Interindividual variability in flower pickiness by foraging bumblebees

Mélissa Armand[1], Christoph Beckenbauer[1], Aurore Avarguès-Weber[2], Mathieu Lihoreau[2] and Tomer J. Czaczkes[1]

[1] Animal Comparative Economics Laboratory, Department of Zoology and Evolutionary Biology, University of Regensburg, 93053 Regensburg, Germany

[2] Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI); CNRS, University Paul Sabatier – Toulouse III, France

ORCID IDs

Mélissa Armand: **0000-0002-3190-5852**

Christoph Beckenbauer: **0009-0005-6445-1577**

Mathieu Lihoreau: **0000-0002-2463-2040**

Aurore Avarguès-Weber: **0000-0003-3160-6710**

Tomer J. Czaczkes: **0000-0002-1350-4975**

ABSTRACT

Pollinators navigate complex and heterogeneous "flower markets", where floral resources vary in quality, availability, and distribution. Bumblebees, as generalist foragers, visit numerous flowers during their foraging bouts. Yet, the factors influencing their flower choices and the notable individual differences in foraging behaviour among bees are still not well understood. We hypothesised that early foraging experiences influence bees' subsequent flower choices. To test this, we observed individual *Bombus terrestris* workers forage for three consecutive bouts in two artificial flower arrays. One array simulated a favourable environment with patches alternating high- and low-quality flowers (40% vs. 20% w/w sucrose solution), while the other array presented a more challenging environment with patches of high-quality flowers alongside unrewarded flowers (40% w/w sucrose solution vs. plain water). In both arrays, bees rapidly improved their foraging efficiency, increasing sucrose intake per unit time across bouts. In the favourable array, most bees became highly selective for high-quality flowers, while some continued visiting both flower types. Their degree of pickiness was influenced by early experiences: bees initially exposed to high-quality flowers became more selective, whereas those encountering low-quality flowers first were less selective in subsequent foraging. Despite differences in pickiness and array conditions, bees achieved comparable sucrose intake rates within three bouts. This study highlights the adaptability of bee foraging behaviour and emphasizes the role of early foraging experiences in driving individual differences.

Keywords: *foraging behaviour, bees, decision-making, foraging efficiency, interindividual variability*

Significance statement

To forage efficiently, pollinators must navigate complex "flower markets", where floral resources vary in quality and availability. We observed *Bombus terrestris* workers forage across three bouts in two artificial flower arrays: a favourable array with flower patches alternating high- and low-quality flowers (40% vs. 20% w/w sucrose solution), and an extreme array with high-quality and non-rewarding flowers (40% w/w sucrose solution vs. plain water). We found that bees initially exposed to high-quality flowers became highly selective, whereas those encountering low-quality flowers first were less picky, collecting both flower types. Despite these differences, bees rapidly improved foraging efficiency over successive bouts, achieving similar sucrose intake rates within three bouts. This study highlights the foraging flexibility of bumblebees and suggests that early experiences can have lasting effects, influencing flower choices dozens of visits later.

INTRODUCTION

Pollinators such as bees, bats, and birds forage in highly diverse and dynamic "flower markets", where optimising food collection is a complex task. Optimal Foraging Theory (OFT) posits that animals forage in ways that optimise net energy gain, i.e. by maximising energy return per unit of time spent foraging (Pyke, 1984; Schmid-Hempel et al., 1985; Pyke and Starr, 2021). There is no single method for enhancing foraging efficiency across heterogeneous environments — whether by increasing speed, improving accuracy, or maximising nectar volume or quality. Bumblebees are highly efficient central-place foragers, playing a crucial role in pollinating both wild plants and agricultural crops (Velthuis and Doorn, 2006). With a visit rate of 10 to 20 flowers per minute, they can visit several hundreds of flowers daily (Heinrich, 1979a). Notably, considerable interindividual variability has been observed in how bees exploit their environment (Woodgate et al., 2016). Despite extensive research on bee foraging behaviour (see review by Sommer et al., 2022), the factors driving these individual differences remain poorly understood. Early foraging experiences and initial environmental conditions likely play a key role in shaping foraging behaviour. However, why some bees initially accept or reject flowers of varying quality, and how these early choices influence subsequent foraging, remain unclear.

Natural environments are highly dynamic, with nectar availability and quality fluctuating across flowers and throughout the day (Goulson, 2003). For example, aging flowers can alter nectar rewards and change colour (Weiss, 1991; Willmer, 2011). Furthermore, many flowers lack nectar entirely, with up to 70% on a single plant being nectarless (Real and Rathcke, 1988; Cresswell, 1990; Thakar et al., 2003). Nectar quality also varies greatly, with sugar concentrations ranging from 10% to 80% w/w (Kevan and Baker, 1983). Additionally, individual bees face internal constraints that affect their foraging behaviour. For instance, wing wear can lead bumblebees to favour denser floral patches to minimise flight distances (Foster and Cartar, 2011). Bumblebees differ significantly in size, impacting the amount of nectar they can carry and their overall foraging success, with larger bees showing higher foraging rates (Heinrich, 1979a; Goulson et al., 2002; Spaethe and Weidenmüller, 2002). Experience further shapes foraging, as more experienced bees make more direct and efficient flights (Osborne et al., 2013; Woodgate et al., 2016), although learning ability varies between individuals

(Evans and Raine, 2014). Given the high energetic needs of foraging (Darveau et al., 2014; Vaudo et al., 2016), bees must carefully navigate these constraints to maximise efficiency.

Foraging bees typically collect nectar from more than one flower type throughout their lives (Hagbery and Nieh, 2012; Russell et al., 2017), and their floral choices are highly variable across environments and individuals. Naive bees, for instance, often show innate preferences for violet or blue flowers (Gumbert, 2000; Raine and Chittka, 2007), larger flowers, which are easier to locate (Ohara and Higashi, 1994; Spaethe et al., 2001), and large flower patches (Makino and Sakai, 2007). Bumblebees also exhibit flower constancy — the tendency to forage predominantly on a single flower species — (Chittka et al., 1999), though they do so more flexibly than honeybees (Osborne and Williams, 2001; Gegear and Laverty, 2004). However, both innate preferences and constancy can be overridden with experience (Gumbert, 2000; Makino and Sakai, 2007). While bees generally prefer higher sugar concentrations (Whitney et al., 2008), they do not always choose nectar-rich flowers. For instance, Abrol (2006) showed that honeybees favoured plants with high flowering density and lower nectar concentration over patches with fewer, nectar-rich flowers. Furthermore, Frasnelli et al. (2021) observed that smaller-size bumblebees invested equal effort in memorising flowers with high and low sugar concentration. Preferences for nectar volume have received less attention, and findings are inconsistent (see: Menzel and Erber, 1972; Waddington and Gottlieb, 1990; Lihoreau et al., 2011). Nonetheless, bees appeared more responsive to changes in nectar concentration than volume (Cnaani et al., 2006). In addition to these factors, floral choices are influenced by the specific energetic needs of bees, as they adjust their foraging behaviour to meet both their individual needs and those of their colony (Molet et al., 2008; Vaudo et al., 2016; Hendriksma et al., 2019).

Depending on environmental conditions, bees may employ various foraging “tactics” to efficiently navigate floral resources. In simpler flower patches, they often follow a nearest-neighbour rule, moving sequentially to the closest unvisited flower until resources are depleted (Saleh and Chittka, 2007; Ohashi et al., 2007). In denser or aggregated patches, bees switch to a near-far search strategy, staying longer in nectar-rich areas and making short flights between rewarding flowers (Heinrich, 1979b; Dukas and Real, 1993), and leaving quickly or taking longer flights when resources diminish (Pyke, 1984; Chittka et al., 1997; Cartar, 2004). In larger-scale environments, bees alternate between exploration and exploitation flights to establish foraging routes (Kembro et al., 2019). They often employ traplining — following fixed routes to maximise rewards while avoiding revisited, depleted flowers (Ohashi et al., 2007; Lihoreau et al., 2010). These routes are gradually refined through iteration, balancing shorter paths with prioritising high-reward flowers (Reynolds et al., 2013). However, foraging patterns in heterogeneous environments are inconsistent (Lihoreau et al., 2012), with individual bees showing marked differences in patch fidelity, the balance between exploration and exploitation, and the duration and frequency of foraging bouts (Woodgate et al., 2016). How bees navigate complex environments is still not well understood.

