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Flower choice copying in bumblebees

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We tested a hypothesis originating with Darwin that bees outside the nest exhibit social learning in flower choices. Naive bumblebees, *Bombus impatiens*, were allowed to observe trained bees or artificial bees forage from orange or green flowers. Subsequently, observers of bees on green flowers landed more often on green flowers than non-observing controls or observers of models on orange flowers. These results demonstrate that bumblebees can change flower choice by observations of non-nest mates, a novel form of social learning in insects that could provide unique benefits to the colony.

Keywords: bumblebees; social learning; stimulus enhancement; social information

1. INTRODUCTION

Information exchange about food resources in social hymenoptera commonly occurs through communication among individuals within the nest or through scent marks outside the nest (Detrain *et al.* 1999). Based on field observations, Darwin proposed a different, complementary mechanism, suggesting that bees outside the nest learn to exploit a resource by watching other bees forage (Romanes 1884). Darwin further proposed that bees might have imitated the motor patterns of other bees (observational learning, or imitation).

Darwin's hypothesis raises the possibility that bees of one colony might, through social learning, exploit information about resources acquired by another colony. While there is evidence that the presence of conspecifics at resources increases attraction to those resources in wasps (e.g. Richter & Tisch 1999; D'Adamo *et al.* 2003), bees (Slaa *et al.* 2003) and flies (Prokopy *et al.* 2000; Pinero & Prokopy 2004), such attraction does not necessarily involve learning and no social learning is claimed in those studies. To date, no formal evidence of social learning involving copying of behaviour outside the nest has been reported in social insects. Indeed, work on social learning has focused almost entirely on vertebrates (Heyes & Galef 1996, but see Fiorito & Scotto 1992). We therefore undertook an analysis of social effects on flower foraging in bumblebees.

Bumblebees are social animals with many sister-workers foraging and performing nest duties in a common colony. Information exchange among nest mates permits the colony to track changes in quality and abundance of resources. Successful foragers stimulate foraging activity of nest mates, and workers

learn the scent of nectar carried by foragers into the nest (Dornhaus & Chittka 2004, 2005). Colony size in bumblebees is comparatively small—often fewer than 100 workers (Morse 1982)—suggesting that information available from returning foragers may be limited. Observation of behaviour of bees outside the nest, including that of non-nest mates, might not only affirm information communicated within the nest but could provide additional information about resources otherwise unavailable to the colony. Here we tested whether flower choice by bumblebees was influenced by direct observation of conspecifics outside the nest, and in particular of non-nest mates.

2. MATERIAL AND METHODS

(a) *Insects and arena*

Bumblebee (*Bombus impatiens* CRESSON) colonies were obtained from Koppert Biological Systems (Michigan, USA). Bee colonies were fed fresh pollen daily. Bees from two colonies were tested in a gray rectangular foraging arena (figure 1a). On one wall, six feeder holes were arranged in two vertical rows of three each (figure 1b). When not being tested, bees had access to cotton dental wicks (Richmond Dental, Charlotte) soaked in 20% weight/volume sucrose without any colour cues.

(b) *Live bee models*

Testing of observer bees consisted of two stages, a 10 min observation period immediately followed by a testing phase in which the test bee could access the coloured 'flowers'. The observation period began when a single bee from the observer colony was allowed to enter the observation box adjacent to the foraging arena. Bees from the model hive that had been trained to feed from either orange or green flowers fed freely from the flowers during the observation period. In a previous experiment, bees were able to learn both colours with equal success (Worden *et al.* 2005). To ensure a continuous source of models during the observation period, the model hive was connected directly to the arena so all workers had access to the feeders. After the observation period, model foragers (range = 3–12; mean = 6.3) were removed from the arena, and a new random array of flowers of each colour was placed on the feeder wall with clean, water-soaked wicks. An observer bee was then released into the arena and landings recorded. We analysed the first six landings (one landing per flower in array) that a bee made. Bees that landed fewer than six times were excluded from analysis. Ten bees completed trials in each treatment group: live models on green (LMG), live models on orange (LMO), and a control (C) consisting of the array with no model bees present.

(c) *Artificial models*

A variation on this experiment was performed using a new observer hive, and using artificially constructed bees as models instead of actual bees. The use of artificial bees precluded active communication (including olfactory) between models and observers. Two artificial bees (see electronic supplementary material for details) were placed directly on two wicks of the modelled colour, and two others were suspended by string directly in front of flowers of the modelled colour. Air blown across the arena caused the models to move in a manner similar to hovering bees. Because test bees landed at lower frequency than in the experiment with live models, all landings during the first 10 min in the arena were tallied. Twelve to fourteen bees were tested in each of the following treatment groups: artificial models on green (AMG), artificial models on orange (AMO), and a control (C) consisting of the array with no model bees present.

