trial lasted 1 h. In total eleven trials were completed by 246 bees from three colonies. All bumble bees were allowed to forage throughout the experiment, as we intended on testing if social behaviour was important in foraging choice. It was not possible to record data blind because our study involved focal animals in the field.

Statistical analyses

Testing the attractiveness of the high-quality flower

We first confirmed that flower C was the most preferred of the three flowers during the training session while it still contained nectar using Welch's ANOVA with the independent variable being the flower types (A, B or C), and the dependent variables being the number of visits to each flower by individual bees. A Welch's ANOVA was used as the data were not normally distributed. We used a Dunn's post hoc test to establish if the flower C was most visited overall during the 30-min training when all flowers were present and full of nectar.

Bees that foraged after the training period ended were not marked. Unmarked bees (2,935 of 10,109 visitation observations) were removed from the following analyses as we were unable to distinguish between individuals. There was no difference in the flower preference of bumble bees when unmarked bumble bees were excluded (data not shown).

The effect of empty flowers on foraging preferences of bumble bees

We determined if bumble bees changed their preference for flowers A or B in the presence or absence of an

Fig. 3 Test phase of experiment. Bees were introduced to 12 flowers which contained 2 groups of flowers in the binary treatment and 3 groups of all three flowers, with the empty flower (coloured in the darkest blue) flower empty of nectar during the empty flower treatment
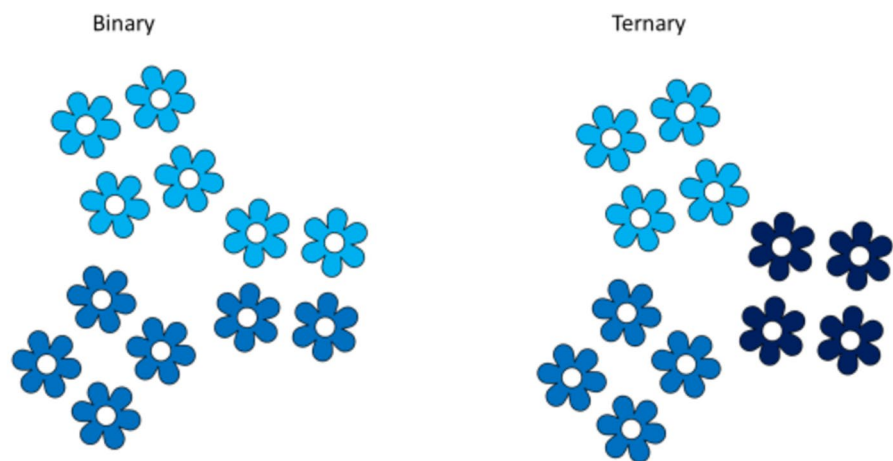
Test phase consisted of one hour of foraging on the binary choice set, and one hour on the ternary choice set in a randomised order.

empty flower. For all analyses, we set flower choice as a binary choice, with flower A assigned as the target flower. Flower choice referred to the flower that an individual landed on during a foraging visit. To test the effect of the empty flower on floral choices by individual bumble bees, we used a generalised linear mixed model (GLMM) with binomial error distribution and a link logit function (Table 2). We specified floral choice (either flower A or B) as a binary response variable. We included treatment (binary or empty flower), level of experience (experienced/ inexperienced), and the number of bumble bees (explained below) present on the flower at the time of visitation as fixed effects, and individual bumble bee identity nested within its colony and the date of the experiment as a random effect. The trial order for each colony was also included as a fixed effect to establish if retesting individuals within the colony resulted in changes in preference over time. GLMMs were created using the lme4 package (Bates et al. 2015) in R version 4.1.2 (R Core Team 2021).

Experienced forager analysis

We were interested in testing whether bees that were experienced with the flower types were more likely to change their preferences in the presence of an empty flower than those without foraging experience. For bumble bees to be considered experienced, they had to visit all three flower types at least five times during the training sessions, and then needed to visit the patch of flowers at least ten times during the binary and empty flower treatments. We tested whether experienced bees were more or less likely to have significant preferences for flower A or B between binary and empty flower treatments using a GLMM with a binomial distribution. We specified flower choice (A or B) as a binary response variable and included treatment (binary or empty flower treatment), trial number and the number of bumble bees present on the flower at the time of visitation as predictor variables. Bumble bee colony and identification nested within the date of experiments was specified as a random effect.

