RESEARCH ARTICLE

Bumblebees occupy: when foragers do and do not use the presence of others to first find food

C. M. S. Plowright · K. A. Ferguson · S. L. Jellen · V. Xu · E. W. Service · A. L. Dookie

Abstract The aim of this study was to determine whether an unlearned preference by bumblebees for flowers that are occupied by other bees is frequency dependent and whether it depends on the size of the flower. In three experiments, bees leaving their colony for the first time were given 20 unrewarded choices of occupied versus unoccupied floral patterns in a radial arm maze. In Experiment 1, the relative frequency of occupiers was manipulated. In Experiment 2, a variety of large ($\geq$6 cm diameter) artificial flowers was used. In Experiment 3, floral patterns were eliminated in an effort to reduce the similarity between "occupied" and "unoccupied". A significant unlearned preference was found only under the combination of conditions in which occupied flowers were comparatively rare and the occupier to flower size ratio was relatively high. Otherwise, the preferences were non-significant, though the stimuli were discriminable because control groups given prior discrimination training acquired a preference. Our results narrow down the conditions under which foragers respond to the presence of others when making their first floral choices.

Introduction

Social learning, i.e. learning from other individuals, has become a topical area of research in a variety of species

C. M. S. Plowright (✉) · K. A. Ferguson ·
S. L. Jellen · V. Xu · E. W. Service · A. L. Dookie
School of Psychology, University of Ottawa, Ottawa,
ON K1N 6N5, Canada
e-mail: cplowrit@uottawa.ca

(Shettleworth, 2010). It is thought to be important to animals for a variety of reasons. For instance, it can lead to faster individual learning compared to trial and error learning and it can reduce costly mistakes by inexperienced individuals (Dukas, 2008). Though bumblebees (*Bombus* spp.) are social creatures par excellence, only recently has the issue of social learning begun to be addressed in these species (Dukas, 2008). Recent evidence shows that bumblebees favour flower types on which other foragers have been observed (Worden and Papaj, 2005). They are attracted to patches of flowers that include other bees (Baude et al., 2008). Moreover, bumblebees can learn to discriminate between rewarding and unrewarding flowers based on the presence or absence of another individual on the flowers (Leadbeater and Chittka, 2007, 2009; Dawson and Chittka, 2012). The other individual need not be a conspecific, since bumblebees learn from the presence of honeybees as well (Dawson and Chittka, 2012). The cognition underlying these social effects has begun to be investigated. The question of how other individuals are perceived has been raised. Perhaps the occupier is perceived as a part of the flower such as a floral nectar guide (Baude et al., 2008). Perhaps the occupier is perceived much as an inanimate object such as a coin or a plastic disk (Dawson and Chittka, 2012). The mechanisms underlying social effects on behaviour have also begun to be delineated. Pavlovian associations (Dawson et al., 2013) have been documented. Stimulus enhancement or local enhancement (Worden and Papaj, 2005; Kawaguchi et al., 2006; Leadbeater and Chittka, 2007), whereby one individual attracts another to a particular stimulus or particular location, has also been implicated.

We approach the question of the use of social cues from the perspective of what helps bees to discover sources of food before they have ever been rewarded on a flower (Simonds and Plowright, 2004; Plowright et al., 2006; Séguin

and Plowright, 2008; Orbán and Plowright, 2013). In other words, when bees first leave their colony, what cues might lead them to potential flowers as opposed to non-rewarding objects? A priori, it is not self-evident that there should be a preference for objects occupied by other bees, whether conspecific or not. The presence of another forager may possibly be irrelevant: in nature floral cues can be effective in attracting bees on their own and the presence of additional aids may be superfluous. Alternatively, the presence of another forager on an object may well signal that the object is a flower, and so choosing occupied objects may well be a "best bet" for first time foragers. The presence of another forager, however, may just as well signal that though the object is indeed a flower, it is likely to be empty or on its way to being emptied, having just been partially or completely depleted by the occupier. If so, a preference for occupied objects would exact foraging costs from inexperienced bees, while avoidance would confer advantages. A similar argument has been made by Baude et al. (2011): conspecifics can act as informers as to resource quality or as competitors for those resources. Perhaps the informational value of conspecifics is context dependent, in which case a preference or avoidance of occupied flowers should be learned from experience in local environments, but would not be expected of inexperienced foragers.

