Hindawi Publishing Corporation
Psyche
Volume 2013, Article ID 768108, 8 pages
http://dx.doi.org/10.1155/2013/768108

Research Article

Social Learning in Bumblebees (*Bombus impatiens*): Worker Bumblebees Learn to Manipulate and Forage at Artificial Flowers by Observation and Communication within the Colony

Hamida B. Mirwan and Peter G. Kevan

Canadian Pollination Initiative (CANPOLIN), School of Environmental Sciences, University of Guelph, Guelph, ON, Canada N1G 2W1

Correspondence should be addressed to Hamida B. Mirwan; hmirwan@uoguelph.ca

Received 17 May 2013; Revised 7 September 2013; Accepted 8 September 2013

Academic Editor: James C. Nieh

Social learning occurs when one individual learns from another, mainly conspecific, often by observation, imitation, or communication. Using artificial flowers, we studied social learning by allowing test bumblebees to (a) see dead bumblebees arranged in foraging positions or (b) watch live bumblebees actually foraging or (c) communicate with nestmates within their colony without having seen foraging. Artificial flowers made from 1.5 mL microcentrifuge tubes with closed caps were inserted through the centres of blue 7 cm plastic discs as optical signals through which the bees could not forage. The reinforcer reward syrup was accessible only through holes in the sides of the tubes beneath the blue discs. Two colonies (A and B) were used in tandem along with control (C and D) colonies. No bee that was not exposed (i.e., from the control colonies (C and D)) to social learning discovered the access holes. Inside colony B, we imprisoned a group of bees that were prevented from seeing or watching. Bees that saw dead bumblebees in foraging positions, those that watched nest-mates foraging, and those that had only in-hive communication with successful foragers all foraged successfully. The means of in-hive communication are not understood and warrant intense investigation.

1. Introduction

Social learning is defined by ethologists as any learning from conspecifics [1] (but we note that social learning between species is known) and mostly involves observation, imitation by observing and replicating another's behavior, and modeling to transmit the learned behaviour from one individual to others [2]. Social learning through individuals' interactions with other animals or their products encompasses attention, memory, and motivation; social theory calls social learning a bridge between behaviourism (i.e., learning based upon behaviour that is acquired through conditioning which occurs through interaction with the environment) and cognitive learning (i.e., learning by using reason, intuition, and perception) [3–6]. Research on social learning has focused largely on vertebrates [7, 8]. However, a growing number of researchers have shown recently that bees and other small brained animals can also learn through acquisition of information by social transmission [9–12]. Nonetheless, the possibility that social learning might extend to practical knowledge (skills), in addition to simple declarative knowledge (facts), remains mostly untested in invertebrates [9].

Insects, especially eusocial bees, show remarkably complex learning abilities [11, 13–15], and social information often leads to the relatively long-term changes in behaviours that constitute social learning. The dance communication of honeybees (*Apis* spp.) [16, 17], sounds in *Melipona costaricensis* [18], and other means of communication in other bees [19], ants [20], wasps [21, 22], and Octopuses [23] serve as examples. As Giurfa's short but informative review notes simple mechanisms based on elemental associations, either Pavlovian or operant conditions may account for social learning in animals with miniature brains, so social learning should not be considered surprising or a highly cognitive ability [11].

To assess the potential for social learning in bumblebees (*Bombus impatiens*), we investigated the spread of foraging techniques from experienced bees to inexperienced bees in the same and different colonies. We explored the following three different paradigms: (a) using a model (positioned dead bees), (b) observation with imitation (of foraging live bees), and (c) intracolony communication within the domicile.

2. Material and Methods

2.1. General Methods. Experiments were made in indoor screened flight cages (2.15 m long × 1.20 m wide × 1.80 m tall) with grey floors. The bees used were foragers of *Bombus impatiens* (Cresson, 1863) (Hymenoptera: Apoidea) from queen-right colonies of 30–40 workers/colony (supplied by BioBest Biological Systems, Canada (Leamington, Ontario)). Moveable screens on one side of the cages allowed experimenter access. Four colonies were used in this experiment, colony A was placed in cage I, colony B was placed in cage II, and colonies C and D (control) were placed in cages III and IV. Each was connected to a small, outer cage (30 × 23 × 20 cm) (holding area) attached to the main flight cage (testing arena) by gated, wire-mesh tunnels that allowed experimental control of the bees' entry to and egress from the flight cage. Colonies, when not being tested, had constant pollen supplies and their diets were supplemented with sugar syrup. Individually, foragers were marked on the thoracic dorsal surface with uniquely numbered and coloured tags (Opalith Plättchen, Christian Graze KG, Germany).

The experimental arena of artificial flowers (Figure 1) was placed in the flight cage 165 cm from where the bees entered and exited. It comprised a green Styrofoam base 45 × 35 × 5 cm with 8 artificial flowers. The first step was to allow naive bees to encounter simple centrifuge tubes which were mounted in a green Styrofoam base (the tubes were hidden and the forager could access the syrup only through the opening of the tube). Once they were accustomed to foraging at those tubes for a week to ten days, they were marked individually and then challenged with learning tasks as described for each experiment (below).

