

Socially acquired flower colour preference in honey bees (*Apis mellifera anatolica*) without direct observation of the task

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Abstract

Social learning occurs when animals acquire information from other individuals. In honey bees, studies of social learning have primarily focused on direct observational paradigms in which naïve individuals observe demonstrators interacting with floral resources within the same foraging setting. However, it remains unclear whether socially influenced foraging preferences can emerge in the absence of direct observation of demonstrators during foraging. We explored whether naïve honey bees, *Apis mellifera anatolica*, would shift their flower colour preference following a period of cohabitation with trained demonstrators, without direct observation of demonstrators at the artificial flower patch. Demonstrator bees were trained to forage on yellow artificial flowers and subsequently remained with naïve bees within the same hive during a period of cohabitation. Naïve bees were then tested individually on the artificial flower patch, where both yellow and blue flowers were equally rewarded. Compared with baseline visitation, naïve bees showed a marked shift towards yellow flowers, although the strength and temporal pattern of this response varied substantially among individuals. Most naïve bees visited yellow flowers at least once, providing preliminary evidence that exposure to trained demonstrators can influence flower colour preference even when demonstrator behaviour is not directly observed at the foraging site. These findings raise the possibility that socially acquired information in honey bees may be expressed across different foraging contexts and potentially generalised beyond the specific stimuli encountered during social exposure.

1. Introduction

Social learning, defined as learning influenced by or through observation of conspecifics (Heyes, 1994), is a widespread phenomenon documented across a broad range of animal taxa, from insects to primates (see Whiten, 2021 for a review). Social learning can be particularly adaptive when learning about resources, as it provides access to information faster and at lower cost than individual trial-and-error learning (Hoppitt & Laland, 2013; Rendell et al., 2010; van Schaik, 2010). By observing or interacting with conspecifics, animals can learn to locate food resources and discriminate between edible and inedible options (e.g., Galef & Giraldeau, 2001; Koethe et al., 2020).

In social insects such as bees, social information can improve colony foraging success under certain ecological conditions (Schürch & Grüter, 2014; Sherman & Visscher, 2002). Floral resources vary in quality, spatial distribution, and temporal availability, creating a dynamic and often unpredictable foraging environment for bees (Ogilvie & Forrest, 2017; Roulston & Goodell, 2011). Such variability reduces the reliability of individually acquired information, as nectar quality and variability can fluctuate unpredictably across flowers and over time (Smolla et al., 2016). Social information can therefore serve as a valuable shortcut, allowing individuals to identify profitable resources without the costs of independent exploration (Laland, 2004; cf. Avarguès-Weber et al., 2018).

In bees, visual cues constitute a central component of floral resource information and play a pivotal role in guiding foraging decisions, particularly through flower colour perception and discrimination processes

(Chittka & Menzel, 1992; Dyer & Chittka, 2004; Giurfa et al., 1995). Bees are known to exhibit foraging preferences for flowers with specific colour wavelengths, often favouring blue and violet hues over colours such as yellow and white (Chittka & Menzel, 1992; Dyer et al., 2016; Giurfa et al., 1995). Such preferences have long been considered largely innate and attributed to constraints of the nervous system (Gegebar & Lavery, 2005; Hill et al., 1997; also see Grüter & Ratnieks, 2011 for a review of differing hypotheses). However, recent findings suggest that these preferences are not entirely fixed (e.g., Balamurali et al., 2018) and that social information from conspecifics can modify and even override innate colour preferences during foraging (Dawson & Chittka, 2012; Romero-González et al., 2020).

Most studies in animal social learning have focused on *observational learning* (see Galef & Laland, 2005; Hoppitt & Laland, 2013, for review). Observational learning paradigms that have been used in the literature have typically employed experimental designs in which naïve individuals, who lack prior experience or training with the target stimulus, directly observe conspecific demonstrators performing the target behaviour (e.g., Bugnyar & Kotrschal, 2002; Call et al., 2005; Romero-González et al., 2020). A key feature of such paradigms is that naïve individuals observe demonstrators at the location where the relevant stimulus is present, thereby providing direct information about both the behaviour and the context to which it is directed.