In view of the considerations above, we seek to evaluate the generality of recent reports that there is a preference for occupied flowers by bumblebees making choices on their first foraging trip in a laboratory setting. Workers with no previous experience on flowers land preferentially on occupied rather than unoccupied artificial flowers, whether they be rewarding (Kawaguchi et al., 2006) or unrewarding (Leadbeater and Chittka, 2009). Two aspects of the procedures used in previous studies are relevant to our purposes. The first is that where the preferences were found, the size of the artificial flowers on which occupiers were pinned was only slightly greater than that of the occupiers themselves: floral diameters were in the range of 10 mm [see photos in Fig. 1 in Leadbeater and Chittka (2007, 2009)] to 3 cm (Kawaguchi et al., 2006). Though flowers of this size are to be found in nature, they do not represent the full range of sizes of floral stimuli, which can extend to include the size of a panicle of lilac or of a sunflower [e.g. see photos in Fig. 1 in Kawaguchi et al. (2007) and Fig. 2 in Dawson and Chittka (2012)]. In our study, we manipulated the size of flowers to reduce and increase the proportion of the area on the flower that is occupied.

The second methodological issue pertains to a possible frequency dependence of choice. Where the proportion of flowers that are occupied was one third (Leadbeater and Chittka, 2009) the possibility that the preference reflected a general preference for comparatively rare flower types could not be excluded. If a preference for occupied flowers
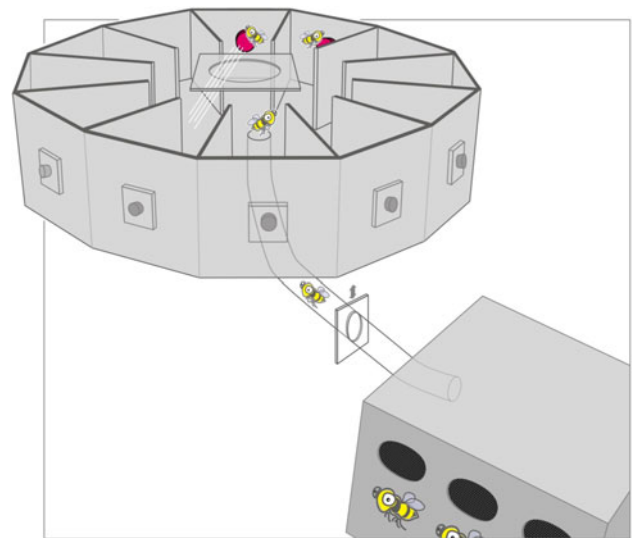
Fig. 1 Diagram of the radial arm maze used in the three experiments. A tunnel leads from the colony into the maze through an opening in the centre of the floor. The feeder tubes, containing either water or sugar solution, were placed at the ends of the ten corridors in use (two being blocked off) in the positions shown in *red*. In the occupied corridors, a dead bee was pinned above the feeder tube
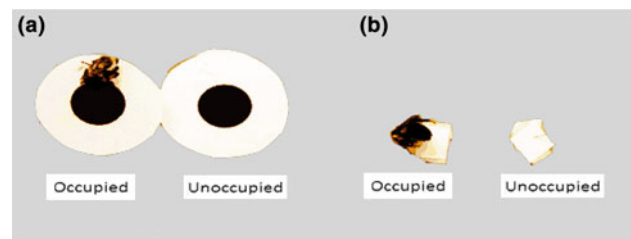
Fig. 2 "Occupied versus Unoccupied" (**a**) in Experiment 2 where the floral patterns were *black* and *white* concentric patterns (**b**) in Experiment 3 where the removal of the patterns leaves a discrimination between the presence or absence of an occupier attached to the back wall of the corridor

