Take it or leaf it: bees learn leaf shape as a cue when flower colour is easily learned

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Over a century of research has demonstrated that pollinators, such as bees, associatively learn diverse flower cues, including tactile, visual and olfactory cues, to find food rewards. However, floral cues are not always reliable, as flowers of different plant species often differ in terms of the qualities of their food rewards, even when flower types resemble each other. At the same time, some nonfloral traits, such as leaf shape, can differ among plant species and might be associatively learned by bees to improve foraging success. In this laboratory study, we tested whether generalist bees (*Bombus impatiens*) can (1) associatively learn differences in leaf shape to discriminate rewarding from unrewarding flowers and (2) rely more on differences in leaf shape when a flower colour cue is harder to discriminate. We therefore assigned bees to either of two treatments: in one treatment, rewarding and unrewarding artificial targets ('flowers') differed greatly in petal colour, and in the other treatment, they differed little; each treatment's targets differed in leaf shape in the same way. As expected, bees learned significantly faster when flower petal colours were more dissimilar and thus relatively easier to discriminate. These bees also learned and recalled the correct combination of petal colour and leaf shape. Yet when petal colours differed relatively little, bees had a much harder time learning petal colour and did not show evidence of having remembered leaf shape. Our results demonstrate that leaf shape is a cue that foraging bees can learn to associate with a pollen food reward. However, leaf shape may be learned secondarily to, or only in combination with, floral cues (such as petal colour). We discuss evidence of compound learning and overshadowing and implications of our results for pollinator-mediated selection on nonfloral plant traits.

A central question in animal behaviour is how animals decide which cues to use to find food (Kamil & Roitblat, 1985; Stephens, 2008). Generalist animals frequently encounter situations of uncertainty while foraging, such as when a cue cannot reliably be associated with food (Mclinn & Stephens, 2006; Page & Jones, 2016). Generalist pollinators frequently learn to associate tactile, visual, olfactory and other cues produced by flowers with floral food rewards (e.g. nectar and pollen) (Chittka & Raine, 2006; Clarke et al., 2013, 2017; Harrap et al., 2017; Riffell, 2011; Whitney et al., 2009). However, pollinators also often encounter uncertainty while foraging on flowers. For instance, many plant species deceive their pollinators by offering floral cues that do not honestly indicate reward presence, quality or amount (Ashman, 2009; Lichtenberg et al., 2020; van der Kooi et al., 2023). Furthermore, co-flowering plant species may share similar floral cues but offer food rewards that differ in quality (e.g. Internicola et al., 2007), making those shared cues unreliable. For instance, up to 5% of

plant species offer no rewards at all and instead attract pollinators by mimicking the floral displays of rewarding co-flowering plant species (Gigord et al., 2002; Lichtenberg et al., 2020; Schiestl, 2005; Fig. 1). Consequently, particularly when floral cues are unreliable, we expect pollinators should learn cues from other parts of the plant that can be reliably associated with floral rewards. However, whether and when nonfloral plant cues alone or in combination with flower cues are used to discriminate among flower types by foraging pollinators has scarcely been explored (see Cepero et al., 2015).

Over the past century, the vast majority of research conducted on how pollinators locate floral food rewards has focused solely on the role of floral cues (see Chittka & Thomson, 2005; Giurfa, 2007). Flower colour, pattern, shape and scents can differ significantly between species of flowering plants, enabling pollinators to learn and develop strong, stable preferences associated with these floral cues (Essenberg et al., 2015; Hempel de Ibarra & Somanathan, 2019; Nicholls et al., 2022). However, nonfloral traits such as leaf shape also often differ between animal-pollinated flowering plant species. For instance, leaves of a given plant species may be strap-

Figure 1. Three plant species whose flowers resemble each other and are thought to be involved in (a, b) Batesian and (c) Müllerian mimicry, but whose leaves vary in shape. Flower and leaves of (a, d) an unrewarding mimic, *Epidendrum ibaguense*, (b, e) the rewarding model, *Lantana camara*, and the (c, f) co-occurring rewarding Müllerian mimic, *Asclepias curassavica*. Photo credits: (a) Dick Culbert, (b) Vineeth Vengolis, (c) Fan Wen, (d) Yercaud Elango, (e) Vineeth Vengolis, (f) Juan Carlos Fonseca. Licensing: (a) CC BY 2.0, (b) CC BY-SA 4.0, (c) CC BY-SA 4.0, (d) CC BY-SA 4.0, (e) CC BY-SA 4.0, (f) CC BY-SA 4.0. https://creativecommons.org/licenses/by-sa/4.0/. The photographs have been cropped.

like or obovate, or pinnately or palmately compound (Fowler, 2016; Kidner & Umbreen, 2010). Notably, leaf shape can differ between plant species engaged in floral Batesian mimicry (when rewarding flowers of one plant species are mimicked by the unrewarding flowers of another plant species) and floral Müllerian mimicry (when flowers of multiple co-flowering plant species are rewarding and resemble one another) (Fig. 1) (Bierzychudek, 1981). That leaf shape differs between plant species, especially when floral cues may be unreliable, raises the possibility that pollinators can learn to associate differences in leaf shape with floral rewards.

Leaf shape is often learned by animals in other contexts. For instance, various butterfly and fly taxa learn to use leaf shape to locate host plants for oviposition (Allard & Papaj, 1996; Degen & Städler, 1996; Dell'Aglio et al., 2016; Wiklund, 1984). Similarly, braconid wasp parasitoids readily learn leaf shape to locate their caterpillar hosts (Wäckers & Lewis, 1999). In addition, honey bees, bumble bees and monarch butterflies, *Danaus plexippus*, can learn to associate flower shape with a nectar reward (Cepero et al., 2015; Gould, 1985; Zhang et al., 1995), suggesting that pollinators might also be able to learn the shape of leaves while foraging. Even still, other floral visual cues are learned preferentially over flower shape (Rusch et al., 2017). Additionally, relative to other floral cues (e.g. scent, colour and pattern), flower shape is more difficult to learn for even generalist bees, a model system for the study of pollinator learning and memory (Gould, 1993; Lehrer, 1993; Lehrer et al., 1985; Menzel, 1967; and references within). Assuming similar challenges when learning leaf shape, we expect that generalist bees may attend little to leaf shape when floral cues are easy to learn and instead rely primarily on floral cues. At the same time, because compound cues have enhanced saliency and facilitate associative learning (Telles et al., 2017), when floral cues are hard

to learn, we expect that bees should attend to leaf shape and that leaf shape should be learned in compound with floral cues.