(d) *Analyses*

All statistical analyses were performed using SPSS v. 12.0 (SPSS Inc., Chicago, IL). Landings on green or orange flowers were converted to proportions for each individual. Proportion data were arcsine square-root transformed prior to analysis with ANOVA and post hoc comparisons with Bonferroni adjustment.

3. RESULTS

(a) *Flower choice with live models*

The experiment with live models showed that model training colour significantly affected colour choices

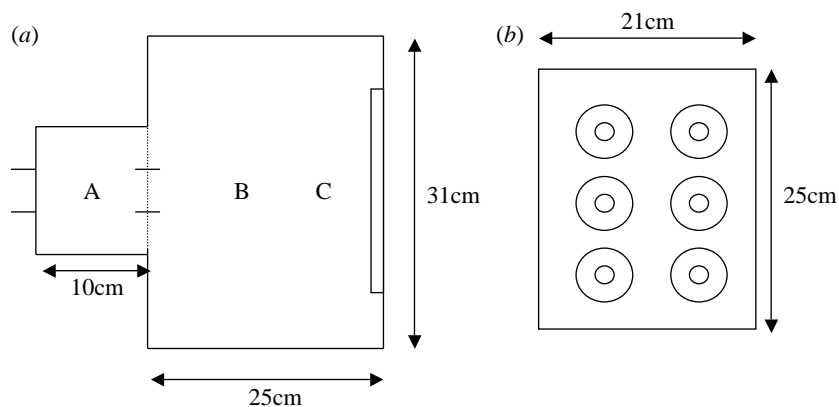


Figure 1. Schematic of the experimental apparatus. (a) The observation box (A) was attached to the modelling arena (B). The observer bee in (A) could view the foraging array (C) that was located 25 cm from the observation box. The barrier separating A from B consisted of a Plexiglas wall bordered by fine wire screening. (b) A close-up view of the foraging array showing the arrangement of the coloured 'flowers'. 'Flowers' were 2.5 cm and 5.5 cm apart vertically and horizontally, respectively, and consisted of coloured paper rings surrounding a central wick.

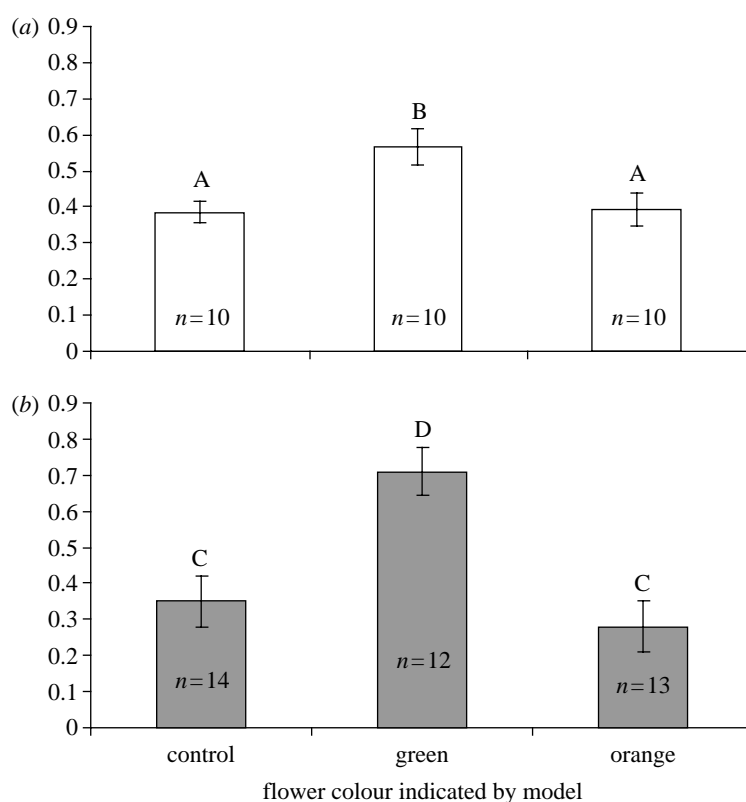


Figure 2. The proportion of landings on green flowers for bees that watched (a) live foraging bee models and (b) artificial models (\pm s.e.). Values within a panel indicated by different letters are significantly different. Pairwise-comparisons between model colours were made with Bonferroni adjustment: (a) GM/C, $p < 0.03$; GM/OM, $p < 0.01$; OM/C, $p > 0.90$ and (b) GM/C, $p = 0.001$; GM/OM, $p < 0.001$; OM/C, $p > 0.90$.