Here, we conducted a lab-based experiment to investigate how bees improve their foraging efficiency in heterogeneous flower markets. We examined how the quality difference between good and poor flowers within patches influences the foraging behaviour of *Bombus terrestris* workers. Individual bees foraged for three consecutive bouts in two distinct artificial flower arrays. The first array simulated a

favourable environment, with patches containing high- and low-quality flowers, alternating ("High vs. Low" array; 40% vs. 20% w/w sucrose solution). The second array represented a more challenging environment, with patches offering a single rewarding flower type alongside unrewarded flowers ("High vs. Water" array; 40% w/w sucrose solution vs. plain water). We hypothesized that early foraging experiences and environmental conditions would shape the bees' subsequent foraging behaviour. Specifically, we predicted that the more extreme conditions in the High vs. Water array would allow bees to learn flower quality more quickly and improve foraging efficiency faster than the bees in the High vs. Low array. Nevertheless, we predicted that bees in both flower arrays would increase their energy gain per unit time over successive bouts, consistent with optimal foraging theory (Pyke, 1984; Schmid-Hempel et al., 1985).

MATERIAL AND METHODS

Bees

Four commercial *B. terrestris* colonies (Koppert, The Netherlands) were maintained under controlled laboratory conditions (22–24°C, 14:10 light:dark cycle; lights on from 6:30 a.m. to 8:30 p.m.) with ad libitum pollen. Colonies were housed in wooden nestboxes, each connected to its respective flight arena (60 x 50 x 35 cm) through a transparent tube fitted with shutters (see apparatus in **Fig. 1**). Between experimental sessions (i.e., pre-training), bees had unrestricted access to six artificial flowers in the arena. Each flower provided ad libitum 20% w/w sucrose solution through a damp cotton mesh soaked in solution and protruding through a central hole. Bees that foraged regularly were individually marked on the thorax with uniquely coloured, numbered tags and selected for the experiment. A total of 52 bees from four colonies were tested over a 20-day period in October–November 2021 (see Supplement **S1** for further colony details). Additionally, six bees from two other colonies were tested in January 2024 in a complementary experiment, to determine whether bees collected the entire sucrose solution drop from the artificial flowers or only part of it. This experiment mirrored the main setup but reversed the flower colours and included weighing the flowers before and after each foraging bout. Results showed that bees typically either fully collected the sucrose drop or rejected the flower without drinking (see Supplement **S2** for detailed analysis).

Artificial flowers

Each flower consisted of a transparent plastic cup (diameter = 38 mm, height = 70 mm) topped with a coloured laminated paper disk. The flowers used during the experiment were either blue (with a peak reflectance at approx. 450 nm) or yellow (with a peak reflectance from approx. 530 to 700 nm, see Supplement **S3** for reflectance curves). Sucrose solution was pipetted onto a small white dot in the centre of each flower, to aid the bees in locating rewards (Heuschen et al., 2005; see **Fig. 1** below). During pre-training, the artificial flowers were made of two halves, one blue and one yellow, following the method of Raine and Chittka (2008). These bicoloured flowers ensured that the bees could associate sucrose rewards equally with each flower colour, which we later used as separate flower types in the experiment.

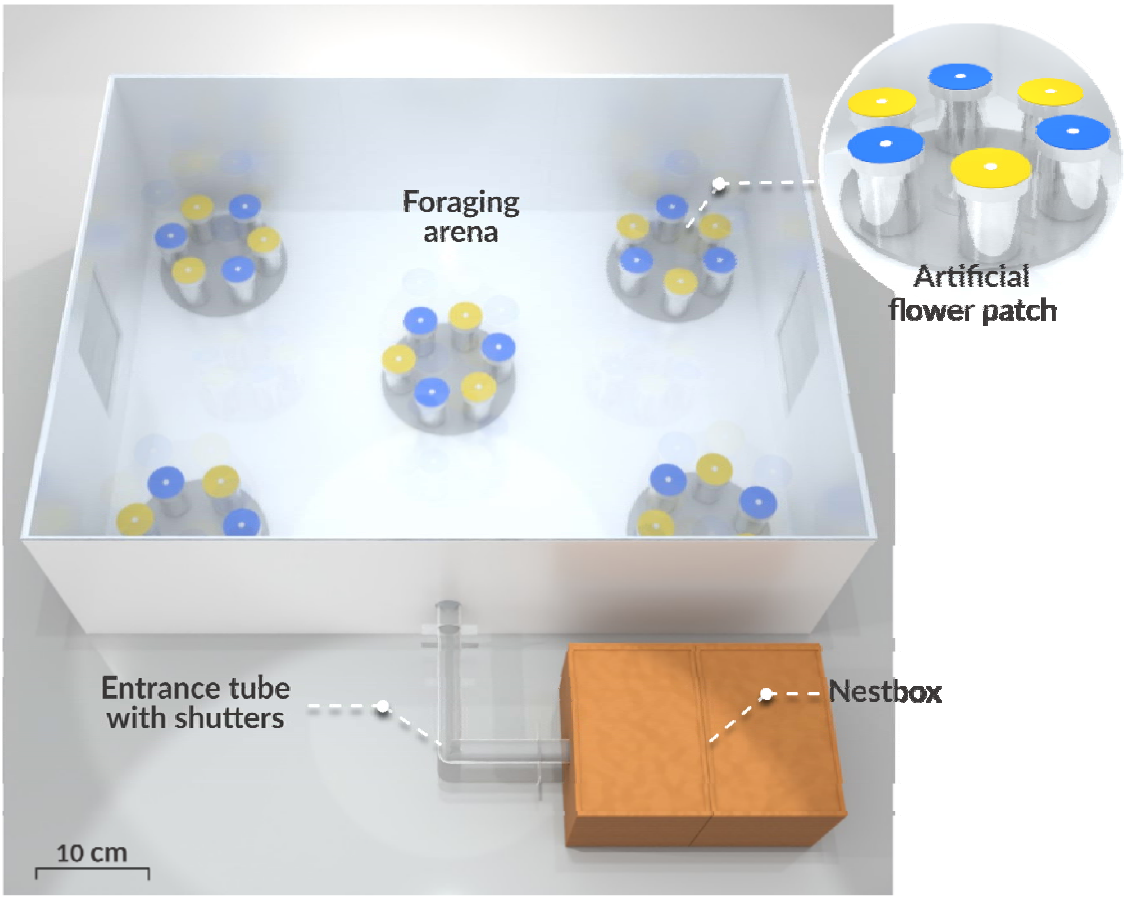

Figure 1: Top view of the scaled experimental setup. The 3D model, created in Blender, illustrates layout pattern A of the flower array (see Supplement **S4** for all layout patterns). Flower patches were positioned 15–50 cm from the arena entrance and mounted on transparent white, circular plastic bases (15 cm diameter, 0.5 cm thick), with flowers within each patch spaced 1.5 cm apart. The flowers were removed and rearranged after each foraging bout using the arena's side doors.

Experiment

Individual bees performed three consecutive foraging bouts to a flower array consisting of five blue/yellow dimorphic flower patches. Each patch contained six flowers arranged in a circle, with alternating blue and yellow flowers ensuring that neighbouring flowers were always of different colours. The patches were arranged pseudo-randomly in an all-white arena using four different layout patterns (see Supplement **S4** for layout patterns). This design ensured that each new foraging bout presented a novel foraging array, preventing the bees from relying on spatial memory from previous bouts. In the main experiment, yellow flowers consistently offered high-concentration sucrose solution to counteract bees' innate preference for blue (as cited in Gumbert, 2000) and to prevent a bias toward blue flowers. To further reinforce the robustness of our setup, the colour assignments were nonetheless reversed in the complementary experiment. The bees were tested on one of two different flower arrays:

(1) High vs. Low flower array (N = 37 bees): For 31 bees, yellow flowers contained 14 µL of concentrated sucrose solution (40% w/w), and blue flowers contained 14 µL of diluted sucrose solution (20% w/w). For the remaining six bees in the complementary experiment, the colours were reversed. This array simulated a favourable environment, with neighbouring flowers offering varying nectar quality. We expected bees in this array to be less selective in their flower choices and to show a slower improvement in foraging efficiency compared to the extreme array described below.