In this laboratory study, we assessed whether and within what context a generalist bee can learn to associate a floral food reward (pollen) with leaf shape. Given that shape is considered a difficult cue to learn, we hypothesized that bumble bees (*Bombus impatiens*) would learn leaf shape, but only when flower colour was relatively difficult to learn (e.g. when the saliency of leaf and flower colour cues are more similar). We tested this hypothesis via an associative learning assay in which bees were trained to associate a pollen reward with a given combination of leaf shape and petal colour (each combination is a 'target'). In one treatment, petals of different target types differed greatly in bee colour space, which we predicted would be easier for bees to learn; in the other treatment, petals of different target types differed little in bee colour space, which we predicted would be harder for bees to learn. Leaf shape differed among target types in the same way across treatments. Finally, we predicted that to reduce uncertainty when the petal colour learning task was more difficult, bees would be more likely to learn specific combinations of leaf shape and petal colour associated with the floral reward.

METHODS

Bees and Housing

We used 79 workers from four captive-bred and commercially obtained (Biobest U.S.A. Inc., Romulus, MI, U.S.A.) colonies of *Bombus impatiens* bumble bees, maintained following Russell et al. (2017). To summarize, bees were permitted to forage on artificial feeders providing nectar solution (2 M sucrose) and pulverized honey bee collected pollen (Plant Products Inc., Leamington, ON,
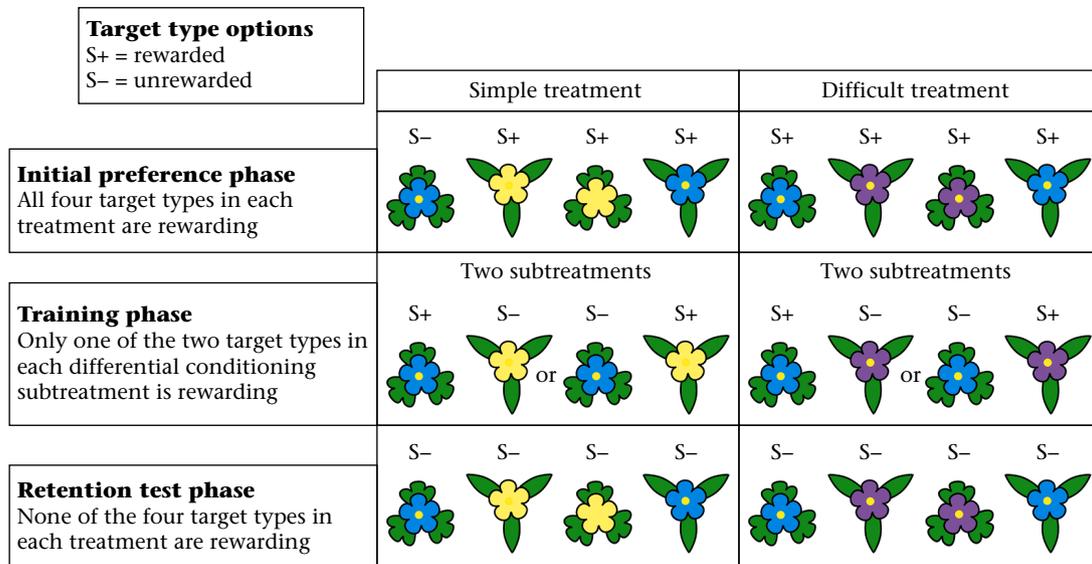
Figure 2. Schematic of the two treatments. Treatments differed in terms of how similar the petal colours are in bee colour space. Leaf shapes differed in the same way for both treatments. In the initial preference phase, we allowed a naïve bee to forage on one of two sets of artificial rewarding (S+) flowers of four types. In the simple treatment: blue petal, short leaves; yellow petal, long leaves; yellow petal, short leaves; blue petal, long leaves. In the difficult treatment: blue petal, short leaves; purple petal, long leaves; purple petal, short leaves; blue petal, long leaves. The artificial anther is depicted as the yellow dot in the centre of all of the flowers. After 24–48 h, the bee was differentially conditioned on an array of two flower types in a training phase, where only one flower type was rewarding (S+/S-) (depending on the subtreatment). In the simple treatment: blue petal, short leaves; yellow petal, long leaves; in the difficult treatment: blue petal, short leaves; purple petal, long leaves. Up to 1 h after training, the bee was given all four flower types it had been exposed to in its initial preference phase, in an unrewarding (S-) retention test.

Canada) ad libitum. Bees were contained within a plywood arena (L × W × H: 82 × 60 × 60 cm) painted grey on the floor and sides with a clear acrylic ceiling, lit from above and set to a 14:10 h light:dark cycle.

Artificial Flowers

To precisely manipulate petal colour and leaf shape, we cut plastic (Polypropylene Heavy Duty Plastic Folders, Amazon Basics, https://www.amazon.com) into the shape of petals and leaves and hot-glued them to microcentrifuge tubes, with leaves offset 2 cm behind the petals. Petal shape was identical across all treatments and the two types of leaf shapes had identical total surface area (measured using ImageJ, National Institutes of Health, Bethesda, MD, U.S.A., http://rsbweb.nih.gov/ij/). We mounted a disposable artificial anther (a uniformly sized yellow chenille stem) to the centre of each artificial flower's corolla ('petal'). We used chenille stems as artificial anthers following Russell and Papaj (2016), as they can hold and present precise amounts of pollen to foraging bees. To prevent bees from visually or olfactorily assessing pollen presence or absence, pollen and artificial anthers were a similar hue of yellow and unrewarding anthers were pollen scented following Muth et al. (2016).

