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RESEARCH ARTICLE

Flower patterns improve foraging efficiency in bumblebees by guiding approach flight and landing

Robin Richter | **Alexander Dietz** | **James Foster** | **Johannes Spaethe** | **Anna Stöckl**

Behavioral Physiology and Sociobiology (Zoology II), University of Würzburg, Würzburg, Germany

Correspondence
Anna Stöckl
Emil:
Email: anna.stoeckl@uni-konstanz.de

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Abstract

1. Colourful patterns on flowers are thought to benefit both pollinators and the plants they visit, by increasing the plants' pollination success via an increased foraging efficiency of the pollinators. This increased efficiency is assumed to result from a guidance effect of the flower patterns, correspondingly termed 'nectar guides', which indicate the position of the nectary to visiting pollinators, thus reducing their flower handling time.
2. Although it is well established that flower patterns play an important role in flower choice, the mechanisms by which they improve the foraging efficiency of flower-visiting insects remain poorly understood.
3. In this study, we quantified the contributions of patterns to all phases of flower interaction in the buff-tailed bumblebee *Bombus terrestris*. We analysed the bees' flight paths, as well as landing positions and walking tracks on artificial flowers with different pattern types.
4. We reveal that flower patterns reduced the overall flower handling time of the bees by up to 30%, by guiding their approach flight, landing positions and departure decisions. Surprisingly, we observed no improvement in nectary discovery time after the bees landed on the flower.
5. Since we tested experienced foragers, which represent the majority of insect pollinators active in nature, the newly described nectary-independent guidance effects of flower patterns are of high ecological relevance.

KEYWORDS
flower pattern, foraging, insect, nectar guide, pollination

1 | INTRODUCTION

The fascinating range of colourful patterns that flowers display has long been considered to be of great importance to animals that visit flowers for their daily food supply (Dafni & Giurfa, 1999; de Ibarra et al., 2015; van der Kooi et al., 2019). Already in the late 18th century, C.K. Sprengel proposed that these 'sap marks' (*Saftmale*) may guide pollinators to the nectary (Sprengel, 1793). The assumption that such *nectar guides* mutually benefit pollinators and the plants they visit is supported by the presence of these patterns within numerous plant families, which possess colour and contrast ranges that are readily detected by insects (Chittka et al., 1994; Dafni et al., 1997; Dafni & Kevan, 1996; De Ibarra & Vorobyev, 2009; Penny, 1983). On the other hand, pollinators of various insect groups show innate preferences for artificial patterns whose structure resembles that of natural flowers, in particular radial patterns and central elements (Dafni et al., 1997; Hansen et al., 2011; Heuschen et al., 2005; Johnson & Dafni, 1998; Kelber, 2002; Lawson et al., 2017; Lunau et al., 2009).

Pollinators are thought to benefit from flower patterns via two main mechanisms: flower patterns help them to memorise and select nectar-rich flowers, in addition to other visual and sensory cues (de Ibarra et al., 2015; Latty & Trueblood, 2020; Orbán & Plowright, 2014; Stöckl & Kelber, 2019), and they can improve the efficiency of flower visits, by reducing handling time. Distinctly shorter handling times with patterned artificial flowers, as compared to uniform ones, have been observed in hymenopteran, dipteran and lepidopteran pollinators (Dinkel & Lunau, 2001; Goodale et al., 2014; Goyret, 2010; Goyret & Kelber, 2012; Johnson & Dafni, 1998; Lawson et al., 2017; Leonard & Papaj, 2011; Waser & Price, 1985). For the plants, both an increased attractiveness and higher visitation rates (due to shorter handling times) result in an increased chance of pollen dispersal (Nepi et al., 2018; Valenta et al., 2016).

Although the role of patterns for both innate and acquired flower selection is well established (de Ibarra et al., 2015; Latty & Trueblood, 2020; Orbán & Plowright, 2014; Stöckl & Kelber, 2019), the mechanisms by which patterns increase foraging efficiency, measured as the ultimate reduction in time spent moving between flowers (Waser & Price, 1985) or on the flower preceding nectary discovery (Goyret, 2010; Goyret & Kelber, 2012; Lawson et al., 2017; Leonard & Papaj, 2011), still remain largely elusive. To understand these effects, it is important to subdivide the flower visit into its component stages: the approach flight, the choice of landing position and control of landing, the movement across the flower towards the nectary and the decision for take-off after nectar uptake (Figure 1a). Very little is known about the role of flower patterns in the stages before and during landing. Previous evidence suggests that honeybees and bumblebees only recognise patterns in the immediate vicinity of flowers (de Ibarra et al., 2002), and do not use them to control their approach flight over longer distances (Free, 1970; Manning, 1956). There are indications that bees land more centrally on a flower with a pattern in its centre (Free, 1970, Manning, 1956)—though this was tested with flowers distinctly larger than those frequently visited by bees in nature (Dafni et al., 1997; Dafni & Kevan, 1997). To reveal whether and how patterns guide the first two stages of flower interaction—approach and landing, quantitative observations with a variety of flower patterns on flowers in the natural size range are required.

In contrast to the approach and landing phase, there are clear indications that flower patterns guide the third stage of flower interaction: the pollinator's movement across the flower to the nectary. Bumblebees, which typically walk to the nectary after landing, require less time to find the nectary when patterns are present (Leonard & Papaj, 2011). Similarly, hovering hawkmoths require shorter exploration times to guide their proboscis to the nectary when radial patterns are present (Goyret, 2010; Goyret & Kelber, 2012). However, in bumblebees, this effect only occurred when the bees were trained on patterned flowers and then presented with uniform ones, not vice versa. Furthermore, the effect decreased over a limited number of consecutive flower visits (Leonard & Papaj, 2011), suggesting that flower patterns are particularly important for learning the position of the nectary in inexperienced foragers. Considering that honeybee and bumblebee foragers perform hundreds if not thousands of flower visits per day (Abrol, 2012; Pasquaretta et al., 2019), it remains an open question what, if any, advantage floral guides convey to experienced foragers, which perform the majority of flower visits. Interestingly, flower patterns also appear to play a role in the last stage of flower interaction, after nectar collection, in reducing the time bumblebee foragers spent exploring artificial flowers before take-off (Leonard & Papaj, 2011). Given that considerable time can pass from nectar uptake to take-off, how patterns affect the take-off decision of flower pollinators could have a distinct impact on the overall handling time of flowers with and without patterns.

To reveal the mechanisms by which flower patterns impact the efficiency of flower handling in insect pollinators, we characterised all stages of flower interaction in a model pollinator, the buffed-tailed bumblebee, *Bombus terrestris*. To represent the natural situation of foragers that are experienced with the general flower configuration, we tested flower-experienced but pattern-naïve bumblebees. Using high-speed videography, we analysed their body orientation and flight speed during approach, their touchdown position, as well as their walking paths before and after nectar uptake on natural-sized artificial flower models with different pattern types. Our results highlight key mechanisms by which patterns influence flower handling in experienced foragers: first, artificial patterns guided bumblebees to their landing positions, thereby reducing the approach time they required before landing. Second, flower patterns did not reduce the walking time to the nectary, except in a visual conflict configuration. Third, they shaped the inspection paths on the flower after nectar uptake. Together, these effects resulted in a 30% overall reduction of handling time in experienced bumblebee foragers for flowers with radial patterns.

Significance Statement

Colourful flower patterns—often referred to as 'nectar guides'—are thought to lead insect pollinators to a plant's nectary, thereby improving the pollinator's foraging efficiency and the plant's pollen dispersal. Although most insect pollinators are innately attracted to flower patterns, the mechanisms by which they improve flower handling efficiency remain poorly understood. Our comprehensive analysis of bumblebee—flower interactions revealed that flower patterns reduced the flower handling time by up to 30% without a reduction in nectar discovery time. Instead, the patterns were involved in guiding approach flight, landing and departure decisions. We revealed these effects on flower-experienced foragers. Since these represent the majority of active pollinators, the nectary-independent impact of flower patterns must be considered fundamental to plant–pollinator interactions under natural conditions.