For social insects, information regarding resources can be transmitted both directly (e.g., via waggle dance in honey bees; von Frisch, 1967) or indirectly (e.g., via scent-marking; Giurfa & Núñez, 1992). However, the ‘direct-observation paradigm’ has also been dominant in studies of social learning of flower colours in bees, in which naïve bees observe or interact with trained demonstrators (either live or artificial model bees) foraging in the same testing context (e.g., Avarguès-Weber et al., 2018; Romero-González et al., 2020; Tait et al., 2025; for a review, see Leadbeater & Chittka, 2007). For example, Romero-González et al. (2020) tested whether initial flower preferences of honey bees could be socially modified. In their study, bees were first assessed for baseline colour preferences and then tested in a controlled foraging context containing artificial flowers of different colours that were equally rewarding. Following this, naïve bees were allowed to *directly observe* either a conspecific or a heterospecific demonstrator foraging on one of the available flower colours. Within this setup, honey bees with an initial preference for magenta flowers shifted towards yellow after observing a demonstrator feeding on yellow flowers. This finding highlights the capacity of social information to reshape individual (and possibly colony-level) foraging preferences in honey bees through observation.

It should be noted, however, that in honey bees, information is also transmitted through non-observational means. Foragers may transmit information about the distance and location of profitable floral resources to nestmates through the waggle dance (Seeley, 1995; von Frisch, 1967), and floral odour information can be shared within the hive via trophallaxis (Farina et al., 2005). Yet it remains underexplored whether honey bees can acquire foraging preferences from conspecifics without directly observing them perform the relevant behaviour in a shared foraging context, beyond these well-established mechanisms of social learning (e.g., observational learning and trophallaxis). Although evidence from other species suggests such social learning is a possibility (e.g., Arbon et al., 2023), direct

evidence in honey bees does not exist. The lack of evidence is notable given that honey bee cognition more broadly suggests a capacity for flexible learning and generalisation; for instance, honey bees can form colour associations and transfer learned rules across novel stimuli, indicating generalisation beyond specific training cues (Giurfa, 2003; Giurfa et al., 1995; MaBouDi et al., 2025; Srinivasan, 1994; for a review, see Avarguès-Weber & Giurfa, 2013).

In the present study, we explored whether naïve honey bees (*Apis mellifera anatolica*) would shift their flower colour preference following a period of cohabitation with trained demonstrators, without any direct experience or observation of demonstrators at the artificial flower patch. Specifically, we asked whether information acquired by demonstrators at one foraging site (an artificial flower patch) could be transmitted to naïve nestmates during cohabitation and subsequently expressed by those naïve bees when encountered with the same foraging context for the first time. As this represents a largely unexplored question in honey bee social learning, we focus on establishing whether such cross-context transfer of socially acquired colour preferences can occur at all, rather than investigating the specific mechanisms through which it might arise.

2. Materials and methods

2.1 Subjects and housing

The study was conducted using a colony of honey bees (foragers; *Apis mellifera anatolica*) housed in a standard Langstroth hive on a university campus in Istanbul, Turkey. The free-flying colony had free access to the surrounding environment both during and outside of the study period. This setup allowed us to test the ecologically valid question of whether social information was acquired outside of the testing arena and sessions.

2.2 Ethical note

All procedures were conducted in accordance with standard ethical practices for behavioural research on invertebrates and in line with the principles of the 3Rs (Replacement, Reduction, and Refinement). As we were working with invertebrates, no ethical approval was required to carry out this study.

2.3 Overall procedure

The study consisted of four phases: (i) baseline, (ii) demonstrator training, (iii) cohabitation, and (iv) naïve bee testing, conducted across six sessions in total (see 2.5 Experimental Phases for details). We utilised an artificial flower patch to collect data on the flower colour preferences in every phase of the study (Wells et al., 1981; see subsection 2.4 Artificial Flower Patch for details). Before each session, bees were individually marked on their thorax at the hive entrance to confirm colony origin, and all bees trained to the artificial flower patch (i.e., all subjects included in testing) were marked on the abdomen for individual identification as soon as they landed on the patch, using Testors (Rockford, Illinois, USA) waterproof marker pens appropriate for use on bees (Borofsky et al., 2020). Care was taken to avoid markers containing acetone-based or solvent-based inks and to avoid covering the spiracles or

compound eyes so as not to interfere with respiration or vision. Throughout all sessions, any unmarked bees that arrived at the patch were captured into vials as soon as they landed on a flower and released after the session, to prevent uncontrolled individuals from gaining patch experience that could confound naïve bee testing (see 2.5 Experimental Phases).