in fact reflects a preference for rare (Smithson and MacNair, 1997) flowers, then a situation in which occupied flowers are common should translate into a preference for unoccupied rather than occupied flowers. One recent study reported no effect on first visits of a manipulation of frequency of conspecific foragers (Baude et al., 2011). In that study, however, the foraging environment was patchy, and so the frequency of conspecifics depended on the area over which it was assessed: 20–60% (i.e. occupied flowers less versus more frequent than unoccupied) within local patches of flowers but only 10–30% (i.e. occupied flowers rare compared to unoccupied in both cases) when evaluated over the whole foraging environment. In the present study, where we reversed the proportions of occupied and unoccupied flowers, the flowers were presented in a radial maze so that all flowers were equidistant from the centre. The use of a radial maze also offers the advantage over a binary choice

procedure, either in a flight cage (Kawaguchi et al., 2006) or in a Y-maze (Perreault and Plowright, 2009), that each time a bee leaves the colony it can encounter several flowers and so occupier frequency (3 out of 10 versus 7 out of 10) can be manipulated.

This paper focuses on the behaviour of bumblebees leaving their colony for the first time, and aims to determine whether preferences for occupied flowers are to be found in general, or under a restricted set of laboratory conditions. We examined the first few choices of unrewarding occupied versus unoccupied artificial flowers by bumblebees that had no prior experience outside of their colony. To ascertain that the bees could distinguish the stimuli, even if they had no preferences, we used control groups for which they were given discrimination training (rewarding occupied flowers versus unrewarding unoccupied flowers), prior to being given choices of those same flowers when they were unrewarding. In Experiment 1, we manipulated the relative frequencies of occupiers. In Experiment 2, we incorporated a variety of floral patterns, which were larger than in previous studies (≥6 cm diameter, so quadruple the area of a flower that was 3 cm in diameter) so as to reduce the size ratio of occupier to flower. In Experiment 3, we eliminated the patterns altogether.

Methods

Colonies

Six colonies of *Bombus impatiens* (Cresson 1863) from Koppert Canada and from Biobest Canada were used: one in Experiment 1, three in Experiment 2 and two in Experiment 3. They were fed pollen *ad libitum*. Prior to training and testing, their access to sugar solution was restricted to stimulate foraging. Untrained bees were removed from the colony after they were tested for their preferences. Each trained bee was individually labelled using a coloured numbered tag glued to its thorax.

Apparatus

Two twelve-arm radial mazes were used, one for training and one for testing [see photo in Fig. 1 in Plowright et al. (2011)]. In the maze used for training, a hole in the centre of the back wall of each corridor allowed a feeder to intrude into the maze. The feeder was either filled with water if it was unrewarding or with sugar solution (2:1, sugar:water, by volume) if it was rewarding. No feeders were used in the maze used for testing.

The central area of the maze was 22 cm wide. The entrance to each corridor was 6 cm wide. Ten of the twelve corridors were used. The other two, opposite each other, were blocked off at their entrance. The corridors were

15 cm long. The back wall of each corridor, on which stimuli were positioned, was 14 cm wide × 15 cm high. The walls of the maze were made of opaque grey Plexiglas® and the ceiling was transparent. A metallic screen tunnel connected to the colony allowed the bumblebees to enter the maze from an opening (2.5 cm in diameter) in the centre of the floor (Fig. 1). A gate allowed the experimenter to control access to the maze.

Three light fixtures were positioned over the apparatus, each holding a high-frequency (>40 kHz) light ballast (Sylvania Quicktronic T8 QHE4x32T8/112) and four fluorescent light bulbs (Sylvania model FO32/841/XP/SS/EC03). The use of a frequency greater than 200 Hz should have minimized the risk of disruption of behaviour due to the perception of flicker (Srinivasan and Lehrer, 1984).

