



Flower choice by the stingless bee *Tetragonula carbonaria* is not influenced by colour-similarity to a higher-reward flower in the same patch

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Abstract – Floral choice by bees is influenced by the bees' previous experience with flowers. For example, bees may learn to associate particular flower colours with rewards and prefer flowers of that colour in a given patch. In this study, we assessed whether floral choice by the stingless bee *Tetragonula carbonaria* was influenced by colour similarity to a high-quality neighbour flower, while it contained nectar, and then when it was empty of nectar. We trained *T. carbonaria* to visit highly rewarding artificial flowers (50% (v/v) honey solution) within a patch that also contained two types of less-rewarding artificial flowers (20% (v/v) honey solution): one of the same colour (though different pattern) as the high-quality flower and one a different colour (and pattern) to the other two flowers. Colonies were tested with blue and yellow colour sets, where either the blue flower was most rewarding and the yellow the least, or vice versa. We then compared preferences between the two equal-quality flowers in the patch under two conditions: (i) when nectar was available from the high-quality flower, and (ii) when the nectar was removed from the high-quality flower. We found that, when available, high-quality flowers were always visited more than low-quality flowers. Under this condition, adjacent lower-quality flowers in the patch received similar levels of visitation, regardless of their colour. When the reward was removed from the high-quality flower (simulating an emptied flower), foragers quickly switched to using the remaining two equal-quality flowers in the patch, but again showed no preference for the similar-coloured flower. Our results indicate that *T. carbonaria* are adaptable foragers capable of quickly learning and responding to floral reward changes in their foraging environment. At least under our experimental conditions, we found no evidence that *T. carbonaria* floral choice is influenced by colour similarity to a high-quality resource in the same foraging location.

Stingless bee / Pollination / Artificial flower / Colour

1. INTRODUCTION

Nectar acts as a nutrient-rich reward to floral visitors and, by attracting floral visitors to flowers for nectar rewards, plants gain assistance in

pollen transfer and therefore pollination benefits. However, the production of nectar can be costly (Pyke 1991). Many plants, therefore, have strategies to tune their nectar production to floral visitor behaviour in ways that ensure adequate pollination benefits without an overproduction of nectar. One consequence of this is that not all flowers contain nectar at any given time. For example, climate, floral attractiveness, and time of day can all impact nectar availability in

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flowers (Langenberger and Davis 2002; Waser and Price 2016; Wright 1988).

The presence of flowers empty of nectar (“empty flowers”) in an environment can impact the foraging choices of floral visitors (Langenberger and Davis 2002; Waser and Price 2016; Wright 1988). Over time, insects may learn to generalize floral traits associated with unrewarding flowers (Smithson and MacNair 1997), resulting in decreased visitation to morphologically similar neighbouring flowers (Smithson and Gigord 2003). For example, where unrewarding flowers are common in a patch, bumble bees *Bombus terrestris* will tend to avoid flowers similar in colour to the unrewarding variety and instead visit flowers of dissimilar colours (Smithson and Gigord 2003; Internicola et al. 2009). In humans, such behaviour is known as a dissimilarity effect. Conversely, empty flowers could potentially increase visitation to similar flower types (a “similarity effect”). That is, if a normally rewarding flower is recently unavailable, bees may seek out morphologically similar flowers for rewards (Dyer and Murphy 2009; Gigord et al. 2002; Internicola et al. 2009). Flowers that never contain nectar such as orchids have even evolved to mimic rewarding flowers to reap the benefits of colour generalisations made by bees towards rewarding flowers (Papadopoulos et al. 2013).

Highly rewarding neighbouring plants can also impact the probability that a flower is visited by bees (Horna Lowell and Murphy 2022). “Magnet plants” are those whose flowers are highly desirable to floral visitors (Ghazoul 2006; Gilpin et al. 2019a; Johnson et al. 2003). For example, lousewort (*Pedicularis sylvatica*) and lavender (*Lavandula* spp.) are often considered magnet plants for honey bees and bumble bees (Gilpin et al. 2019b; Lavery 1992). By attracting floral visitors to the vicinity, magnet plants can increase pollination benefits to nearby plants due to “spillover effects” (Ghazoul 2006; Johnson et al. 2003). Such spillover effects are strongest where magnet plants are similarly coloured to neighbouring plants. Thus nectarless orchids of similar colour to adjacent magnet plants are more likely to gain pollination benefits than other nearby plants of distinct colours (Johnson et al. 2003; Peter and Johnson 2008).

To date, most of our understanding of how bees respond to the colour similarity of flowers in a patch, whether they contain nectar or not (i.e. nectarless or nectar-depleted) has come from studies on two groups of social bees: bumble bees and honey bees. Stingless bees (tribe Meliponini) are the other major clade of social bees, yet their foraging behaviour and floral choices are comparatively understudied. Stingless bees are abundant and important pollinators in tropical ecosystems across the globe, visiting upwards of 215 plant families (Bueno et al. 2021). They are also pollinators of a variety of tropical crops and are increasingly used as managed pollinators in agro-ecosystems (Grüter 2020). In Australia, the stingless bee *T. carbonaria* is the species most widely propagated for commercial trade and is an effective pollinator of crops including macadamia, avocado, and blueberry (Heard 1994; Kendall et al. 2020). *T. carbonaria* colonies comprise a single queen and typically 5000–10,000 workers (Heard 1999). The species is common throughout both forests and disturbed environments in tropical and subtropical Eastern Australia.