We then tested if overall visits by each trained individual bee resulted in a preference for a flower type. To determine if individual bumble bees in the experienced subset significantly preferred flower A or B, we tested if the bumble bee visited flower A or B more than expected by chance using a binomial test, where the expected probability was 0.5. If the binomial test was significant, we classified the bumble bee as having a 'preference'. Bees that showed no significant preference were classified as 'indifferent'. We also corrected for multiple comparisons using Bonferroni corrections.

Ethical note

No certificate or licencing numbers or ethics approval was required, as study of this species does not require any government or institutional approval through Sydney University's Animal Ethics requirements.

Results

We recorded visits by 246 individually marked bumble bees during test phases, with 29 considered 'experienced'. Overall, 132 individual bees visited the empty flower during the test phase, including 23 of the 29 experienced bumble bees.

Testing the attractiveness of the high-quality flower

Overall, bumble bees showed a significant preference for flower C (55% cotton ball; Welch's test, $F_{2, 229} = 35.382$, $\alpha < 0.001$), thereby confirming a preference for the decoy when it contained nectar. Individuals had similar preferences for the remaining two flowers, A and B (Fig. 4). Bumble bees were able to visit multiple flowers in a bout, which were also included in determining the overall preference by bumble bees.

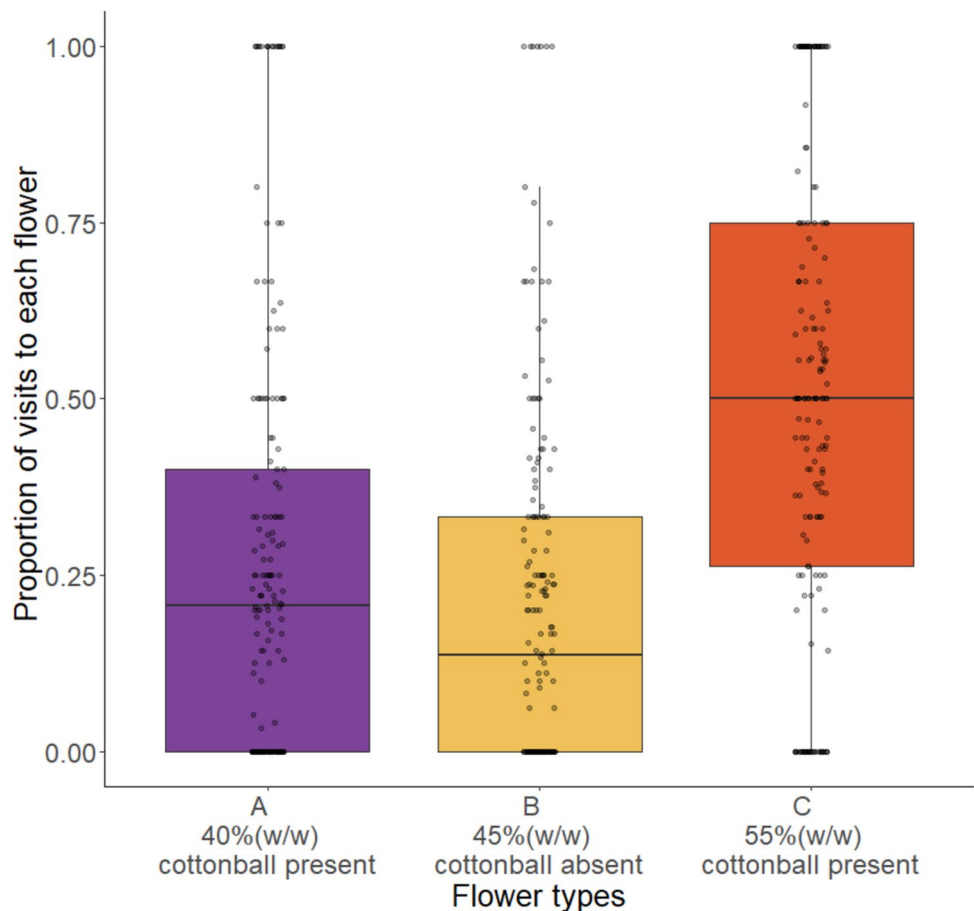### Effect of empty flowers on foraging preferences in groups of bumble bees

The presence of an empty flower had no impact on the preference between flower A and B in the binary or empty flower treatments by bumble bees (Fig. 5). Inexperienced bumble bees, however, were more likely to visit flowers that already had conspecifics feeding in comparison to experienced bumble bees (Table 2). This did not hold for the subset of bees that were experienced in the choice set. Their choices were not influenced by the number of bees already foraging on flowers (Table 2). During the experiment, there were between 0 and 6 individuals counted visiting a single flower.