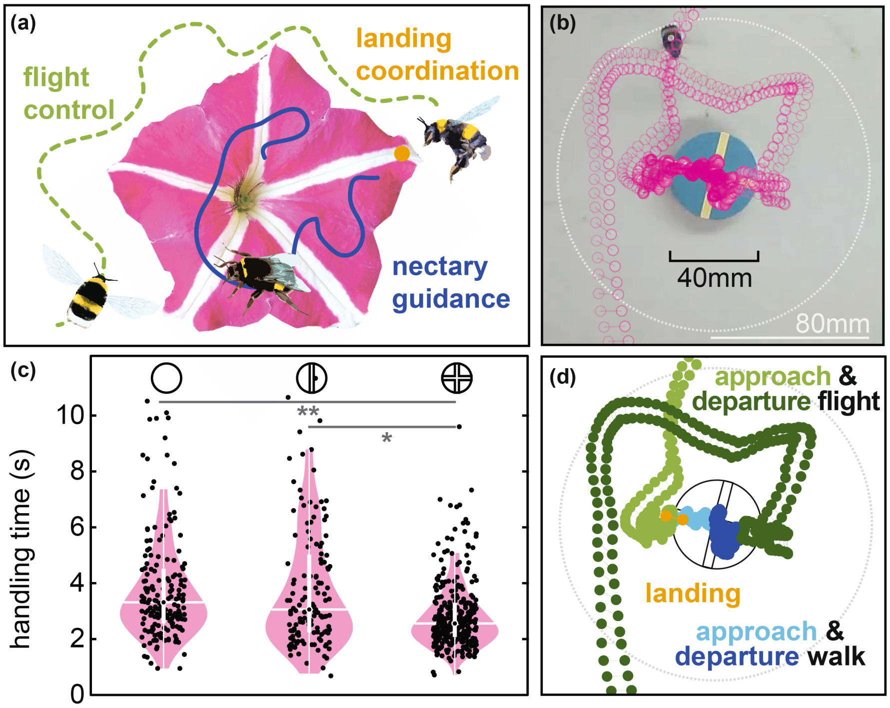

FIGURE 1 The functional significance of flower patterns for bumblebee foragers. (a) Flower patterns provide important visual cues for several stages of flower interaction: for orientation and flight control during the approach flight, for landing control, and as a visual guide to the nectary. (b) We investigated the functional role of flower patterns in these different stages by filming the entire interaction of bumblebee foragers with artificial flowers, which were mounted horizontally 10 mm off the ground, and presented flower patterns of different shapes and colours (see Figure S1). The head and thorax position of each individual bumblebee were tracked at 60 fps. (c) Total flower handling time of bumblebee foragers (from approaching the flower at a perimeter of 80 mm, shown in (b), to take-off, excluding time during nectar uptake) with three different flower patterns: *no*, *line* and *cross* pattern. Dots show data from individual flight paths (number of individuals n: 21, 16, 31; number of trials N: 178,140,305). The asterisks depict the statistical results of a generalised linear mixed-effects model (GLMM, see Section 2, Table S1). Only significant results of the pairwise comparisons of the *pattern-type* and *foraging-time* factors are shown. (d) To investigate which stages of flower interaction contributed to pattern dependence of flower handling time, and what their underlying mechanisms were, we analysed different stages of flower interaction: the approach (and departure) flight, the landing position and orientation, and the walking paths before and after nectar uptake.

2 | MATERIALS AND METHODS

2.1 | Animals

Colonies of *Bombus terrestris* were obtained from commercial breeders (Koppert, Berkel en Rodenrijs, Netherlands and Biobest, Westerlo, Belgium). The experiments did not require ethical approval. The colonies were housed in a two-chamber wooden nesting box (28 cm × 16 cm × 11 cm), which provided one chamber for nest-building and one for feeding. Before experiments, the bees were fed ad libitum with Apiinvert (Südzucker, Germany), a 70% sucrose solution, and with pollen (Bio-Blütenpollen, Naturwaren-Niederrhein, Germany).

2.2 | Setup and experimental procedure

For free flight experiments, the nesting boxes were connected to a flight arena (120 cm × 100 cm × 35 cm) via an acrylic tube. The arena was constructed from plywood, with a UV-transparent acrylic lid. It was illuminated from directly above by two fluorescent tubes (Osram, Biolux, L58W/965) connected to an electric ballast, as well as indirect light through the room's windows, resulting in a light intensity of 510 lx at the bottom of the arena pointing upwards, with the spectrum shown in Figure S1. The floor of the arena was covered by grey cardboard (Mi-Taintes #122, Canson SAS, Annonay Cedex, France), and the same cardboard was used for the training feeders (see below). Bumblebees visiting the flowers were recorded using an ELP USB camera (2.0 Megapixel [1080p], Ailipu Technology), operated at 60 fps with 1280 × 720 pixel using the software ContaCam 7.9.0 beta7 (Contaware) in motion detection mode for automatic video acquisition. The camera was directly attached to the acrylic lid to minimise reflections from the overhead lighting, and positioned above the respective stimuli that were imaged.

2.3 | Stimuli

All artificial flowers were constructed from round paper or cardboard cut-outs of 40 mm diameter, mounted on 10 mm high dark grey platforms of 40 mm diameter. The grey training stimuli were constructed from the same cardboard used for the floor of the arena, and the coloured test stimuli were printed on un-bleached paper ('Classic White', Steinbeis, Glückstadt, Germany) using a laser colour printer (C3325i, Canon, Germany). All stimuli were subsequently laminated with a matt foil (S-PP525-22 matt, Peach, PRT GmbH, Tannheim, Germany). The yellow colours were printed as C = 0%, M = 0%, Y = 100%, K = 0%, and the blue as C = 70%, M = 15%, Y = 0%, K = 0%. The relative reflectance spectra of the resulting colours are shown in Figure S1. We used three different main categories of stimuli: blue and yellow artificial flowers without patterns (*no* pattern), and artificial flowers with a *line*, and a *cross* pattern, which were either presented in yellow on blue background or vice versa. The arms of all lines or crosses were 4 mm wide, and the central point of the cross positioned at the flowers' centre. These patterns are highly abstract versions of two major spatial arrangements of flower patterns found in nature: radially and bilaterally symmetric patterns (Dafni & Kevan, 1996).

In this study, we performed two experiments, in which different pattern types were shown to separate groups of bumblebees. In the first experiment, six stimuli in total were presented: yellow and blue artificial flowers without a pattern (*no* pattern), a *line* and a *cross* that extended to the rim of the flower. The second experiment consisted only of cross-type stimuli: the same *cross* as in the first experiment, an *inner cross* with arms of 20 mm length from the centre of the flower, and an *outer cross*, which consisted only of 20 mm-long arms extending from the rim of the flower to the centre, but lacking the central part of the cross (Figure S1). In each experiment, we presented the two possible colour combinations of each of the three stimuli to each bumblebee, resulting in six different pattern conditions per individual.

2.4 | Experimental procedure

Bombus terrestris foragers were selected for experiments by tracking their foraging activity in the flight arena on grey training flowers covered generously with 30% sugar solution. They were marked on the thorax with individual number tags. In each experimental session, before being presented with the test stimuli, five grey training flowers were positioned in the arena in a random arrangement, with one placed directly under the central camera. They were prepared with 10 μl of 50% sugar solution in the centre of the flower. At the start of each experiment, a single marked forager was selected and allowed to forage for three foraging bouts on the grey flowers. Foraging bouts were separated by the forager's return to the colony and comprised between 10 and 20 flower visits each. Each flower was refilled immediately after the bumblebee departed and shuffled to different positions after each visit. Feeders were cleaned between foraging bouts. After the three initial foraging bouts on grey flowers, the first test stimuli were presented. Five flowers of the same type were randomly arranged in the arena with the same system of sugar reward. The central one was placed under the camera as for the grey stimuli. Five visits to the central flower of each bumblebee, representing five trials, were recorded, which were contained within a maximum of three foraging bouts. After that, one foraging bout on grey flowers was conducted, followed by the next pattern type, until all three pattern types in both colour combinations were tested. Pattern types and colour combinations were presented in a randomised order. Typically, all data from one forager were collected within a single day. In cases where the forager aborted their foraging activity before all six stimuli could be tested, missing data were collected on the following day. We only analysed data of bees for which a complete set of pattern types within one colour combination was obtained. In two instances of the *no* pattern condition, individual videos could not be analysed, even though the bees had performed the trial so that only four instead of five trials per individual and pattern type were included in the analysis. Eight individuals in the *no* pattern, four individuals in the *line* and one in the *cross* pattern condition performed only in one colour combination. The number of individual bees tested (*n*), as well as the number of trials obtained from the individual bees (*N*) for each experiment are provided in each figure depicting the datasets.