2.1.1. Artificial Flowers. Artificial flowers were made of 1.5 mL centrifuge tubes inserted into the centres of blue plastic discs, 7 cm in diameter. The centrifuge tube was capped so that the bees could not obtain the contained syrup (50% sucrose w:w as the reinforcer reward; the amount of syrup was not controlled but was replenished as soon as it was exhausted) from the surface of the plastic disc. Instead, a small hole (0.5 cm in diameters) had been drilled into one side of each centrifuge tube just below the lip; see Figure 2. The artificial flower was then attached to a yellow pipette tube mounted on 35 × 52 cm Styrofoam base. Eight flowers in two rows of four flowers were each arranged with the bored holes facing the central aisle between the rows of flowers and so presented to the bees in each experiment.

Thus, the bees could orientate to the blue disc of the artificial flower but could not obtain syrup except by going under the disc to the hole in the tube's wall. Test bees were assessed based on their abilities to learn and replicate foraging behaviours without actually having performed them.

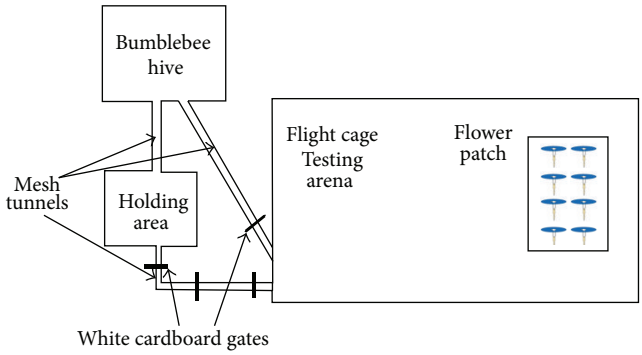

Figure 1: Experiment setup with hive, holding area, flight cage, testing arena, patch of artificial flowers, and mesh tube routes with gates by which the bees were allowed to enter and exit the flight cage. The bees, in training or trained, exited from the hive and could take only one route through the holding area to the testing arena in the main flight cage. The exiting bees were not allowed to use the diagonal route because the gate in it was kept closed. The gates after the holding area were opened and closed to allow single bees to enter the testing arena during testing. The bees returned to their hive from the testing area via the diagonal mesh tube route, the gate of which was opened as necessary. Note that the main flight cage's end wall, through which the mesh tunnels ran, was a wooden panel so that the bees in the tunnels or in the holding area could not see the flower patch.

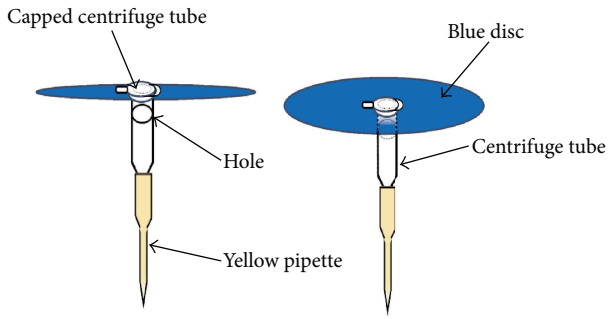

Figure 2: Artificial flowers were made of 1.5 mL centrifuge tubes inserted into the centres of blue plastic discs, 7 cm in diameter. The centrifuge tube was capped so that the bees could not obtain the contained syrup from the surface of the plastic disc. Instead, a small hole (0.5 cm in diameters) had been drilled into one side of each centrifuge tube just below the lip.

The Experimental Groups Were as Follows

(1) A group of foragers from colony A (A2) were used from which bees were tested without a model for 2 trials with 30 minutes of giving-up time; then, the model (dead bee) was introduced and the group was allowed to forage alongside models pinned in the robbing position.

(2) A group of foragers from colony A (A1) were provided with enough food (syrup and pollen) while imprisoned so that they could observe group A2 foragers for 10 hours. They were then released and allowed to forage alone.

(3) A group of foragers from colony B (B1) were provided with enough food (syrup and pollen), while imprisoned and treated as foragers in group A1, except that they were able to watch foragers from a different colony (colony A) rather than from their own colony.

(4) A group of foragers from colony B (B2) were kept contained inside the colony and not allowed to forage from the artificial flowers. They had the opportunity to interact (inside the nest) with group B1 for 24 hours and then were allowed to forage alone.

(5) Foragers from control colonies (colony C with 15 subject bees and colony D with 10 subject bees) were challenged to forage through "the access holes" of the artificial flowers without models nor opportunity to watch other foragers on the artificial flowers nor opportunity to communicate with foragers that had successfully foraged at the artificial flowers. They were allowed 30 minutes to succeed, but none did.

2.1.2. Experimental Procedures. Over a period of several days, individually marked bees were trained to forage from simple centrifuge tubes (described above).

Following the initial training, the bees from the control colonies, colonies C and D, were tested by challenging them with the 8 artificial flowers described and arranged above with 30 minutes of giving-up time. There was no need to replace the flowers in this experiment because no bee foraged successfully at them.