At the beginning of each experimental session, bees were trained from the hive to the flower patch using a gravity feeder containing a 30% sucrose solution. The feeder was an inverted glass jar set on a 46-groove Plexiglas plate, which rested on a plastic stool. The underside of the plate was covered in black velvet, which prevented the plate from sliding on the stool and, showing through the clear Plexiglas, gave the sucrose solution in the grooves visual contrast that helped bees locate it. The feeder was placed in front of the hive and, once bees had gathered on it, was moved gradually towards the patch in approximately ten steps of two metres each, pausing at each step until bees had settled on the feeder before proceeding. Upon reaching the patch, the feeder was placed in the centre and left until bees began landing on the flowers. Once bees were habituated to the patch and started to forage on the flowers, the feeder was removed, and data collection began.

All sessions lasted one hour and were conducted using the same flower patch. Flowers were filled with 10 μL of unscented 30% (w/w) sucrose solution using a micropipette. Flower positions were randomised at the beginning of each session, and the patch was rotated 90° along the x-axis every 15 minutes to minimise positional bias. After each session, the flower patch and individual flowers were washed to prevent the confounding effects of scent-marking and residual sucrose odour.

Data Collection and Coding. The study was carried out from August 29th to September 9th, 2022, during the summer. Flower visits were recorded manually across all sessions. Each *visit* was defined as a landing event on a flower, and colour choices were scored for yellow and blue flowers across four 15-min intervals per session, totalling 1 h per session. Individual bee identities were not tracked during the baseline and demonstrator training phases (see 2.5 Experimental Phases).

Different bees participated in each phase of the study, as bees were selected exclusively from individuals bearing no previous mark, confirming they had not been recruited during any prior session. Since all bees that had previously participated in any session received at least a thorax mark, existing marks served as a reliable indicator of prior patch experience. In this study, we refer to “*naïve*” bees as individuals that have not been trained to forage on either flower colour and have no prior experience with the flower patch.

2.4 Artificial Flower Patch

The artificial flower patch consisted of 32 square-shaped Plexiglass flowers (6 mm) coloured in blue or yellow (16 yellow and 16 blue), and they were mounted in a 6 x 6 array, 4 positions in the middle were left empty for the initial feeder placement, with colours being placed randomly, on a wooden board spray-painted in brown to mimic real-life foraging colour contrasts (Fig. 1) (see Rükün et al., 2025 for a visual analysis of the same flower patch demonstrating this contrast). The flower patch was placed on a

foldable table. Each flower contained a small filling hole through which sucrose solution could be filled. The same patch was used across all experimental phases.

2.5 Experimental Phases

There were four phases as listed below (see Fig. 2).

i) Baseline

A single baseline session was conducted to establish the colony's initial colour preferences prior to experimental conditions, with both blue and yellow flowers on the flower patch filled equally with the sucrose solution. Bees were observed across four 15-minute intervals, and the number of visits to blue and yellow flowers at the artificial flower patch was recorded. This session served as the reference point against which subsequent naïve bee test data were compared.

ii) Demonstrator Training

The demonstrator training phase was carried out to train a cohort of bees from the colony to forage from yellow flowers, establishing them as experienced individuals whose foraging behaviour could subsequently influence naïve nestmates. We trained a total of 42 bees as demonstrators across three training sessions. Bees were marked on the abdomen upon arrival at the patch to designate them as demonstrators, with each training group receiving a different abdomen colour depending on the session. We removed unmarked honey bees that arrived at the flower patch during training, ensuring that no individuals other than the trained demonstrators could learn that only yellow flowers were rewarding. Since the baseline data showed a strong innate preference for blue flowers, only yellow flowers were filled with sucrose solution while blue flowers remained empty, reinforcing a yellow flower preference in trained individuals. Demonstrators returned to the colony after each training session over the three-day training period.