To create treatments that differed in the difficulty of the colour learning task, we selected two pairs of petal colours that were closer and further apart in bee colour space, respectively (Fig. 2, Fig. 3a–c, Supplementary Fig. S1). We closely matched the colour of the artificial plastic leaves to live leaves collected from the Missouri State University campus (*Amelanchier* sp., *Philodendron* sp., *Tulipa* sp.) (Fig. 3b–d).

Spectral Analyses

Following Russell et al. (2021), we measured the colour reflectance of the artificial petals and leaves (Amazon Basics) and

live leaves with a UV-VIS spectrometer (USB2000, Ocean Optics, University, FL, U.S.A.), tungsten-deuterium light source (DH2000-BAL, Ocean Optics), a fluoropolymer white standard (WS-1-SL Spectralon, Ocean Optics) and an RPH reflectance probe (Ocean Optics), shielded from extraneous light. We measured irradiance within the flight arena at the centre of the flower array using a 50 ms integration time and 50 ms averaging, CC-3-UV-S cosine-corrected (180 degrees) irradiance probe (Ocean Optics), Q400-7-SR UV/VIS optical fibre (Ocean Optics) and a tungsten-deuterium calibration light source (DH-3P-CAL, Ocean Optics). Each reflectance spectrum consisted of the mean of 10 measurements, taken from different petals, leaves or parts of the arena wall background.

To characterize what bees perceived, we used our reflectance and irradiance measurements to plot artificial petals (Fig. 3a) and leaves (Fig. 3b) within a colour space (e.g. the colour hexagon) for *Bombus impatiens* following Russell et al. (2017). We crafted a colour space diagram using ultraviolet (UV)-blue-green trichromat receptor sensitivities following Chittka (1992) and Skorupski and Chittka (2010), then transformed them to spectral sensitivity curves following Stavenga et al. (1993), as in the 'pavo' and 'colourvision' R packages (Gawryszewski, 2018; Maia et al., 2019). In colour space, the maximum distance from the centre to the vertex of each photoreceptor (blue, UV or green) is 1, or the maximum excitation of that photoreceptor. We used the grey-painted test arena wall, where the flowers were displayed, as the background stimulus for the colour hexagon (Fig. 3c), and we used the irradiance of the overhead arena lights to calculate the receptor excitation values (Fig. 3e).

We selected the colours for our artificial flower petals and leaves by how they differed in bee colour vision. Bumble bees have difficulty discriminating colours that are close in colour space and fail to discriminate colours that are less than 0.04 colour units apart (distance in bee colour space according to a hexagon colour model of bee vision) (Dyer & Chittka, 2004). Previous research
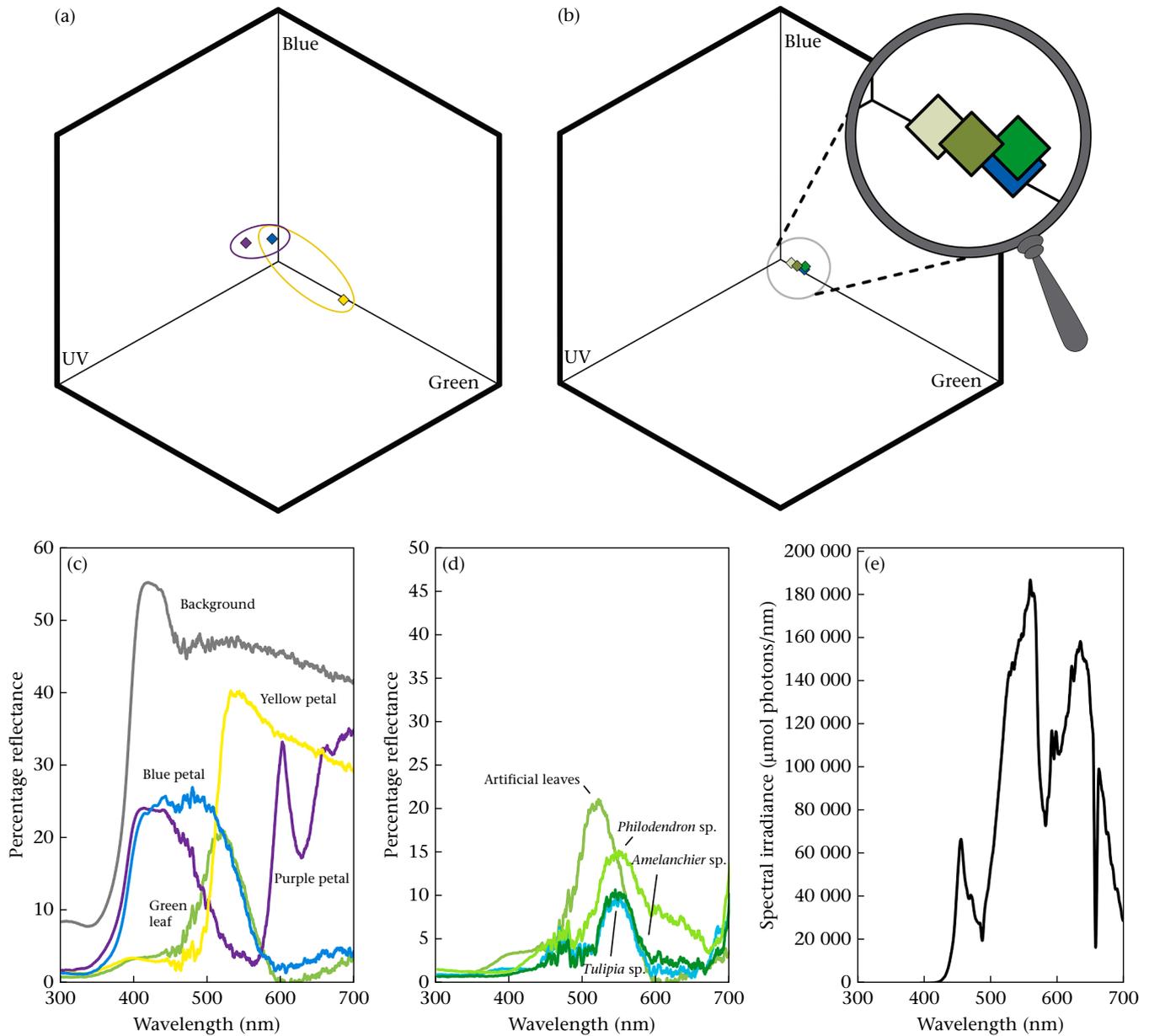
Figure 3. The loci in *B. impatiens* colour space of (a) artificial blue (blue diamond), purple (purple diamond) and yellow (yellow diamond) petals and (b) live (*Amelanchier* sp., *Philodendron* sp., *Tulipa* sp.) and artificial leaves against the test arena background. Petal colours used in the simple and difficult treatments are encircled in yellow and purple, respectively. Blue and purple petals differed by 0.1 colour units (difficult to learn; Dyer & Garcia, 2014) and from the background by 0.1 and 0.15 colour units, respectively, according to a hexagon colour model of bee vision. Blue and yellow petals differed by 0.41 colour units (easy to learn; Dyer & Garcia, 2014), and the yellow petals differed from the background by 0.32 units. Artificial leaves differed from live leaves by a mean ± SE of 0.037 ± 0.019 colour units, and the green plastic differed from the background by 0.11 colour units. (c) The reflectance spectra of the foraging arena background, the artificial petals and leaf, and (d) the live leaves compared to the artificial leaf. (e) The irradiance at the centre of the flower array of the LED panel illuminating the arena.