(2) High vs. Water flower array (N = 15 bees): Yellow flowers contained 14 µL of concentrated sucrose solution (40% w/w) and blue flowers 14 µL of plain water. This array represented an extreme environment, with only one rewarding flower type and half the flowers offering no reward. We expected bees in this array to be highly selective and to rapidly improve their foraging efficiency.

In both flower arrays, each flower type provided enough sucrose solution (210 µL per bout) for a bee to fill its crop by visiting a single flower type. This volume exceeds the average crop capacity of bumblebee foragers (120–180 µL; Lihoreau et al., 2010). To prevent chemical marks from influencing flower choices, all flower surfaces were wiped clean with paper towel moistened with 70% ethanol after each bees' foraging bout (Goulson et al., 2000; Saleh et al., 2007).

After the third foraging bout, the bees completed a "test" bout in which the arena contained two monochromatic flower patches, one yellow and one blue, both unrewarded (plain water). The patches were positioned against the back wall, facing the arena entrance, and the bee's first flower visit was recorded as an indicator of its flower type preference.

Data collection

Each foraging bout was video-recorded using a camera (Sony HDR CX405) placed above the flight arena. Bee behaviour was analysed using an event-logging software (BORIS, v8.6), recording: (1) foraging bout durations (i.e., time from entering the arena to returning to the nest), (2) flower visits (bee landing on a flower), (3) flower revisits (bee landing on a previously visited flower within the same bout), and (4) reward collection (bee licking a drop of sucrose solution for over five seconds). Based on video analysis, we considered the bees to either reject, or accept and fully consume the sucrose drop on visited flowers (see Supplement **S5** for video examples). This categorisation was further validated in the complementary experiment, where flowers were weighed before and after each foraging bout (see Supplement **S2** for methodology and results). Bees that accepted a flower overwhelmingly consumed the entire drop, regardless of whether it was high- or low-concentration.

Data analysis

Data processing was performed with Python (v3.11, Python Software Foundation, 2023) using the following libraries: *pandas* (McKinney, 2010) for data structuring, *seaborn* (Waskom, 2021) and *Matplotlib* (Hunter, 2007) for data visualisation, and *Scikit-learn* (Pedregosa et al., 2011) for data

clustering. Statistical analyses were carried out with R (v4.1, R Core Team 2022) using the packages *glmmTMB* (Brooks et al., 2017) for Generalised Linear Mixed Models (GLMM), and *emmeans* (Lenth, 2020) for post-hoc tests. Model residuals were evaluated using the *DHARMa* package (Hartig, 2020). The datasets from the main experiment and the complementary experiment, where flower colours were reversed, were merged for analysis. The type of experiment (main or complementary) was included as a random effect to control for potential differences in experimental conditions. Individual bees were also treated as random effects, nested within their respective colonies, to account for variations within colonies. Complete statistical analyses and datasets are available on Zenodo (https://doi.org/10.5281/zenodo.14524634).

(A) Bee clustering

To assess bee pickiness for high-quality flowers in the High vs. Low flower array (see results below), we performed a Principal Component Analysis (PCA) on three key variables from the last foraging bout:

(1) Proportion of visits to high-quality flowers: number of visits to high-quality flowers divided by the total number of visits,

(2) Proportion of high-concentration sucrose solution collected: number of high-quality flowers collected divided by the total number of flowers collected, and

(3) Proportion of low-concentration sucrose solution rejected: number of non-depleted low-quality flowers visited and not collected, divided by the total number of visits to low-quality flowers.

The first two principal components (PC1 and PC2) were retained, as they together explained 100% of the variance, capturing the combined influence of the three variables. We then combined PC1 and PC2 into a single "pickiness metric" by calculating their weighted sum based on the proportion of variance each component explained (see Supplement **S1** for full analysis).

Additionally, we applied K-Means clustering to classify bees into two distinct groups based on the combined influence of PC1 and PC2. The algorithm identified two clusters (**Fig. 2B**): (1) Low pickiness (N = 9 bees), representing bees with the lowest "pickiness metric" scores, and (2) High pickiness (N = 28 bees), representing bees with the highest scores.

(B) Estimation of absolute sucrose intakes

We inferred the absolute sucrose intakes of bees based on video analysis, using the number of high- and low-quality flowers collected per foraging bout and the theoretical sucrose content of 20% and 40% w/w sucrose solutions: (1) 20% w/w sucrose solution: with a density of 1.081 g/mL (Hofmann, 1977), a drop of 14 µL drop weighs approximately 15.134 mg, comprising 12.106 mg of water and 3.027 mg of sucrose, and (2) 40% w/w sucrose solution: with a density of 1.176 g/mL (Hofmann, 1977), a 14 µL drop weighs approximately 16.464 mg, comprising 9.882 mg of water and 6.588 mg of sucrose.

RESULTS

The datasets from the main experiment and the complementary experiment (which replicated the main experiment with reversed flower colours; see Supplement **S2** for methodology and results) were combined for analysis. Naive bees in both experiments showed a tendency to visit yellow flowers first, with 60.9% (18/28 bees) and 67% (4/6 bees) making their very first visit to a yellow flower in the main and complementary experiments, respectively.

1. Bees in the High vs. Low flower array increased their foraging efficiency with experience

We first examined whether bees foraging on flower patches containing both high- and low-quality flowers favoured the high-concentration sucrose solution or collected solution from both flower types. Over successive foraging bouts, the bees significantly increased: (1) their proportion of visits to high-quality flowers, calculated as the number of visits to high-quality flowers divided by total visits (post-hoc Tukey test, bout 1 vs. bout 3: 50.5% ± 4.2% vs. 68.3% ± 4.2%, t-ratio = -6.20, $p < 0.0001$; N = 37 bees; **Fig. 2A**); (2) their proportion of high-concentration sucrose solution collected, calculated as the number of high-quality flowers collected divided by total flowers collected (post-hoc Tukey test, bout 1 vs. bout 3: 55.6% ± 4.6% vs. 87.7% ± 4.7%, t-ratio = -10.55, $p < 0.0001$; N = 37 bees; **Fig. 2A**), and (3) their proportion of low-concentration sucrose solution rejected, calculated as the number of non-depleted low-quality flowers visited and not collected, divided by total visits to low-quality flowers (post-hoc Tukey test, bout 1 vs. bout 3: 29.4% ± 7.0% vs. 74.0% ± 6.2%, t-ratio = -5.51, $p < 0.0001$; N = 37 bees; **Fig. 2A**).

(A) Bees in the High vs. Low flower array showed variability in pickiness

We observed high variability in the proportions of high-quality flower visits, high-concentration sucrose collection, and low-quality flower rejection (**Fig. 2A**), reflecting substantial interindividual differences in foraging behaviour. To capture these differences, we performed a Principal Component Analysis (PCA) on these three variables from the final foraging bout, when bees were expected to have developed stable foraging behaviour after three successive bouts. We then applied K-means clustering, identifying two distinct bee clusters (**Fig. 2B**): High pickiness (N = 28 bees) and Low pickiness (N = 9 bees).

After three foraging bouts, bees in the high pickiness cluster made significantly more visits to high-quality flowers than those in the low pickiness cluster (GLMM: $\chi^2 = 16.41$, df = 1, $p < 0.0001$; mean last bout = 75% ± 0.03 for High pickiness cluster vs. mean last bout = 51.78% ± 0.04 for Low pickiness cluster; **Fig. 2C**). High pickiness bees also collected a higher proportion of high-concentration sucrose solution (GLMM: $\chi^2 = 53.79$, df = 1, $p < 0.0001$; mean last bout = 97.82% ± 0.01 for High pickiness cluster vs. mean last bout = 57.33% ± 0.04 for Low pickiness cluster; **Fig. 2C**), and rejected a greater proportion of low-concentration sucrose solution (GLMM: $\chi^2 = 43.01$, df = 1, $p < 0.0001$; mean last bout = 98.13% ± 0.01 for High pickiness cluster vs. mean last bout = 36.63% ± 0.08 for Low pickiness cluster; **Fig. 2C**).