iii) Cohabitation

The cohabitation phase was carried out to allow trained demonstrators and naïve bees to interact naturally within the colony environment, providing an opportunity for social transmission of flower colour preference information to occur outside of the artificial flower patch context. Demonstrator training took place each morning during the three-day training period (see 2.5. ii), leaving demonstrators and naïve bees free to interact within the hive and forage together each afternoon throughout this period. Following the final demonstrator training session, demonstrators and naïve bees continued to remain together in the hive for a further three days, during which they could interact freely within the colony and forage outside the hive. At no point during this period (the training-day afternoons and the three days following training) did naïve bees have access to the artificial flower patch, and they therefore did not directly observe demonstrators interacting with the experimental stimuli. This phase, therefore, was intended to allow any potential social transmission of information to occur through naturally occurring colony interactions.

iv) Naïve Bee Testing

Following the cohabitation phase, the naïve bee testing phase was conducted to assess whether the cohabitation experience with trained demonstrators had influenced naïve bees' flower colour preferences. Across two sessions conducted on separate days, individually marked naïve bees were observed on the flower patch, where all flowers were filled equally. A total of 13 individuals participated in this phase across two sessions. To ensure that only truly naïve individuals were tested, bees bearing thorax and/or abdomen markings from previous sessions were excluded from the naïve bee testing sessions, as such markings confirmed prior patch experience. No demonstrators were present during naïve bee test sessions (Naïve Test 1 and Naïve Test 2), and any demonstrators (and bees with markings representing other sessions and/or phases) that arrived at the patch were captured in vials and removed from the flower patch, ensuring that naïve bees could not directly observe demonstrators and/or patch-experienced individuals foraging on the flowers. Any preference shift observed among naïve bees, therefore, occurred in the absence of concurrent observation of demonstrators at the experimental flower patch and is consistent with information acquired indirectly during the cohabitation period.

2.6 Statistical Analysis

In the baseline session, visit counts were aggregated across intervals as individual bee identities were not tracked. For the two Naïve Test sessions, bees were individually identified using unique abdomen colour markings, and interval-level visit counts were summed for each bee to yield one observation per individual (NT1: $n = 8$; NT2: $n = 5$; total $n = 13$). PropYellow was calculated as $\text{Yellow Visits} / (\text{Yellow Visits} + \text{Blue Visits})$.

To assess whether yellow visitation occurred in a greater proportion of naïve bees following exposure to demonstrators, the proportion of bees making at least one yellow visit was compared between the baseline session and each naïve test condition (NT1, NT2, and the pooled naïve test dataset) using one-tailed Fisher's exact tests. The one-tailed approach was used because the *a priori* hypothesis predicted an increase in yellow visitation following exposure to demonstrator bees. As individual bee identities in the baseline session were unavailable, the baseline comparison was reconstructed conservatively using $n = 12$ bees (considering there were *at least* 12 bees), with the single recorded yellow visit treated as having been made by one individual. A two-tailed Fisher's exact test was used to compare the proportion of yellow-visiting bees between NT1 and NT2. Odds ratios (ORs), 95% confidence intervals (CIs), and exact p -values are reported, with ORs representing the odds of yellow visitation in the baseline group relative to the corresponding naïve test group. As a sensitivity analysis, Wilcoxon rank-sum tests were used to compare individual-level PropYellow values between the naïve test bees and reconstructed baseline distributions under alternative assumptions about the allocation of the single baseline yellow visit; these analyses were interpreted cautiously because individual baseline visit data were unavailable. All statistical analyses were conducted in *R version 4.5.2*.

3. Results

3.1 Group-level preference shift

Across both naïve test sessions, yellow flowers accounted for a substantially greater proportion of recorded visits than during the baseline session (Table 1). During the baseline session, yellow visits comprised only 0.54% of all recorded visits (1 yellow, 185 blue; $N = 186$). In NT1, yellow visits accounted for 56.8% of all visits (201 yellow, 153 blue; $N = 354$), while in NT2 they accounted for 46.2% (84 yellow, 98 blue; $N = 182$). Across both naïve test sessions combined, yellow visits comprised 53.2% of all recorded visits (285 yellow, 251 blue; $N = 536$).

At the individual level, 9 of 13 naïve bees made at least one yellow visit, while only 1 of ~ 12 bees did so in the baseline session. A one-tailed Fisher's exact test indicated that the proportion of bees visiting yellow at least once was significantly higher in the pooled naïve test dataset than during baseline ($OR = 0.047$, 95% CI [0.000, 0.395], $p = .003$), with the odds ratio indicating substantially lower odds of yellow visitation in the baseline group than in the pooled naïve test group. The same pattern was observed in NT1, where 7 of 8 bees visited yellow at least once compared with 1 of ~ 12 bees at baseline ($OR = 0.020$, 95% CI [0.000, 0.246], $p < .001$). In contrast, only 2 of 5 bees visited yellow in NT2, and this did not differ significantly from baseline ($OR = 0.158$, 95% CI [0.000, 2.605], $p = .191$). The proportion of yellow-visiting bees also did not differ significantly between NT1 and NT2 ($p = .217$).