From test colony A, which was placed in cage I, individually marked worker bees were segregated into two groups of bees (A1 with 12 bees and A2 with 14 bees). One group (A1) was removed from the colony and imprisoned in a mesh tube (20 cm long and 3 cm diameter with 0.4×0.4 mm mesh) kept out of sight of the experimental cage; these bees were provided with enough food (syrup and pollen). These bees were to be placed later in the aisle between the two rows of artificial flowers. Group A2 (14 individuals) were prevented from leaving the colony and foraging until testing could be started the next day. Once the A1 bees had been sequestered, bees in group A2 were used for testing one by one. Each bee from group A2 was released and allowed to forage at the artificial flowers without dead bees in place for two trials with 30 minutes of giving-up time; none of them were successful to forage. After two trials of giving up, a model (dead bee) was introduced. At this point, newly killed bees were placed on the artificial flowers with their heads at the access hole. The dead bees came from the same colony (A) and had been killed by freezing at -18°C one day before the experiment and allowed to thaw and warm to ambient air temperature for 3 hours before the experiment started. Each bee from group A2 was released and allowed to forage at the artificial flowers with dead bees in place. After each bee from group A2 had made three successful foraging visits to any one of the artificial flowers, dead bees in place, we replaced the used artificial flowers with cleaned ones that did not have dead bees in place. This avoided the possibility that pheromone signals could influence the results. The visits of each of the A2 bees to the artificial flowers with (3 trials for each of 10 bees) and without dead bees (7 trials for each of the same 10 bees) were observed and timed for a total of 10 foraging bouts; access time was measured by using a stop watch, and the time started when the subject bee entered the testing arena and stopped when the subject bee started to probe for the syrup.

In the follow-up experiment, the cohort of 10 bees from the same colony (group A1) that had been imprisoned was placed in a mesh tube size (as described above) between the array of artificial flowers so that they could watch the successful experienced foragers (A2 bees) noted above. The A1 bees had the opportunity to watch the A2 bees at work for 10 daylight hours and were not allowed to return home until the next morning (at 8 am.), so preventing them from having communication with their nestmates (except for watching during the day), for 20 hours. The A1 bees, upon release in the morning, voluntarily and immediately returned to their hive but within 5 minutes started to reemerge from the domicile. They were then allowed to forage singly at the experimental array of new and clean artificial flowers without the experienced A2 bees present. The visits of each of these A1 bees to the artificial flowers were observed and timed for a total of 10 foraging bouts.

In a tandem experiment to test if the bees could communicate within the hive how to forage on the artificial flowers, we used a completely different colony (B) which was placed in cage II. In colony B, we segregated two cohorts of 12 sister or half-sister worker bees each of individually marked bees (as above). The workers in colony B (cage II) were allowed to forage freely from 8 microcentrifuge tubes not provided with artificial floral discs or holes in the walls. One cohort (B1) was later imprisoned in a mesh tube; these bees were provided with enough food (syrup and pollen) (as described above) and transported to cage I, where they were placed in the array of artificial flowers (as described above for A1 bees) and allowed to watch foragers from colony A forage for 10 hours. The same protocol for A1 bees was used to treat the imprisoned workers from colony B, except that the mesh tube prison and its inmates were removed from cage I for the night to the bench supporting the cage. In the morning the prison and its inmates of B1 bees were returned to cage II, where the inmates were released. As with the A1 bees as described above, the B1 bees voluntarily and immediately returned to their hive but within 5 minutes started to reemerge from the domicile. At the same time, the second cohort (B2) was allowed to forage freely at plain microcentrifuge tubes. Thus, the B2 bees had no opportunity to come into contact with, or to see, the artificial flowers with the holes in the microcentrifuge walls; group B2 was prevented from leaving the colony and foraging until they were tested after their nestmate B1 finished testing.

After the B1 bees had been returned to their home cage in the morning, after being imprisoned in the mesh tube overnight, and had reentered their home domicile, bees from both cohorts started to exit from their domicile but were denied access to the main cage. At this time, an array of

8 artificial flowers (with discs and holes in the walls) was placed into cage II. Then, only B1 bees were allowed to forage individually at that array and the B2 bees were denied entry into the main part of the cage. The B1 bees were each allowed to forage from the artificial flowers (newly cleaned for each trial and each bee) three times. After that, they were allowed to forage at the flowers 7 more times. Thus, the B2 bees still had no opportunity to come into contact with, or to see, the artificial flowers with the holes in the microcentrifuge walls, but they had contact with experienced nestmates, the B1 bees. The next day, B2 bees were allowed to forage at newly cleaned artificial flowers in the standard array. These bees were observed for 3 trials, followed by another 7 (as described above), and the durations of the foraging bouts were recorded. At this time, all bees from the first cohort (B1) were prevented from entering the main cage. At no time during the experiment were bees of both cohorts allowed to forage at the artificial flowers at the same time.

2.2. Statistical Analyses. To compare between groups and trials, we used one-way repeated measurement (using sigma plot statistic v12.0), and to isolate the group or groups that differed from the others we used a multiple comparison procedure. The duration for the manipulation of the artificial flowers on the first visit by foragers was used for interexperimental comparisons both within and between colonies (groups). Power of performed test with alpha = 0.050 : 1.000. We used Multiple Comparison Procedures (Holm-Sidak method): All pairwise and overall significance level = 0.05.

For comparison between the two groups of learning through observation, we used *t*-test.

3. Results

Bees from the control colonies (C and D) in cages III and IV had no opportunity for social learning, and all subject bees, 15 bees from colony C and 10 bees from colony D, which were observed proved incapable of foraging successfully at the artificial flowers, with 30 minutes of giving-up time.