(B) The degree of pickiness was correlated with the quality of the first flowers visited

Bees in the High pickiness cluster were more likely to make their first-ever visit to a high-quality flower compared to those in the Low pickiness cluster (post-hoc Tukey test, High pickiness cluster vs. Low pickiness cluster: 60.1% ± 16.4% vs. 27.6% ± 19.4%; z = 1.48, p = 0.138, N = 37 visits; **Fig. 2D**). This effect became statistically significant when considering only the first two flower visits (post-hoc Tukey test, High pickiness cluster vs. Low pickiness cluster: 61% ± 8.13% vs. 28.2% ± 11.36%; z = 2.19, p = 0.028, N = 74 visits; **Fig. 2D**). This finding suggests that early exposure to high-quality flowers drive bees to become more selective, whereas initial visits to low-quality flowers may decrease selectivity in subsequent choices.

2. Bees across arrays and clusters improved foraging efficiency through variable foraging behaviour

Next, we examined the foraging behaviour of bees across bouts, comparing flower arrays (High vs. Low and High vs. Water) and clusters (High pickiness and Low pickiness). All groups significantly increased their estimated sucrose intake per unit of time with each successive bout (GLMM: $\chi^2 = 90.76$, df = 2, $p < 0.0001$, N = 52 bees). This improvement rate was consistent across groups at the same foraging stage (GLMM: $\chi^2 = 0.77$, df = 2, $p = 0.68$). We then analysed the foraging behaviour of each bee group in more detail:

(A) High pickiness bees

High pickiness bees maintained consistent foraging durations across bouts (post-hoc Tukey test, bout 1 vs. bout 3: 3.96 min ± 0.53 vs. 3.41 min ± 0.45, z-ratio = 1.06, $p = 0.54$; **Fig. 3A**). They increased the number of flowers collected (post-hoc Tukey test, bout 1 vs. bout 3: 10.24 flowers ± 0.89 vs. 12.22 flowers ± 1.04, z-ratio = -2.73, $p = 0.017$; **Fig. 3B**) but did not significantly increase the proportion of high-concentration sucrose solution collected (post-hoc Tukey test, bout 1 vs. bout 3: 61.6% of high-quality flowers collected ± 3.59 vs. 97.6% ± 1.01, z-ratio = -1.81, $p = 0.17$; **Fig. 3C**).

The bees reduced revisits to previously depleted flowers (post-hoc Tukey test, bout 1 vs. bout 3: 7.44 revisits ± 1.74 vs. 4.62 revisits ± 1.15, z-ratio = 2.63, $p = 0.02$; **Fig. 3D**). Overall, bees from this cluster showed an increase in estimated sucrose intake across bouts (post-hoc Tukey test, bout 1 vs. bout 3: 45.7 mg ± 4.66 vs. 61 mg ± 6.04, z-ratio = -4.47, $p < 0.0001$; **Fig. 3E**). In the final test, 92.6% of bees first visited the high-quality flower patch (**Fig. 3F**).

(B) Low pickiness bees

By contrast, Low pickiness bees increased their foraging duration over bouts (post-hoc Tukey test, bout 1 vs. bout 3: 6.80 min ± 0.52 vs. 4.14 min ± 0.31, z-ratio = 6.16, $p < 0.0001$; **Fig. 3A**). They decreased the number of flowers collected (post-hoc Tukey test, bout 1 vs. bout 3: 12.68 flowers ± 0.61 vs. 10.57 flowers ± 0.52, z-ratio = 5.11, $p < 0.0001$; **Fig. 3B**) while significantly shifting their collection of sucrose solution towards high-quality flowers (post-hoc Tukey test, bout 1 vs. bout 3: 39.1% of high-quality flowers collected ± 6.74 vs. 55.2% ± 6.57, z-ratio = -7.18, $p < 0.0001$; **Fig. 3C**).

The bees reduced flower revisits (post-hoc Tukey test, bout 1 vs. bout 3: 12.59 revisits ± 1.85 vs. 9.78 revisits ± 1.46, z-ratio = 3.26, p = 0.003; **Fig. 3D**), while their estimated sucrose intakes remained stable across bouts (post-hoc Tukey test, bout 1 vs. bout 3: 65.2 mg ± 3.47 vs. 68.8 mg ± 3.65, z-ratio = -1.69, p = 0.21; **Fig. 3E**). In the final test, 55.6% of bees first visited the high-quality flower patch (**Fig. 3F**).

(C) High vs. Water flower array

In this flower array, where only high-concentration sucrose solution was available, bees nearly halved their foraging duration over successive bouts (post-hoc Tukey test, bout 1 vs. bout 3: 7.42 min ± 0.77 vs. 3.88 min ± 0.4, z-ratio = 5.96, p < 0.0001; **Fig. 3A**) while maintaining a steady number of flowers collected (post-hoc Tukey test, bout 1 vs. bout 3: 10.13 flowers ± 0.69 vs. 9.49 flowers ± 0.65, z-ratio = 1.25, p = 0.42; **Fig. 3B**).

Bees reduced flower revisits by nearly threefold (post-hoc Tukey test, bout 1 vs. bout 3: 24.04 revisits ± 3.99 vs. 8.8 revisits ± 1.57, z-ratio = -1.81, p < 0.0001; **Fig. 3D**), while their estimated sucrose intakes remained consistent across bouts (post-hoc Tukey test, bout 1 vs. bout 3: 66.9 mg ± 4.9 vs. 62.2 mg ± 4.59, z-ratio = 1.61, p = 0.24; **Fig. 3E**). In the final test, 86.7% of bees first visited the high-quality flower patch (**Fig. 3F**).