Table 1
Flower Visit Counts and Yellow Visit Proportions by Condition

Condition	Blue Visits	Yellow Visits	Total	Yellow Visit Proportion	n (individual)
Baseline	185	1	186	.0054	approx. 12
Naïve Test 1	153	201	354	.568	8
Naïve Test 2	98	84	182	.462	5
Naïve Test (pooled)	251	285	536	.532	13
<i>Note.</i> Baseline yellow visit proportion was calculated from aggregated visit counts (1 yellow / 186 total visits = .00538), as individual bee identities were not recorded during this session. For the naïve test sessions, yellow visit proportions were calculated from the aggregated numbers of yellow and blue visits shown in the table.					

3.2 Learning patterns in flower colour preference

Despite the overall shift towards yellow visits, individual bees showed substantial variation in both the magnitude and temporal pattern of yellow preference (Table 2). Three broadly distinguishable patterns were apparent in the interval-level data: strong cohabitation learners, possible on-the-spot learners and non-learners.

The first pattern was characterised by a strong yellow bias from the beginning of the test session, representing *strong cohabitation learners*. Three bees (abdomen colour: Green & White, Grey, and White &

Dark Blue) showed PropYellow values exceeding .90 in every interval in which they made flower visits. Their yellow-biased response was already evident during the first 15-min interval, during which they made exclusively yellow visits, indicating that they entered the test with an established yellow preference and therefore likely acquired this preference during cohabitation, before encountering the test flowers.

A second pattern involved an increase in yellow responding across successive intervals, representing possible *on-the-spot learners*. Three bees (Black, Gold, and Pink & White) showed relatively low or moderate PropYellow values during the first interval, followed by higher values in later intervals. Black showed PropYellow values of .40, .93, .91, and 1.00 across the four intervals; Gold showed .14, .45, .38, and 1.00; and Pink & White showed .27, .75, .53, and .91. Although the magnitude and consistency of the increase varied among individuals, all three showed predominantly yellow-biased preference by the final interval. Yellow & Dark Blue showed a less consistent pattern, with no visits recorded during the first and third intervals, but exclusively yellow visits during the second interval and predominantly yellow visits during the final interval (PropYellow = 1.00 and .94, respectively), making its response difficult to classify.

The remaining six bees showed predominantly blue-biased preference, representing *non-learners*. Grey & Dark blue, Pink, and Yellow made no yellow visits across any interval in which they were active. Red made a single yellow visit during the final interval (PropYellow = .08), while Dark blue was active during only one interval and made no yellow visits. Yellow & White showed a declining yellow response, with PropYellow values of .11, .08, .00, and .00 across successive intervals. This pattern is consistent with little or no acquisition of the yellow preference, either during cohabitation or on-the-spot.

Overall, the interval-level data showed that the group-level increase in yellow visitation was not expressed uniformly across individuals. Some bees showed a strong yellow preference from the outset, some increased their yellow response over the course of the test session, whereas others remained predominantly blue-biased. The possible sources of the individual variation are considered in the Discussion.

Table 2
Interval-Level Yellow and Blue Flower Visit Counts for Individual Naïve Bees

Response pattern	Bee ID	Session	Interval (min)	Yellow visit	Blue visit	PropYellow
Strong cohabitation learners	Green & White	NT1	0–15	12	0	1.00
			15–30	11	0	1.00
			30–45	18	1	0.95
			45–60	13	1	0.93
	Grey	NT1	0–15	5	0	1.00
			15–30	17	0	1.00
			30–45	20	1	0.95
			45–60	11	1	0.92
White & Dark Blue	NT2	0–15	14	0	1.00	
		15–30	14	0	1.00	
		30–45	17	0	1.00	
		45–60	20	1	0.95	
Possible on-the-spot learners	Black	NT1	0–15	2	3	0.40
			15–30	13	1	0.93
			30–45	10	1	0.91
			45–60	7	0	1.00
	Gold	NT1	0–15	1	6	0.14
			15–30	5	6	0.45
			30–45	5	8	0.38
			45–60	14	0	1.00
Pink & White	NT1	0–15	3	8	0.27	
		15–30	12	4	0.75	
Note. Yellow and blue columns indicate the number of flower visits recorded during each 15-min interval. PropYellow = YellowVisits / (YellowVisits + BlueVisits). A dash (–) indicates intervals in which no flower visits were recorded, making the proportion undefined.						