notes that the difficulty of the colour learning task is a reliable way to quantify bee perceptual difficulty of a visual task (Dyer & Garcia, 2014). Therefore, petal colours selected for the simple treatment (blue versus yellow, which differ by 0.41 colour units) should be more easily discriminable than petal colours selected for the difficult treatment (blue versus purple, which differ by 0.1 colour units). Artificial leaves were a close match to live leaves in bee colour space and differed on average by 0.037 colour units. Colours of artificial petals and leaves differed from the background by at least 0.1 colour units. See Table S1 for receptor excitation values.

Experimental Protocol

Behavioural trials were conducted in a cleaned and grey-painted plywood test arena (L × W × H: 82 × 60 × 60 cm) with a clear acrylic ceiling, lit from above by 38 W, 4281 lumen LED lights (2 × 2 LED Panel; 5000K, Bees Lighting, Chatsworth, CA, U.S.A.), following Russell and Ashman (2019). To summarize, artificial flowers were spaced 7 cm apart in a Cartesian grid design attached to the arena wall opposite a marking surrounding an artificial nest entrance.

Each of 79 flower-naïve worker bees (hereafter 'naïve bee') from four colonies was assigned to one of two treatments. For both treatments, we first tested the initial petal colour and leaf shape preference of each individual bee using a 4 × 4 array of four types of pollen-rewarding artificial flowers and systematically alternated flower position in the grid. The four types of flowers (the 4 flower petal and leaf combinations) present in the array depended on the assigned treatment (see Fig. 2, Supplementary Figs S1−S2). We systematically alternated flower positions for each trial. The artificial anther of each rewarding flower was loaded with 5.5 mg of cherry pollen (*Prunus avium*, Antles Pollen Inc., Wenatchee, WA, U.S.A.). After each trial (initial, training, retention), we discarded the artificial anthers and thoroughly cleaned the artificial flowers with 70% ethanol to be reused following Russell and Ashman (2019), as bees leave chemical footprints when foraging (Roselino et al., 2016). At the conclusion of each trial, and before starting again, the testing arena floor was cleaned.

To initiate an initial preference trial, we first set up flowers vertically on the arena wall and allowed one naïve bee into the arena. Each bee visited nearly all of the flowers in its trial at least once, which familiarized them with foraging in the array and on each flower type and its component parts. To ensure trials were comparable, trials were terminated after the naïve bee made up to 40 pollen-collecting visits in its single initial preference trial, did not approach any flower for a period of 5 min or attempted to leave the arena via the nest entrance, whichever came first. The bee was then recaptured, marked with a unique paint colour using nontoxic oil-based markers (Sharpie, https://www.sharpie.ca/) and returned to its colony. Of 79 bees, 14 did not collect pollen within their initial preference trial and were not included in the experiment.

After 24−48 h, marked bees were individually differentially conditioned ('trained') to the specific rewarding leaf and petal combination within their assigned treatment (see Giurfa, 2007) (Fig. 2, Supplementary Fig. S2). Bees were allowed to forage individually on a 5 × 4 training assay of 20 flowers with one rewarding flower type of the respective treatment (S+) and one unrewarding flower type (S-), with flower types alternated by position. Anthers of rewarding flowers were loaded with 5.5 mg of cherry pollen and anthers of unrewarding flowers were pollen-scented. We alternated which of the two training flower types were rewarding across trials, thus creating two subtreatments per treatment (Fig. 2, Supplementary Fig. S2). We permitted bees to forage until they had made 8 of their last 10 rewarding visits to the rewarding flower type, which we considered evidence of the bee having learned. Bees that did not meet this learning criterion in their first training treatment (i.e. did not visit any flower for a period of 5 min, or made several consecutive nest entrance visits) were returned to their colony to unload pollen and subsequently given a second training trial (16 of the 38 successful bees). Of 65 total bees that were included in training, nine did not collect pollen within their first or second training trial and a further 10 bees did not meet the learning criterion even after two trainings; these data were not used in analyses.