2.5 | Video tracking

We used DeepLabCut (Mathis et al., 2018) to automatically identify the bees' head and thorax position (Figure 1b; using 4100 frames, merged from five different recordings as a training dataset). All videos were manually curated afterwards using the DLTdv7 software (Hedrick, 2008) in Matlab 2017b (The Mathworks), to ensure a high precision of tracking throughout the entire video. The flower position (marked by four points on the flowers' circumference parallel to the cardinal axes) and pattern position (marked on all pattern edges) were indicated in each video using DLTdv as well. Furthermore, the landing position was marked manually, with landing defined as the touchdown of at least the two front legs with no immediate subsequent take-off. We did not observe any antennal probing of the flowers before touch-down, which conforms with previous observations of bumblebee and honeybee landing on horizontal platforms (Reber et al., 2016). We also marked the initiation and end of the drinking phase (indicated by the extension of the proboscis into the sugar solution, and its retraction, respectively), to separate flight and walking trajectories before and after nectar uptake (*approach* and *departure*, Figure 1c). Data were then further processed using custom-written Matlab scripts.

2.6 | Data analysis

From the bumblebees' approach flight trajectory, we calculated the time from entering an 80 mm perimeter around the flowers' centre to the bumblebees' landing (Figure 2a). We further analysed the approach and departure trajectories 500 ms before landing and after take-off, respectively, to calculate the average forward velocity as the mean projected ground speed between consecutive tracking points

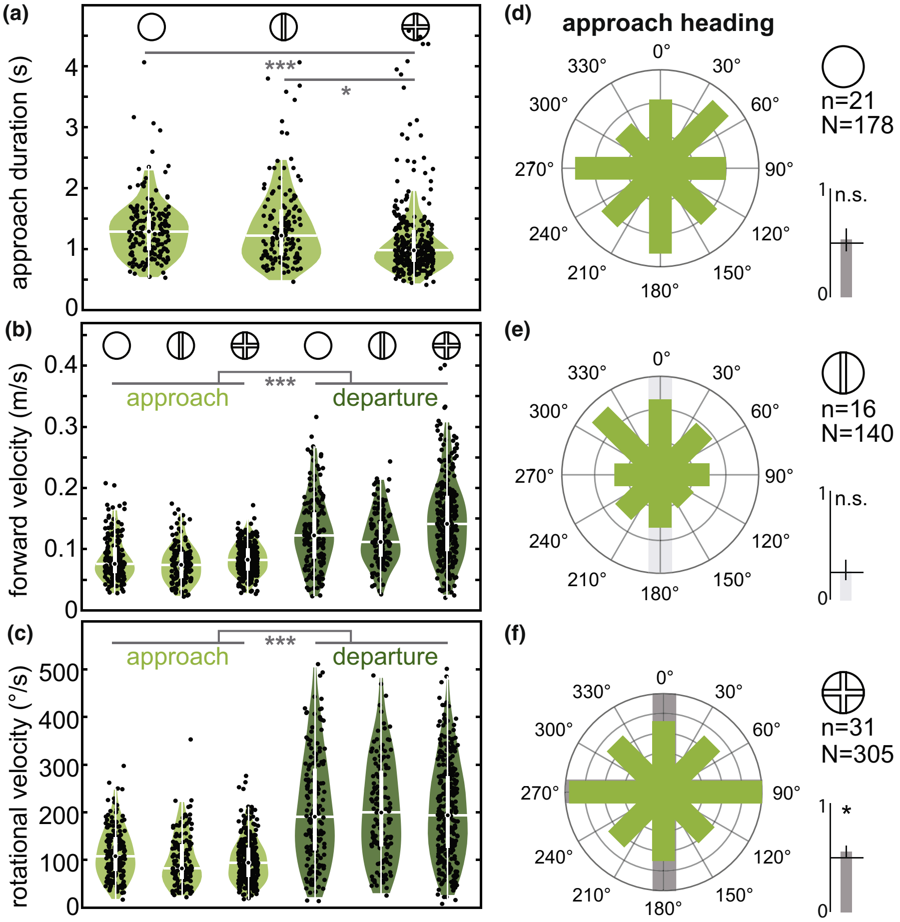

FIGURE 2 Approach and departure flight characteristics with different flower patterns. (a) shows the total approach duration, calculated as the time from entering a radius of 80 mm from the flower centre to landing, (b) depicts the average forward velocity and (c) the yaw rotation velocity of the *approach* and *departure* flight paths in a 500 ms window before landing and after take-off, respectively, for the three pattern types (*no* pattern, *line* pattern, *cross* pattern). Dots show data from individual flight paths including multiple trials (*N* as in d–f) of the individual bumblebees (*n* as in d–f). The asterisks depict the statistical results of a generalised linear mixed-effects model (GLMM, see Section 2, Tables S2–S4). Only significant results of the pairwise comparisons of the *pattern-type* and *foraging-time* factors are shown. (d–f) Show circular histograms of the average heading angle of each bumblebee's body axis (defined by the head and thorax position) in the 500 ms approach flights for the three pattern conditions. All data from conditions with patterns were re-orientated so that the patterns aligned with the cardinal axes (the *line* pattern always aligns with the *Y*-axis). The *no* pattern condition remained in the original configuration. Thus, in the *no* pattern condition the cardinal axes represent the axes of the video camera's field-of-view. The heading angles were binned into eight sectors, of which two contain the pattern directions for the *line* pattern (0 and 180°, e) and four contain the pattern directions for the *cross* pattern (0, 90, 180 and 270°, e), as indicated by the grey shades. The statistical results of a generalised linear mixed-effects model implementing a binomial comparison of heading angles (see Section 2, Table S10) that fall into pattern vs no-pattern sectors are shown as bar graphs next to each histogram. These graphs depict the mean and confidence intervals of heading angles that fell into pattern sectors, relative to the probability of landing in these sectors randomly.

(Figure 2b, Figure S2A,B), and the rotational velocity as the change in orientation angle of the longitudinal body axis (Figure 2c, Figure S2C,D). We determined the longitudinal body axis using the head and thorax tracking points. We furthermore used the 500 ms approach and departure trajectories to calculate the bees' mean heading direction as the circular mean of frame-by-frame body axis orientations (Figure 2d–f, Figure S2E–G). Where patterns were presented, the heading directions were calculated relative to the pattern axes (so that the patterns aligned with the cardinal axes, where the *line* pattern always aligned with the *Y*-axis, Figure 2e,f). In the *no* pattern condition, heading directions were analysed relative to the flower's absolute position in the arena so that the cardinal axes represent the axes of the video camera's field-of-view (Figure 2d). This condition thus provided a control for potential biases in the absolute approach directions.

We sorted the approach and departure headings into eight evenly spaced sectors (bin centres of 0°, ±45°, ±90°, ±135°, 180°), relative to the pattern's orientation (or camera axes for the *no* pattern condition): with the *line* pattern, two of the sectors contained the pattern directions (0 and 180°, Figure 2e, grey shade in histogram) and four with the *cross* pattern (0, 90, 180 and 270°, Figure 2e, grey shade in histogram). We used the same histogram bins for the landing positions (Figures 3d–f and 4d–f), as well as