In this study, we asked the following: (1) When a high-quality flower is present in a patch, do *T. carbonaria* foragers visit nearby flowers of similar colours more than those of dissimilar colours?, and (2) When a high-quality flower is depleted of nectar, do foragers initially visit nearby flowers of similar colours more than those of dissimilar colours? We tested foragers visiting resources in their natural social context; that is, workers foraging in the presence of nestmates, rather than lone foragers absent of all social information.

We predicted that *T. carbonaria* would generalise flower colour after learning the quality of flowers, as previously shown for the bumble bee *B. terrestris* (Dyer and Chittka 2004; Gumbert 2000; Rohde et al. 2013) and the honey bee *Apis mellifera* (Dyer and Murphy 2009; Rohde et al. 2013). That is, we expected that *T. carbonaria* would preferentially visit flowers that were similar in colour to the most rewarding flower in the group. Following nectar depletion, we hypothesised that foragers

would again be influenced by flower colour, but that their floral choices would differ in the short term and longer term after nectar removal. We predicted that when a highly rewarding flower is removed from a choice set, foragers would initially have a preference for similar coloured flowers to the high-quality flower. When a once highly rewarding flower had been empty for an extended period, we predicted that foragers would learn that this flower type was persistently unrewarding and begin to prefer the adjacent flowers that were least similar in colour.

2. METHODS

2.1. Colonies

We used 14 colonies of *T. carbonaria* maintained by The University of Sydney and Kuringai Council Nursery, Sydney, Australia. Each colony was housed in a three-part Original Australian Trigona Hive (OATH) style wooden hive (Heard 1999). To ensure that foragers were naive to the local natural flower locations (therefore encouraging foraging on our patch of artificial flowers), colonies were moved one at a time from their usual location to the yards of private houses in Lidcombe or Baulkham Hills, Sydney for the period of data collection. Experiments were conducted between December 2021 and March 2022.

2.2. Artificial flowers

To assess the impact of high-reward flowers on other flowers in the patch, we created a patch of artificial flowers with three flowers that differed in colour and pattern (Table I). Two flowers contained a reward of equal concentration (Flowers A and B; 5 ml of 20% honey solution) and one which was of higher concentration (Flower C, the “high-reward flower”; 5 ml of 50% honey solution). Flower A had a circular pattern, Flower B had no pattern, and Flower C

(“high-reward”) was the same colour as Flower A, but with a radiating pattern. Patterns were used as additional associative cues. We chose blue and yellow as flower colours since they are colours that can be readily discriminated by *T. carbonaria* (Spaethe et al. 2014). To control for any innate colour preferences, two colour sets were used: one set in which A and C were yellow and B was blue, and a second set in which A and C were blue, while B was yellow (Table I).

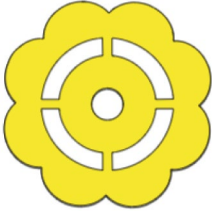
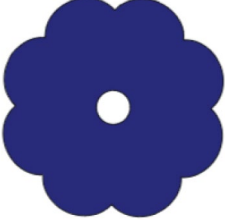

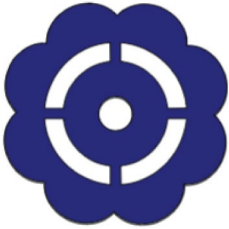
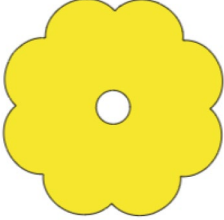

Artificial flowers consisted of the coloured paper flower cut to shape using a precision cutting machine (Cricut Maker) and placed underneath a 75-mm-diameter clear Perspex disc containing radiating lines indented in the top to hold the honey solution. The honey solution was placed on a cotton ball that was put on top of the artificial flower, to allow the honey solution to seep into indentations on the artificial flowers.

Briefly, we confirmed the discriminability of our three floral colours to bees by using spectrometry to record the reflectance of cardboard, before estimating their colour difference using the colour hexagon model of Chittka (1992), with the visual phenotype of honeybees (Maia et al. 2019). All three stimuli were separated by distances well above documented absolute discrimination thresholds (Supplementary Figure S1), and so should be readily separable by our focal bees.

2.3. Pretraining and training

For each colony, we first trained foragers to a gravity feeder to encourage them to forage at the test location, which was a green wooden board 1 m directly in front of the hive entrance (level with the colony). The gravity feeder consisted of a plastic plate covered by a single sheet of paper towel, onto which we positioned an upside-down cup containing a 50% (v/v) honey solution so that the solution progressively seeped onto the towel. The gravity feeder was initially placed right next to the hive, touching the colony entrance. Once 20 foragers were present on the feeder, we slowly shifted it to the test location. The training feeder was then removed and replaced by our three

Table 1 Sets of artificial flowers used in this study and the relative reward offered (honey:water solution). Flower C is the “high-reward” flower, with 50% solution, while Flowers A and B were lower-reward concentrations (20% solution), with Flower A sharing the same colour as C (i.e. colour-similar to the high-reward flower) while Flower B was a different colour

	Flower A (similar to C)	Flower B (dissimilar to C)	Flower C (high-reward)
Reward	20%	20%	50%
Yellow set			
Blue set			

artificial flowers. Artificial flowers were placed edge-to-edge with each other during the 30-min training phase. During this time, bees were able to freely forage on all three flower types. We could confirm foragers were coming from our trained colony by observing their flight to and from the hive entrance.