Stimuli

In all experiments, the bees were tested for their preference of occupied versus unoccupied corridors. Occupiers were previously frozen dead bees. According to Leadbeater and Chittka (2007), bumblebees respond to dead occupiers much as they do to live ones. We used dead queens rather than dead workers to maximize the chances that they would be detected by virtue of their larger size. In nature, the times at which workers and queens forage within a season overlap and so workers could well encounter other queens. The occupier was pinned to a visual pattern (e.g. a photo of a flower) that was attached to the back wall of a corridor using Velcro®, or, in cases where no pattern was used (Experiments 1 and 3), it was pinned directly to a piece of white Velcro® attached to the wall (Fig. 2). The unoccupied corridors were identical to the occupied corridors except that no dead bee was attached to the pin.

Four visual patterns were used to test for a possible preference for occupied patterns in Experiment 2. Two were photographs of flowers on a green background: a thistle and a sunflower. The 7 × 7 cm photographs were printed in colour and laminated. Two were concentric patterns: a white circle 6 cm in diameter with a black centre 2.5 cm in diameter printed on paper and glued to cardboard, and a fluorescent yellow circle with a blue centre of the same dimensions cut out of sheets of foam.

To determine that preferences could be detected using our procedure, we also pitted the concentric patterns described above against radial patterns (also 6 cm in diameter), since our previous research has shown a preference for radial patterns in this experimental setup when the patterns were yellow and blue (Simonds and Plowright, 2004; Plowright et al., 2006) as well as when they were black and white (Séguin and Plowright, 2008). The radial patterns consisted of six alternating wedges of blue and yellow or black and white.

Procedure

Training

In each of Experiments 2 and 3, one group of bees from one of the colonies was given discrimination training with occupied patterns or corridors being rewarding (S+) and unoccupied being unrewarding (S−). In Experiment 2, black and white concentric patterns were used, and in Experiment 3, the patterns were removed (Fig. 2). To maximize exposure to the contingency, half of the corridors contained an S+ and half an S−, with a new random assignment of the corridors each day. Frozen dead queens were replaced periodically to minimize the use of odour cues and were also replaced prior to testing.

Bees were given unrestricted access to the maze during training for a minimum of 4 h per day for a minimum of 5 days, after which foraging activity seemed, on the whole, to be concentrated on the rewarding stimuli. A period of monitoring individuals followed so as to ensure that the bees that were subsequently tested would have each experienced reward during training. To be selected for testing, a bee had to be seen ten times to insert its proboscis in feeders containing sugar solution. In Experiment 2, each forager was tested upon it having attained the criterion of ten rewards. In Experiment 3, training continued until a group of bees had attained criterion, so ten rewards was a minimum.

Testing

Bees were tested individually in the maze offering no reward. The trained bees from one colony in Experiment 2 and one colony in Experiment 3 were tested in the same way as the untrained bees from all the other colonies.

In Experiment 1, "approaches" to the stimuli, i.e. crossing an imaginary line half way across the corridor, were tabulated separately from "touches" of the back wall or some element of the display. In Experiments 2 and 3, a choice was defined as walking or flying past the head of the pin on the back wall of the corridor. "Dithering" within a corridor never counted as repeating choices: for a new choice to be counted, the bee always had to first fly out of the corridor to the centre of the maze.

In all experiments, the proportions of choices for the occupied over unoccupied stimuli were based on 20 choices. Because all the stimuli were unrewarding, the bees did not interrupt their sequence of choices to return food to the colony. We have shown previously using the same apparatus and procedure that the first four choices of unrewarding stimuli are comparable to the first 16 choices (Plowright et al., 2011). Also, within 20 choices, little if any change in approach behaviour to unrewarding radial patterns is evident (Simonds, 2002), though between repeated

sessions of 20 choices, habituation occurs and there is a decline in preference (Plowright et al., 2006).