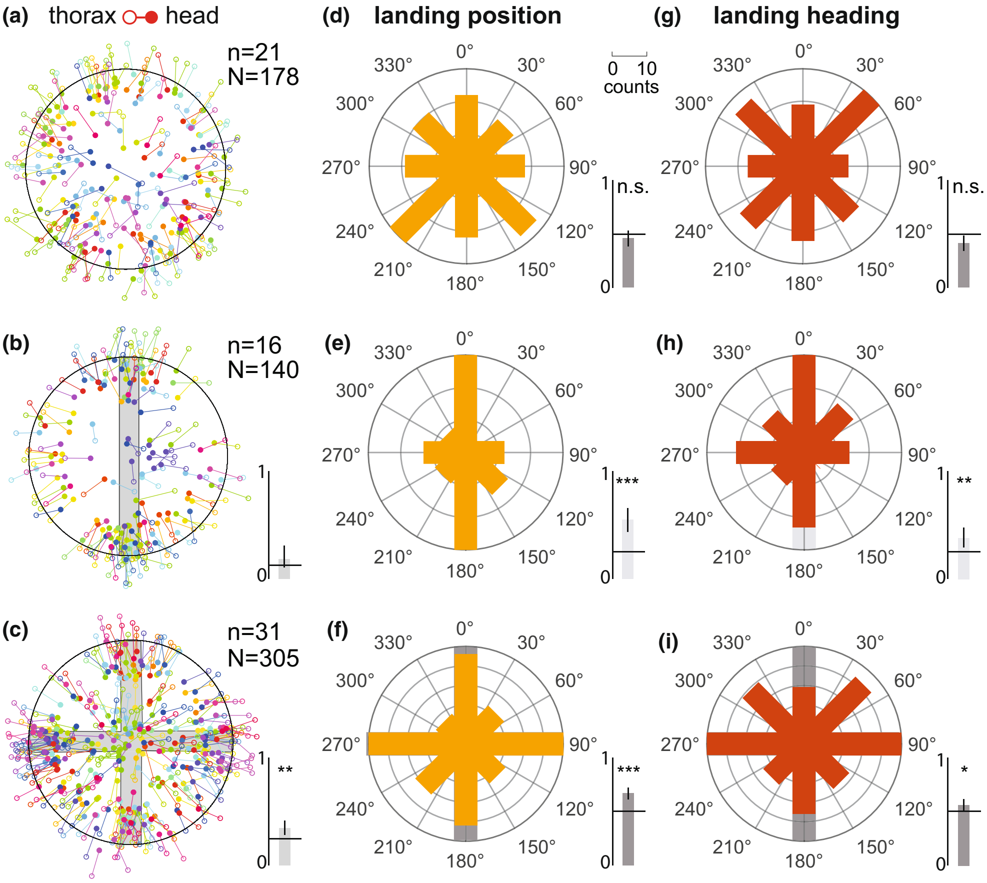

FIGURE 3 Landing headings and positions with different flower patterns. (a–c) The head (filled circle) and thorax (open circle) position of each bumblebee upon landing is shown for each pattern (indicated in grey). The colours mark individual bumblebees (*n*), which approached the flowers in multiple trials (*N*). The inset bar graphs in (b and c) depict the results of a statistical test (GLMM with binomial distribution, see Section 2, Tables S9 and S10) to assess whether the bumblebees' were more likely to land directly on the patterned area than on the background. Depicted are the mean and confidence interval of the probability of a pattern landing, as well as the prediction for random choices (line), which equals the proportion of the flower surface covered by the respective patterns. (d–f) Circular histograms of each bumblebee's angular landing position (orange) and the orientation of their body axis (defined by the head and thorax position) upon landing (g–i, red). The grey shades indicate the pattern sectors in the respective histograms. The inset bars graphs show the statistical results of two GLMMs (see Section 2, Tables S9 and S10) testing the frequency of landing positions and heading angles in the pattern sectors.

for the landing headings (the orientation of the body axis of the bumblebee upon touchdown, Figure 3g–i). We furthermore quantified the distance of the landing positions from the flowers' centre (Figure 4g, Figure S3A), and calculated the relative frequency of landings inside the perimeter of half the flowers' radius and outside of it (Figure 4h, Figure S3B).

Using the touchdown and take-off timestamps, as well as the timestamps of nectar retrieval on the flower, we separated the bumblebees' walking paths on the flower into approach and departure tracks (Figure 5a). We calculated the paths' total duration (Figure 5b) and the tortuosity (as the paths' length divided by the distance between its start and end point, Figure 5c). We furthermore calculated the relative frequency of occupation for each pixel position on the flower, based on the departure tracks of each bumblebee (Figure 5d). To compare the bees' occupation frequency at different distances from the flower centre, we calculated the relative frequency of occupation in four circular sectors spaced at 5 mm steps in distance from the flower centre for each bumblebee flower visit (Figure 5e).

For visual presentation, we pooled the data obtained from blue patterns on yellow background and yellow patterns on blue background, since the statistical analysis did not reveal any significant interaction of pattern colour with the analysed measures (see Section 2.7).

2.7 | Statistical analysis

To statistically analyse the effect of pattern type, pattern colour and individual identity on the flight, landing and walking parameters of the bumblebees, we used generalised linear mixed-effects models (GLMMs) with R v4.1.2 (R Foundation for Statistical Computing).

To analyse the heading, landing position and landing orientation data, we used GLMM with the formula

$$\text{sector choice} \sim \text{patternColour} + (1 + \text{patternColour} \mid \text{animalID}).$$

These estimated the fixed-effect of pattern colour on the relative probability of a landing in a pattern or non-pattern sector—scored for each individual flight as 0 or 1, accounting for individual biases and differences in response to pattern colour. For the *no* pattern condition, the sectors containing the cross pattern were identified as part of the target region, to test for any general preference for landings along the cardinal axes of the camera's field-of-view (and thus also of the flight cage). Thus, the random choice probability for the *no* and *cross* pattern condition was 0.5, and for the *line* condition it was 0.25 (see Table S10).

Since the *patternColour* factor did not significantly reduce model deviance with any of tested parameters (assessed by comparing the deviance of the full and reduced model below using a likelihood-ratio test, Table S9), we combined the data for all colour conditions, and fitted the following model, accounting only for individual biases, for all subsequent analyses:

$$\text{sector choice} \sim 1 + (1 \mid \text{animalID}).$$

The resulting model (mean and confidence intervals) is shown in each figure as an inset bar graph. The statistical results are summarised in Table S10.

To analyse the total duration of the approach flight, the forward and rotational velocity of the flight tracks, and the total duration of the walking paths and their tortuosity, we fitted a GLMM with the formula

$$\begin{aligned}&\text{track parameter} \sim \text{foragingPhase} \times \text{patternType} \times \text{patternColour}\\&+ (1 + \text{foragingPhase} \times \text{patternType} \times \text{patternColour} \mid \text{animalID})\end{aligned}$$

For the analysis of approach duration, the *foragingPhase* (approach, departure) factor was not included in the model, since this analysis was only conducted on the approach data. All data were log-transformed to ensure normality of the residuals.

Where the patternColour factor did not significantly reduce model deviance (see Tables S1–S8), we combined the data for all colour conditions for the subsequent analysis, and fitted the following model:

$$\begin{aligned}&\text{track parameter} \sim \text{foragingPhase} \times \text{patternType}\\&+ (1 + \text{foragingPhase} \times \text{patternType} \mid \text{animalID}).\end{aligned}$$

Where the *patternColour* factor significantly reduced model deviance, we always analysed the full model with the factor (including cases where the data were pooled across colour conditions in the figures for better visibility). The statistical results are summarised in Tables S1–S8.

3 | RESULTS

We quantified the role of flower patterns for different stages of flower interaction: approach flight, landing and floral exploration before and after nectar uptake in experienced *Bombus terrestris* foragers. Individual foragers were filmed when foraging from flower models of similar size to their grey training models, but with novel colour and pattern features (Figure 1a). Overall, bumblebees required shorter handling times (from entering an 80 mm radius around the flower to take-off after nectar uptake, excluding the time for nectar uptake) with *cross* patterned flower, compared to *no* pattern and to the *line* pattern (Figure 1c, GLMM: p(*no*–*line*) = 1.0, p(*no*–*cross*) = 0.004, p(*line*–*cross*) = 0.033, Table S1). We quantified their head and thorax positions throughout all stages of floral interaction (Figure 1b,d) upon multiple flower visits, to assess the mechanistic role of flower patterns for the different interaction stages.

3.1 | Radial patterns guide approach flight and reduce approach duration

When approaching the flower, the total approach duration (from entering an 80 mm radius around the flower to landing) was significantly shorter for flowers with the *cross* pattern than either the *line* or *no* pattern (Figure 2a, GLMM: p(*no*–*line*) = 0.98, p(*no*–*cross*) = 0.004, p(*line*–*cross*) = 0.037, Table S2). As the bumblebees came closer to landing, they reduced their forward velocity (Figure S2A). This resulted in a significantly lower forward velocity in the 500 ms before touchdown, compared to the 500 ms after take-off when the bees were departing the flower (Figure 2b, GLMM: p[*approach*–*departure*] < 0.001). There were no significant differences in approach velocity during the final 500 ms before touchdown for the different pattern types (Table S3). As for the forward velocity, the rotational velocity of the approaching bumblebees around their yaw axis differed significantly between the approach and departure flights (Figure 2c, GLMM: p[*approach*–*departure*] < 0.001, Table S4). Bumblebees kept a more stable body angle to the flower during approach, but rotated more freely around their yaw axis upon departure. There were no significant differences in either approach or departure rotational velocity for the different pattern types (Table S3).