2.4. Test phase

During the test phase, the three artificial flowers were positioned in a triangular configuration, with flowers 10 cm apart from each other. The test phase had two parts (Figure 1). In the first 50 min of the experiment, all three flowers in the test set had a honey solution available. Just before the 60-min observation interval, we removed the honey solution from Flower C.

Nectar removal was done by replacing the flower with a new clean feeder with a cotton ball containing no nectar on top. All flowers were also replaced with new clean Perspex top-feeders at this stage. During the second part of the test phase (60–150 min), all three flowers were available for the bees to visit, but only Flowers A and B offered any food. We performed forager counts on artificial flowers at 10-min intervals throughout the test phase (i.e. five counts before removing the reward from Flower C, and ten counts after removal). We counted every stingless bee that landed and fed on a flower for 1 min. One minute was chosen to prevent pseudoreplication, as it was a short enough period of time to prevent bees from returning to the feeder after previously feeding. Between each count, foragers were allowed to continue accessing the flowers. However, before each new count, flowers were

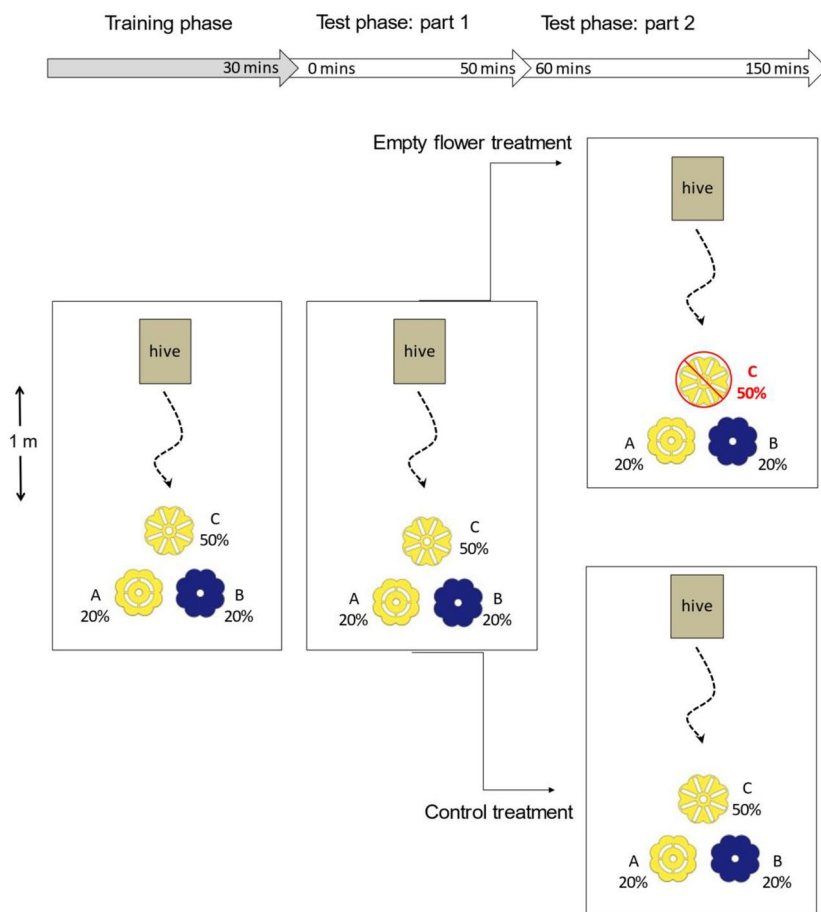


Figure 1. Overview of the experimental design used to assess if flower choice by *T. carbonaria* foragers is influenced by colour-similarity to high-reward flowers (either full or emptied) in a patch (high reward=Flower C). The reward was removed from Flower C during test phase part 2 in the experimental (“empty-flower”) treatments but not the control treatments. Percentages indicate the percentage of honey used in each solution (v/v). Note, that the layout of the three flowers was randomised during each time interval where data was recorded.

replaced with new flowers. All flowers were cleaned with 70% ethanol before being used again and rotated in the triangular configuration to reduce any effects of their location and remove any scent marks.

To confirm that any responses to nectar removal from Flower C were due to the removal, and not just the passage of time, we performed both our experimental treatment (Flower C reward was removed during the test phase; $N=12$ trials) and a control treatment (no reward removal during the test phase; $N=10$ trials). In the experimental treatment, eight colonies were

used, with three colonies used more than once (two colonies used twice with different colour sets, and one colony used twice with the blue set and once with the yellow set). In our control treatment, eight colonies were used across all trials, with two colonies used twice with different colour sets. We initially ran trials for 100 min as we anticipated that colonies would reach satiation and stop foraging within that time period. However, the first two colonies we tested were still foraging strongly after 100 min. Since we were interested in how *T. carbonaria* behaviour changed following the switch in flower quality,

we decided to increase the observation time to 150 min. As a result, we have 150 min of foraging data for 8 colonies, and 100 min for two colonies. We retained these shorter trials in our dataset because 100 min represented the maximum “post-flower-removal” timepoint in our analysis (i.e. 40-min post-reward removal in the experimental treatment; Figure 1), and evidence from all remaining colonies was that forager choice did not vary significantly between 100 and 150 min.

2.5. Data analysis

All analyses were conducted in R version 4.1.2 (R Core Team 2021). To establish if the high-quality flower was the most preferred artificial flower, we performed a Kruskal–Wallis test considering all visits to flowers before the 60-min observation interval. The Kruskal–Wallis test was used due to a lack of normality in data (McKnight and Najab 2010). We then used post hoc pairwise tests to compare forager numbers on Flowers C vs A and B (Dunn test), with p -values adjusted for multiple testing via the Benjamini Hochberg Method (Benjamini and Hochberg 1995).