To test whether trained bees retained the learned preference, each was given a single retention test 1 h after training. Each bee was individually tested and presented with unrewarding, pollen-scented flowers in a 4 × 4 array with the same flower types as in that bee's initial preference assay. We allowed each bee in the retention test to make up to 40 flower visits. After a bee completed its retention test, the bee was euthanized. Of 46 bees that were included in the retention tests, eight would not visit flowers and their data were not used in analyses.

We recorded flower-visiting behaviour following Muth et al. (2016). To summarize, we recorded flower 'visits', which we

defined as a bee touching the scented or pollen-covered anther. When bees collected pollen from rewarding flowers (scraped from anthers by 'scrabbling'; see Russell & Papaj, 2016), the visit was recorded as 'rewarded'. When bees visited unrewarding flowers, the visit was recorded as 'unrewarded'. In the rare cases when bees visited rewarding flowers but did not collect pollen from them, we excluded the visit from analyses because we could not be sure whether the visit reinforced or inhibited learning. Bees never depleted rewarding flowers of pollen and rarely filled their pollen baskets during trials.

Data Analyses

We analysed how rate and strength of learning was affected by treatment and how preferences for the trained rewarding petal colour, leaf shape and/or the combination changed with experience. All data were analysed using R statistical software, using R version 4.2.2 (R Core Team, 2022) and RStudio version 2023.09.1+494 (Ushey et al., 2022). We calculated the effect sizes using the 'emmeans' package (Lenth, 2025) and report Cohen's *d* in all cases.

Do bees learn more quickly when the learning task is easier?

In the differential conditioning assay, we assessed whether bees made more visits to the rewarding flowers with successive visits (i.e. learned which flower type was rewarding) and whether the pattern differed by treatment. To accomplish this, we analysed only bees that met our learning criterion and used a binomial generalized linear mixed effects model (GLMM) similar to Russell and Ashman (2019). We fitted a model using the 'glmmTMB()' function from the 'glmmTMB' package (Brooks et al., 2017), specifying type II Wald chi-square (χ^2) tests via the 'Anova()' function in the 'car' package (Fox & Weisberg, 2019), and checked model assumptions using the 'DHARMa' (Hartig & Lohse, 2022) and 'sjPlot' (Lüdecke, 2024) packages. We specified 'visit type' (rewarded or unrewarded) as the response variable and 'treatment' (simple or difficult) and 'visit number' as the explanatory variables. We included visit number as a repeated measure, nested within 'bee ID', nested within 'colony ID' as our random effects.

Do bees learn the leaf−petal combination regardless of the difficulty of the learning task?

To analyse differences in preference across the four flower types for each group of bees in each treatment (Fig. 2), before and after learning, we used a hierarchical Bayesian model ('BayesPref' package; Fordyce et al., 2011) for multinomial count data, following Russell et al. (2018). Detailed information regarding the advantages of this model is given in Fordyce et al. (2011), Forister and Scholl (2012) and Gompert and Buerkle (2012). For each analysis, we ran MCMC for 40 000 generations and discarded the first 10 000 runs as burn-in. We confirmed even mixing for all posteriors using the 'plot' Russell et al. (2018) function. To identify significant differences among estimates of preference for each of the four flower types in each treatment, we used pairwise comparisons of posterior probabilities (PP) (BayesPref package; Fordyce et al., 2011). When preference for a particular flower type is greater than preference for another flower type, or when preference for a particular flower type after experience (i.e. the retention test) is greater than the initial preference for that flower type in more than 95% of the sampled MCMC steps, the preference estimates are considered to be significantly different (Fordyce et al., 2011). Although we use a Bayesian approach for examining pairwise differences, we can interpret posterior probability values similarly to the frequentist $P − \alpha$ (where $\alpha = 0.05$). While pairwise comparisons offer complementary values for both choice A over B

and B over A, we report only the smaller value to align with a frequentist interpretation. See Russell et al. (2018) for a complete explanation.

Is associative learning mediated equivalently by petal colour and leaf shape?

To determine whether treatment influenced whether bees learned to associate petal colour or leaf shape with the pollen reward, we first calculated the mean percentage of each bee's visits to the trained petal colour or leaf shape in the initial preference assay and retention test. We compared initial to test preference for petal colour or leaf shape via GLMMs as above. The response variable was 'percentage preference' (for the rewarded petal colour or leaf shape) and 'experiment phase' (initial versus test) was the explanatory variable. For these models, we specified bee ID, nested within colony ID as our random effects.

Ethical Note

No approval from a regulatory body was required for these experiments. However, we made every effort to minimize stress to our subjects, and the bees were maintained and handled only by experienced researchers. Colonies had ad libitum access to food outside the daily experimental period. Bees were handled only during individual marking, after which they were allowed to recover and acclimate in their nestbox. The bees moved freely in the testing arenas and were never forced to participate. The feeding arenas and tubing to the feeding arenas were cleaned regularly. At the end of the experiments, we euthanized bees by freezing in accordance with standard practice.

RESULTS

Bees Learned More Quickly When the Learning Task Was Easier

Bumble bees visiting artificial targets ('flowers') rapidly learned via differential conditioning whether a given flower type was associated with the pollen reward. Bees in both training treatments made more flower visits across consecutive visits to the rewarding flower type (GLMM: visit number effect: $\chi^2_1 = 5.579$, $P = 0.019$; treatment effect: $\chi^2_1 = 2.472$, $P = 0.116$; effect size = 0.305). However, when the petal colours of the two artificial flower types were perceptually more dissimilar (simple treatment), bees learned significantly more quickly than when the petal colours of the two flower types were perceptually more similar (difficult treatment) (GLMM: visit number × treatment interaction: $\chi^2_1 = 6.016$, $P = 0.015$; Fig. 4). This difference corresponds to a 41% better performance in the mean number of flower visits to reach the learning criterion (mean number of visits ± SE: trained in simple treatment: 48.9 ± 5.0, $N = 17$ bees; trained in difficult treatment: 68.9 ± 8.3, $N = 21$ bees).