We next assessed whether the rather stable heading angle of the bees during approach flight (Figure 2c) aligned with the flower patterns. We therefore calculated the circular mean of the heading angle over the final 500 ms of flower approach and analysed which of the flowers' 8 angular sectors it fell within, where 2 and 4 of the sectors included the pattern in the *line* and *cross* condition, respectively (Figure 2d–f). With the radial *cross* pattern, the approach heading angles were significantly more frequently in the pattern sectors (Figure 2f, dark grey shades) than in the background sectors (GLMM with binomial distribution: $p = 0.026$, Table S10). This suggests that the bees used the patterns to control the heading of their approach flight. This was not the case for the approach heading angles in the *no* (Figure 2d, $p = 0.277$) and *line* pattern conditions (Figure 2e, $p = 0.373$). Importantly, the approach heading angles in the *no* pattern condition did not reveal any clusters (Figure 2d), suggesting there were no preferred approach directions, as might have been caused by features of the foraging arena (such as the position of the room's window, or the entrance to the arena from the hive). Thus, compared to *no* pattern, the *cross* pattern duration of the approach flight was significantly reduced, combined with an alignment of the bumblebees' heading axis with the pattern axes during the approach.

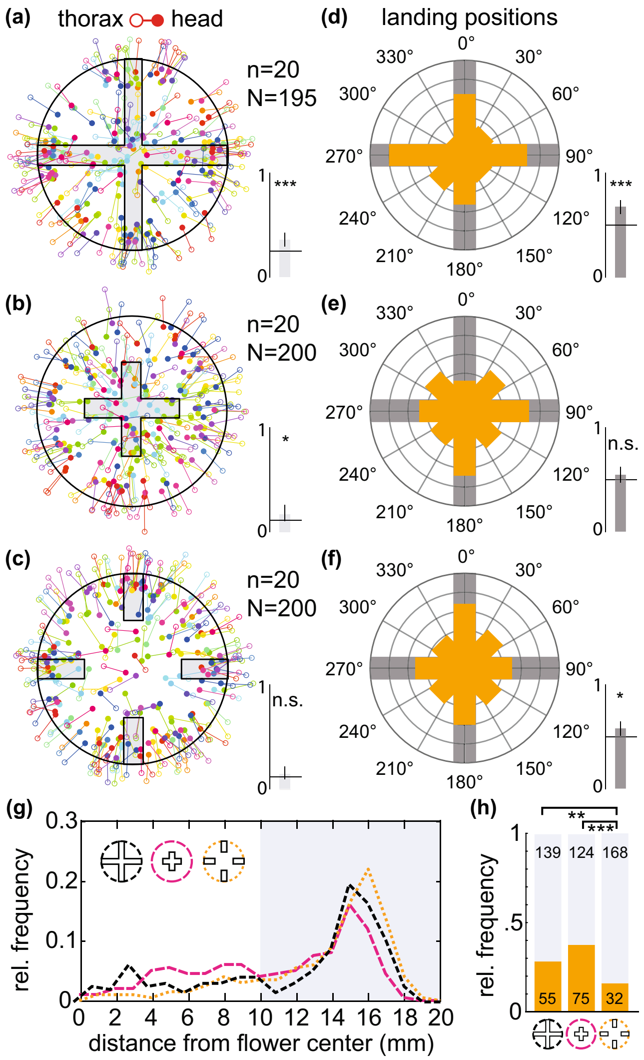

FIGURE 4 Landing positions with flower patterns of different eccentricity. (a–c) The head (filled circle) and thorax (open circle) position of each bumblebee upon landing is shown for each pattern (indicated in grey). The different colours indicate individual bumblebees (*n*), which approached the flowers in multiple trials (*N*). The inset bar graphs in (a–c) depict the results of a statistical test (GLMM with binomial distribution, see Section 2, Tables S9 and S10) to assess whether the bumblebees' landed directly on the pattern or on the background. Depicted are the mean and confidence interval of the probability of a pattern landing, as well as the prediction for random choices (line), which equals the proportion of the flower surface covered by the respective patterns. (d–f) Circular histograms of each bumblebee's angular landing position (orange). The grey shades indicate the pattern sectors in the respective histograms. The inset bars graphs show the statistical results of two GLMMs (see Section 2, Tables S9 and S10) testing the frequency of landing positions and heading angles in the pattern sectors. (g) The relative frequency of landings for the three pattern types with respect to the distance from the flower centre, binned at 1 mm intervals. The shaded background highlights two groups for further analysis in (h): landings closer than 10 mm to the centre and landings further than 10 mm. (h) The number of landings in the inner 10 mm (orange) and outer 10 mm (grey) of the flower was compared for all pattern types (Fisher's exact test, ● = 0.05, * < 0.05, ** < 0.01, *** < 0.001).

3.2 | Flower patterns guided the bumblebees' landing position

Without a pattern, the bumblebees' landing positions were spread over the entire angular range of the flower, and over the radial extent (Figure 3a), though with a higher frequency of landings at the edge than at the centre (Figure S2A). This general strategy to land at the edge of the flower was also visible in the *line* and *cross* conditions (Figure S2A). However, in the patterned conditions, there was also an increased proportion of landings close to or on the *line* and *cross* patterns (Figure 3b,c). We therefore analysed whether bumblebees landed more frequently directly on the patterned area than on the background. Indeed, a significantly higher proportion of bumblebees landed directly on the pattern area for the *cross* pattern (Figure 3c, GLMM with binomial distribution: $p_{cross} < 0.001$), and showed a non-significant trend for the *line* pattern ($p_{\mathrm{line}} = 0.096$, Table S10). Yet, many bumblebees did not land directly on the patterns, but very close to them. To quantify this effect, we analysed the frequency of landing in the pattern sectors of the flower. For the *line* and *cross* patterns, the landing positions fell significantly more frequent within the pattern sectors than non-pattern sectors (Figure 3e,f, $p_{\mathrm{line}} < 0.001$, $p_{\mathrm{cross}} < 0.001$, Table S10). Without a pattern, there were no clusters in their landing positions, and there was no increased frequency of landing points in the four cardinal pattern sectors ($p_{\mathrm{no}} = 0.884$). This strongly suggests that the bumblebees used the patterns as landing targets, in particular at the outer rim of the flowers.

We further checked whether the bees aligned their body axis with the pattern axis upon landing so that they landed on or close to the pattern while facing the centre of the flower. Alternatively, bees might have targeted the pattern for landing, but approached it from different angles not aligned with the pattern axes (keeping the pattern perpendicular upon approach, for example), particularly with the *line* pattern. Indeed, for the *line* and *cross* pattern, the frequency of body axis angles aligned with the pattern axes was significantly increased (Figure 3h,i, $p_{\mathrm{line}} = 0.001$, $p_{\mathrm{cross}} = 0.015$, Table S10). Although there were notable exceptions (see Figure 3b,c), there was a significant population strategy to land on or close to the patterns aligned with the pattern axes, predominately at the edge of the flower.