We used ANOVAs to compare the number of foragers visiting each of the neighbouring flowers (Flowers A and B) to a high-reward flower (Flower C) at three key time points: one directly before nectar removal from Flower C (after 50 min, i.e. count 5), one directly after nectar removal (70 min; count 7) and one after 100 min (i.e. after foragers had time to learn that Flower C was now consistently unrewarding). Significant differences in forager counts between Flowers A and B at any of these time points would indicate a preference for the option that was either similarly coloured or differently coloured to Flower C.

Finally, we assessed whether the removal of reward from Flower C caused changes in the number of total foragers using the patch after the nectar was removed in the empty flower treatment, using a Kruskal–Wallis test. That is, we assessed whether foragers abandoned the

patch once the best quality flower was no longer available.

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

3. RESULTS

When a high-reward artificial flower was available in the patch, foragers showed a strong preference for this flower (i.e. Flower C), with around twice as many foragers visiting Flower C than each of Flowers A or B at the end of part 1 test phase in both experimental and control treatments (Table II, Figure 2; $\chi^2(2)=30.391$, $p<0.0001$, where post hoc pairwise tests for Flowers A vs. C and B vs. C both $p<0.0001$). There was no difference in visitation rates between Flowers A and B at this time ($F(1)=0.866$, $p=0.729$); that is, while some foragers did use the lower-reward flowers adjacent to a high-quality flower, there was no preference among these for flowers similarly-coloured to the high-reward option.

Once the nectar was removed from the high-reward flower, visitation to this flower decreased rapidly within 10 min, indicating foragers quickly learnt it was now empty (Table II; Figure 2). Foragers shifted at this time to use the remaining rewarding flowers (A and B) with similar numbers on each ($F(1)=0.25$, $p=0.621$; Table II, Figure 2). Foragers continued to show no preference between Flowers A and B after a longer interval post-nectar removal from the high-reward flower (i.e. once they had time to learn that Flower C was now consistently unrewarding; $F(1)=0.942$, $p=0.338$; Table II). Overall visitation to the patch by *T. carbonaria* decreased in the presence of a previously rewarding, but now empty, flower (experimental treatment vs control treatment: $\chi^2(1)=61.687$, $p=<0.001$; Figure 2; Table II).

4. DISCUSSION

We investigated whether foragers of the stingless bee *T. carbonaria* were influenced by the colour of a high-quality flower when choosing between flowers