by observer bees (ANOVA, $F_{2,30} = 7.16$, $p < 0.005$). Model number varied between trials, but we found no effect of model number on the proportion of landings on each flower colour when model colour was taken into account (ANOVA, $F_{1,20} = 1.19$, $p > 0.25$). In general, trained models made few landing 'mistakes' in the presence of observers (maximum = 16.7% of landings on unrewarded colour, mean = 5.2 ± 5.6 (s.d.)%). Foragers in the LMG treatment landed proportionately more on green flowers during the test phase than did control bees or bees in the LMO treatment (figure 2a). Examining only first landings made by test bees showed a proportionally greater

effect. Eighty percent of test bees in the LMG treatment landed first on green compared with only 30% and 40% in the C and LMO treatments, respectively (Chi squared tests; $\chi^2_1 = 5.05$, $p < 0.03$, $\chi^2_1 = 3.33$, $p = 0.07$). Landings in the LMO treatment versus control group did not differ.

(b) Flower choice with artificial models

Observers landed 3.7 ± 2.3 (range 2–12) times during the test phase. Results with artificial bee models resembled those with live models. Model treatment significantly affected landings ($F_{2,39} = 11.9$, $p < 0.001$, figure 2b). Test bees in the AMG treatment made

more landings on green flowers than control bees or bees that observed orange models (figure 2b). As with live models, observers of models on orange flowers did not differ from control bees in flower choice (figure 2b). Bees in AMG treatment made 67% of first landings on green compared with 36% by control bees or 23% by AMO bees (Chi squared tests: $\chi_1^2 = 2.48$, $p = 0.12$; $\chi_1^2 = 4.81$, $p = 0.03$, respectively).

4. DISCUSSION

The most parsimonious explanation for our results is that bumblebees are attracted to stimuli that they have seen in association with the presence of live or artificial bees. Our results cannot be explained by bees copying the locations of models because flower location was changed between observation and testing phases. Rather, it appears that bees were copying responses to the coloured target stimuli per se.

An important distinction should be made between the demonstration of direct attraction to a model or signals produced by a model (Richter & Tisch 1999; Prokopy *et al.* 2000; D'Adamo *et al.* 2003; Slaa *et al.* 2003; Pinero & Prokopy 2004), and our demonstration of attraction to floral stimuli even when model or model signals are not present. The former process requires no learning, whereas the latter is generally considered social learning (Heyes 1994).

Categories and terminology for social learning remain ambiguous and in debate (Heyes 1994; Heyes & Galef 1996). In some frameworks (Galef 1988), our results would be considered evidence of stimulus enhancement and local enhancement, which are lumped together. In other frameworks (Whiten & Ham 1992), our results would qualify as stimulus enhancement but not local enhancement. Alternatively, this may be an example of observational conditioning, whereby observers matched the models' responses to green flowers (Heyes 1994; C. M. Heyes, personal communication).

The present results may be of profound importance in how effectively a bee colony tracks spatial and temporal change in floral resources. Because multiple colonies typically forage in the same general area (Chapman *et al.* 2003), copying of non-nest mates may provide information about productive food sources that have not yet been discovered by a given colony. The finding that bees copy the behaviour of non-nest mates raises the intriguing possibility that bees might learn from watching other species of insects forage in the field. Indeed, Darwin's observations (Romanes 1884) of honeybees and bumblebees suggested to him that this occurs. Recent work by Slaa *et al.* (2003) demonstrated that attraction by stingless bees to artificial flowers depends on the presence or absence of another bee species. Whether stingless bees show social learning in conjunction with this attraction remains to be tested; certainly, such attraction could facilitate a copying process by promoting observation of individuals. In this vein, preliminary field data on bumblebees (*B. morrisoni* CRESSON) suggests that wild free-foraging bees are attracted to flowering plants that bear artificial bees (B. Worden, unpublished data).

Field studies of bees might not only confirm the relevance of our work to bee behaviour in nature but could elucidate contexts in which social learning is used. In our experiments, for example, social learning was selective, being observed toward green flowers but not orange ones. This selectivity could reflect an innate bias towards orange overwhelming effects of social learning. Alternatively, bees may be inherently more likely to copy flower choices when the observed flower is of a novel or less-preferred colour. For example, capuchin monkeys copied the token preferences of models when tokens were novel, but not when tokens were familiar (Brosnan & de Waal 2004). It would be useful to know if variation in copying occurs in relation to variation in flower types in nature.

In closing, evidence continues to mount that there is no strict dichotomy between vertebrate and invertebrate cognition (Fiorito & Scotto 1992; Giurfa *et al.* 2001; Srinivasan & Zhang 2003). Our work adds to the growing body of research in social hymenoptera that demonstrates that brain size does not necessarily limit an animal's cognitive abilities.

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