



## Food restriction and threat of predation affect visual pattern choices by flower-naïve bumblebees



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### ABSTRACT

The aim of this study was to determine whether a preference by flower-naïve bumblebees could be created or enhanced by manipulating variables relevant to food collection and to defense against predation. In two experiments, colonies of bumblebees (*Bombus impatiens*) were deprived of pollen, exposed to CO<sub>2</sub>, or neither. Choices of individual workers in a radial arm maze were monitored. In Experiment 1, both variables lead to a preference for corridors occupied by a conspecific bee. The effect was specific: no change in preference for corridors occupied by other objects (a coin and a piece of Styrofoam) was detected. In Experiment 2, radial and concentric patterns were used, both of which were unoccupied. Only pollen deprivation increased preference for radial stimuli, while CO<sub>2</sub> had no discernible effect. Preferences for visual patterns by bees leaving their colony for the first time are modulated by variables that affect the internal state of the bees in problem-specific ways.

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The possibility that foraging bees use the presence of other insects on flowers to govern their own floral choices has received little if any support in the field. For instance, one survey of counts of floral visitors found on flower heads of sunflowers (*Helianthus annuus* L.) and onion flowers (*Allium cepa* L.) addressed the question of whether there would be attraction or avoidance of inflorescences that were already occupied by one or more individuals. The distribution of insects, including honeybees (*Apis mellifera* L.) and bumblebees (*Bombus* spp. Latreille), followed a Poisson distribution (Tepedino & Parker, 1981): there were neither more nor less flowers with just one forager than would be expected by chance. The notion that insects forage independently of other insects may, however, have been dismissed prematurely by field biologists. Recently, an examination of the details of social effects on foraging in the laboratory has revealed that bees use associative learning to take advantage of cues that predict important outcomes such as presence of floral reward (Avarguès-Weber & Chittka, 2014a; Dawson, Avarguès-Weber, Chittka, & Leadbeater, 2013; Leadbeater & Chittka, 2009) and presence of predators (Dawson & Chittka, 2014)—in general, social information is used by insects strategically (Grüter & Leadbeater, 2014). Moreover, workers that have just left their colony for the first time also show a significant preference for flowers that are already occupied by another forager (Kawaguchi, Ohashi, & Toquenaga, 2006; Leadbeater & Chittka, 2009), though this effect is most evident when the flowers are rare and the occupiers are large relative to the flowers (Plowright et al., 2013). Because of the difficulty in obtaining the pre-experimental histories of bees seen foraging in the field, these sorts of effects may have eluded detection in nature.

In this paper, our focus is on the behaviour of “flower-naïve” bumblebee workers: bees that leave their colony for the first time, and as such, have had no prior experience with flowers. One view regarding the preferences for occupied flowers

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by flower-naïve bees is that they may help inexperienced bees to locate sources of food: a pattern with another bee on it is likely to be a flower. One difficulty with this interpretation is that it is *post hoc*. Indeed, the exact opposite argument can be made *a priori*: a flower that is occupied by a forager is likely to be empty or well on its way to being depleted, and so it ought not to be preferred but avoided. In other words, other foragers may possibly act as competitors rather than as informers (Baude, Danchin, Mugabo, & Dajoz, 2011). Another view is that the presence of an occupier on a flower has little to do with signalling resource availability. Field observations have suggested that interactions among bees on a flower are in fact aggressive (Kikuchi, 1963). Indeed, in the course of a prior study on pattern preferences of flower-naïve bees (Orbán & Plowright, 2013), we captured a few such interactions on film (Videos 1 and 2 in the Supplementary Materials): the behaviours of the bee landing on the flower seemed more directed at the occupier than at the flower, which suggests that the occupier might have been perceived as a predator or a competitor.