Response pattern	Bee ID	Session	Interval (min)	Yellow visit	Blue visit	PropYellow
	Yellow & Dark blue	NT2	30–45	9	8	0.53
			0–15	0	0	—
			15–30	4	0	1.00
			30–45	0	0	—
			45–60	15	1	0.94
Non-learners	Yellow & White	NT1	0–15	1	8	0.11
			15–30	1	11	0.08
			30–45	0	18	0.00
			45–60	0	8	0.00
	Red	NT1	0–15	0	10	0.00
			15–30	0	13	0.00
			30–45	0	17	0.00
			45–60	1	11	0.08
	Dark Blue	NT1	0–15	0	0	—
			15–30	0	7	0.00
			30–45	0	0	—
			45–60	0	0	—
	Grey & Dark blue	NT2	0–15	0	4	0.00
			15–30	0	0	—
			30–45	0	2	0.00
			45–60	0	9	0.00
	Pink	NT2	0–15	0	2	0.00
			15–30	0	11	0.00
			30–45	0	13	0.00
Note. Yellow and blue columns indicate the number of flower visits recorded during each 15-min interval. PropYellow = YellowVisits / (YellowVisits + BlueVisits). A dash (—) indicates intervals in which no flower visits were recorded, making the proportion undefined.						

Response pattern	Bee ID	Session	Interval (min)	Yellow visit	Blue visit	PropYellow
			45–60	0	17	0.00
	Yellow	NT2	0–15	0	5	0.00
			15–30	0	9	0.00
			30–45	0	13	0.00
			45–60	0	11	0.00
Note. Yellow and blue columns indicate the number of flower visits recorded during each 15-min interval. PropYellow = YellowVisits / (YellowVisits + BlueVisits). A dash (–) indicates intervals in which no flower visits were recorded, making the proportion undefined.						

4. Discussion

The present study explored whether flower colour preferences learned by demonstrator honey bees at an artificial flower patch could be transmitted to naïve nestmates during a period of cohabitation and subsequently expressed by those naïve bees upon their first encounter with the same foraging context. Across both naïve test sessions combined, bees showed a marked shift towards yellow flowers relative to baseline, where yellow visits comprised less than 1% of all recorded visits. This shift was also evident when the two naïve test sessions were considered separately, with both NT1 and NT2 showing significantly different distributions of yellow and blue visits from baseline. The distribution of visits also differed between NT1 and NT2, with a higher proportion of yellow visits in NT1, although both sessions showed a clear shift towards yellow relative to baseline.

Our experimental design ensured that naïve bees had no prior experience with the artificial flower patch and were not present during demonstrator training sessions. Any shift in colour preference is therefore most plausibly attributed to information acquired through indirect social exposure rather than through personal foraging experience or direct observation of demonstrators at the flower patch. This finding extends prior work demonstrating that honey bee colour preferences can be modified by social information (Romero-González et al., 2020), suggesting that such social influence may operate through routes beyond direct observation or interaction at the exact foraging site.

The heterogeneity in individual responses warrants further attention. Although the group-level analyses showed a clear shift towards yellow visitation, individual bees varied substantially in the extent and temporal pattern of this response. Some bees showed a strong yellow preference from the outset, whereas others showed little or no yellow visitation across the test session. The interval-level patterns provide additional insight into how the observed preference shift may have developed. In both naïve test sessions, at least one individual showed an almost exclusive preference for yellow flowers starting from the very first 15-minute interval of testing (Green & White and Grey in NT1; White & Dark Blue in NT2).

Given that these bees had no opportunity to encounter yellow flowers on the test patch before testing began, their behaviour should have already been acquired during the cohabitation period.