Bees Learned the Leaf—Petal Combination When the Learning Task Was Easier

Relative to their initial preference, experienced bees in unrewarded retention tests for the simple treatment significantly preferred the flower type that had been rewarded (flower types with the correct petal colour and leaf shape) and avoided flower types with the incorrect petal colour or incorrect petal colour and leaf shape but did not alter their preference when only leaf shape was incorrect (Table 1, Fig. 5). Experienced bees also significantly preferred flowers with the correct petal colour over flowers with the incorrect petal colour, regardless of leaf shape (Table 1, Fig. 5). In contrast, bees in the difficult treatment did not alter their
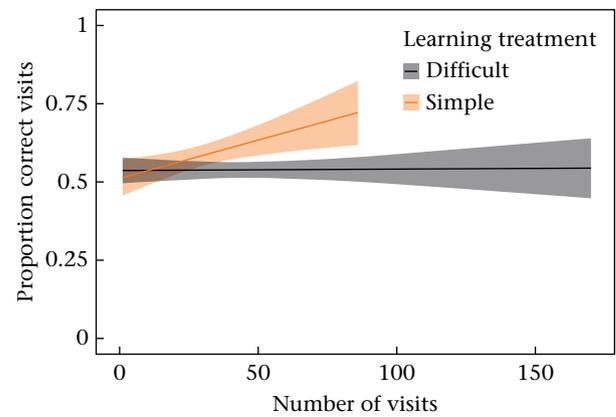

Figure 4. Mean proportion of correct (rewarded) visits to the rewarding flower type during the training phase for bees in the simple treatment ($N = 17$) and the difficult treatment ($N = 21$). Plotted lines indicate means and shaded regions indicate 95% confidence intervals.

preference for any flower type with experience (Table 2, Fig. 5). For preferences divided among subtreatments for both treatments, see Supplementary Tables S2—S5 and Supplementary Fig. S3.

Initially naïve bees showed no preference for any one flower type over any other flower type, regardless of treatment (Table 1, Fig. 5).

Associative Learning Was Primarily Mediated by Petal Colour

Learned preferences for petal colour, but not leaf shape, were retained for at least 1 h by bees assigned to the simple treatment. Relative to their initial petal colour preference and independent of leaf shape, these experienced bees significantly preferred the correct petal colour (GLMM: $\chi^2_1 = 11.743$, $P = 0.0007$, effect size = 1.18; Fig. 6a). Conversely, experienced bees in the difficult treatment did not similarly retain their petal colour preference (GLMM: $\chi^2_1 = 1.095$, $P = 0.295$, effect size = 0.349; Fig. 6a). However, in one of the two subtreatments there was a trend for experienced bees to recall the correct petal colour (GLMM: trained to flowers with purple petals and long leaves: $\chi^2_1 = 3.785$, $P = 0.052$, effect size = 0.973; trained to flowers with blue petals and short leaves: $\chi^2_1 = 0.005$, $P = 0.945$, effect size = 0.031). In contrast, regardless of treatment or subtreatment, experienced bees did not retain their preference for leaf shape independent of flower colour (GLMMs: simple treatment: $\chi^2_1 = 1.803$, $P = 0.180$; effect size = 0.461; difficult treatment: $\chi^2_1 = 0.033$, $P = 0.857$; effect size = 0.060;

Table 1
Differences in posterior probabilities via a Bayesian analysis for bees assigned to the simple treatment

	Initial preference	Test preference	Initial vs Test
CPIL vs CPCL	0.400	0.262	
CPIL vs IPIL	0.345	0.007	
CPIL vs IPCL	0.287	0.013	
CPCL vs IPIL	0.264	0.009	
CPCL vs IPCL	0.208	0.003	
IPIL vs IPCL	0.432	0.470	
CPIL			0.084
CPCL			0.007
IPIL			0.022
IPCL			0.020

CP: correct petal colour; CL: correct leaf shape; IP: incorrect petal colour; IL: incorrect leaf shape.
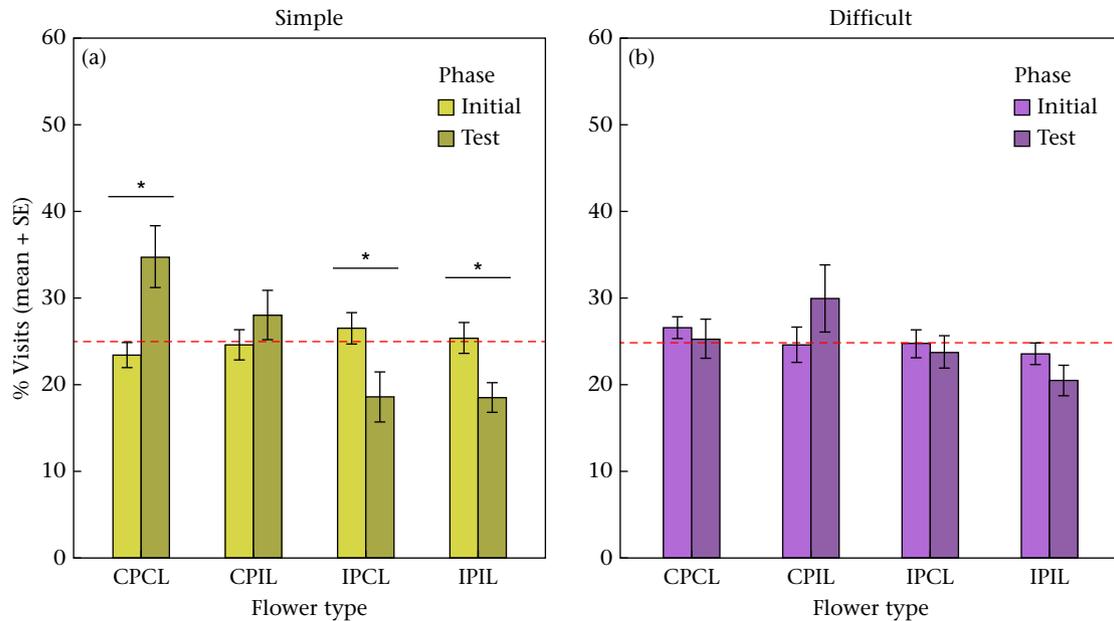
Figure 5. Initial and unrewarded retention test preference for each flower type for bees in (a) the simple treatment ($N = 17$ bees) and (b) the difficult treatment ($N = 20$ bees). Asterisks indicate pairwise differences for each flower type for the initial versus retention test at posterior probabilities <0.05. Dashed line at 25% indicates random expectation for an assay with four choices. In reference to the trained rewarding flower target, C = correct, I = incorrect, P = petal colour, L = leaf shape; therefore, CPCL = correct petal colour−correct leaf shape; CPIL = correct petal colour−incorrect leaf shape; IPCL = incorrect petal colour−correct leaf shape; IPIL = incorrect petal colour−incorrect leaf shape.

