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# Bumble-bees learn the value of social cues through experience

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**Natural selection should lead animals to use social cues (SC) when they are useful, and disregard them when they are not. Theoretical investigation predicts that individuals should thus employ social learning 'strategies', but how might such context specificity be achieved on a proximate level? Operant conditioning, whereby the use of SC is reinforced through rewarding results, provides a potential mechanism. We investigate the role of reinforcement in joining behaviour in bumble-bees, *Bombus terrestris*. When bees visit unfamiliar flower species, they prefer to probe inflorescences where others are also foraging, and here we show that such behaviour is promoted through experience when conspecific presence reliably predicts reward. Our findings highlight a straightforward, but rarely discussed, mechanism by which animals can be selective about when to use SC.**

**Keywords:** social cues; social information; bee cognition

## 1. INTRODUCTION

The hypothesis that animals should use cues about the environment provided by conspecifics, termed social cues (SC), only in the specific circumstances where they are most useful has been developed extensively in recent years (Laland 2004; Kendal *et al.* 2005). Less attention, however, has been devoted to the question of how individuals could achieve the flexibility to decide when SC are meaningful and when they should be discarded. A potential mechanism (Laland 2004) is associative learning, whereby experience leads to an association between an action made by the animal and a rewarding or non-rewarding stimulus (the reinforcer). If a social cue offers a consistent short cut to success, reliably predicting a rewarding outcome, its use should be reinforced, just as would be the case with an asocial cue. Here, we explore whether the use of meaningful SC is promoted through learning, using an insect model, the bumble-bee *Bombus terrestris*.

During their search for nectar and pollen to bring back to their colony, bumble-bees visit a highly variable floral array (Heinrich 1979). Individuals use asocial cues, including shapes, colours and scents, to identify rewarding flowers (Keasar *et al.* 1997; Blarer *et al.* 2002), and can quickly learn that particular floral features predict high rewards (Raine *et al.* 2006). Bumble-bees also make use of cues provided inadvertently by their foraging conspecifics, which influence how individuals handle flowers (Leadbeater & Chittka 2008), which flower species they choose to forage upon (Worden & Papaj 2005; Leadbeater & Chittka 2007; Baude *et al.* 2008) and which individual flowers they visit (Leadbeater & Chittka 2005; Kawaguchi *et al.* 2006; Saleh & Chittka 2006). The available evidence suggests that individuals may also modify their use of SC through learning, just as they do asocial cues, according to local conditions. For example, bees learn to accept or reject flowers on which they can detect the olfactory 'footprints' of conspecifics depending on whether such cues have previously been associated with high rewards (Saleh & Chittka 2006).

In this study, we focus on a simple social cue—the presence of a feeding conspecific. When bees visit a new flower species for the first time, they prefer those inflorescences where conspecifics are also foraging. However, they quickly begin to ignore the presence of conspecifics on subsequent visits, implying that foragers use conspecific presence to identify rewarding species but not rewarding flowers (Leadbeater & Chittka 2005; Kawaguchi *et al.* 2007). Sometimes, however, conspecific presence might provide a valuable cue as to floral reward levels; for example, when the nectar rewards offered by individual inflorescences deplete slowly because they contain many nectaries (e.g. sunflowers *Helianthus annuus*). Under these conditions, do bees continue to ignore social information, even though using it might improve foraging efficiency, or can operant conditioning allow for phenotypic flexibility in the use of SC? Here, we manipulate the value of SC in a laboratory set-up, to ascertain whether joining behaviour in bumble-bees is modified through experience.

## 2. MATERIAL AND METHODS

Subjects derived from commercially obtained colonies, housed in a wooden nest-box, connected to a flight arena (figure 1*a*). Bees had never been previously fed in the arena, sucrose solution (50% v/v) having been placed into nest honeypots. Three colonies of number-marked bees were used sequentially.

The arena contained 12 bicoloured yellow-and-blue artificial flowers, each comprising a dental wick within a glass vial, which held 5 ml of either sucrose solution or water (figure 1*b*). This sucrose volume is sufficient to fill a bee's nectar stomach. Each flower was scented to encourage visitation (lavender oil, 5 µl : 50 ml oil : water). Flowers were washed (50% ethanol), dried, refilled and the wick replaced, before subjects entered the arena in both learning and testing phases.