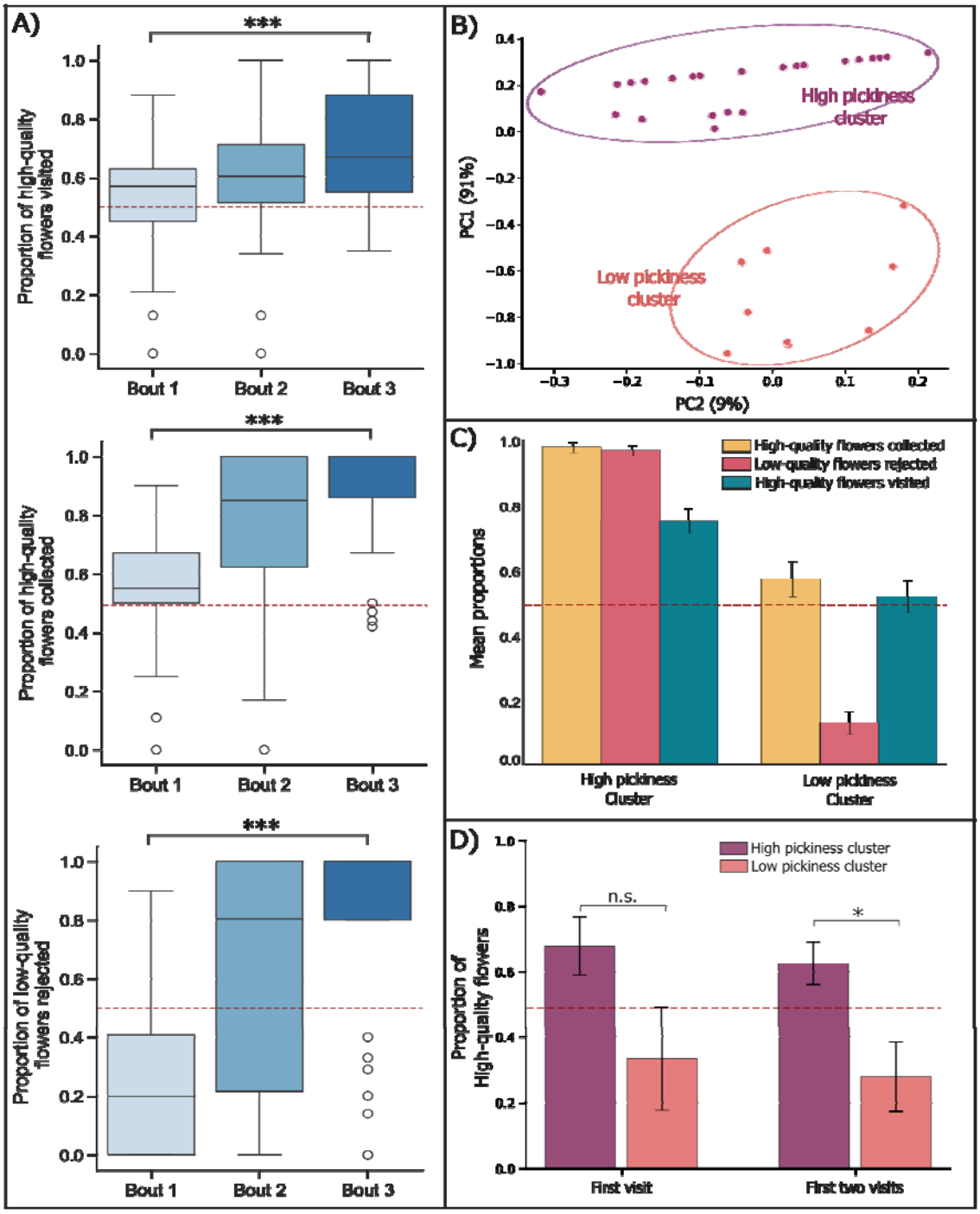

Figure 2: Foraging efficiency in the High vs. Low flower array. A) Box plots of the proportions of bees: (1) visiting high-quality flowers, (2) collecting high-quality flowers, and (3) rejecting low-quality flowers across foraging bouts (N = 37 bees). Boxes represent the interquartile range (IQR), the inner line the median, and whiskers extend to the smallest and largest values within 1.5 times the IQR from the quartiles. Statistical significance is indicated as *** ($p < 0.001$, post-hoc Tukey test); **B)** Scatter plots of bee clustering based on PCA of the three foraging pickiness variables (1), (2), and (3). The y-axis shows the first principal component (PC1), explaining 91% of the variance, and the x-axis shows the second principal component (PC2), explaining 9% of the variance. Each point represents a bee (N

= 37), colour-coded by cluster: Low pickiness (N = 9) and High pickiness (N = 28), as determined by K-means clustering; **C)** Bar plots of the mean proportions of variables (1), (2), and (3) for each pickiness clusters; **D)** Bar plots of the proportions of high-quality flowers visited during the first flower visits for each bee cluster. Error bars represent standard errors of the means, and statistical significance is indicated as ***** ($p < 0.05$) and **n.s.** ($p > 0.05$, post-hoc Tukey tests).

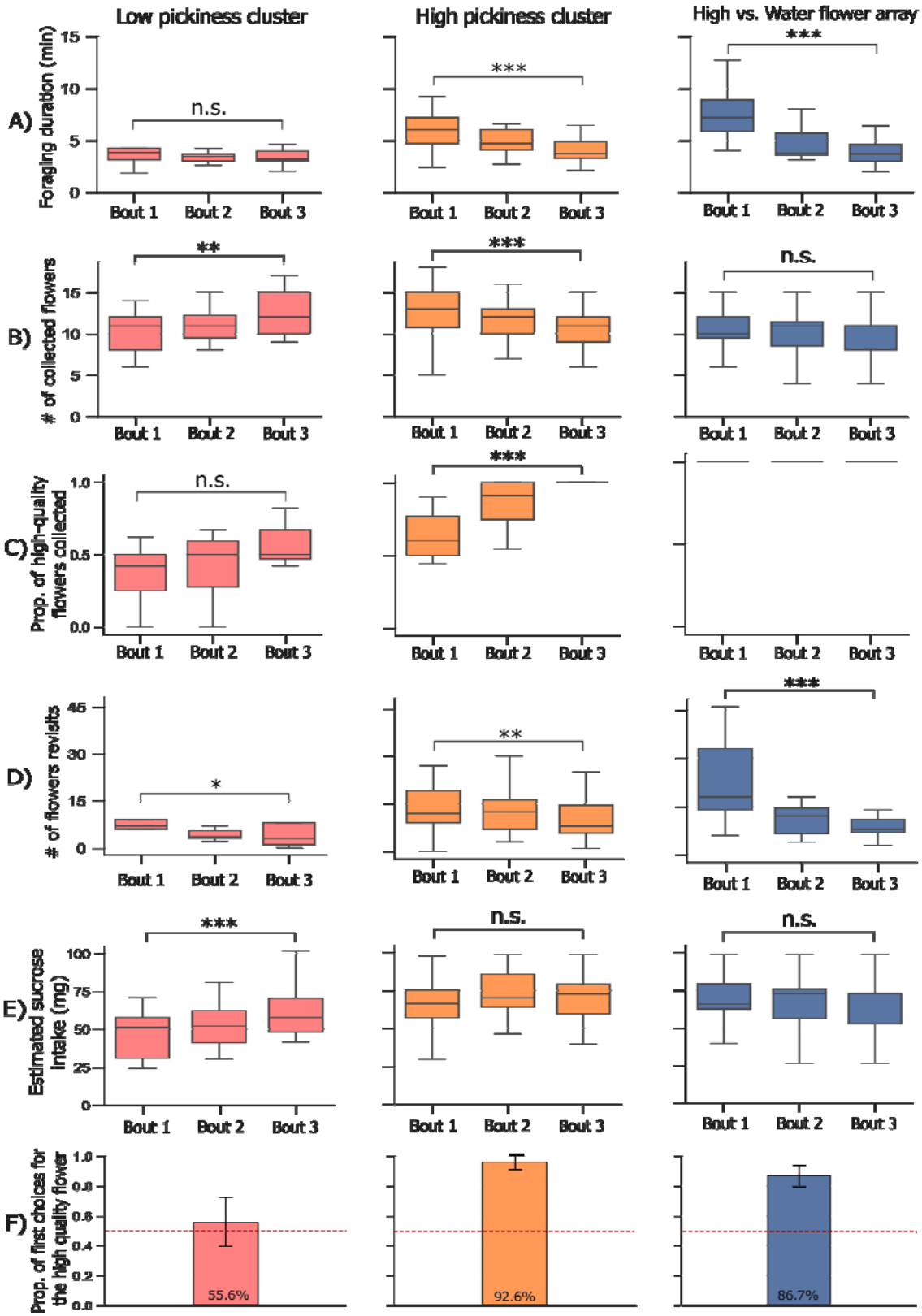

Figure 3: Foraging efficiency of bees across flower arrays. A) Foraging duration per bout (minutes); **B)** Number of flowers collected per bout; **C)** Proportion of high-concentration sucrose solution collected per bout; **D)** Number of flowers revisited per bout; **E)** Estimated sucrose intake per

foraging bout (mg), and **F)** Proportion of first visit on the high-quality flower in the final test (N = 52 bees). Each boxplot shows the median (centre line), interquartile range (IQR, represented by the box), and whiskers extending to the smallest and largest values within 1.5 times the IQR from the quartiles. Error bars represent standard errors of the predicted probabilities. Statistical significance is indicated as ******* ($p < 0.001$), ****** ($p < 0.01$), ***** ($p < 0.05$), and **n.s.** ($p > 0.05$), based on post-hoc Tukey tests.