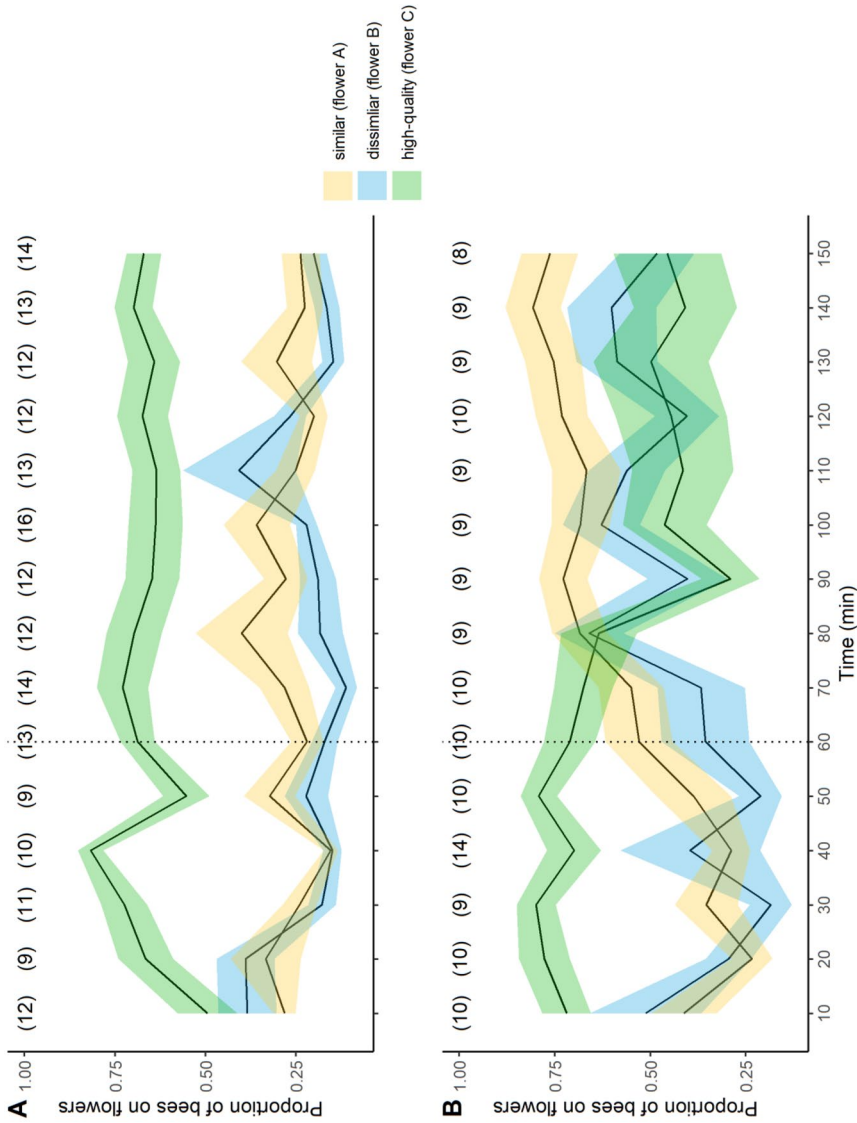








Figure 2. The mean proportion (\pm S.E.) of *T. carbonaria* foragers feeding on artificial flowers in our patch throughout the test phase (150 min) for **A** Control treatments ($N = 10$ colonies), and **B** experimental treatments ($N = 12$ colonies); the dotted line indicates the time at which nectar was removed from the high-quality flower in the experimental treatment). Counts were made for 1 min at 10-min intervals. The mean forager numbers for each count interval are indicated in parentheses at the top of the plots. Flower C (green plot) was a high-reward flower (50% honey solution). Flower A was similar in colour to Flower C but lower reward (yellow plot; 20% honey solution) and Flower B was dissimilar in colour to Flower C and also lower reward (blue plot; 20% honey solution).

Table II Mean numbers (\pm S.E.) of *T. carbonaria* foragers visiting artificial flowers in a patch during three-time points in the test phase (50, 70 and 100 minutes) for experimental and control treatments. Flower C was high-reward while Flowers A and B were equal, lower reward flowers. Flowers C and A were the same colour, while Flower B was a different colour. In the experimental treatment, the feeding solution (“nectar”) was removed from Flower C at the end of part 1 of the test phase (i.e. after 60 minutes) and the flower remained empty for the rest of the test phase. Images in this table show the “yellow set” flower colours as examples

Timepoint		50 minutes (bees/min)	70 minutes (bees/min)	100 minutes (bees/min)
Experimental treatment (N = 12)		High-reward Flower C available	High-reward Flower C recently depleted	High-reward Flower C depleted for >30 mins
	Flower A 	2.91 (\pm 0.83)	4.00 (\pm 1.16)	2.81 (\pm 0.65)
	Flower B 	2.13 (\pm 0.74)	3.57 (\pm 0.92)	3.45 (\pm 1.01)
	Flower C 	4.47 (\pm 1.02)	2.53 (\pm 0.49)	2.67 (\pm 0.50)
Control treatment (N = 10)	High-reward flower (C) always available			
	Flower A 	2.22 (\pm 0.22)	3.88 (\pm 0.83)	4.43 (\pm 0.68)
	Flower B 	2.00 (\pm 0.37)	2.00 (\pm 0.21)	3.40 (\pm 0.54)
	Flower C 	4.70 (\pm 0.68)	7.60 (\pm 1.44)	7.80 (\pm 1.28)

of similar and dissimilar colours to the high-quality flower in a patch, including after the preferred flower became nectar-depleted. We found that while *T. carbonaria* readily foraged on less-rewarding artificial flowers adjacent to the high-quality flower, they were no more likely to choose those flowers if they colour-matched the high-reward resource than if they did not. Nor were foragers’ flower choices between neighbouring nectar-containing flowers influenced by the presence of an empty, previously high-quality flower in the patch. That is, in all, *T. carbonaria* foragers showed a consistent lack of preference between two flowers of equal reward but different colours, regardless of the availability of a high-quality neighbour flower.

Honey bees and bumble bees have been shown to quickly learn to make generalisations about flowers based on colour across a range of foraging contexts (Dyer and Chittka 2004; Dyer and Murphy 2009; Giurfa 1991; Gumbert 2000; Rohde et al. 2013). At least in bumble bees, this colour generalisation extends to a preference for flowers that are similar in

colour to those that have been previously rewarding (Gigord et al. 2002; Johnson et al. 2003). Why then did we detect no evidence of colour generalisations in our experiment with foraging *T. carbonaria*? A key difference between our study and previous ones on other bee species is that we assessed the collective foraging choices of *T. carbonaria* in a social environment, rather than those of lone foragers in isolation. That is, foragers in our study could see and smell their nestmates using flowers in the same patch. Social behaviour is likely an important factor in foraging choice in stingless bees, and by allowing interactions with nestmates we ensured that we were assessing foraging responses in the most ecologically relevant context. For example, *T. carbonaria* uses scent marks at food sources to recruit nestmates to profitable resources (Bartareau 1996; Gloag et al. 2021), as do other stingless bee species (Bartareau 1996; Roselino et al. 2016; Schmidt et al. 2003; Schorkopf et al. 2007; Sommerlandt et al. 2014). Many bees, including stingless bees, also rely on visual local enhancement, where the presence of a conspecific

can increase visitation to a flower (D'Adamo et al. 2000; Slaa et al. 2003; Sommerlandt et al. 2014). Presumably, social bees will rely less on their personal experience with particular colours when selecting flowers if they also have available the social information provided by nestmates. Alternatively, some foragers in our experiment may simply have been sufficiently experienced with all three flower types in our sets (i.e. had visited and could recall the relative values of Flowers A, B, and C) such that they had no need to make generalisations about flower colour once the preferred flower was empty. Indeed, some visitation of the low-quality flowers (A and B) persisted throughout the pre-removal stage of trials, though we cannot confirm whether this was the result of a few foragers repeatedly visiting these flowers, or many different foragers visiting them infrequently. Whichever the case, we cannot rule out that *T. carbonaria* will sometimes respond to high-reward flowers by later selecting similar colour choices (e.g. in cases where no social information is available, and/or if they have no direct experience with other flower types in a patch). Ultimately, tests of individual *T. carbonaria*, in the absence of social information, would be needed before direct comparisons with previous studies on bumble bees or honey bees can be made.