Experienced bee analysis

Of all bees in the experiment, only 27 were considered experienced. The presence of the empty flower did not affect preferences towards flower A (Fig. 6; Table 3). The flower choice of experienced bumble bees was not impacted by the number of individuals on the flower before landing. Treatment order did impact the floral choices bees made. Bees were more likely to pick flower A if the empty flower treatment occurred before the binary treatment (Table 3).

Of the 27 individual bumble bees that were considered experienced and had visited flowers in each treatment at least ten times, 12 initially showed a preference shift between

Fig. 4 The mean proportion of visits by individual bees to all flower types during the 30-min training set ($n = 183$). Flower A (purple) refers to the flower with 40% sucrose and a cotton ball, flower B (yellow) refers to the flower with 45% sucrose and no cotton ball, flower C (orange) represents the flower with 55% sucrose and a cotton ball. Black lines refer to the median percent of visits. Error bars refer to standard error, with the median proportion of visits represented by horizontal lines in the boxplot. Asterisk refers to significant difference in the proportion of visits between flower types

Discussion

We tested the impact of empty flowers on foraging choice using bumble bees in a foraging task that provided an opportunity for social foraging. A small subset of experienced individuals changed their preferences in the presence of an empty flower, suggesting there is a small possibility empty flowers could impact some individuals, though the robustness of this finding is tempered by a relatively small sample size of experienced bees. We found that inexperienced individuals were more likely to use social context—the number of conspecifics foraging on a flower. Social context no longer had an effect when considering only the subset of trained

binary and empty flower treatments. With Bonferroni corrections for multiple comparisons, this was reduced to five individuals (Supplementary Table 2). Of these five individuals, one moved from a preference for flower B in binary trials to no preference (in empty flower trials), one from no preference (binary trials) to flower B (empty flower trials) and three from no preference (binary trials) to flower A (empty flower decoy trials).

foragers, whose choices appeared unaffected by the presence of other foragers.