DISCUSSION

This study investigated how the difference between good and poor flowers in mixed-quality patches influence bees' flower choices, addressing the gap in understanding interindividual variability in the foraging behaviour among bees. We showed that foragers rapidly improved foraging efficiency across successive bouts, achieving similar sucrose intake rates after three bouts, regardless of the flower array ("favourable", with high- and low-quality flowers, or "extreme", where only half the flowers were rewarding). This main finding supports our prediction and is to some degree in line with Optimal Foraging Theory (OFT) predictions, which suggests that nectarivores should maximise their net energy intake rate (Heinrich, 1979a; Waddington and Holden, 1979; Pyke and Starr, 2021). Additionally, we observed substantial variability in foraging behaviour, particularly in flower selectivity, with some bees showing a strong preference for high-quality flowers while others were less selective. This result is consistent with the high interindividual variability reported in bumblebees foraging in heterogeneous environments (Woodgate et al., 2016).

Bees in our study showed considerable variability in how they improved their foraging efficiency; High pickiness bees collected less sucrose solution over bouts but of higher concentration, thus prioritising quality over quantity. In contrast, bees from the low pickiness cluster increased the total volume of sucrose they collected, regardless of sucrose concentration. While bees from both clusters learned and improved with each bout, they still maintained distinct foraging behaviours across bouts. These findings align with those of Chittka et al. (2003), where individual bees demonstrated consistent speed-accuracy trade-offs, retaining their initial foraging behaviours even as they learned. Similar trade-offs have been observed in other studies, with bees balancing speed and accuracy (Burns and Dyer, 2008), or reward value and foraging effort (Lihoreau et al., 2011; Pattrick et al., 2023). Such variability in foraging behaviour may be advantageous in natural environments, given the spatial and temporal unpredictability of resources. Moreover, variability in individual foraging behaviour may enhance overall colony performance (Muller and Chittka, 2008; Holland et al., 2021). In line with this, Hagbery and Nieh (2012) observed that generalist bumblebees which do not specialise exclusively in nectar or pollen, could flexibly adapt their foraging behaviour in response to shifts in the colony workforce.

Interestingly, most bees did not increase their estimated absolute sucrose intake over successive bouts; only low pickiness bees showed an increase. Bees in this cluster had lower estimated intakes during the first two foraging bouts compared to high-pickiness bees and those foraging in the array with only one rewarding flower type. For high-pickiness bees, their focus on high-quality flowers likely constrained their ability to collect significantly more sucrose over bouts: in our setup, only half of the

flowers in each patch were either highly rewarding or rewarding at all, increasing the likelihood of revisiting previously depleted flowers as the best rewards diminished. Previous studies have shown that bees do not visit all flowers in a patch (Goulson, 2000; Hemingway et al., 2024). According to the optimal departure rule, pollinators should leave a patch when their reward acquisition rate declines (Cresswell, 1990; Goulson, 2000). However, we found that naive bees, regardless of group, did not collect markedly fewer rewards during their first bout despite longer foraging durations and frequent revisits to depleted flowers. This suggests that bees did not return to the nest when sucrose acquisition rates decreased; otherwise, we would have observed lower estimated sucrose intakes on the first bout, due to reduced foraging efficiency. Instead, it is likely that inexperienced bees were exploring their new environment, similar to wild bumblebees making exploration flights during their initial foraging trips (Woodgate et al., 2016). Notably, high-pickiness bees collected over 15% fewer flowers in their final bout compared to their first, while maintaining constant total sucrose collection. This behaviour suggests that bees may aim for a fixed energetic target before returning to the nest, rather than a fixed collection volume or foraging duration. Furthermore, it indicates that bees are willing to return with partially empty crops (see Schmid-Hempel et al., 1985). However, explicit testing would be necessary to confirm such fixed energetic target hypothesis.

One result to further consider is that all bee groups in our study improved their foraging efficiency at a similar rate, achieving comparable estimated sucrose intakes by the same bout. This suggests that bees, to some extent, may be capable of compensating for less favourable initial conditions by adapting their foraging behaviour. This finding should nonetheless be considered with caution, as we did not directly measure the bees' actual sucrose intakes but rather inferred it through video analysis and calculations (see B. in the data analysis section). Notably, our results may underestimate the sucrose solution collected from low-quality flowers, as these were often probed for less than a second and thus considered non-collected in the analysis. However, Lechantre et al (2021) showed that bumblebees can imbibe up to 2 µL of solution per second, indicating that even brief probing may yield measurable rewards.

Our study also raises questions about the factors influencing differential foraging behaviours, such as flower-quality pickiness. In the favourable array containing both high- and low-quality flowers, the majority of bees became highly selective for high-quality flowers. The degree of pickiness was correlated with the bees' initial flower visits, which were predominantly on flowers with high-concentration sucrose solution. One potential explanation for this variability in pickiness is flower constancy. Previous studies have shown that bees remain constant to flowers offering high rewards but explore alternative options when rewards are low (Chittka et al., 1999; Grüter and Ratnieks, 2011; Nityananda and Chittka, 2020). This mechanism may explain why bees in our study strongly favoured high-quality flowers when first exposed to them, whereas bees initially visiting low-quality flowers exhibited greater variability in subsequent choices. While flower constancy was long thought to result from cognitive limitations (Waser, 1986, 1986; Chittka et al., 1999), more recent studies suggest it may function as an adaptive strategy (Gegear and Thomson, 2004). Recent simulations have shown that highly flower-constant bee colonies exploited only 30–50% of available flower species, while indiscriminate foragers exploited nearly all species (Grüter et al., 2024).

Can pickiness be solely attributed to the quality of the first few flower visits? The relative strength of the correlation suggests that other factors may also be at play. For example, bees are known to have variable sensitivity thresholds for sucrose, which could drive individual differences in specialisation on rewards of varying quality (Page et al., 2006; Riveros and Gronenberg, 2010). Additionally, differences in learning ability among bumblebees (Raine et al., 2006) might explain why bees in the low pickiness cluster did not favour the high-quality patch in the final test. Although all bees in our study increased their visits to high-quality flowers over successive bouts, they did not do so at the same rate. Would every bee have eventually become highly selective in our setup? Shifting foraging behaviour can be energetically costly, especially in dynamic environments (DeWitt et al., 1998), like our changing flower array layouts in each bout. An interesting research direction would be to experiment with varying starting conditions to determine whether bees eventually converge on the same optimal foraging behaviour, and when this convergence happens, providing insights into the limits of foraging flexibility.

It is important to note that most high-concentration flowers were yellow in this experiment. Contrary to our expectation that blue flowers would attract bees first due to innate preferences (Gumbert, 2000; Raine and Chittka, 2007), over two-thirds of the first visits were made to yellow flowers. This unexpected preference may stem from yellow flowers reflecting more light across a broader range of wavelengths, resulting in higher overall brightness. Brightness is a key factor influencing bee preferences (Sletvold et al., 2016) and may explain this initial preference, even though the blue flowers in our setup had greater spectral purity and saliency in the white arena — traits typically associated with higher bee attraction (Lunau, 1990; Goulson, 2000).

While our findings suggest that bees aimed to optimise energy intake, it is important to note that not all energetic costs of foraging were fully accounted for, such as the cost of flight: in our setup, flowers within patches were positioned closely enough for bees to walk between them, allowing those who visited neighbouring flowers to potentially conserve energy. Additionally, the energy expenditure of individual bees likely varied depending on the weight of the sucrose loads carried by each bee (Wolf et al., 1989; Combes et al., 2020). While bees quickly learned in our simple flower arrays within a few consecutive bouts, natural environments are far more complex, with differences between rich and poor flowers being less distinct and predictable. Moreover, our small flight arena represented a "local" scale, as described by Sommer et al. (2022). In this controlled setting, bees likely encountered flower signals almost immediately (Heinrich, 2004), which is not typically the case in natural environments. Nonetheless, our findings highlight the rapid adaptability of foraging bumblebees within just three bouts and open interesting research avenues to explore how environmental conditions, initial experiences, and foraging behaviour interact. A deeper understanding of these mechanisms could provide valuable insights into the ecological success of bumblebees as pollinators across diverse and dynamic habitats.

SUPPLEMENTARY MATERIAL

Supplementary Material **S1** presents the statistical analysis of the main experiment, while **S2** provides the statistical analysis of the complementary experiment. **S3** includes the reflectance curves of the

artificial flowers, and **S4** the layout patterns of the flower arrays. **S5** features video examples of bees foraging during the experiment. **S6** and **S7** contain the datasets for the main and complementary experiments, respectively. All statistical analyses and datasets are publicly available on Zenodo (https://doi.org/10.5281/zenodo.14524634).