Design

Experiment 1: manipulating frequency of occupiers

Occupiers occurred at either High frequency (7 out of 10 corridors were occupied) or Low frequency (3 out of 10). Twenty bees were tested in each condition. A Latin square design was used for counterbalancing: each corridor was occupied equally often across bees in each condition (High versus Low). The conditions were alternated from one bee to the next so as to un-confound possible age effects with the experimental conditions. No floral patterns were added to the feeders, and so the discrimination appeared as in Fig. 2b. Twenty bees were tested in each condition.

Experiment 2: using different floral patterns

In one colony, four floral patterns were used to test for preference of 3 occupied versus 7 unoccupied flowers, with 20 bees in each group. Two more groups of 20 bees were used to test for a preference for radial over concentric patterns. A second colony was used just with black and white concentric patterns in the event that there might be colony differences.

A third colony was used to train a group of 20 bees on a discrimination between concentric black and white patterns that were occupied or unoccupied (Fig. 2a). The group was divided into two groups of ten bees for testing on unrewarding patterns, which occurred for each bee on the day on which it had completed training. One group was tested on the discrimination on which it had been trained. The other was tested on new flowers (photos of thistles), in an effort to determine whether learning was restricted to one particular configuration ("concentric-pattern-with-dead-bee" is rewarding) or whether it generalized.

Experiment 3: eliminating the floral pattern

One colony was used for testing bees without any prior experience (20 bees) while the other was used for testing bees that had been trained (11 bees). The patterns used in Experiment 2 were eliminated, and so the discrimination at the time of testing appeared as in the Low-frequency condition of Experiment 1 (Fig. 2b). The proportion of occupied corridors was 3/10.

Statistics

A replicated goodness-of-fit test using the G-statistic (Sokal and Rohlf, 2012) was used to compare choice proportions to

a theoretical value of chance (the number of occupied flowers in the maze out of ten) since the data collected were binary (occupied versus unoccupied) and there was replication within bees (20 choices per bee). Two G values were obtained: (1) the G_P value (P for Pooled) determines whether the pooled data, i.e. group choice proportions, differ significantly from a theoretical value of chance, and (2) the G_H value (H for Heterogeneity) determines whether there are individual differences. Where the G_H value was significant, the G value was partitioned into individual contributions. G values were compared to χ^2 values in tests of significance.

The statistics above compare observed proportions to a theoretical value. We also compared choice proportions of different groups of bees to each other. In Experiment 2, we fit a logistic model to our data using GLIM (Generalized Linear Interactive Modelling; Francis et al., 1993), which specifies a binomial error term, to test for differences in choice proportions among four groups. In Experiment 3, we used an independent measures t test to compare two groups.
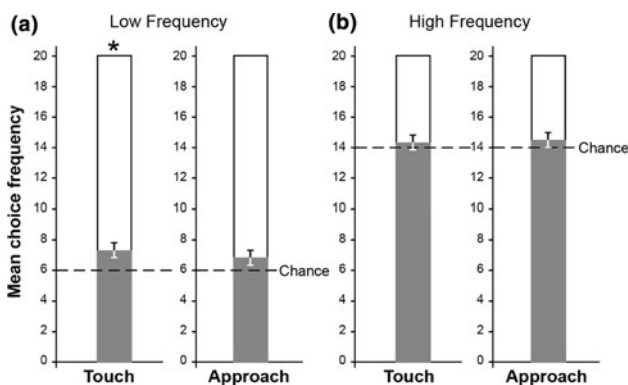
Fig. 3 Group choice proportions by untrained bees in Experiment 1, with standard *error bars*, of (**a**) Low frequencies (3/10) and (**b**) High frequencies (7/10) of occupied corridors. In the *stacked bars*, the shaded portions show the frequencies of choices of the occupied corridors, and the unshaded portions show the frequencies of choices of the unoccupied corridors. Two different measures of choice are shown: approach and touch. No reward was given. The *asterisk* indicates a choice proportion significantly greater than chance

Results

Experiment 1: manipulating frequency of occupiers

Figure 3 shows the proportions of approaches and touches. In the Low-frequency condition (Fig. 3a), where 3 out of 10 corridors were occupied, there was a significant preference for "occupied" when touches were measured ($G_P = 8.15$, 1 *df*, $P = 0.004$), which seemed evident even in the first four choices (1.45 out of 4, or 36%). The choice proportion did not differ from chance when approaches were measured, though the effect was in the same direction ($G_P = 2.98$, 1 *df*, $P = 0.085$).