The natural foraging landscape for *T. carbonaria* may also help to explain why we did not detect colour generalisations by foragers in response to empty flowers in this study. In Australia, many naturally occurring mass flowering plants are trees containing thousands of flowers of the same species, such as those in the family Myrtaceae (e.g. eucalypts (Somerville 2019) and Australian stingless bees often forage in trees (Bueno et al. 2021; Grüter 2020). Compared to meadows, where bees are likely to encounter multiple flower species growing next to each other, mass-flowering trees represent a less heterogeneous foraging environment. Future efforts to understand the responses of stingless bees to empty flowers may require therefore a better understanding of how they experience foraging spaces with both high and low flower heterogeneity. For example, *T. carbonaria* and other stingless bees may regularly need to respond to empty flowers within inflorescences on a single

plant, rather than within patches of closely positioned different flowers.

Social insect colonies may benefit from having some workers that visit food sources other than those known to be the most profitable. For example, in mass recruiting ant species, not every ant will follow pheromone trails. Individuals that are not following the main trail may find new resources and may make colonies quicker to reallocate foragers if the most profitable food source becomes unavailable (Deneubourg et al., 1983; Deneubourg et al. 1987; Vittori et al., 2006). In bees, variation in the foraging strategies of individual bees can similarly allow colonies to adapt quickly to changes in resource availability. Bumble bees (*B. terrestris*) that are more likely to visit less profitable flowers in a patch are also more likely to visit novel flowers (Evans and Raine 2014), suggesting that these more error-prone individuals are most likely to be first to locate newly available resources. In *A. mellifera*, individual bees may have different foraging search strategies (different foraging 'personalities'; Dyer et al. 2014; Smithson and Gigord 2003). Some foragers are fast to learn the value of new resources, while others are slow to change preferences once established. The efficiency of these different strategies varies depending on how often flower quality changes in a patch (Dyer et al. 2014). Worker bees may also vary in their reliance on social information to make foraging choices, ensuring an optimal balance between benefiting from group knowledge and finding new resources. (Gigord et al. 2002; Johnson et al. 2003). Although our experiments record only collective-level foraging responses, our data is consistent with *T. carbonaria* foragers from the same colony showing variability in their response to the same floral cues, given that all three flowers in a patch were used by at least some foragers. Further work is needed to better understand how variation in foraging decisions between workers, or "error" in foraging decisions, contributes to the foraging ecology of stingless bees.

High-quality flowers can sometimes facilitate increased visitation to the lower-quality flowers in the same patch (spillover caused by a "magnet plant" effect). Magnet plant effects are potentially important in the context of crop pollination, either

because they can be used to entice wild or managed pollinators to crop blooms which might otherwise be a less-preferred floral resource (Johnson et al. 2003; Montero-Castaño et al. 2016; Horna Lowell and Murphy 2022), or because the magnet plant competes with the crop for pollinators. Given the promising prospects of *T. carbonaria* as a pollinator of some Australian crops (Heard 1994, 1999; Kendall et al. 2020), we recommend that the susceptibility of this species to magnet plant effects is a fertile area for future investigation. In our study, while we found no evidence for flower colour generalisation in foraging decisions (and thus no support for the idea that magnet plants near crops must share flower colour with the crop to be effective), we do find that *T. carbonaria* foragers continually visited the lower-quality flowers adjacent to the highest-quality flower in our experimental patch, consistent with a possible magnet effect of the high-reward flower. Further experimental work comparing *T. carbonaria* visitation to experimental patches with and without high-reward plants is now needed, as well as field data of natural foraging behaviour in this species, to better understand how co-located plants impact foraging choice. Indeed, magnet plant effects remain largely unstudied for all pollinators in Australian agricultural or natural ecosystems (Gilpin et al. 2019a).

In all, our experiment demonstrates that *T. carbonaria* are versatile social foragers, capable of quickly learning to abandon previously rewarding but unavailable resources when foraging alongside nestmates. Their floral choice in a patch was not influenced by colour similarity to high-quality flowers, and some foragers visited lower-quality resources in a patch even when high-quality options were present. We suggest that *T. carbonaria*'s ability to adapt quickly to new resources, and willingness to forage on resources irrespective of their quality, may make them suitable targets for magnet plants in a crop pollination context, and warrants further investigation. If and when their foraging choices are influenced by floral colour generalisations, and whether such behaviour

impacts pollination networks in Australia, also requires further study.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-023-00997-y>.

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AUTHOR CONTRIBUTION

CYF: conceptualisation, methodology, investigation, formal analysis, and writing—original draft. FM: methodology and investigation. DFH: supervision, and writing—editing. TEW: supervision, data curation, formal analysis, and writing—editing. TL: supervision, conceptualisation, methodology, resources, and writing—editing. RG: supervision, conceptualisation, methodology, resources, and writing—editing. All Authors approved the final draft.

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DATA AVAILABILITY

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

CODE AVAILABILITY

Code for analyses is available on GitHub and can be shared upon reasonable request.