Table 2
Differences in posterior probabilities via a Bayesian analysis for bees assigned to the difficult treatment

	Initial preference	Test preference	Initial vs Test
CPIL vs CPCL	0.424	0.364	
CPIL vs IPIL	0.353	0.079	
CPIL vs IPCL	0.292	0.214	
CPCL vs IPIL	0.299	0.150	
CPCL vs IPCL	0.232	0.338	
IPIL vs IPCL	0.422	0.257	
CPIL			0.181
CPCL			0.227
IPIL			0.132
IPCL			0.277

CP: correct petal colour; CL: correct leaf shape; IP: incorrect petal colour; IL: incorrect leaf shape.

Fig. 6b). For further details regarding bee preferences by sub-treatment, see Supplementary Tables S2−S5 and Fig. S3.

DISCUSSION

Our study sheds light on the role a common nonfloral plant cue plays in pollinator learning. We found that generalist bumble bees can learn to associate leaf shape with a pollen food reward, but whether bees learned leaf shape depended on how readily the simultaneously available floral colour cue was learned. However, our prediction for when bees would learn leaf shape did not align with our results. We predicted that bees would learn to discriminate flower types more slowly when presented with a difficult flower colour perceptual learning task (see Niggebrügge et al., 2009). We also predicted that when the petal colour learning task was more difficult, bees would readily learn the other available cue, leaf shape, alone or in combination with petal colour, to facilitate learning. When the colour perceptual learning task was difficult, bees indeed learned to discriminate flower types 29%

more slowly, but they did not remember leaf shape alone or in combination with petal colour. Instead, only when the colour perceptual learning task was easier did bees remember the correct combination of petal colour and leaf shape. We also found that the effectiveness of training within this treatment depended on which target was rewarded: bees trained to flowers with yellow petals and long leaves had much greater retention than bees trained to flowers with blue petals and short leaves. Whether this is evidence of a bias or prepared learning (Dexheimer & Dunlap, 2025) will require future study. Altogether, while foraging bees can attend to a nonfloral cue like leaf shape, at least when compared to a flower colour cue, leaf shape is less important for associative learning.

Compound floral stimuli facilitate significantly stronger learning and memory for bees (Kunze & Gumbert, 2001; Leonard et al., 2011a; Leonard et al., 2011b; Mansur et al., 2018; Rusch et al., 2017; Stach et al., 2004). Our results extend prior research by demonstrating that bees can also be conditioned to a compound of flower and leaf cues. However, this compound stimulus was forgotten just 1 h later by bees in our difficult colour perceptual treatment. One possible explanation is that bees attempted to attend primarily to petal colour, even when the colour perceptual task was difficult. Consistent with this, bees in the difficult colour perceptual treatment did not remember the correct leaf shape, but still showed modest recall of petal colour. This bias could have occurred if the stimulus saliency of leaf shape was always significantly weaker than that of petal colour in our experiment, thus resulting in weaker recall of leaf shape (see Gil-Guevara et al., 2022). Indeed, even in the simpler colour perceptual learning treatment, bees learned petal colour independently of leaf shape, but did not learn leaf shape independently of petal colour. Altogether, our results seem to provide further evidence that differences in stimulus saliency affect learning processes and memory of compound stimuli (Katzenberger et al., 2013).

