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Bumblebee social learning can lead to suboptimal foraging choices

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Bumblebees are influenced by socially acquired information when deciding on which flowers to forage. In some circumstances, however, this attraction towards conspecifics may lead to suboptimal foraging performance because the presence of multiple pollinators typically results in a faster rate of nectar depletion in the flower. We tested the capacity of bees to learn to avoid flowers occupied by conspecifics when they offered a lower reward than unoccupied similar flowers. Bumblebees were able to discriminate between poorly and highly rewarding flowers by using the presence of a nonsocial cue (a wooden rectangular white block). When poorly rewarding flowers were indicated by social cues (model bees), however, bees did not discriminate between the two flower types except when an additional cue was provided (flower colour). These findings indicate that bumblebees attach particular meaning to conspecific presence on flowers, even when this could lead to suboptimal foraging performance. The relatively lower flexibility in the use of social than nonsocial cues suggests a biased positive value of conspecifics as indicators of rewarded flowers.

A wide range of animals use information that originates from other individuals to make vital decisions regarding habitat, food, mates or predators (Danchin, Giraldeau, Valone, & Wagner, 2004; Galef & Giraldeau, 2001; Hoppitt & Laland, 2013; Leadbeater & Chittka, 2007b). For example, by attending to the outcome of conspecific behaviour, animals can reduce the costs of trial-and-error sampling associated with personal exploration (Galef & Giraldeau, 2001; Hoppitt & Laland, 2013). However, these social learning strategies are only valuable if enough individuals within the group also provide individually acquired knowledge (Rieucau & Giraldeau, 2011). Social learning inevitably increases intraspecific competition and limits alternative and independent sampling, thus potentially leading to suboptimal choices and, in the worst scenario, to informational cascades as observed in market crashes in economics or false flock alarm flight, for example (Giraldeau, Valone, & Templeton, 2002; Rieucau & Giraldeau, 2011). Consequently, animals should not always rely on social cues when they are available, but attach different values to social and individual information depending on the context. Theoretical analyses have predicted strategies about when animals should copy and from whom (Laland, 2004). In some circumstances determined through personal experience or from evolutionary processes, animals should ignore social stimuli or even actively avoid them while in others it may pay individuals to selectively attend to conspecific cues.

Bumblebees are influenced by the behaviour of conspecifics when deciding from which flower species to forage (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b; Dawson, Avarguès-Weber, Leadbeater, & Chittka, 2013; Kawaguchi, Ohashi, & Toquenaga, 2006; Kawaguchi, Ohashi, & Toquenaga, 2007; Leadbeater & Chittka, 2005, 2007a, 2009; Mirwan & Kevan, 2013; Plowright, et al., 2013; Smolla, Alem, Chittka, & Shultz, 2016; Worden & Papaj, 2005). Uninformed individuals tend to land on flowers occupied by conspecifics and foragers can decide, by observing conspecifics' behaviour, which flower species might be profitable (Dawson, et al., 2013; Worden & Papaj, 2005). Such behaviour is not indiscriminate: bumblebees tend to rely more on social cues when they do not have personal information available about the surrounding floral resources (Jones, Ryan, & Chittka, 2015; Kawaguchi, et al., 2007; Leadbeater & Florent, 2014) or when flower investigation is costly (Saleh, Ohashi, Thomson, & Chittka, 2006). They also tend to avoid occupied flowers in highly competitive contexts (Baude, Danchin, Mugabo, & Dajoz, 2011; Plowright, et al., 2013) or if social information is less reliable than other flower features (Dunlap, Nielsen, Dornhaus, & Papaj, 2016). Finally, bumblebees have been shown to ignore social cues if they are not informative (Leadbeater & Chittka, 2009) and to flexibly treat them as attractive or repellent cues depending on the associated outcome (Dawson, et al., 2013; Saleh & Chittka, 2006).

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In the current study we investigated whether attraction towards a conspecific bee can also be modulated by the relative value of the information acquired socially. Flowers that were occupied by conspecifics offered relatively lower reward than the other flowers. Would the bees succeed in learning to suppress their attraction to conspecifics and selectively visit unoccupied flowers? We compared the capacity of bees to modulate their initial preference for occupied flowers both in a social (model bees used as indicators) and in a nonsocial context (flower colours or wooden blocks used as indicators).

METHODS

Three bumblebee, *Bombus terrestris*, colonies, provided by Syngenta Bioline Bees (Weert, the Netherlands), were used. The colonies were housed in wooden nestboxes (28 × 16 cm and 11 cm high) connected to a flight arena (117 × 72 m and 30 cm high) covered by a UV-transparent Plexiglas ceiling. Light conditions mimicked the natural daylight spectrum and the flicker frequency of the light was set beyond bumblebee's flicker fusion frequency (Skorupski & Chittka, 2010). The nestboxes and the flight arenas were connected via a Plexiglas tube with sliding doors allowing a controlled individual access to the arena. Individual bees were identified by paint marks, and were removed from the colony after testing. Bees were fed daily with pollen and with a 30% (volume/volume) sucrose solution provided in perforated plastic tubes placed inside the nestbox when necessary. The nest was kept in dim red light (hard to detect for bees) when food was supplied to minimize the chance of bees forming positive associations between food and the visual appearance of nestmates within the nest. However, the bees could see each other in a nest compartment in which food was never provided. The social cues used during the experiments were artificial model bees (see ‘social cue’ in ‘Treatment groups’ section below for details) to exclude any possibility of olfactory-mediated recognition. The bees were not allowed to forage in the arena before the experiment.