On the other hand, several other individuals (Black, Gold, and Pink & White) began the session with weaker or mixed preferences but progressively increased their proportion of yellow visits across successive intervals. This temporal pattern suggests that the naïve bees did not all acquire or express the socially transmitted information in the same way. Whereas some individuals appeared to arrive at the flower patch with an already established preference for yellow, others appeared to develop or strengthen that preference during the course of the test. From an ecological perspective, such within-patch social learning would not be unexpected, as honey bees are known to use the foraging choices of conspecifics when exploiting floral resources (e.g., Romero-González et al., 2020).

Naïve bees that preferred yellow from the beginning could, in principle, have acted as inadvertent demonstrators to other naïve bees in the same session. This was a natural consequence of the group testing procedure and could not be avoided without individual-by-individual testing. However, this does not undermine our interpretation. Given the near-exclusive blue preference observed at baseline, it is unlikely that any naïve bee would have visited yellow flowers spontaneously without prior exposure to social information favouring yellow. Any within-session transmission would therefore still presuppose that at least some individuals had acquired a yellow preference during cohabitation. The interval-level data are consistent with this interpretation: bees whose yellow preference increased gradually during the session (Black, Gold, and Pink & White) were foraging alongside individuals (Green & White and Grey in NT1; White & Dark Blue in NT2) that already exhibited an almost exclusive preference for yellow from the first observation interval. Although these data cannot demonstrate within-session social transmission directly, they are compatible with the possibility that early cohabitation learners subsequently served as demonstrators for other naïve bees, reinforcing or facilitating additional social learning during the test itself.

Some individuals (e.g., Red, Pink, and Yellow), on the other hand, almost exclusively preferred blue flowers across intervals. The varying proportions of flower colour preference, ranging from an exclusive preference for yellow to an exclusive preference for blue, could reflect differences in the amount of exposure these individuals had to the demonstrators during the cohabitation phase. Alternatively, these individuals may have been more conservative in their foraging decisions (Armand et al., 2025).

Such individual variation is consistent with differences in social learning reported in honey bees (Tait & Naug, 2022), where slow–fast cognitive differences have been proposed to reflect variation in the relative reliance on individual versus social information. Variation in the amount of contact that individual naïve bees had with returning demonstrators during cohabitation may also have contributed to the observed heterogeneity, although such interactions were not tracked in the present study.

The question of how such indirect social transmission might have occurred is speculative at this stage, but two candidate mechanisms deserve consideration and may have operated in combination. The first concerns the possibility that demonstrators, having learned that yellow is rewarding on the artificial

flower patch, carried this preference over to their natural foraging behaviour in the field. Given that honey bees generalise learned colour information to novel stimuli according to perceptual similarity (Giurfa et al., 1995; Martínez-Harms et al., 2014; Avarguès-Weber et al., 2014), trained demonstrators may have preferentially (or more frequently than before) visited yellow flowers in the surrounding environment during the cohabitation period, after learning that yellow flowers are also profitable in the training sessions. Naïve bees, which had free access to the same environment as the demonstrators, then could, in principle, have observed this behaviour and socially learned that yellow flowers are rewarding, subsequently generalising this information back to the artificial patch when tested.

This explanation is consistent with the broader literature suggesting that honey bees can transfer colour associations across novel stimuli and contexts (Giurfa et al., 2001; Srinivasan, 1994), and would imply that generalisation served as both the mechanism of initial preference transfer and its subsequent expression at the patch. This account is especially relevant given that even the strong blue preference observed at baseline likely reflects a form of generalisation, in which bees transferred their innate predisposition towards *natural* blue flowers to the *artificial* blue flowers used in the present study, suggesting that such transfer across contexts may be a general feature of bee flower colour learning rather than an exceptional outcome. However, we acknowledge that this possibility arises partly from a limitation of our design, as the cohabitation period was not controlled for exposure to natural flowers, and therefore, it cannot be confirmed or ruled out based on the present study.

A second, perhaps complementary, possibility is that naïve bees acquired more abstract information from demonstrators during cohabitation, not a specific colour preference per se, but a broader disposition to explore non-default options. Honey bees are capable of abstracting relational rules and transferring learned information to novel stimuli and situations (Giurfa et al., 2001; Stach et al., 2004; Avarguès-Weber et al., 2012; Avarguès-Weber & Giurfa, 2013), and it is plausible that social contact with demonstrators whose behaviour differed from the predominant colony-level pattern may have increased naïve bees' propensity to sample non-preferred stimuli (i.e., yellow flowers). Under this interpretation, the shift towards yellow would reflect not a specific learned association but a more general increase in exploratory behaviour towards potentially rewarding alternatives, consistent with evidence that social information can broaden individual exploration strategies (Tait & Naug, 2022).