At the beginning of each trial, a bee was selected from those attempting to leave the nest, and allocated to one of four treatment groups: Naive; SC informative; SC redundant; or No SC. Groups were allocated in sequential order, to avoid over-representation of the most motivated foragers (those to leave the colony first) in any one treatment. Each group experienced different conditions during the learning phase, except for the group Naive, which did not participate in this phase.

For bees in the group SC informative, the presence of foraging conspecifics was reliably associated with a sucrose reward. Out of the 12 flowers in the arena, only four contained sucrose, and unrelated dead 'demonstrator' bees were pinned in a foraging position to these flowers (figure 1*a*). Previous work has established that responses to dead, freshly freeze-killed, demonstrators are comparable with those of live foragers (Kawaguchi *et al.* 2006, 2007; Leadbeater & Chittka 2007). Demonstrators (eight per subject for training and testing) had been frozen to −4°C, then defrosted at room temperature and pin-mounted before use. The remaining flowers provided only water.

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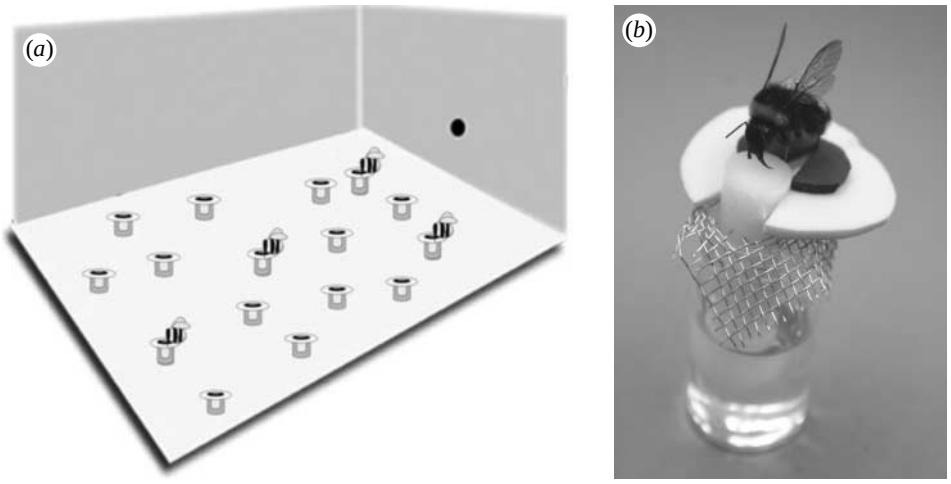


Figure 1. (*a*) Demonstrator bees were pinned to four artificial flowers from an array of 12, in a rectangular wooden flight arena with a transparent lid (105×70×30 cm) (*b*) 'Demonstrators' were pinned to artificial flowers. Flowers comprised a dental wick (3 cm high) in a vial of sucrose/water, surrounded by circular yellow-and-blue foam discs.

For group SC redundant, demonstrators were again pinned to four flowers, but in this case, all 12 flowers were rewarding. Thus, conspecific presence provided no useful information about reward levels.

Bees in group No SC were included as a control, to ensure that any observed difference in behaviour between bees in groups SC informative and SC redundant derived from differences in the value of SC during the learning phase, rather than from the differences in the variance of reward levels experienced by the two groups. These subjects foraged on an identical array to group SC informative, but no demonstrator bees were present. Each subject was allowed to forage alone for five foraging bouts (3–11 min per bout), interspersed with voluntary return visits to the nest-box to offload sucrose solution, during the learning phase.

Testing took place immediately after the learning phase, and tests were identical for every subject. All 12 of the flowers contained only water, and demonstrators were pinned to four arbitrarily chosen flowers. All flower visits completed before the bee attempted to return to the colony were recorded. Since naive bees often ceased foraging when they received no reward, we allowed up to three bouts on the same flowers in group Naive. The total number of visits recorded thus did not differ significantly between groups (Kruskal–Wallis test: $\chi^2_3 = 1.3$, $p < 0.7$, mean $= 11 \pm 0.3$ (s.e)). A complete dataset was collected from 10 bees in each group—40 bees in total.