In the High-frequency condition (Fig. 3b), where 7 out of 10 corridors were occupied, a preference for rare stimuli should have translated into a preference for the unoccupied corridors, i.e. an avoidance of the occupied. The proportions did not differ, however, from chance, either for approaches ($G_P = 0.98$, 1 *df*, $P = 0.32$) or for touches ($G_P = 0.30$, 1 *df*, $P = 0.58$), though the differences were in the direction of preference rather than avoidance of occupied stimuli. No preference was evident when only the first four touches were examined: the occupied corridors were chosen on average of 2.85 times (71%). Individual differences for both measures in both conditions were non-significant ($G_H \leq 21.46$, 19 *df*, $P \geq 0.31$).

Experiment 2: using different floral patterns

Table 1 shows the choice proportions for four groups of 20 untrained bees given 20 choices of 3 occupied versus 7 unoccupied patterns (photos of thistle flower, photos of sunflower etc.). Fitting a logistic model to the data showed no differences among the four groups ($\chi^2 = 0.399$, 3 *df*, $P = 0.94$), and so the data were pooled. Overall, no significant difference was found between the observed choice proportion and a chance value of 0.3 ($G_P = 1.08$, 1 *df*, $P = 0.30$). Individual differences, however, were significant ($G_H = 177.59$, 79 *df*, $P < 0.0001$): occupied flowers were preferred by 5 of the 80 bees, while they were avoided by 11 others.

Table 1 Choice frequencies by groups of 20 untrained bees given 20 choices between 3 occupied and 7 unoccupied unrewarding patterns in Experiment 2

Stimulus	No. choices			Choice proportion for occupied flowers
	Occupied	Unoccupied	Total	
Colony 1				
Thistle flower photo	112	288	400	0.28
Sunflower photo	119	281	400	0.30
Blue and yellow concentric circles	113	287	400	0.28
Black and white concentric circles	117	283	400	0.29
Total	461	1139	1600	0.29
Colony 2				
Black and white concentric circles	110	290	400	0.28

Table 2 Choice frequencies by 20 trained bees given 20 choices between 3 occupied and 7 unoccupied unrewarding patterns in Experiment 2

Stimulus	No. choices			Choice proportion for occupied flowers
	Occupied	Unoccupied	Total	
Old: black and white concentric patterns	74	126	200	0.37
New: thistle flower photos	69	131	200	0.35
Total	143	257	400	0.36[a]

All bees were given prior discrimination training (Occupied S+ versus Unoccupied S−) on black and white concentric patterns. Half the bees were tested on old and half on new patterns

[a] Proportion significantly greater than chance value of 0.3

In a second colony with a group of 20 bees tested just with black and white concentric patterns, the choice proportion for the occupied pattern was again not different from chance ($G_P = 1.21$, 1 df, $P = 0.27$), though individual differences were significant again ($G_H = 38.97$, 19 df, $P = 0.004$), with two bees showing almost exclusive preference for unoccupied patterns (0–1 choices out of 20) and another showing a strong preference for the occupied patterns (11 out of 20, where chance was 3/10).

Preferences in untrained bees were detectable using our method. Though a choice proportion of 0.33 for radial over concentric coloured patterns was no greater than the chance value of 0.30 ($G_P = 1.17$, 1 df, $P = 0.28$), a preference of 0.40 for radial patterns was found when the fluorescent blue and yellow were replaced by black and white ($G_P = 18.96$, 1 df, $P = 0.00002$).