In two experiments, we manipulated internal states of flower-naïve bees. To promote food finding behaviours, we manipulated the availability of pollen, which is needed for feeding to larvae. To promote aggressive or defensive behaviours, we exposed the bees to CO<sub>2</sub> to simulate the presence of a mammalian predator. Predators of bumblebee colonies (Goulson, 2010) include mice (*Mus domesticus*), badgers (*Meles meles* L.) in Europe, and skunks (*Mephitis mephitis* Schreber) in North-America. Bumblebees perceive CO<sub>2</sub>: they respond to mammalian breath and to currents of air containing 5 or 10% CO<sub>2</sub> by hissing, which serves as an inter-specific defence signal (Kirchner & Röschard, 1999).

If a preference for occupied stimuli is engaged when bees are food searching, then pollen deprivation should create or increase the preference. If the preference is engaged in situations that trigger aggressive behaviours, then exposure to CO<sub>2</sub> should create or increase the preference. Experiment 1 tested these two predictions. In addition, by comparing the preference for stimuli occupied by another bee with the preference for stimuli occupied by non-organic objects (a coin, as in Dawson and Chittka (2012), and a piece of Styrofoam), we began to address the question of whether any preference for occupied stimuli was indeed social.

Aggressive tendencies ought to be directed at other individuals and not at flowers themselves. Heightening an aggressive tendency ought not to increase a preference for a pattern that is more “floral” than another. To determine whether the effects of our variables were specific to social preferences, Experiment 2 examined their effects on preference for floral patterns with no occupiers. Given that radial patterns (illustrated in the legend of Fig. 3) are, by and large, preferred over concentric patterns (Orbán & Plowright, 2013) as they are thought to resemble flowers in nature (Lehrer, Horridge, Zhang, & Gadagkar, 1995), we examined the effect of food deprivation and CO<sub>2</sub> exposure on relative choice of these patterns. Food deprivation ought, if anything, to increase preference for radial patterns, while CO<sub>2</sub> should not. Given that larger bumblebees tend to invest themselves in foraging duties while smaller bees tend to the nest (Goulson, 2010), though task specialization is not as marked as in honeybees, we reasoned that the effect of food deprivation might interact with body mass.

## Methods

### Subjects

Three commercial colonies of *Bombus impatiens* Cresson in plastic nest boxes (19.5 cm × 17.5 cm × 12 cm high) were supplied by Koppert Canada. Because the colonies were covered with an opaque lid, they received little light, as in nature. In Experiment 1, 48 bees from each of two colonies were used, for a total of 96. In Experiment 2, 60 bees from the third colony were used. All bees were tested the first time they left the colony: they had no pre-experimental experience outside of the nest box. In all conditions, to motivate the bees to exit the colony, the wick that absorbed sugar solution from a plastic bag beneath the nest box was capped for one or two days prior to testing.

### Apparatus

The 12-corridor maze that we used, modelled on that of Lehrer et al. (1995), is diagrammed in Fig. 1. Photographs are shown in Plowright, Evans, Chew Leung, and Collin (2011, Fig. 1). It was constructed of grey Plexiglas® with a clear cover. From the central area (22 cm wide, 15 cm high), 12 corridors radiated outwards. The bees entered the maze *via* a screen tube that connected their colony exit hole to an entrance hole in the center of the floor of the maze. The exit was stoppered when the colony was not in use during the experiment: bees were not allowed to travel to and from the apparatus prior to testing. The entrance to the maze was gated during testing sessions: bees were let into the maze individually. The corridors were 6 cm wide at their entrance from the center of the maze and 15 cm long. The back walls were 13 cm wide.

The maze was illuminated from above by high-frequency (>40 kHz) lighting equipment (three Sylvania Quicktronic T8 QHE4x32T8/112 light ballasts, each with four Sylvania model FO32/841/XP/SS/EC03 fluorescent light bulbs).

### Stimuli

In both experiments, the stimuli were mounted with Velcro® on the back walls of the corridors in the maze, as shown in Fig. 1.

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