3.3 | The radial extent of flower patterns was crucial for landing guidance

Although the bumblebees clearly used the *line* and *cross* patterns to determine their angular landing position and body orientation on the flower, these experiments could not delineate how they chose the distance from the centre at which to land. Since both the *line* and *cross* pattern extended to the rim of the flowers, the bees might either have used the edges of the patterns at the rim as landing targets or only used their general orientation to align their body axis, choosing their subsequent landing eccentricity independent of the pattern, preferably at the flowers' edge. To

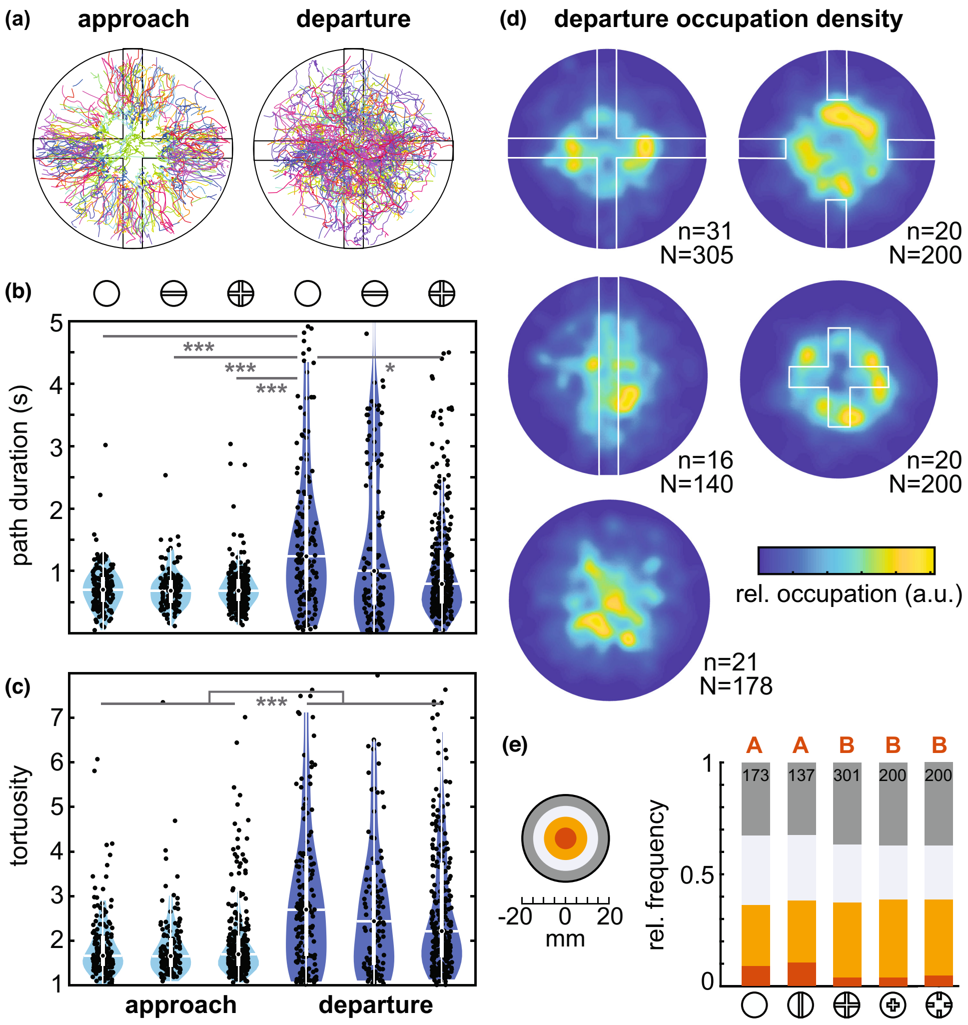

FIGURE 5 Walking paths before and after nectar uptake with different flower patterns. (a) The walking paths of individual bumblebees after landing until first proboscis contact with sucrose (*approach*) and after drinking until take-off (*departure*). The different colours indicate individual bumblebees (*n*) with multiple trials (*N*, as indicated in d). (b, c) Path duration (b), and tortuosity (c) of the *approach* and *departure* walks, respectively, in three pattern conditions. Dots show data from individual flight paths (*N*), including multiple trials for individual bumblebees (*n*, see d). The asterisks depict the statistical results of a generalised linear mixed-effects model (GLMM, see Section 2, Tabled S5 and S6). Only significant results of the pairwise comparisons of all conditions (pattern type, flight type) are shown. (d) Heat maps show the average relative occupation density of the bumblebees' departure walks on the different pattern types. These were generated from the normalised occupation density generated from each individual bumblebee, where each position per timeframe contributed one entry to the individual's occupational density, which was then averaged across all animals. (e) The relative frequency of occupation of departure walks in sectors of different radial distances from the flower centre. These frequencies were generated from individual occupational densities and subsequently averaged. The relative frequency of occupation in the centre sector (red) was compared with all pattern types (Wilcoxon rank sum test with Benjamini–Hochberg correction for multiple testing at alpha <0.05, Table S11).

disentangle these effects, we tested a new group of bumblebees with two variations of the *cross* pattern in addition to the original version (Figure 4a): a *central cross* pattern with 10 mm long arms that extended across only half the flowers' radius (Figure 4b), and an *outer cross* pattern (Figure 4c), that consisted of 10 mm long arms in a cross-orientation, starting at the flowers' edge, thus leaving the centre free.

With respect to the angular landing position, only the *cross* and *outer cross* pattern resulted in a significantly increased frequency of landings in pattern sectors (Figure 4d,f, $p_{\text{cross}} < 0.001$, $p_{\text{outer cross}} = 0.017$). The frequency of landing positions aligned to the inner cross pattern did not differ from chance (Figure 4e, $p_{\text{inner cross}} = 0.131$). The 4 mm wide arms of the inner cross pattern were still well within a bumblebee's threshold for spatial resolution: with a spatial resolution of 1° in their frontal visual field (Taylor et al., 2019), a bumblebee could resolve the pattern arm at a distance of 22.9 cm. Thus, we conclude that bumblebees only used patterns that extended to the edges of a flower to guide their angular landing position, but not patterns that were restricted to the flower's centre, despite their clearly visible directional components.

We next assessed how the position of the patterns' edges affected the bees' control of landing eccentricity—the distance from the flower centre. The majority of bumblebees landed at the flowers' edge (in the outer 10 mm) for all conditions (Figure 4g). Nevertheless, there was a clear effect of flower pattern on landing eccentricity: the proportion of bees that landed in the centre was significantly higher for the *inner cross* pattern than the *outer cross* (Fisher's exact test, $p < 0.001$), and showed a trend to be higher than for the *cross* pattern ($p = 0.054$). Furthermore, the proportion of bees landing on the outer rim was also significantly higher for the *outer cross* pattern than the *cross* ($p = 0.003$). Thus, despite the prominent contrast of the flower's edge to the background serving as a strong visual cue for landing control, patterns on the flower did play a role in determining the eccentricity of landing positions.

3.4 | Patterns guided movements on the flower after nectar uptake

We next investigated whether the flower patterns we presented guided the bumblebees' approaching walks to the nectary after landing. After landing, the overwhelming majority of individuals walked straight to the presented food reward in the centre of the flower (Figure 5a). This was visible in short straight approach walking tracks from the landing position to the flower centre (Figure 5b,c). The duration and tortuosity of the tracks did not differ between the *no*, *line* and *cross* pattern conditions (duration: Figure 5b, GLMM: $p_{\text{no-}line} = 0.719$, $p_{\text{no-}cross} = 0.542$, $p_{line\text{-}cross} = 0.983$, Table S6, tortuosity: Figure 5c, $p_{\text{no-}line} = 0.986$, $p_{\text{no-}cross} = 0.854$, $p_{line\text{-}cross} = 0.776$, Table S5). There was also no significant difference in approach duration between the *cross* and *inner cross* patterns (Figure S4A, Table S7). Thus, the bumblebees made their way to the nectar reward on the straightest path possible, irrespective the presence or type of the flower patterns. The walking paths of bumblebees with the *outer cross* pattern were the only exception to this trend, requiring significantly longer to reach the nectary than for all other cross patterns (Figure S4A, $p_{cross\text{-}ocross} = 0.036$, $p_{icross\text{-}ocross} = 0.031$, Table S7). This indicates that the bees did indeed perceive the patterns after landing on the flower and approaching the nectary, and moreover, that visual patterns can interfere with the bees' approach to the nectary.

The movement tracks of the animals after nectar uptake were much more variable than during approach, ranging from a few steps before take-off to long explorative paths on the flower (Figure 5a). This resulted in a broader range in duration and tortuosity of the departure walks than approach walks (Figure 5b,c). Indeed, approach and departure were a significant factor in walk tortuosity (GLMM: $p_{\text{approach-departure}} < 0.001$, Table S5), and in walking path duration (GLMM: $p_{\text{approach-departure}} < 0.001$, Table S6). Although the tortuosity differed significantly between the approach and departure portions of all the paths in all pattern conditions (Table S5), this was only the case for some of the patterns, approach/departure and flower colour interactions, in particular those with *no* pattern (Table S5), where the departure walks of the *no* pattern were significantly longer.