Though the group choice proportions for untrained bees showed no discrimination between occupied versus unoccupied patterns, they were discriminable, since Table 2 shows a preference for occupied flowers by trained bees. No difference was detected between the 10 bees tested on the patterns used during training versus the 10 bees tested on new patterns ($\chi^2 = 0.27$, 1 df, $P = 0.6$) and so the data were pooled. The overall preference for occupied flowers, though weak (0.36, compared to a chance value of 0.30), was significant ($G_P = 6.09$, 1 df, $P = 0.014$) and once again, individual differences were significant ($G_H = 36.71$, 19 df, $P = 0.009$).

Experiment 3: eliminating the floral pattern

The choice proportion for the untrained bees was comparable to that found under the same conditions in Experiment 1 in the Low-Frequency condition. The preference for the occupied corridors was significantly greater than a chance value of 3/10 ($G_P = 20.81$, 1 df, $P < 0.0001$) and the individual differences were not significant ($G_H = 24.82$, 19 df, $P = 0.17$). Prior discrimination training amplified the preference (Fig. 4): not only was the group proportion significantly greater than chance ($G_P = 77.15$, 1 df, $P < 0.0001$) but there was a significant difference between
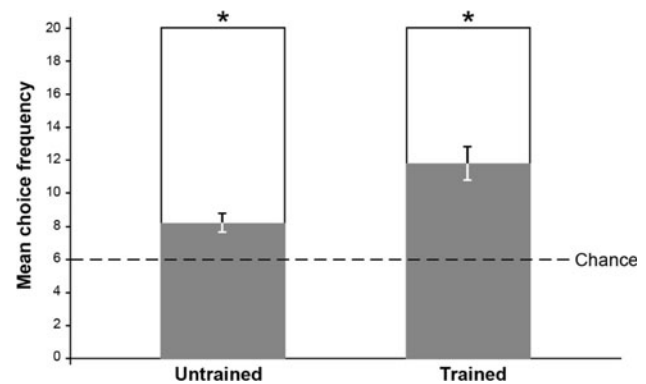
Fig. 4 Group choice proportions, with standard *error bars*, in the testing for preference for Occupied versus Unoccupied by 20 untrained bees and 11 bees given prior discrimination training (Occupied S+ versus Unoccupied S−) in Experiment 3. In the *stacked bars*, the shaded portions show the frequencies of choices of the occupied corridors, and the unshaded portions show the frequencies of choices of the unoccupied corridors. No reward was given during testing. The *asterisks* indicate that the proportions in both groups were significantly greater than chance. The difference between the two groups was significant

the two groups ($t_{(29)} = 3.47$, $P < .0016$). Individual differences were significant ($G_H = 22.20$, 10 df, $P = 0.014$).

Discussion

A preference for occupied flowers cannot be attributed to a general tendency to preferentially visit uncommon flower types: the preference for occupied flowers over unoccupied flowers when their relative frequencies were 3:7 did not reverse when the relative frequencies were switched to 7:3. The preference, however, did disappear, and so there is frequency dependence in choice. Moreover, even though this study used 100 bees drawn from two colonies and used a variety of large artificial floral patterns, no general preference by inexperienced bees for "Occupied" was found. Occupied flowers were chosen preferentially by inexperienced bumblebees in our study, but only under a restricted set of conditions: when occupied flowers were comparatively rare and the occupier to flower size ratio was

relatively high, the floral pattern having been eliminated. These results should serve as a caution against overgeneralizing the results of laboratory demonstrations to situations where they clearly do not apply.

Two aspects of our data are in line with other reports: (1) A preference for occupied flowers can be acquired through rewarded experience (Leadbeater and Chittka, 2009). (2) Experience on a discrimination between occupied versus unoccupied on one flower type can generalize (Dawson and Chittka, 2012) to new flower types. To further investigate the possible role of the formation of associative bonds, future research should include reversed contingencies (Unoccupied S+ versus Occupied S−) as well as random controls (Rescorla, 1967).