None of the 14 tested bees colony A (in cage I) group (A2) when challenged by presenting the artificial flowers without dead bees in place for two trials with 30 minutes of giving-up time were successful to forage. 10 out of 14 (the rest gave up and did not show up for more testing) of the group (A2) were able to see dead bees at all of the 8 flowers as they foraged freely from their colony. When they foraged, they did so by climbing the artificial stem (pipette tube) of the flower, positioning themselves beside the dead bee under the disc, and taking syrup. These bees were not at first fully adept at foraging beside the dead bees, but after about 3 trials they became adept at the task (Figure 3). After having had that experience and when the dead bee was absent, those same experienced bees foraged successfully from new and cleaned artificial flowers. However, they did not require familiarization with the dead bee-less artificial flowers and were fully adept on their first visit (Figure 3).

In the follow-up experiment, a cohort of 10 different bees from the same colony (A1) that had been imprisoned in the

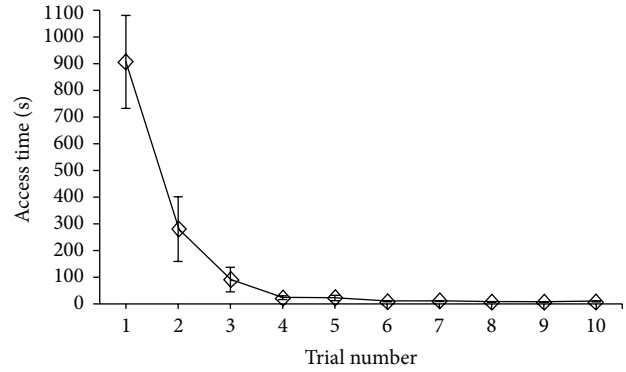

Figure 3: The learning curve (time/sec) (±SE) taken to access and forage on syrup for 10 initially naive workers of *Bombus impatiens* which were allowed to forage freely, but only one at a time, at artificial flowers with and without dead bees present. After the bees had demonstrated their ability to forage at the flowers with dead bees present (i.e., after 3 trails), those flowers were replaced with cleaned ones without dead bees present. The activities of the foragers were recorded for a further 7 visits. H_0 showing that the durations for successful foraging are independent of experience is rejected ($F_{9,9} = 19.7$; $P < 0.001$).

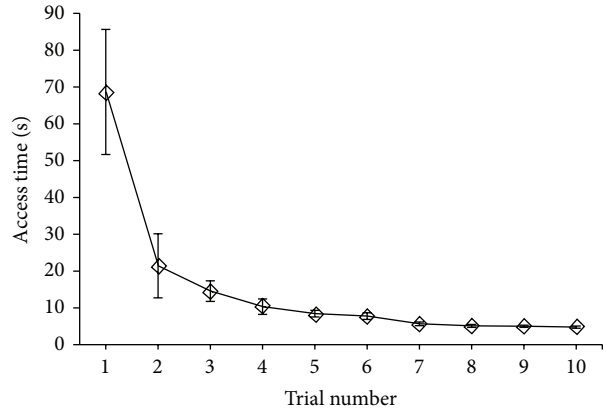

Figure 4: The learning curve (time/sec) (±SE) taken to access and forage on syrup for 9 workers of *Bombus impatiens* which were allowed to watch experienced foragers at artificial flowers for 10 hours and held incommunicado overnight. In the morning these bees demonstrated their ability to forage at the flowers after 3 trails. The flowers were replaced with cleaned ones after each of the first three trials and for each individual bee tested. The activities of the foragers were recorded for a further 7 visits. H_0 showing that the durations for successful foraging are independent of experience of having watched nestmates forage is rejected ($F_{8,9} = 10.7$; $P < 0.001$).

mesh tube was placed between the arrays of artificial flowers, so that they could watch successful experienced foragers for a day (the A2 bees) at first, typically land on the upper surface of the coloured disc of the artificial flower, and then crawl under and down to access the reinforcer syrup through the holes in the sides of the microcentrifuge tubes. After about 3 visits, these A1 bees flew directly to the openings on the sides of the microcentrifuge tubes to forage (Figure 4).

To assess the importance of watching active foragers versus the presence of the dead-bee model, we compared

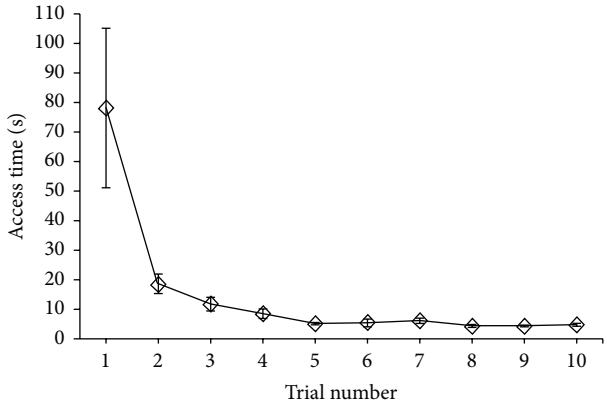

Figure 5: The learning curve (time/sec) (±SE) taken to access and forage on syrup for 9 workers of *Bombus impatiens* which were allowed to watch experienced foragers (from different colony (colony A)) at artificial flowers for 10 hours and held incommunicado overnight. In the morning these bees demonstrated their ability to forage at the flowers after 3 trails. The flowers were replaced with cleaned ones after each of the first three trials and for each individual bee tested. The activities of the foragers were recorded for a further 7 visits. H_0 showing that the durations for successful foraging are independent of experience of having watched other, non-nestmate, bees forage is rejected ($F_{8,9} = 7.7$; $P < 0.001$).