Given that flower patterns influenced not just the duration, but also the straightness of the departure walks, we next investigated whether the patterns also influenced where the bees walked on the flower. Indeed, the areas the bumblebees frequented most during their departure walks differed across pattern types (Figure 5d): with *no* pattern present, the frequency of occupation was significantly higher in the centre of the flower than for the *cross* pattern types (Figure 5e, Table S11). With the *line* pattern, the bees occupied a more elongated area along the pattern and also had a significantly higher occupation frequency in the centre of the flower (Figure 5e, Table S11). With all three *cross* pattern types, the occupied area formed a ring shape around the centre (Figure 5d), leading to significantly lower occupation densities in the centre (Figure 5e). Taken together, the analysis reveals that unlike for approach walks, which were directed straight to the centre of the flower, the patterns played a distinct role in shaping the duration and spatial structure of departure walks.

4 | DISCUSSION

Flower patterns are thought to have evolved to improve foraging efficiency by reducing handling times of the pollinator during a flower visit (Dinkel & Lunau, 2001; Goodale et al., 2014; Goyret, 2010; Goyret & Kelber, 2012; Johnson & Dafni, 1998; Lawson et al., 2017; Leonard & Papaj, 2011; Waser & Price, 1985). In this study, we demonstrated how flower patterns reduce the flower handling of experienced bumblebee foragers at several stages of their flower visit, by analysing their flight and walking behaviour for the entire flower interaction. Unlike previous results from naïve foragers, we found no significant reduction in the nectary discovery time after landing associated with flower patterns. The strong reduction in overall handling time resulted from the patterns' role in guiding the bumblebees' approach flight and landing, as well as their walking paths on the flower before departure.

4.1 | The role of patterns for approach and landing guidance

While the identification and approach of the nectary is an important aspect of flower foraging, it first requires a safe approach to and landing on the flower for the majority of insect pollinators. Our results highlight the role of flower patterns in this stage of foraging. The 31% reduction in approach duration facilitated by radial patterns (Figure 2a) shows that even though the bees' nectary discovery time once landed on the flower was not reduced by the patterns, the flight guidance effect provided a substantial improvement in the overall foraging efficiency. We could pinpoint how the patterns contributed to a reduction in approach flight duration: they served as guides for both the angular bearing (Figure 3) and the eccentricity of the landing position (Figure 4, Figure S3). Thus, by providing clearly visible landing guides, flower patterns may reduce the inspection time approaching bumblebees require to initiate landing, consequently reducing their overall approach flight time. The observed pattern-based control of eccentricity occurred despite a strong preference of the bees to land at the edge of the flowers in all pattern conditions, likely aided by the strong visual contrast between the flower and the grey background. This confirms previous observations on much larger artificial flowers (Free, 1970; Manning, 1956), and provides strong evidence that these guidance effects also occur on biologically relevant flower sizes.

The effects of patterns on angular landing positions have not been observed previously. They were closely related to the alignment of the bees' body axis to the flower patterns during approach flight (Figure 2c–e) and landing (Figure 3g–i). This suggests that the bumblebees used the pattern arms as cues to stabilise their approach flight before touchdown. As has been shown in honeybees (Rusch et al., 2021) and flies (Maimon et al., 2008), many insects fixate elongated targets, for example stripes, in their central visual field when they move. The arms of the flower patterns we presented could have served as such fixation targets.

However, we observed distinct differences in the bumblebees' responses to the different pattern types: although the *line* pattern resulted in pattern-related angular landing positions (Figure 3e) and body orientations during landing (Figure 3f), it did not induce an alignment of the body orientation with the pattern, or a significant reduction in the approach duration compared with the *cross* pattern (Figure 2a). One major difference between the *line* and *cross* pattern is that the *cross* pattern provides translational optic flow and alignment cues at the same time: if an approaching bumblebee aligned their body axis with one arm of the *cross* pattern, the respective cross-bar of the pattern generated translational optic flow. The *line* pattern, on the other hand, either provided translational optic flow cues (if bees approached the pattern perpendicularly) or alignment cues (if they approached in parallel). Previous studies on honeybees demonstrated the importance of translational optic flow cues to control the flight speed upon landings on horizontal surfaces (Srinivasan et al., 2000) and of motion cues to identify edges suitable for landing on horizontal targets (Lehrer & Srinivasan, 1993). Thus, the bees benefitted from aligning with the arms of the *cross* pattern and landing at their contact with the flowers' edge in all aspects of their approach flight and landing. In contrast, an alignment with the *line* pattern would have only been partly beneficial, as optic flow cues for flight control would have been generated most strongly by a perpendicular approach. In addition, the radial pattern generated stronger expansion cues upon approach than the line pattern—which are important for landing control in bees (Baird et al., 2013). These differences in approach and landing guidance between pattern types strongly suggest that the bumblebees used patterns both for flight stabilisation, in addition to selecting a unique landing position.

4.2 | The role of flower patterns as guides to the nectary—Landing position

One straightforward way by which flower patterns could reduce the overall foraging time of pollinators is that they indicate the position of the nectary, allowing the insects to land as close as possible to the nectary, and thus reducing the walking time. Our results do not provide clear evidence that bumblebee foragers used the patterns, particularly the cross patterns, which provided radial guides to the nectary in the centre of the pattern, as landing indicators for the nectary position. The majority of bees landed at the edge of the flower (Figures 3 and 4 and Figure S3) rather than in the centre close to the nectary with either type of pattern (Figure 4g and Figure S3A), even though all foragers had experienced the nectary position in the centre of the flower at least 30 times on the grey pattern-less training flowers during pre-training. They could also see the sugar reward placed openly as a small drop on the flower surface (see Section 2).

It is important to note that there was indeed a significant shift of landing positions from edge to central landings with the *cross* pattern, compared with *no* and *line* patterns, even though bees landed closer to the edge overall (Figure S3). This suggests that at least some bees used the radial information in the cross pattern as an indicator for the location of the nectary and landed closer to it. However, combined with the fact that the landing positions shifted further to the flowers' edge with the *outer cross* pattern (Figure 4), which also presents radial guides towards the centre, this suggests that bumblebees did not interpret the spatial layout as nectar guides, but were most likely attracted by their colour or achromatic contrast of the pattern in general. This is in line with previous observations, which showed that honeybees and bumblebees did not land on the convergence point of pattern lines presented on artificial flowers. Instead, they landed all along the lines in irregular orientations (Free, 1970, Manning, 1956). Thus, while guiding the foragers' approach flights and landing on the flower, bumblebees did not use radial patterns to extrapolate the position of the nectary and to land there directly. This also suggests that a controlled and safe landing might be of higher importance in the bees' foraging strategy than a closer landing to the nectary. It would be very informative to test this hypothesis in future experiments by setting visual cues that indicate the nectary and visual landing guides into conflict.

4.3 | The role of flower patterns as guides to the nectary—Walking approach

Our results did not provide evidence that flower patterns improved the efficiency of nectary discovery once the bumblebees landed, as there was no difference in walking time across the *no*, *line* and *cross* pattern conditions (Figure 4b). Instead, for all conditions except the *outer cross*, the bumblebees walked in rather straight paths from their landing position to the food reward in the centre of the flower (Figure 4a). At first sight, this contradicts a previous study with comparably sized and patterned artificial flowers, which described a significantly reduced time until the discovery of the nectary after landing when patterns were present, suggesting a guidance function of the patterns (Leonard & Papaj, 2011). However, this discrepancy might be due to a different role of the flower patterns in the respective foraging setting: Leonard and Papaj (2011) presented the patterns in the context of a learning task, where only a subset of flowers with patterns, or respectively without, was rewarded. Thus, differences in search times might be due to the time required for flower identification and discrimination, rather than nectary location—a well-demonstrated function of flower patterns during search behaviour by flower visitors (Dafni et al., 1997; Hansen et al., 2011; Heuschen et al., 2005; Johnson & Dafni, 1998; Kelber, 2002; Lunau et al., 2009). In our task, all flowers were rewarded so that the flower patterns did not indicate a reward, but might act as potential landing and nectar guides.