While there was no overall impact of empty flowers at the population level, 5 of the 27 individual bees in our study showed a significant switch in preference in the presence of the decoy. For example, one bee had no preferences in the binary treatment but preferred flower B in the empty flower treatment, while another bumble bee preferred flower A in the binary but had no preference in the empty flower treatment. Variation in individual preferences in the presence of a decoy has been seen in other species. Individual-level preference switches have been observed in *Apis cerana*, where the presence of an empty flower caused individual bees to pick flowers more similar in attribute space to the empty flower, there was some variation in individual preferences observed (Tan et al. 2015). Similarly, hummingbirds showed individual-level variation in their direction of preference for artificial flowers when an empty third option was added, with 4 of the 11 birds changing their preference in the predicted direction, and 5 of 11 changed their preferences in the opposite direction (Bateson et al. 2003). Taken together, the literature (and our work) suggests that some individuals might be more susceptible to decoy effects than others. Individuals may have had different innate preferences, sensory
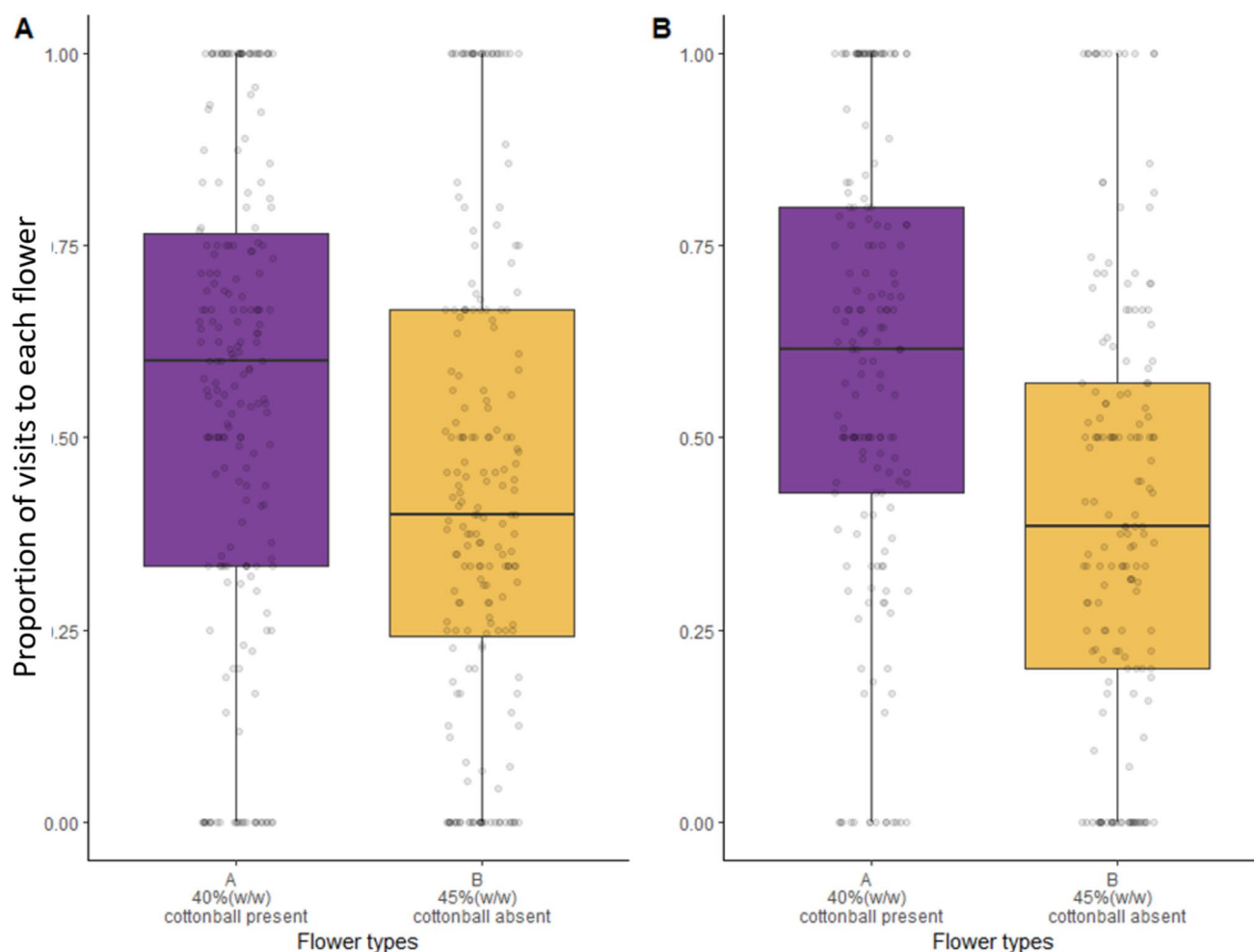
Fig. 5 Proportion of visits by individual bees in the in the binary (**A**), and empty flower treatment (**B**) for *all* bees ($n = 246$). Flower A (purple) refers to the flower with 40% sucrose and a cotton ball, and flower B (yellow) refers to the flower with 45% sucrose. Error bars refer to standard error, with median proportion of visits represented by horizontal lines in the boxplot. There was no significant flower choice made by bees in either treatment

Table 2 GLMM output for the effect of treatment on flower choice by bees

Parameter	Estimate	Standard error	Z	P
Intercept	0.168	0.241	0.696	0.486
Treatment	0.097	0.689	1.407	0.159
Experience	−0.078	0.121	−0.644	0.519
Number of bees present	0.168	0.050	3.361	0.000***
Treatment order	0.301	0.211	1.429	0.153
Trial Number	0.005	0.062	0.083	0.933

Predictor variables are treatment, whether or not bees had previous experience with all flower types, the number of bees present on a flower when a new bee landed, and the order in which bees were exposed to treatments. Asterisks represent significance at $\alpha < 0.05$. Variance of random effects: Bee identity: 0.215, Date: 0.001

biases, or levels of experience with the foraging choice that could have impacted how they chose which flowers to forage on. Our results only show a small number of preference shifts (5 out of 27 individuals), so the impacts of decoys in this experimental context should be interpreted with caution. A larger study may be necessary to understand the variation in decoy susceptibility.