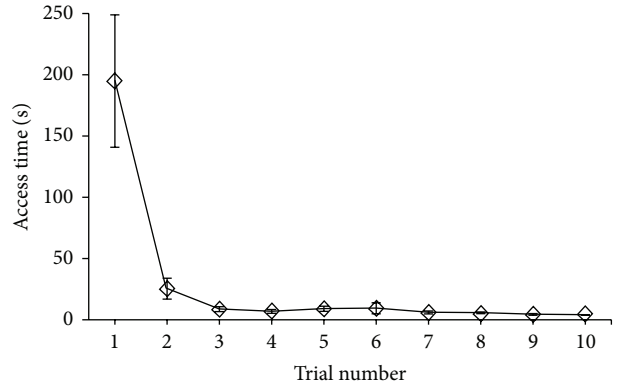

Figure 6: The learning curve (time/sec) (±SE) taken to access and forage on syrup for 9 workers of *Bombus impatiens* which were allowed to contact with their nestmates B1 (i.e., they were watching the experienced bees from colony A). The B2 bees were kept inside the hive and then, after release to forage, had apparently learned to manipulate the artificial flowers through communication with their nestmates. H_0 showing that the durations for successful foraging are independent of experience of having communicated with their nestmates is rejected ($F_{8,9} = 21.4$; $P < 0.001$).

the time it took for the bees to manipulate (i.e., to land on the flowers, orient to their correct positions to forage, and then to imbibe syrup) the flowers on their first visit (cf. Figures 4 and 3). The difference in time is huge. In the model with dead bees, the initial visit to succeed at obtaining the reinforcer syrup was 900 ± 174.8 secs (mean ± SE; $n = 10$ bees), whereas after watching, the bees took only 69 ± 17.4 secs ($n = 9$ bees) to forage successfully (Student's $t = 4.53$; df = 17; $P = 0.0003$).

Following experiments on the first colonies (colonies A, C, and D), we introduced to the experimental set-up, another colony (colony B) in another cage (II).

The watcher worker bees from colony B, cohort 1 (B1 bees), showed the same behaviour as A1 bees (from colony A) when challenged with the artificial flowers (see Figures 4 and 5).

To assess the importance of watching active nestmate foragers versus non-nestmate foragers, we compared the time it took for the bees to manipulate the flowers on their first visit (cf. Figures 4 and 5). There is no statistical difference in time for either group to succeed at obtaining the reinforcer syrup which was 69 ± 17.42 secs (mean ± SE; $n = 9$ bees) after watching nestmates versus 78 ± 27.14 secs ($n = 8$ bees) after watching non-nestmates (Student's $t = 0.3$; df = 15; $P = 0.77$).

The bees in cohort B2 had no chance to see artificial flowers with or without dead bees in foraging positions nor to observe their nestmates or non-nestmates foraging at the artificial flowers. Cohort B2 bees had only the opportunity to communicate with their nestmates, while their nestmates were foraging, with exclusive access, to the artificial flowers. Figure 6 presents the surprising results that B2 bees had somehow learned how to forage from the artificial flowers.

To assess the importance of communicating with active nestmate foragers versus no communication and versus learning by observing a model (dead bees) or active foragers (nestmates or not), we compared the time it took for the bees to manipulate the flowers on their first visit (cf. Figures 6, 3, 4, and 5). The bees that had opportunity for in-nest communication only before foraging took longer time than the bees that had watched either nestmates (Figure 5) or non-nestmates (Figure 4) forage. However, they were quicker than the bees that had learned by having only the dead-bee models in place (Figure 3). Statistical analysis by ANOVA supports those observations ($F_{3,9} = 2.3$; $P = 0.046$); durations to successfully obtaining the reinforcer syrup on the first experimental encounter rank in the following order: watcher of nestmates (69 secs; Figure 4) = watcher of non-nestmates (78 secs; Figure 5) < communicators (195 secs; Figure 6) < observers of dead bees (906 secs; Figure 3) < no clues provided (all 15 bees unsuccessful; ∞ secs).

We provide the detailed statistical tables for the results of our one-way repeated measures for ANOVA (Table 1).