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REFERENCES

Abrol DP (2006) Foraging behaviour of bees as influenced by quality and quantity of rewards from flowers. J Asia-Pac Entomol 9:145–148. https://doi.org/10.1016/S1226-8615(08)60285-X

Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400. https://doi.org/10.3929/ethz-b-000240890

Burns JG, Dyer AG (2008) Diversity of speed-accuracy strategies benefits social insects. Curr Biol 18:R953–R954. https://doi.org/10.1016/j.cub.2008.08.028

Cartar RV (2004) Resource tracking by bumble bees: responses to plant-level differences in quality. Ecology 85:2764–2771. https://doi.org/10.1890/03-0484

Chittka L, Dyer AG, Bock F, Dornhaus A (2003) Bees trade off foraging speed for accuracy. Nature 424:388. https://doi.org/10.1038/424388a

Chittka L, Gumbert A, Kunze J (1997) Foraging dynamics of bumble bees: correlates of movements within and between plant species. Behav Ecol 8:239–249. https://doi.org/10.1093/beheco/8.3.239

Chittka L, Thomson JD, Waser NM (1999) Flower constancy, insect psychology, and plant evolution. Naturwissenschaften 86:361–377. https://doi.org/10.1007/s001140050636

Cnaani J, Thomson JD, Papaj DR (2006) Flower choice and learning in foraging bumblebees: effects of variation in nectar volume and concentration. Ethology 112:278–285. https://doi.org/10.1111/j.1439-0310.2006.01174.x

Combes SA, Gagliardi SF, Switzer CM, Dillon ME (2020) Kinematic flexibility allows bumblebees to increase energetic efficiency when carrying heavy loads. Sci Adv 6:eaay3115. https://doi.org/10.1126/sciadv.aay3115

Cresswell JE (1990) How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot Monarda fistulosa (Lamiaceae)? Oecologia 82:450–460. https://doi.org/10.1007/BF00319785

Darveau C-A, Billardon F, Bélanger K (2014) Intraspecific variation in flight metabolic rate in the bumblebee Bombus impatiens: repeatability and functional determinants in workers and drones. J Exp Biol 217:536–544. https://doi.org/10.1242/jeb.091892

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. Trends Ecol Evol 13:77–

81. https://doi.org/10.1016/S0169-5347(97)01274-3
Dukas R, Real LA (1993) Effects of recent experience on foraging decisions by bumble bees. Oecologia 94:244–246.https://doi.org/10.1007/BF00341323
Evans LJ, Raine NE (2014) Changes in learning and foraging behaviour within developing bumble bee (Bombus terrestris) colonies. PLoS One 9:e90556. https://doi.org/10.1371/journal.pone.0090556
Foster DJ, Cartar RV (2011) Wing wear affects wing use and choice of floral density in foraging bumble bees. Behav Ecol 22:52–59. https://doi.org/10.1093/beheco/arq160
Frasnelli E, Robert T, Chow PKY, et al (2021) Small and large bumblebees invest differently when learning about flowers. Curr Biol. https://doi.org/10.1016/j.cub.2020.11.062
Gegear RJ, Laverty TM (2004) Effect of a colour dimorphism on the flower constancy of honey bees and bumble bees. Can J Zool 82:587–593. https://doi.org/10.1139/z04-029
Gegear RJ, Thomson JD (2004) Does the flower constancy of bumble bees reflect foraging economics? Ethology 110:793–805. https://doi.org/10.1111/j.1439-0310.2004.01010.x
Goulson D (2000) Why do pollinators visit proportionally fewer flowers in large patches? Oikos 91:485–492. https://doi.org/10.1034/j.1600-0706.2000.910309.x
Goulson D (2003) Bumblebees: Their Behaviour and Ecology. Oxford University Press, Oxford
Goulson D, Peat J, Stout JC, et al (2002) Can alloethism in workers of the bumblebee, Bombus terrestris, be explained in terms of foraging efficiency? Anim Behav 64:123–130. https://doi.org/10.1006/anbe.2002.3041
Goulson D, Stout JC, Langley J, Hughes WOH (2000) Identity and function of scent marks deposited by foraging bumblebees. J Chem Ecol 26:2897–2911. https://doi.org/10.1023/A:1026406330348
Grüter C, Ratnieks FLW (2011) Flower constancy in insect pollinators: adaptive foraging behaviour or cognitive limitation? Commun Integr Biol 4:633–636. https://doi.org/10.4161/cib.16972
Grüter C, Segers FHID, Hayes L (2024) Extensive loss of forage diversity in social bees owing to flower constancy in simulated environments. Proc R Soc B 291:20241036. https://doi.org/10.1098/rspb.2024.1036
Gumbert A (2000) Color choices by bumble bees (Bombus terrestris): innate preferences and generalization after learning. Behav Ecol Sociobiol 48:36–43. https://doi.org/10.1007/s002650000213
Hagbery J, Nieh JC (2012) Individual lifetime pollen and nectar foraging preferences in bumble bees. Naturwissenschaften 99:821–832. https://doi.org/10.1007/s00114-012-0964-7
Hartig F (2020) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.3.
Heinrich B (1979a) “Majoring” and “minoring” by foraging bumblebees, Bombus vagans: an experimental analysis. Ecology 60:245–255. https://doi.org/10.2307/1937652
Heinrich B (1979b) Resource heterogeneity and patterns of movement in foraging bumblebees. Oecologia 40:235–245. https://doi.org/10.1007/BF00345321
Heinrich B (2004) Bumblebee Economics. Harvard University Press, Cambridge
Hemingway CT, Pimplikar S, Muth F (2024) Wild bumblebees use both absolute and relative evaluation when foraging. Behav Ecol 35:arad112. https://doi.org/10.1093/beheco/arad112
Hendriksma HP, Toth AL, Shafir S (2019) Individual and colony level foraging decisions of bumble bees and honey bees in relation to balancing nutrient needs. Front Ecol Evol 7:177.

https://doi.org/10.3389/fevo.2019.00177
Heuschen B, Gumbert A, Lunau K (2005) A generalised mimicry system involving angiosperm flower colour, pollen and bumblebees' innate colour preferences. Plant Syst Evol 252:121–137. https://doi.org/10.1007/s00606-004-0249-5
Hofmann G (1977) Iscotables: a handbook of data for biological and physical scientists. Instrumentation Specialties Company, Illinois
Holland JG, Nakayama S, Porfiri M, et al (2021) Body size and behavioural plasticity interact to influence the performance of free-foraging bumblebee colonies. Insects 12:236. https://doi.org/10.3390/insects12030236
Hunter JD (2007) Matplotlib: a 2D graphics environment. Comput Sci Eng 3:90–95. https://doi.org/10.1109/MCSE.2007.55
Kembro JM, Lihoreau M, Garriga J, et al (2019) Bumblebees learn foraging routes through exploitation–exploration cycles. J R Soc Interface 16:20190103. https://doi.org/10.1098/rsif.2019.0103
Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. Annu Rev Entomol 28:407–453. https://doi.org/10.1146/annurev.en.28.010183.002203
Lechantre A, Draux A, Hua H-AB, et al (2021) Essential role of papillae flexibility in nectar capture by bees. Proc Natl Acad Sci USA 118:e2025513118. https://doi.org/10.1073/pnas.2025513118
Lenth RV (2020) emmeans: estimated marginal means, aka least-squares means. R package version 1.5.3. CRAN
Lihoreau M, Chittka L, Raine NE (2011) Trade-off between travel distance and prioritization of high-reward sites in traplining bumblebees. Funct Ecol 25:1284–1292. https://doi.org/10.1111/j.1365-2435.2011.01881.x
Lihoreau M, Chittka L, Raine NE (2010) Travel optimization by foraging bumblebees through readjustments of traplines after discovery of new feeding locations. Am Nat 176:744–757. https://doi.org/10.1086/657042
Lihoreau M, Raine NE, Reynolds AM, et al (2012) Radar tracking and motion-sensitive cameras on flowers reveal the development of pollinator multi-destination routes over large spatial scales. PLoS Biol 10:e1001392. https://doi.org/10.1371/journal.pbio.1001392
Lunau K (1990) Colour saturation triggers innate reactions to flower signals: flower dummy experiments with bumblebees. J Comp Physiol A 166:827–834. https://doi.org/10.1007/BF00187329
Makino TT, Sakai S (2007) Experience changes pollinator responses to floral display size: from size-based to reward-based foraging. Funct Ecol 21:854–863. https://doi.org/10.1111/j.1365-2435.2007.01293.x
McKinney W (2010) Data structures for statistical computing in Python. Proc SciPy 56–61
Menzel R, Erber J (1972) The influence of the quantity of reward on the learning performance in honeybees. Behaviour 41:27–42. https://doi.org/10.1163/156853972X00176
Molet M, Chittka L, Stelzer RJ, et al (2008) Colony nutritional status modulates worker responses to foraging recruitment pheromone in the bumblebee Bombus terrestris. Behav Ecol Sociobiol 62:1919–1926. https://doi.org/10.1007/s00265-008-0623-3
Muller H, Chittka L (2008) Animal personalities: the advantage of diversity. Curr Biol 18:R961–R963. https://doi.org/10.1016/j.cub.2008.09.001