Moreover, our experiments also differed from those of Leonard and Papaj (2011) in the bumblebees' experience of the flower's configuration, and how they learned to locate the nectary. They showed that foraging experience drastically reduced walking time to the nectary in both flower types, with and without patterns. They furthermore showed that the influence of patterns on the approach time depended on which patterns had been rewarded during training. Bees that were initially rewarded on un-patterned flowers did not decrease their approach time with patterned flowers. The opposite was the case for the reversed order of presentation. Without patterns during learning, bees might thus learn the nectary configuration relative to the flowers' shape, but if patterns are present, bees might learn the nectary position relative to the patterns, and thus require longer to locate the nectary without them. In our study, the foragers were extensively trained to pattern-less grey flowers, and likely learnt the nectary configuration. This would explain why the approach walking times did not differ between the patterned and un-patterned flowers (Figure 4), as the bees might have mainly relied on their experience of the flower configuration. However, the bumblebees in our experiments did not entirely ignore the patterns: for the *outer cross* pattern, which created high-contrast visual cues separate from the nectary position, approach walking times were significantly longer than for all other patterns (Figure S4). This suggests that the bees relied on their experience of the pattern configuration even when flower patterns were present, but when patterns provided conflicting cues about the position of the nectary, bees were distracted during their nectary approach.

Thus, we conclude that the role of flower patterns as walking guides to the nectary strongly depends on the previous foraging experience of bumblebees, and on how the pattern cues combine guidance information with the learned flower and nectary configuration.

4.4 | Flower patterns influence departure decisions

Although bumblebees did not reach the nectary faster after landing on flowers with or without patterns, we found that patterns significantly influenced departure decisions: radial patterns reduced the bumblebees' exploration time on the flower after emptying the sugar reward (Figure 5a, Figure S4A). These observations are supported by a previous study (Leonard & Papaj, 2011). Our analysis of the bees' exploration tracks may explain this finding, since the bees' paths on the flowers were shaped by the different pattern types (Figure 5d). The relative time spend in the centre of the flower was significantly higher in the *no* pattern and *line* condition than for the *cross* pattern conditions, suggesting that the flower patterns guided the post-drinking exploration of foragers. A lack of patterns might suggest hidden nectaries or pollen, and thus might encourage an extended search.

Our findings suggests that in future studies, more emphasis should be placed on the post-nectary exploration to better understand the role of flower patterns for foraging efficiency, as it took a considerably larger share of the foragers' time on the flower than the nectary approach (Figure 5b, also in Leonard and Papaj (2011)). Longer exploration times increase the risk of exposure to predators on the flower and reduce the time available to exploit other food sources. Future work may focus on identifying the observed post-drinking exploration patterns in real flowers, which would provide a better understanding of the diverse functions of floral patterns in plant–pollinator interactions.

4.5 | What do these experiments suggest about foraging in the natural world?

Based on our laboratory experiments, a number of key predictions can be made about the relevance of flower patterns for insect pollinators at flowers under natural conditions. Together with insights from comparable studies (Free, 1970; Leonard & Papaj, 2011; Manning, 1956), our results suggest that the role of floral markings for guiding a flower visitor to the nectary after landing strongly depends on its foraging experience. The impact of floral markings drastically decreases with experience, to the point where approach times to the nectary with and without patterns may not differ. Honeybee and bumblebee foragers perform several hundreds to a thousand flower visits during a day (Abrol, 2012; Pasquaretta et al., 2019)—compared with the dozens of visits on which most laboratory observations are based—and are known to improve their natural flower handling with experience (Laverty, 1980). We thus expect that flower patterns play only a minor role for nectary discovery while walking on the flower for the majority of their foraging life. Moreover, on a natural flower, sensory cues beyond visual ones may guide the bee to the nectary after landing: the shape of the flower, as well as mechanosensory, olfactory and humidity cues, thus further diminish the potential importance of flower patterns for nectary guidance after landing. Interestingly though, when flower patterns provided conflicting information about nectary location with regard to the learned configuration, they resulted in increased exploration times even in experienced foragers (Figure S4A). Such scenarios might be employed by some flowers to trick insects into suitable positions for pollination (Dafni, 1984), or deceit pollinators about the availability of nectar (Thakar et al., 2003). Mismatched visual cues and nectary location may also occur in ornamental flowers, where the floral markings have been altered from their natural configurations.

Importantly, our results demonstrate that even for experienced foragers who have learned the position of the nectary on the flower, flower patterns are important to guide their approach flight and landing on the flower, thus significantly reducing handling time. Since approach guidance and landing control cannot be supported by other sensory modalities (except for mechanosensation in the legs and antennae upon contact with the flower, Reber et al., 2016), we expect this effect also to be effective in a natural setting. Indeed, we expect approach guidance and landing control to be of even higher importance than in the laboratory, as flowers in nature are encountered at different heights, tilt angles, and vary in size and shape (Dafni et al., 1997; Dafni & Kevan, 1997), making it harder to transfer learned approach-and-landing strategies between flowers, and therefore relying more on sensory inputs. Additional challenges during flower approach and landing are obstacles such as foliage in the potential approach paths, changing lighting conditions, as well movement of the pollinators and flowers induced by wind (Chang et al., 2016).

Although the exclusively horizontal presentation of our artificial flowers is not representative for all flower types visited by bumblebees, their size and general shape fell well within the natural range of flowers bumblebees typically forage from (Dafni et al., 1997, Dafni & Kevan, 1997). Moreover, choice experiments suggest that bumblebees prefer horizontally arranged flowers (Makino, 2008), from which they also learn cues more flexibly (Wolf et al., 2015) so that this type of flower is highly relevant for bumblebees. The colour contrast and spatial resolution of the patterns in our experiments were designed to ensure reliable detection by the bumblebees. It is currently unclear whether this is comparable to most natural flower patterns of bumblebee pollinated flowers, as unlike the spectral composition, the exact spatial arrangements of the patterns of most insect-pollinated flowers remain largely unquantified (Garcia & Dyer, 2021, but see De Ibarra & Vorobyev, 2009, Vorobyev et al., 1997). With the advent of new multispectral imaging techniques (Garcia et al., 2014; Lunau et al., 2021; Tedore & Nilsson, 2019), in the coming years a higher-throughput quantification of flower patterns will likely provide a better understanding for how natural flower patterns compare to the stimuli used for laboratory experiments, enabling more natural stimulus designs for presentation under controlled laboratory conditions.

5 | CONCLUSIONS

Our results reveal guidance functions of flower patterns that contribute significantly to foraging efficiency. We demonstrate how patterns guide the approach flight and landing control of bumblebees on flowers, and which pattern features play a role in this guidance. Moreover, we demonstrate the role of patterns in the decision to depart or to continue flower inspection after nectar uptake. These insights provide a novel focus for the study of flower–pollinator interactions in the laboratory and in their natural environment, and open up new questions on how deceptive patterns or altered displays on ornamental flowers impact foraging efficiency in insect pollinators.

AUTHOR CONTRIBUTIONS

Conceptualisation: Anna Stöckl and Johannes Spaethe; Methodology: Anna Stöckl and Johannes Spaethe; Validation: Robin Richter, Alexander Dietz, Anna Stöckl, Johannes Spaethe and James Foster; Formal analysis: Robin Richter, Alexander Dietz, James Foster and Anna Stöckl; Investigation: Robin Richter and Alexander Dietz; Resources: Anna Stöckl and Johannes Spaethe; Data curation: Anna Stöckl; Writing—original draft: Anna Stöckl; Writing—review & editing: Robin Richter, Alexander Dietz, James Foster, Johannes Spaethe and Anna Stöckl; Visualisation: Anna Stöckl and James Foster; Supervision: Johannes Spaethe and Anna Stöckl; Funding acquisition: Johannes Spaethe and Anna Stöckl

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The raw data (flight paths of all bumblebees and spectral measurements of the flower patterns) are available at the figshare digital repository: https://doi.org/10.6084/m9.figshare.20089409.v1 (Richter et al., 2022). Detailed results of all statistical tests are presented in supplementary tables.

ORCID

James Foster https://orcid.org/0000-0002-4444-2375
Johannes Spaethe https://orcid.org/0000-0002-0734-2869
Anna Stöckl https://orcid.org/0000-0002-0833-9995

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1.

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