4. Discussion

When naive bumblebee workers first encounter a flower from which they can obtain a reward (e.g., nectar or pollen), they must learn how to manipulate it. Laverty [24] has shown that bumblebee workers (*Bombus impatiens*, *B. fervidus*, *B. vagans*, *B. rufocinctus*, and *B. consobrinus*) become increasingly adept (i.e., by speed and accuracy of manipulation) with increasing experience. Moreover, Dornhaus and Chittka [25, 26] noted that returning foragers stimulated colony-level foraging activity. Baude et al. [12] described the intercolony facilitation in foraging by *B. terrestris* as the use of inadvertent social information (ISI), whereby foragers watched each other's activities and learned from that. Leadbeater and Chittka [27] showed that worker bumblebees (*B. terrestris*) learned to discriminate between two kinds of flowers, depending on

Table 1: Statistical values from repeated one-way Analysis of Variance of the findings from experiments in which dead bees were used as models to aid in the learning process for foraging by living bees, in which living bees were able to watch other living bees (nestmates and nonnestmates) forage to aid in the learning process and in which living bees which had no opportunity to observe models or other living bees foraging learned to forage by within-colony communication.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	Probability
Using dead bees in the foraging position on the artificial flowers (Figure 3)					
Between bees	9	992368	110263		
Between trials	9	7234272	803808	19.68	<0.001
Residual	81	3306794	40824		
Total	**99**	**11533434**			
Watching nestmates (Figure 4)					
Between bees	8	5425	678.14		
Between trials	9	30850	3427.83	10.74	<0.001
Residual	72	22961	318.91		
Total	**89**	**59237**			
Watching nonnestmates (Figure 5)					
Between bees	8	3948	493.55		
Between trials	9	38014	4223.78	7.69	<0.001
Residual	72	39528	549		
Total	**89**	**81490**			
Communication within the domicile (Figure 6)					
Between bees	8	20619	2577.37		
Between trials	9	286156	31795.11	21.37	<0.001
Residual	72	107107	1487.61		
Total	**89**	**413882**			
The difference between four groups of tested bees					
Between learning type	3	105010	35003.61		
Between trial	9	331231	36803.44	2.30	0.046
Residual	27	431755	15990.95		
Total	**39**	**867997**			

whether or not they contained nectar, faster if conspecific foragers were present and foraging at the same time than if they were alone. They also noted that if dead bumblebee models were present in posed foraging positions, the effect was the same; the experimental bees learned faster than if no dead bee was present. Their results indicate that social learning at flowers can be a component of foraging efficiency. More recently they have shown that nectar robbing can spread socially among bumblebees foraging at horizontally oriented tubular artificial flowers [9, 28] (probably by watching other bees and encountering holes already made in the flowers). They state that social learning within the nest is unlikely, but our results indicate otherwise. It is possible that measures of rates of learning (e.g., Figures 3–6 in our study) also indicate effects of stimulation by experience or the presence of other foragers. Even though our results indicate that those bees that watched living foragers (i.e., nestmate or none nestmate) learned faster than those which could see dead bees (cf. Figures 3, 4, and 5). We raise the idea that the difference could reflect stimulation's accelerates social learning. We also noted that Worden and Papaj [29] used stationary and moving model bees and found quicker responses of trained forager bees to the latter. It is also known that bumblebees, as other bees, communicate socially through pheromones [30] and can discriminate between recently visited flowers and flowers which have not been visited for some time [31–33]. Renner and Nieh [34] showed that foragers of *B. impatiens* can associate scentedness of rewarding food sources (flowers) and share this ability with their nestmates. The same phenomenon has also been shown for other species, for example, *B. terrestris* [35–38]. Physical contact, especially antennal and body contact, may be important in the transmission of information on the location, quality, quantity, and nature of floral resources in honeybees [39] and stingless bees [40, 41]. However, little is known about the role of physical contact in the lives of bumblebees. Food exchange (trophallaxis) may be the most primeval form of social communication in eusocial bees, but not bumblebees [42, 43], and may provide information about food quality and odour for some species. Bumblebees may be able to gain such information by sampling resources (nectar and pollen) once deposited in the colony. Observation and social learning strengthen a colony's

foraging efficiency both by intake of more resources by the same colony and by promoting a competitive stratagem by learning from rival colonies [44].

Our experiments were designed to extend our understanding of the potential for social learning in bumblebees following from the work of Worden and Papaj [29], Kawaguchi et al. [45], and Leadbeater and Chittka [9, 46].

We controlled for external cues, such as scentedness of or pheromone residues on the artificial flowers (cleaned as used) and reinforcer syrup (sucrose in water has no vapour pressure and was always made fresh for each experiment). The domiciles used were always in the same locations relative to the arrays of artificial flowers. The visual signals were highly controlled such as the colour of the artificial flowers, the dead bees were posed on them and the active foragers that imprisoned bees could watch.

5. Conclusion

Our results indicate that workers of *B. impatiens* are highly observant and learn through social communication. Although they were relatively slow to learn to forage from artificial flowers with dead conspecifics posed as foragers, they were much faster if they had the opportunity to observe, but not join, active foragers from either their own colony or from another. Surprisingly, when we allowed workers that had never had a chance to visit nor see an artificial flower, but had had contact with nestmates that were successful foragers, the experimental (naive) workers were adept at handling the artificial flowers. All workers that were confronted with the artificial flowers but no opportunity to see posed dead bees, active foragers, or communicate within the colony failed to forage successfully. It would be useful for other researchers to repeat our experiment, with appropriate modifications, to test if our results can be repeated or explained.

It is often assumed that observational learning and imitation (or copying) lie at the heart of social transmission of information and learning [47, 48]; there are other ways novel behaviour can be transmitted socially (e.g., through tactile, vibratory, and olfactory senses), especially in bees. We are not able to explain how workers that had never had a chance to visit nor even see an artificial flower, but only had had contact with nestmates that were successful foragers and only in the nest, became so quickly adept at handling the artificial flowers.