DECLARATIONS

Ethics 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.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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REFERENCES

- Bartareau T (1996) Foraging behaviour of *Trigona carbonaria* (Hymenoptera: Apidae) at multiple-choice feeding stations. *Aust J Zool* 44(2):143–153. <https://doi.org/10.1071/zo9960143>
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J Roy Stat Soc: Ser B (methodol)* 57(1):289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Chittka L (1992) The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *J Comp Physiol A* 170(5):533–543
- D'Adamo P, Corley J, Sackmann P, Lozada M (2000) Local enhancement in the wasp *Vespa germanica* Are visual cues all that matter? *Insectes Soc* 47(3):289–291. <https://doi.org/10.1007/PL00001717>
- Deneubourg JL, Pasteels JM, Verhaeghe JC (1883) Probabilistic behaviour in ants: a strategy of errors? *J Theor Biol* 105(2):259–271. [https://doi.org/10.1016/S0022-5193\(83\)80007-1](https://doi.org/10.1016/S0022-5193(83)80007-1)
- Deneubourg JL, Aron S, Goss S, Pasteels JM (1987) Error, communication and learning in ant societies. *Eur J Oper Res* 30(2):168–172. [https://doi.org/10.1016/0377-2217\(87\)90093-2](https://doi.org/10.1016/0377-2217(87)90093-2)
- Dyer AG, Chittka L (2004) Biological significance of distinguishing between similar colours in spectrally variable illumination: bumble bees (*Bombus terrestris*) as a case study. *J Comp Physiol A* 190(2):105–114. <https://doi.org/10.1007/s00359-003-0475-2>
- Dyer AG, Dorin A, Reinhardt V, Garcia JE, Rosa MGP (2014) Bee reverse-learning behavior and intra-colony differences: simulations based on behavioral experiments reveal benefits of diversity. *Ecol Model* 277:119–131. <https://doi.org/10.1016/j.ecolmodel.2014.01.009>
- Dyer AG, Murphy AH (2009) Honey bees choose “incorrect” colors that are similar to target flowers in preference to novel colors. *Israel Journal of Plant Sciences* 57(3):203–210. <https://doi.org/10.1560/IJPS.57.3.203>
- Evans LJ, Raine NE (2014) Foraging errors play a role in resource exploration by bumble bees (*Bombus terrestris*). *J Comp Physiol A* 200(6):475–484. <https://doi.org/10.1007/s00359-014-0905-3>
- Garcia Bulle Bueno F, Kendall L, Araujo Alves D, Lequerica Tamara M, Heard T, Latty T, Gloag R (2021) Stingless bee floral visitation in the global tropics and subtropics. *BioRxiv* 440550. <https://doi.org/10.1101/2021.04.26.440550>
- Ghazoul J (2006) Floral diversity and the facilitation of pollination. *J Ecol* 94(2):295–304. <https://doi.org/10.1111/j.1365-2745.2006.01098.x>
- Gigord LD, Macnair MR, Stritsky M, Smithson A. The potential for floral mimicry in rewardless orchids: an experimental study. *Proc R Soc Lond B Biol Sci* 269(1498):1389–1395. <https://doi.org/10.1098/rspb.2002.2018>
- Gilpin A-M, Denham AJ, Ayre DJ (2019a) Are there magnet plants in Australian ecosystems: pollinator visits to neighbouring plants are not affected by proximity to mass flowering plants. *Basic Appl Ecol* 35:34–44. <https://doi.org/10.1016/j.baae.2018.12.003>
- Gilpin A-M, Denham AJ, Ayre DJ (2019b) Do mass flowering agricultural species affect the pollination of Australian native plants through localised depletion of pollinators or pollinator spillover effects? *Agr Ecosyst Environ* 277:83–94. <https://doi.org/10.1016/j.agee.2019.03.010>
- Giurfa M (1991) Colour generalization and choice behaviour of the honey bee *Apis mellifera* ligustica. *J Insect Physiol* 37(1):41–44. [https://doi.org/10.1016/0022-1910\(91\)90017-T](https://doi.org/10.1016/0022-1910(91)90017-T)
- Gloag R, Smith JP, Stephens RE, Heard TA, Beekman M (2021) Australian stingless bees detect odours left at food sources by nestmates, conspecifics and honey bees. *Insectes Soc* 68:151–159
- Grüter, C (2020) Stingless bees: an overview. In: Grüter C (ed) *Stingless bees: their behaviour, ecology and evolution*. Springer international publishing, p 1–42. https://doi.org/10.1007/978-3-030-60090-7_1
- Gumbert A (2000) Color choices by bumble bees (*Bombus terrestris*): Innate preferences and generalization after learning. *Behav Ecol Sociobiol* 48(1):36–43. <https://doi.org/10.1007/s002650000213>