Artificial flowers consisted of coloured Perspex squares (25 × 25 mm and 5 mm high) offering 20 μl of sucrose solution from a small hole (diameter 5 mm) in the centre. These were randomly placed in the arena on top of transparent cylinder supports (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b).

The bees were first individually subjected to a pretraining phase, consisting of five foraging bouts in which typically six flower visits were necessary to collect a full crop of 30% sucrose solution. A foraging bout ended when the bee stopped visiting flowers and returned to its nest. In this phase, only green (Green 6205 Perspex from Hamar Acrylic Fabrications Ltd, London, U.K.) flowers were displayed and were all rewarded.

The subsequent training phase also consisted of five foraging bouts, in which bees had to discriminate between flowers containing high rewards (50% sucrose solution) from flowers offering low rewards (10% sucrose solution). A cue informed subjects about which flower was offering a high or low reward, but cues varied between treatment groups (Fig. 1). The flowers were either cream (Cream 128 Perspex) or fuchsia (Red 4415 Perspex) coloured in this phase (Fig. 1). These colours were thus novel for the bee and were easily distinguished from each other (0.3 hexagon units) and from the green flowers (respectively 0.3 and 0.4 hexagon units) used in the previous phase (Chittka, 1992; Dyer & Chittka, 2004). In the hexagon colour space, a level of 70% discriminability corresponds to approximately 0.1 hexagon units. After each foraging bout, the flowers were washed with an ethanol solution to remove scent marks and their positions varied within the arena.

A 3 min nonrewarded learning test followed the training period. In this test, the flowers contained only plain water. Each bee was trained and tested individually.

Treatment Groups

Social cue

Bees ($N = 10$) from this group were first familiarized with conspecifics being associated with rewarding flowers (30% sucrose solution) during the pretraining phase: model bees were placed on six of 12 green flowers displayed with a random spatial arrangement in the arena. The opportunity to associate conspecifics with reward has been shown necessary for social learning to occur (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b). Model bees were shaped using oven-hardening modelling clay (Fimo Soft, Staedtler) and painted with a colour pattern matching that of *B. terrestris*. We used the following paints: yellow (Rheotech, Acrylics Bright Yellow); black (Winsor & Newton, Griffin fast drying oil painting, ivory black) and white (unpainted modelling clay) to reflect natural *B. terrestris* colour properties, as assessed by bumblebee colour vision (Skorupski, Döring, & Chittka, 2007; Stelzer, Raine, Schmitt, & Chittka, 2010) and quantified in a bee colour space model (Chittka, 1992). In the subsequent training phase, six flowers occupied by model bees offered a low reward (10%), while six unoccupied flowers of the same colour offered a high reward (50%; Fig. 1). Only fuchsia flowers were used for half of the tested bees, while the other half experienced only cream flowers, thus avoiding potential colour influence.

Flower colour cue

Bees ($N = 10$) from this treatment group were presented with 12 rewarding (30% sucrose solution) green flowers without any associated cue in the pretraining phase and had to discriminate cream from fuchsia flowers in the training phase. One flower colour (fuchsia or cream depending on bees in a counterbalanced design) was associated with the low (10%) flower reward while the other provided a high (50%) reward (Fig. 1). As these colours can be easily discriminated by the bees, results from this group provide a baseline level of bees' performance in a discrimination task based on reward level comparison.

Nonsocial cue

Bees ($N = 10$) from this group experienced nonsocial cues placed on half of the 12 green flowers in the pretraining phase to allow positive association between the cue and rewarding flowers. Both occupied and unoccupied flowers were equally rewarding (30% sucrose) in this pretraining phase. The nonsocial cues consisted of cuboid, white wooden blocks (Winsor & Newton, Griffin fast drying oil painting, titanium white) of a size similar to the bees (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b). The bees then had to discriminate flowers by the presence of this nonsocial cue on top of them (‘occupied’ versus ‘unoccupied’ flowers) in the training phase (Fig. 1). Occupied flowers offered a low reward (10% sucrose) while unoccupied flowers were highly rewarded (50% sucrose). There were six flowers in each category that were randomly placed in the arena. Their positions varied between foraging bouts. All flowers were of the same colour (fuchsia or cream depending on bees in a counterbalanced design).

Social and flower colour cues

Bees from this group ($N = 10$) were pretrained with model bees. In the training phase, the bees faced six cream and six fuchsia flowers. One type of flower (fuchsia or cream depending on bees in a counterbalanced design) was associated both with model bees and a low reward (10%) while the other type offered a high reward (50%; Fig. 1).

Data collection was run in parallel with two different colonies used sequentially for the following treatments: the flower colours, nonsocial objects or model bees as indicator of the less profitable