Evidence, including that which we present herein, continues to mount that there is no strict dichotomy between vertebrate and invertebrate cognition [23, 49, 50]. 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. More imaginative experiments are needed to determine the role of social learning, the amount and type of information that need to be transmitted, and how that body of information contributes to Darwinian fitness.

Acknowledgments

The authors thank the Ministry of Higher Education, Libya, Canadian Bureau for International Education, Ottawa, Canada, and the Canadian Pollination Initiative (NSERC-CANPOLIN for which this is contribution no. 99) for funding. BioBest Canada, Leamington, Ontario, kindly provided the colonies of *Bombus impatiens* for this study.

References

[1] S. J. Shettleworth, *Cognition, Evolution, and Behavior*, Oxford University Press, Oxford, UK, 1998.

[2] A. Whiten and R. Ham, "On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research," *Advances in the Study of Behavior*, vol. 21, no. C, pp. 239–283, 1992.

[3] A. Bandura, *Social Learning Theory*, General Learning Press, New York, NY, USA, 1977.

[4] A. Bandura, *Social Foundations of Thought and Action*, Prentice-Hall, Englewood Cliffs, NJ, USA, 1986.

[5] L. A. Giraldeau and T. Caraco, *Social Foraging Theory*, Princeton University Press, Englewood Cliffs, NJ, USA, 2000.

[6] L. A. Giraldeau, T. Caraco, and T. J. Valone, "Social foraging—individual learning and cultural transmission of innovations," *Behavioral Ecology*, vol. 5, no. 1, pp. 35–43, 1994.

[7] L. Lefebvre, "The opening of milk bottles by birds: evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission," *Behavioural Processes*, vol. 34, no. 1, pp. 43–53, 1995.

[8] C. Heyes and B. J. Galef, *Social Learning and the Roots of Culture*, Academic Press, San Diego, Calif, USA, 1996.

[9] E. Leadbeater and L. Chittka, "Social transmission of nectar-robbing behaviour in bumble-bees," *Proceedings of the Royal Society*, vol. 275, no. 1643, pp. 1669–1674, 2008.

[10] E. Leadbeater and L. Chittka, "Do inexperienced bumblebee foragers use scent marks as social information?" *Animal Cognition*, vol. 14, no. 6, pp. 915–919, 2011.

[11] M. Giurfa, "Social learning in insects: a higher-order capacity," *Frontiers in Behavioral Neuroscience*, vol. 6, article 57, 2012.

[12] M. Baude, I. Dajoz, and É. Danchin, "Inadvertent social information in foraging bumblebees: effects of flower distribution and implications for pollination," *Animal Behaviour*, vol. 76, no. 6, pp. 1863–1873, 2008.

[13] M. Giurfa, "Cognitive neuroethology: dissecting non-elemental learning in a honeybee brain," *Current Opinion in Neurobiology*, vol. 13, no. 6, pp. 726–735, 2003.

[14] R. Menzel, G. Leboulle, and D. Eisenhardt, "Small brains, bright minds," *Cell*, vol. 124, no. 2, pp. 237–239, 2006.

[15] P. G. Kevan and R. Menzel, "The plight of pollination and the interface of neurobiology, ecology and food security," *Environmentalist*, vol. 32, no. 3, pp. 300–310, 2012.

[16] K. von Frisch, *The Dance Language and Orientation of Bees*, Belknap Press, Cambridge, Mass, USA, 1993.

[17] R. W. K. Punchihewa, N. Koeniger, P. G. Kevan, and R. M. Gadawski, "Observations on the dance communication and natural foraging ranges of the three honeybee species in Sri Lanka," *Journal of Apicultural Research*, vol. 24, no. 2, pp. 168–175, 1985.

[18] I. Aguilar and D. Briceño, "Sounds in *Melipona costaricensis* (Apidae: Meliponini): effect of sugar concentration and nectar source distance," *Apidologie*, vol. 33, no. 4, pp. 375–388, 2002.

[19] J. C. Nieh, "Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini)," *Apidologie*, vol. 35, no. 2, pp. 159–182, 2004.

[20] D. E. Jackson and F. L. W. Ratnieks, "Communication in ants," *Current Biology*, vol. 16, no. 15, pp. R570–R574, 2006.

[21] R. L. Jeanne, "Chemical communication during swarm emigration in the social wasp *Polybia sericea* (Olivier)," *Animal Behaviour*, vol. 29, no. 1, pp. 102–113, 1981.

[22] H. Schöne and J. Tengo, "Competition of males, courtship behaviour and chemical communication in the digger wasp *Bembix rostrata* (Hymenoptera, Sphecidae)," *Behaviour*, vol. 77, pp. 44–66, 1981.

[23] G. Fiorito and P. Scotto, "Observational learning in *Octopus vulgaris*," *Science*, vol. 256, no. 5056, pp. 545–547, 1992.

[24] T. M. Laverty, "Bumble bee learning and flower morphology," *Animal Behaviour*, vol. 47, no. 3, pp. 531–545, 1994.

[25] A. Dornhaus and L. Chittka, "Information flow and regulation of foraging activity in bumble bees (*Bombus* spp.)," *Apidologie*, vol. 35, no. 2, pp. 183–192, 2004.