- Heard TA (1999) The role of stingless bees in crop pollination. *Annu Rev Entomol* 44(1):183–206. <https://doi.org/10.1146/annurev.ento.44.1.183>
- Heard TA (1994) Behaviour and pollinator efficiency of stingless bees and honey bees on macadamia flowers. *J Apic Res* 33(4):191–198. <https://doi.org/10.1080/00218839.1994.11100870>
- Horna Lowell ES, Murphy SM (2022) Neighborhood effects and honey bee foraging behavior. *J Apic Res* 0(0):1–12. <https://doi.org/10.1080/00218839.2022.2045755>
- Internicola AI, Page PA, Bernasconi G, Gigord LDB (2009) Carry-over effects of bumble bee associative learning in changing plant communities leads to increased costs of foraging. *Arthropod-Plant Interactions* 3(1):17–26. <https://doi.org/10.1007/s11829-008-9051-6>
- Johnson SD, Peter CI, Nilsson LA, Ågren J (2003) Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84(11):2919–2927. <https://doi.org/10.1890/02-0471>
- Kendall LK, Gagic V, Evans LJ, Cutting BT, Scalzo J, Hanusch Y, Jones J, Rocchetti M, Sonter C, Keir M, Rader R (2020) Self-compatible blueberry cultivars require fewer floral visits to maximize fruit production than a partially self-incompatible cultivar. *J Appl Ecol* 57(12):2454–2462. <https://doi.org/10.1111/1365-2664.13751>
- Langenberger MW, Davis AR (2002) Temporal changes in floral nectar production, reabsorption, and composition associated with dichogamy in annual caraway (*Carum carvi*; Apiaceae). *Am J Bot* 89(10):1588–1598. <https://doi.org/10.3732/ajb.89.10.1588>
- Laverty TM (1992) Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia* 89(4):502–508. <https://doi.org/10.1007/BF00317156>
- Maia R, Gruson H, Endler JA, White TE (2019) pavo 2: new tools for the spectral and spatial analysis of colour in R. *Methods Ecol Evol* 10(7):1097–1107
- McKnight PE, Najab J (2010) Kruskal-Wallis test. The Corsini Encyclopedia of Psychology 1:1–10. <https://doi.org/10.1002/9780470479216.corpsy0491>
- Montero-Castaño A, Ortiz-Sánchez FJ, Vilà M (2016) Mass flowering crops in a patchy agricultural landscape can reduce bee abundance in adjacent shrublands. *Agr Ecosyst Environ* 223:22–30. <https://doi.org/10.1016/j.agee.2016.02.019>
- Papadopoulos AST, Powell MP, Pupulin F, Warner J, Hawkins JA, Salamin N, Chittka L, Williams NH, Whitten WM, Loader D, Valente LM, Chase MW, Savolainen V (2013) Convergent evolution of floral signals underlies the success of Neotropical orchids. *Proceedings of the Royal Society b: Biological Sciences* 280(1765):20130960. <https://doi.org/10.1098/rspb.2013.0960>
- Peter CI, Johnson SD (2008) Mimics and magnets: the importance of color and ecological facilitation in floral deception. *Ecology* 89(6):1583–1595. <https://doi.org/10.1890/07-1098.1>
- Pyke GH (1991) What does it cost a plant to produce floral nectar? *Nature* 350(6313):58–59. <https://doi.org/10.1038/350058a0>
- R Core Team (2021) R: A language and environment for statistical computing (4.1.2) [Computer software]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rohde K, Papiorek S, Lunau K (2013) Bumble bees (*Bombus terrestris*) and honey bees (*Apis mellifera*) prefer similar colours of higher spectral purity over trained colours. *J Comp Physiol A* 199(3):197–210. <https://doi.org/10.1007/s00359-012-0783-5>
- Roselino AC, Rodrigues AV, Hrncir M (2016) Stingless bees (*Melipona scutellaris*) learn to associate footprint cues at food sources with a specific reward context. *J Comp Physiol A* 202(9):657–666. <https://doi.org/10.1007/s00359-016-1104-1>
- Schmidt VM, Zucchi R, Barth FG (2003) A stingless bee marks the feeding site in addition to the scent path (*Scaptotrigona aff. Depilis*). *Apidologie* 34(3):237–248. <https://doi.org/10.1051/apido:2003021>
- Schorkopf DLP, Jarau S, Francke W, Twele R, Zucchi R, Hrncir M, Schmidt VM, Ayasse M, Barth FG (2007) Spitting out information: *Trigona* bees deposit saliva to signal resource locations. *Proceedings of the Royal Society b: Biological Sciences* 274(1611):895–899. <https://doi.org/10.1098/rspb.2006.3766>
- Slaa EJ, Wassenberg J, Biesmeijer JC (2003) The use of field-based social information in eusocial foragers: Local enhancement among nestmates and heterospecifics in stingless bees. *Ecological Entomology* 28(3):369–379. <https://doi.org/10.1046/j.1365-2311.2003.00512.x>
- Smithson A, Gigord LDB (2003) The evolution of empty flowers revisited. *Am Nat* 161(4):537–552. <https://doi.org/10.1086/368347>
- Smithson A, MacNair MR (1997) Negative frequency-dependent selection by pollinators on artificial flowers without rewards. *Evolution* 51(3):715–723. <https://doi.org/10.2307/2411148>
- Somerville D (2019) Honey and pollen flora of south-eastern Australia, NSW Department of Primary Industries, NSW
- Sommerlandt FM, Huber W, Spaethe J (2014) Social information in the stingless bee, *Trigona corvina* Cockerell (Hymenoptera: Apidae): the use of visual and olfactory cues at the food site. *Sociobiology*, 61(4):401–406. <https://doi.org/10.13102/sociobiology.v61i4.401-406>
- Spaethe J, Streinzer M, Eckert J, May S, Dyer AG (2014) Behavioural evidence of colour vision in free flying stingless bees. *J Comp Physiol A* 200(6):485–496. <https://doi.org/10.1007/s00359-014-0886-2>

- Vittori K, Talbot G, Gautrais J, Fourcassié V, Araújo AFR, Theraulaz G (2006) Path efficiency of ant foraging trails in an artificial network. *J Theor Biol* 239(4):507–515. <https://doi.org/10.1016/j.jtbi.2005.08.017>. (<https://www.sciencedirect.com/science/article/pii/S0022519305003577>)
- Waser NM, Price MV (2016) Drought, pollen and nectar availability, and pollination success. *Ecology* 97(6):1400–1409. <https://doi.org/10.1890/15-1423.1>
- Wright DH (1988) Temporal changes in nectar availability and *Bombus appositus* (Hymenoptera: Apidae) foraging profits. *Southwest Nat* 33(2):219–227. <https://doi.org/10.2307/3671898>

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