Nityananda V, Chittka L (2020) Reward value is more important than physical saliency during bumblebee visual search for multiple rewarding targets. BioRxiv. https://doi.org/10.1101/2020.10.01.322172

Ohara M, Higashi S (1994) Effects of inflorescence size on visits from pollinators and seed set of Corydalis ambigua (Papaveraceae). Oecologia 98:25–30. https://doi.org/10.1007/BF00326086

Ohashi K, Thomson JD, D'Souza D (2007) Trapline foraging by bumble bees: IV. Optimization of route geometry in the absence of competition. Behav Ecol 18:1–11. https://doi.org/10.1093/beheco/arl053

Osborne JL, Smith A, Clark SJ, et al (2013) The ontogeny of bumblebee flight trajectories: from naïve explorers to experienced foragers. PLoS One 8:e78681. https://doi.org/10.1371/journal.pone.0078681

Osborne JL, Williams IH (2001) Site constancy of bumble bees in an experimentally patchy habitat. Agric Ecosyst Environ 83:129–141. https://doi.org/10.1016/S0167-8809(00)00262-0

Page RE, Scheiner R, Erber J, Amdam GV (2006) The development and evolution of division of labor and foraging specialization in a social insect (Apis mellifera L.). Curr Top Dev Biol 74:253–286

Pattrick JG, Symington HA, Federle W, Glover BJ (2023) Bumblebees negotiate a trade-off between nectar quality and floral biomechanics. iScience 26:108071. https://doi.org/10.1016/j.isci.2023.108071

Pedregosa F, Varoquaux G, Gramfort A, et al (2011) Scikit-learn: machine learning in Python. J Mach Learn Res 12:2825–2830

Pyke GH (1984) Optimal foraging theory: a critical review. Annu Rev Ecol Syst 15:523–575

Pyke GH, Starr CK (2021) Optimal foraging theory. In: Starr CK (ed) Encyclopedia of social insects. Springer, Cham, pp 677–685

Raine NE, Chittka L (2008) The correlation of learning speed and natural foraging success in bumble-bees. Proc R Soc B 275:803–808. https://doi.org/10.1098/rspb.2007.1652

Raine NE, Chittka L (2007) The adaptive significance of sensory bias in a foraging context: floral colour preferences in the bumblebee Bombus terrestris. PLoS One 2:e556. https://doi.org/10.1371/journal.pone.0000556

Real L, Rathcke BJ (1988) Patterns of individual variability in floral resources. Ecology 69:728–735. https://doi.org/10.2307/1941021

Reynolds AM, Lihoreau M, Chittka L (2013) A simple iterative model accurately captures complex trapline formation by bumblebees across spatial scales and flower arrangements. PLoS Comput Biol 9:e1002938. https://doi.org/10.1371/journal.pcbi.1002938

Riveros AJ, Gronenberg W (2010) Brain allometry and neural plasticity in the bumblebee Bombus occidentalis. Brain Behav Evol 75:138–148. https://doi.org/10.1159/000306506

Russell AL, Buchmann SL, Papaj DR (2017) How a generalist bee achieves high efficiency of pollen collection on diverse floral resources. Behav Ecol 28:991–1003. https://doi.org/10.1093/beheco/arx058

Saleh N, Chittka L (2007) Traplining in bumblebees (Bombus impatiens): a foraging strategy's ontogeny and the importance of spatial reference memory in short-range foraging. Oecologia 151:719–730. https://doi.org/10.1007/s00442-006-0607-9

Saleh N, Scott AG, Bryning GP, Chittka L (2007) Distinguishing signals and cues: bumblebees use general footprints to generate adaptive behaviour at flowers and nest. Arthropod-Plant Interact 1:119–127. https://doi.org/10.1007/s11829-007-9011-6

Schmid-Hempel P, Kacelnik A, Houston AI (1985) Honeybees maximize efficiency by not filling their

crop. Behav Ecol Sociobiol 17:61–66. https://doi.org/10.1007/BF00299430

Sletvold N, Trunschke J, Smit M, et al (2016) Strong pollinator-mediated selection for increased flower brightness and contrast in a deceptive orchid. Evolution 70:716–724. https://doi.org/10.1111/evo.12881

Sommer J, Rao V, Sprayberry J (2022) Deconstructing and contextualizing foraging behavior in bumble bees and other central place foragers. Apidologie 53:32. https://doi.org/10.1007/s13592-022-00944-3

Spaethe J, Tautz J, Chittka L (2001) Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. Proc Natl Acad Sci USA 98:3898–3903. https://doi.org/10.1073/pnas.071053098

Spaethe J, Weidenmüller A (2002) Size variation and foraging rate in bumblebees (Bombus terrestris). Insectes Soc 49:142–146. https://doi.org/10.1007/s00040-002-8293-z

Thakar JD, Kunte K, Chauhan AK, et al (2003) Nectarless flowers: ecological correlates and evolutionary stability. Oecologia 136:565–570. https://doi.org/10.1007/s00442-003-1304-6

Vaudo AD, Patch HM, Mortensen DA, et al (2016) Macronutrient ratios in pollen shape bumble bee (Bombus impatiens) foraging strategies and floral preferences. Proc Natl Acad Sci USA 113:E4035–E4042. https://doi.org/10.1073/pnas.1606101113

Waddington KD, Gottlieb N (1990) Actual vs perceived profitability: a study of floral choice of honey bees. J Insect Behav 3:429–441. https://doi.org/10.1007/BF01052010

Waddington KD, Holden LR (1979) Optimal foraging: on flower selection by bees. Am Nat 114:179–196. https://doi.org/10.1086/283467

Waser NM (1986) Flower constancy: definition, cause, and measurement. Am Nat 127:593–603. https://doi.org/10.1086/284507

Waskom M (2021) seaborn: statistical data visualization. JOSS 6:3021. https://doi.org/10.21105/joss.03021

Weiss MR (1991) Floral colour changes as cues for pollinators. Nature 354:227–229. https://doi.org/10.1038/354227a0

Whitney HM, Dyer A, Chittka L, et al (2008) The interaction of temperature and sucrose concentration on foraging preferences in bumblebees. Naturwissenschaften 95:845–850. https://doi.org/10.1007/s00114-008-0393-9

Willmer P (2011) Pollination and floral ecology. Princeton University Press, Princeton

Wolf TJ, Schmid-Hempel P, Ellington CP, Stevenson RD (1989) Physiological correlates of foraging efforts in honey-bees: oxygen consumption and nectar load. Funct Ecol 3:417–424. https://doi.org/10.2307/2389615

Woodgate JL, Makinson JC, Lim KS, et al (2016) Life-long radar tracking of bumblebees. PLoS One 11:e0160333. https://doi.org/10.1371/journal.pone.0160333