Our results also suggest that petal colour overshadows learning of leaf shape. If bees only learned compound stimuli, they should have remembered only the correct leaf shape and petal colour
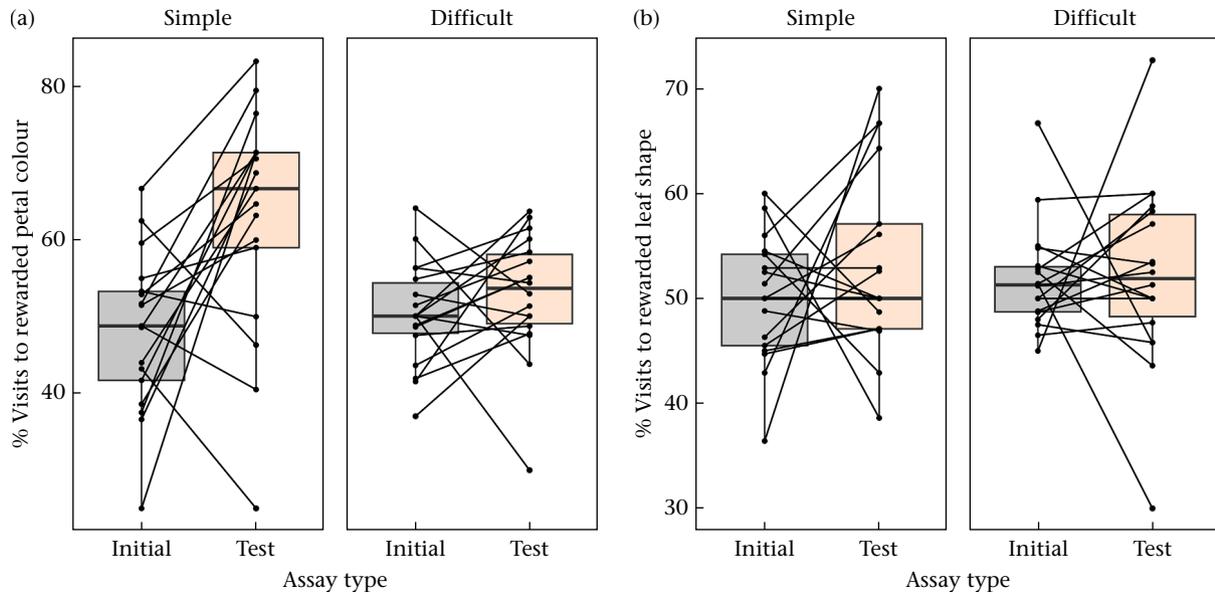
Figure 6. Initial and retention test preference for the trained flower type in the simple and difficult treatment (same raw data as in Fig. 5), pooled by (a) petal colour or (b) leaf shape. Plotted as box plots that show 25% and 75% quartiles (boxes), medians (lines in the boxes) and with raw data indicated via dots joined by lines showing how preference of individual bees changed with experience. $N = 17$ and 21 bees in the simple and difficult treatment, respectively.

combination and avoided all other combinations. Instead, bees remembered the correct petal colour and leaf shape combination, avoided flowers with the incorrect petal colour (regardless of leaf shape) and showed no change in preference when petal colour, but not leaf shape, matched the correct combination. This overshadowing could be a result of a bias in learning, in which bees always learn colour before shape, regardless of which stimulus is more salient (e.g. Lehrer & Campan, 2005; Rusch et al., 2017). Indeed, learning of flower shape is generally more difficult than learning of flower colour (Gould, 1993; Lehrer, 1990, 1993; Lehrer et al., 1985; Menzel, 1967), suggesting a bias in learning (Dexheimer & Dunlap, 2025). Given that depending on the bee's angle of approach to the flower, a shape cue changes substantially more than a noniridescent colour cue and thus may be a less reliable cue, a bias to learn colour before shape could be functional for the bee (Gould, 1993). Additionally, our experimental design potentially facilitated bees to attend to colour over shape. Scent can prepare pollinators to learn a flower colour cue (Leonard et al., 2011a; Leonard et al., 2011a; Leonard & Masek, 2014; Mansur et al., 2018). Both rewarding and unrewarding flowers in this study were pollen-scented, which may have prepared bees to learn petal colour first even when the shape learning task was potentially less perceptually difficult. Finally, perhaps flower cues generally overshadow leaf cues, given that, for instance, leaf cues will not always be reliably associated with the presence of flowers or their rewards. Future work will be required to tease apart the context and causes of overshadowing of shape cues.

How broadly representative are our results? In this study we standardized leaf surface area so that we could test whether bees specifically learned leaf shape of artificial targets. However, both leaf shape and surface area frequently differ between clades of plant species (Kidner & Umbreen, 2010), which could further facilitate associative learning. Yet learning of leaf shape may also be more difficult than our findings suggest. Leaves of closely related plant species are often similar in shape and there may even be variation in leaf shape within a species (Kidner & Umbreen, 2010; Richards et al., 2019), which could make learning this cue more difficult. Additionally, green leaves are often perceived by pollinators against a green background (e.g. the plant's own foliage

or the foliage of other plant species), and green achromatic contrast is especially important in associative learning by bees (Del Valle et al., 2024; Dyer & Spaethe, 2008). Nonetheless, given that bees can learn to discriminate very similar flower shapes (e.g. Symington & Glover, 2024) and that other insects can learn leaf shapes (e.g. Degen & Städler, 1996; Dell'Aglio et al., 2016; Wäckers & Lewis, 1999), learning relatively small differences in leaf shape in the context of floral foraging may also be possible.

In conclusion, given that multimodal floral cues are essential in enabling pollinators to discriminate flowers (Leonard et al., 2011a; Leonard et al., 2011a; Mansur et al., 2018; Rusch et al., 2017), the multimodal sensory billboard (Raguso, 2004) may also comprise leaf cues, including potentially leaf scent (see Caissard et al., 2024; Dufaÿ et al., 2003). Whether these cues are also learned in combination with flower cues will rely on future study. In addition, the capacity of a generalist pollinator to learn a leaf cue has significant implications for plant–pollinator interactions. Pollinator cognition is broadly recognized to drive the evolution of floral cues that are more easily learned and remembered, as such cues facilitate plant reproduction (Gervasi & Schiestl, 2017; Russell et al., 2016; Schiestl & Johnson, 2013). Our results provide rare evidence that pollinator-mediated selection may also directly drive the evolution of leaf traits (see also Caissard et al., 2024; Dufaÿ et al., 2003; Simon et al., 2011). In particular, we expect pollinator-mediated selection on leaf cues to be strongest when co-occurring floral cues are easily learned. However, assuming that learning of flower cues generally overshadows learning of leaf cues such as shape, we would expect reduced selection on leaf cues when flower types are relatively hard to discriminate. Such a pattern might explain why, in floral mimicry systems, leaf shape (and even petal shape) often differ enough between model and mimic to be discriminable (e.g. Fig. 1).

Author Contributions

Anthony Moth T. Castagna: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Jenny K. Burrow: Writing − review & editing, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Ciara G. Stewart:** Writing − review & editing, Validation, Methodology, Investigation, Conceptualization. **Avery L. Russell:** Writing − review & editing, Writing − original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Data Availability

The data sets supporting this article are available as Supplementary Material.

Declaration of Interest

None.

Acknowledgments

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2026.123509.

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