Bees, including bumble bees, also rely on visual local enhancement, where the presence of nestmates can impact visitation to flowers (D'Adamo et al. 2000; Slaa et al. 2003; Sommerlandt et al. 2014). Our results show that bumble bees used group foraging to make decisions as to which flower to visit. We did not separate individuals to understand their preferences in the absence of social information. To identify how foragers respond to empty flowers in the absence of social information, it would be necessary to test individuals one at a time. However, our experiment provided
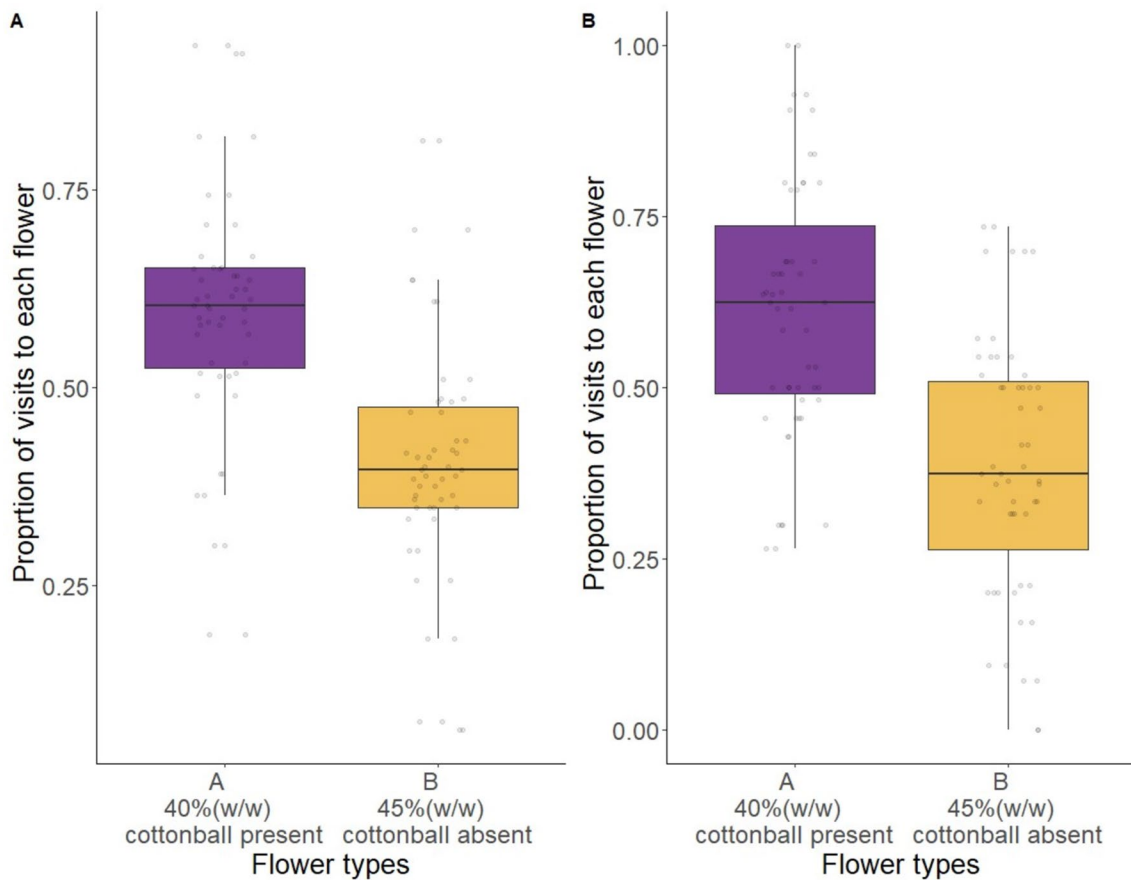
Fig. 6 The mean proportion of visits by individual bees from the experienced subset to flowers in the empty flower (**A**) and binary treatments (**B**) (n=27). Flower A refers to the flower with 40% sucrose and a cotton ball (purple), and flower B refers to the flower with 45% sucrose and no cotton ball (yellow). Error bars refer to standard error, with the median proportion of visits represented by horizontal lines in the boxplot. There was no significant flower choice made by bees in either treatment group

Table 3 GLMM summary for the effect of treatment on flower choice by the experienced subset of bees (n=27)

Parameter	Estimate	± Standard error	Z Value	P-value
Intercept	−0.425	0.224	−0.190	0.849
Treatment	0.079	0.114	0.694	0.487
Number of bees present	0.105	0.090	1.172	0.241
Treatment order	0.693	0.221	3.135	0.001**
Trial number	0.046	0.061	0.751	0.452

Predictor variables are treatment, the number of bees present on a flower when a new bee landed and the order in which bees were exposed to treatments. Asterisks represent significance at $\alpha < 0.05$. (Conditional R^2: 0.092, Marginal R^2: 0.011)

the opportunity to understand foraging responses to empty flowers in a setting similar to natural foraging, where bees are likely to encounter other foraging individuals on a patch.