A similar pattern has been reported in jackdaws, where individuals that observed a conspecific consume one novel food subsequently showed an increased willingness to consume a different novel food, suggesting a generalised influence of social information towards novel foods rather than direct copying of a specific target stimulus (Arbon et al., 2023). These two accounts are not mutually exclusive; natural flower generalisation and rule learning may have both contributed to the observed preference shift, operating through different routes during the cohabitation period. These accounts are especially relevant for understanding honey bee social learning of flower preferences because, unlike direct observational paradigms where learning is constrained to the experimental apparatus, bees typically experience a more complex social and ecological environment in which information can be acquired through multiple, interacting pathways (Grüter & Czaczkas, 2019; Leadbeater & Dawson, 2017).

A further limitation is that individual bee identities were not recorded during baseline, requiring the baseline comparison to be reconstructed from aggregate visit data. Although sensitivity analyses under alternative allocations of the baseline yellow visit yielded the same qualitative conclusion, this reconstruction limits the strength of individual-level comparisons with baseline. Finally, the study was conducted within a single colony, meaning that the findings require replication across colonies before broader conclusions about honey bee social learning can be drawn.

Taken together, the present findings offer preliminary evidence that honey bees can acquire flower colour preferences through indirect social exposure and express them in a novel foraging context. Whether this reflects specific colour transfer via natural flower generalisation, the acquisition of more abstract foraging rules, some combination of both or any alternative mechanism, the results suggest that the capacity for social information acquisition may be broader in honey bees than the existing bee social learning literature shows (e.g., Romero-González et al., 2020; Tait et al., 2025). Further studies using experimental designs that allow these alternative mechanisms to be distinguished, larger sample sizes, and multiple colonies are needed to determine how such socially acquired preferences are transmitted and expressed across individuals and contexts.

Declarations

Competing interests:

- The authors declare no competing interests.

Consent for publication:

- All authors have read the manuscript and approved its submission.

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Data Availability

All data supporting the findings of this study are publicly available at the following DOI:
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Materials availability:

Not applicable.

Code availability:

Not applicable.

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Figures

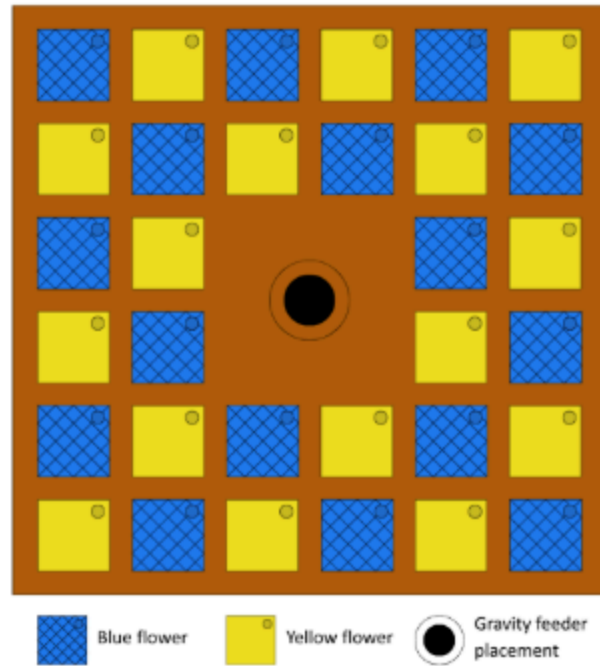


Figure 1

Schematic of the flower patch. The gravity feeder was removed once the bees started to forage from the flowers. The crossed squares denote blue flowers. The artificial flower patch consisted of 32 square-shaped Plexiglass flowers (6 mm) coloured in blue or yellow (16 yellow and 16 blue), and they were mounted in a 6 x 6 array, 4 positions in the middle were left empty for the initial feeder placement, with colours being placed randomly, on a wooden board spray-painted in brown to mimic real-life foraging colour contrasts, this was verified previously using a UV-VIS spectrometry analysis (Rükün et al 2025).