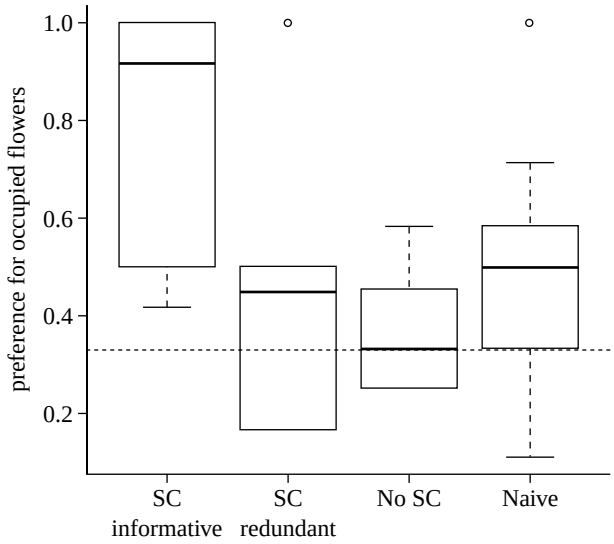


Figure 2. Median preferences for occupied flowers during test trials (social cues, SC). Of the 12 flowers presented, four were 'occupied'; dashed line indicates chance expectations (0.33).

## 3. RESULTS

We found that bees in group SC informative showed significantly higher preferences for occupied flowers than those in each of the other three groups (figure 2; Wilcoxon signed-rank tests; $W = 78$, $p = 0.034$; $W = 94$, $p < 0.01$; and $W = 84$, $p < 0.01$ for groups Naive, No SC and SC redundant, respectively). Thus, when SC were consistently associated with reward, bees made greater use of them than when naive, when they had never previously encountered SC, or when SC had previously proved unreliable.

By contrast, we found no compelling evidence that social cue use degrades when cues prove unreliable, since preferences for the occupied flower did not differ between the groups SC redundant and Naive ($W = 62.5$, $p = 0.36$).

What is the 'default' behaviour in bees that have never had the opportunity to learn about SC? Naive bees showed a preference for occupied flowers, which was significantly higher than chance expectations of 0.33 when only the first flower visit was considered (7 out of 10 subjects chose the occupied flower; binomial test, $p < 0.02$), and bordered on significance overall ($W = 46$, $p = 0.066$). Of the other groups, only bees in group SC informative preferred the occupied flower on the first visit ($p < 0.02$, $p > 0.25$ in both other groups).

## 4. DISCUSSION

When the presence of conspecifics consistently predicted high reward levels, subjects developed a preference for occupied flowers which was significantly stronger than that of naive bees, bees that had foraged alone or bees for which SC had provided no useful information. Naive bees showed a preference for occupied flowers which was significantly above the chance levels on their first flower visit, and a previous study has illustrated that naive bees significantly prefer occupied flowers (Kawaguchi *et al.* 2006); thus, we do not suggest that joining behaviour arises entirely through learning. Instead, our findings demonstrate that joining behaviour in

bumble-bees is a flexible trait that can be positively reinforced through operant conditioning to match local circumstances.

This result complements previous work that has illustrated how animals may learn that a particular socially learnt trait is not useful (Galef & Whiskin 1997), but here we focused on how learning modifies social cue use as a trait in itself, rather than how learning reinforces or degrades socially learnt behavioural preferences. Why does it matter whether learning modifies the use of SC? Laland (2004) pointed out that 'social learning cannot be indiscriminate and individuals should adopt strategies that dictate the circumstances under which they copy from others', based on the combined conclusions of producer–scrounger models (Barnard & Sibly 1981) and evolutionary social learning models (Boyd & Richerson 1985, 1995). Moreover, several empirical results are consistent with the existences of such strategies (Laland 2004; Kendal *et al*. 2005; Toelch *et al*. 2008) including examples from the bee literature. For example, bumble-bees that forage from complex flowers (with long handling times) rely on conspecific scent marks to gauge reward levels to a greater extent than bees that visit only simple flowers (Saleh *et al*. 2006), in accordance with a 'copy when asocial learning is costly' strategy. Experienced honeybee foragers rate their own private information about where particular floral resources are located above spatial information provided by dancers (Grüter *et al*. 2008), but follow dance information if their previous trip was unsuccessful (Biesmeijer & Seeley 2005), in line with a 'copy when established behaviour is unproductive' strategy.

How can such context specificity arise mechanistically? Natural selection may lead to simple preprogrammed heuristics, but positive or negative reinforcement of adaptive or maladaptive use of SC, respectively, seems a straightforward and credible mechanism, at least in a foraging context. Our findings highlight how social cue use, like asocial cue use, can be fine-tuned to local circumstances, allowing animals to be discerning about when to respond to others' behaviour, as theory predicts that they need to be.

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