This experiment provided ad libitum sucrose solutions, which may have impacted choice to some degree in this experiment. While bees were experiencing empty flowers, there was always another floral option available nearby to the empty flowers, which may not always be the case in a real-world scenario. It is possible that floral choices by individuals may have been impacted by the constant supply of nectar, so it would be beneficial to look at the effects of empty flowers when there were also minimal resources available to forage on instead of the high-quality flower.

Previously, animals have chosen items in choice sets in the presence of phantom decoy effects using similarity effects, where individuals are more likely to pick the more similar item to the unavailable one (Scarpi 2011; Tan et al. 2015). However, the realisation that a preferred item is now unavailable can also result in more loss-averse individuals avoiding unavailable options or picking options less related to the unavailable one (See Highhouse (1996) for example). Given a small subset of experienced bees shifted their preferences, it may be necessary to test the impact of phantom decoys using different attributes on

individual bumble bees to untangle to decision-making strategies used by this species.

In our experiment, less experienced individuals were more likely to visit flowers containing that other bees were currently foraging on. We only saw a small number of experienced individuals in our experiment, but similar patterns have been seen, with experienced foragers generally being more efficient foragers in terms of travel speed and nectar collection (Lihoreau et al. 2016), so there is less value in using social information once sufficient information on the foraging environment has been obtained. Only a small subset of the population of bees were truly 'experienced' in the foraging environment, and over time, the number of experienced individuals would likely increase. It is possible that if more individuals had foraging experience on all flowers, there could also be an increase in individuals susceptible to effects of empty flowers. This could in turn change the choices of less experienced individuals. Our study provides further evidence for flexible information use in bumble bees, where individuals can preferentially use private information over social information when they are experienced.

Our flowers acted as a large landing area with a central nectary that allowed multiple visitors to enter the flower at the same time, allowing us to test the impact of other foraging bees on floral choice. Previous studies have shown that bees leave scent marks on previously depleted flowers, which can prevent visitation to unprofitable flowers (Giurfa and Núñez, 1992; Giurfa et al., 1993; Stout et al., 1998; Saleh et al., 2007). On smaller flowers that can be depleted as opposed to containing ad libitum nectar like those in our experiment, it is possible that social information from the presence of other bees, as well as scent marks could result in reduced future visitation. Many flowers only allow single visitors at a time, so it would be beneficial to investigate the impacts of social information on foraging choice on flowers that can only be visited by single individuals.

Groups may be generally less susceptible to decoy effects, particularly in eusocial species. Edwards and Pratt (2009) found that while individual *Temnothorax* ants were susceptible to decoy effects, foraging groups were not. The communication systems of social insects can lead to high degrees of positive feedback which can cause a single option to be greatly preferred over the others (Sasaki and Pratt 2011). Such amplification may lessen the impact of phantom decoys by preventing less experienced individuals from ever encountering the empty flower. In our experiment, bees less experienced with the foraging setting were more likely to pick flowers based on the relative number of bees already foraging on that flower. Over time, it became increasingly likely for individuals less experienced with the foraging setting to never experience the empty flower. The collective nature of bumble bees foraging meant that some bees did not actually experience the complete choice set and were potentially 'unaware' of the presence of the empty flower.

Empty flowers can impact how bees choose flowers, and there is potential that these choices are predictable and can be modelled from phantom decoys used in behavioural economics. Decoy experiments are usually considered in highly controlled environments with artificially created foraging experiences which may result in conclusions that are not necessarily applicable to real-world foraging scenarios, which makes it hard to draw conclusions about their applicability (Latty and Trueblood, 2020). We used controlled flowers in an ecologically relevant social setting for bumble bees to try and further understand how phantom decoys may work in more natural environments. Our experiment showed that empty flowers did not directly impact foraging choice in bumble bees at the population level, suggesting that empty flowers may not affect the valuation of surrounding flowers. We did, however, find an impact of empty flowers on the behaviour of a small subset of experienced bumble bees, although the direction of their preferences shifts was inconsistent. Further, we found that bees less experienced with the foraging setting were more likely to forage on flowers when conspecifics were present. Our study highlights the importance of including social behaviour in understanding the impacts of decoys on social species.

Author contributions CF: conceptualisation, methodology, investigation, data curation, and writing. TEW: editing and supervision. DFH: editing and supervision. RG: editing and supervision. TL: conceptualisation, methodology, investigation, data curation, and writing.

Data availability Data are available on Github: https://github.com/CaitlynForster/data_Bimpatiens_emptyflowers.

Declarations

Conflict of interest There are no conflicts of interest to disclose.

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