The results of this study are in some way paradoxical. Previous research found that the first landing on an occupied flower instead of an unoccupied flower seemed more frequent when the flowers were real *Chrysanthemum* flowers than when they were artificial flowers (Kawaguchi et al., 2006). When we obtained a preference for occupied flowers, it was not by making flowers more realistic, but rather by eliminating the floral pattern altogether. Nonetheless, from a cognitive point of view these results are sensible: a discrimination between two stimuli should be facilitated by the removal of common elements (Pearce and Redhead, 1993).

The heightened performance by the trained bees in Experiment 3 (59 % choice of occupied flowers) compared to those in Experiment 2 (36 % choice) is consistent with the interpretation that the stimuli themselves were more discriminable. We cannot rule out, however, the possibility that the difference was due to extended training in Experiment 3, as the nature of visual processing in bees is known to change over time (Giurfa et al., 2003)—perhaps it is the memories of the stimuli that become more discriminable by virtue of unnecessary information being eliminated with experience (Stach and Giurfa, 2005).

Cautions against anthropomorphism in bee research (Horridge, 2009) bear repeating. Where we presented photographs of flowers, there is no claim that these photographs were perceived as real flowers. Moreover, where we presented dead bees, there is no claim that they were recognized as such. Indeed, if 'photographs of human faces' may be treated by bees as atypical flowers (Avarguès-Weber et al., 2010), then the same may be true of 'dead insects attached to grey panels'.

Though work has begun to elucidate population differences in "innate" colour preferences and learning speed (Ings et al., 2009), individual differences in bee learning and cognition have received comparatively little attention (Jeanne, 1988), and indeed they are typically not even reported [a recent exception being the individual choice data reported by Forrest and Thomson (2009)]. Here, we repeatedly obtained significant individual differences by untrained bees, with a few showing strong preferences for occupied floral patterns and a few others showing the opposite (Experiment 2). One possible explanation is that there are individual differences in perseveration on one or the other flower type in the face of no reward, with a subset of bees showing a high degree of flower constancy. Another very speculative post-hoc explanation might be that conflicting motivations of varying degrees underlie these differences: occupiers might possibly elicit both approach and avoidance tendencies and the balance of the two might differ across individuals. In this light, aggression and other social interactions (Sibbald and Plowright, 2013) observed in another context might be considered as a possible explanatory variable for individual foraging decisions.

The ecological relevance of laboratory demonstrations of preference or non-preference of unrewarding occupied flowers by first foragers depends very much on whether important variables in nature have been captured. Our study expanded the range of floral sizes used in previous laboratory studies, yet they still fall well within the ranges found in nature. The frequencies of occupied flowers in this study, however, were likely much higher than those encountered in nature. The frequencies of flowers occupied by other insect pollinators are undoubtedly small, and even 30 % is an overestimate, let alone 70 %. Nonetheless, if the frequency of occupied flowers is estimated by bees on a small local level (e.g. a patch of 5–10 thistle flowers), it would be possible to find occupancy rates that were comparable to those in this study. The point, however, is not so much whether the absolute frequencies used here mirror those in nature, but whether bees are sensitive to frequencies at all: our results suggest that a preference for occupied flowers is not general but only occurs when the perceived frequency of occupiers is on the lower end of the scale. To further investigate the temporal and spatial characteristics of how bees assess those relative frequencies, future research could use a commonly used procedure of forced-choice of stimuli in an array, in which the experimenter controls access to only one stimulus at a time (so "forced-choice" is a misnomer for "no-choice") followed by free-choice. In this vein, our study highlights an important point made by other researchers working in the area 'cognitive ecology', which informs behavioural ecology with considerations of perception, memory, learning and decision making (Shettleworth, 1989; Dukas, 1998; Chittka and Thomson, 2001; Dukas and Ratcliffe, 2009): the bridge between the laboratory and the field is not given but must be built.

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