[26] A. Dornhaus and L. Chittka, "Bumble bees (*Bombus terrestris*) store both food and information in honeypots," *Behavioral Ecology*, vol. 16, no. 3, pp. 661–666, 2005.

[27] E. Leadbeater and L. Chittka, "Social information use in foraging insects," in *Food Exploitation by Social Insects: Ecological, Behavioral, and Theoretical Approaches*, S. Jarau and M. Hrncir, Eds., CRC Press, Boca Raton, Fla, USA, 2009.

[28] D. F. Sherry, "Social learning: nectar robbing spreads socially in bumble bees," *Current Biology*, vol. 18, no. 14, pp. R608–R610, 2008.

[29] B. D. Worden and D. R. Papaj, "Flower choice copying in bumblebees," *Biology Letters*, vol. 1, no. 4, pp. 504–507, 2005.

[30] T. D. Wyatt, *Pheromones and Animal Behaviour: Communication by Smell and Taste*, Cambridge University Press, Cambridge, UK, 2003.

[31] S. A. Cameron, "Chemical signals in bumble bee foraging," *Behavioral Ecology and Sociobiology*, vol. 9, no. 4, pp. 257–260, 1981.

[32] D. Goulson, S. A. Hawson, and J. C. Stout, "Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species," *Animal Behaviour*, vol. 55, no. 1, pp. 199–206, 1998.

[33] J. Wilms and T. Eltz, "Foraging scent marks of bumblebees: footprint cues rather than pheromone signals," *Naturwissenschaften*, vol. 95, no. 2, pp. 149–153, 2008.

[34] M. A. Renner and J. C. Nieh, "Bumble bee olfactory information flow and contact-based foraging activation," *Insectes Sociaux*, vol. 55, no. 4, pp. 417–424, 2008.

[35] U. Schmitt and A. Bertsch, "Do foraging bumblebees scent-mark food sources and does it matter?" *Oecologia*, vol. 82, no. 1, pp. 137–144, 1990.

[36] U. Schmitt, G. Lübke, and W. Francke, "Tarsal secretion marks food sources in bumblebees (Hymenoptera: Apidae)," *Chemoecology*, vol. 2, no. 1, pp. 35–40, 1991.

[37] D. Goulson, J. C. Stout, J. Langley, and W. O. H. Hughes, "Identity and function of scent marks deposited by foraging bumblebees," *Journal of Chemical Ecology*, vol. 26, no. 12, pp. 2897–2911, 2000.

[38] S. Witjes and T. Eltz, "Influence of scent deposits on flower choice: experiments in an artificial flower array with bumblebees," *Apidologie*, vol. 38, no. 1, pp. 12–18, 2007.

[39] K. Rohrseitz and J. Tautz, "Honey bee dance communication: waggle run direction coded in antennal contacts?" *Journal of Comparative Physiology*, vol. 184, no. 4, pp. 463–470, 1999.

[40] M. Hrncir, S. Jarau, R. Zucchi, and F. G. Barth, "Recruitment behavior in stingless bees, *Melipona scutellaris* and *M. quadrifasciata* II. Possible mechanisms of communication," *Apidologie*, vol. 31, no. 1, pp. 93–113, 2000.

[41] V. M. Schmidt, R. Zucchi, and F. G. Barth, "Recruitment in a scent trail laying stingless bee (*Scaptotrigona* aff. *depilis*): Changes with reduction but not with increase of the energy gain," *Apidologie*, vol. 37, no. 4, pp. 487–500, 2006.

[42] R. J. De Marco and W. M. Farina, "Trophallaxis in forager honeybees (*Apis mellifera*): resource uncertainty enhances begging contacts?" *Journal of Comparative Physiology*, vol. 189, no. 2, pp. 125–134, 2003.

[43] A. G. Hart and F. L. W. Ratnieks, "Task-partitioned nectar transfer in stingless bees: work organisation in a phylogenetic context," *Ecological Entomology*, vol. 27, no. 2, pp. 163–168, 2002.

[44] M. Baude, É. Danchin, M. Mugabo, and I. Dajoz, "Conspecifics as informers and competitors: an experimental study in foraging bumble-bees," *Proceedings of the Royal Society B*, vol. 278, no. 1719, pp. 2806–2813, 2011.

[45] L. G. Kawaguchi, K. Ohashi, and Y. Toquenaga, "Do bumble bees save time when choosing novel flowers by following conspecifics?" *Functional Ecology*, vol. 20, no. 2, pp. 239–244, 2006.

[46] E. Leadbeater and L. Chittka, "The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*)," *Behavioral Ecology and Sociobiology*, vol. 61, no. 11, pp. 1789–1796, 2007.

[47] A. D. Brian, "Differences in the flowers visited by four species of bumble-bees and their causes," *Journal of Animal Ecology*, vol. 26, pp. 71–98, 1957.

[48] E. Leadbeater and L. Chittka, "A new mode of information transfer in foraging bumblebees," *Current Biology*, vol. 15, no. 12, pp. R447–R448, 2005.

[49] M. Giurfa, S. Zhang, A. Jenett, R. Menzel, and M. V. Srinivasan, "The concepts of "sameness" and "difference" in an insect," *Nature*, vol. 410, no. 6831, pp. 930–933, 2001.

[50] M. Srinivasan and S. Zhang, "Small brains, smart minds: vision, perception and "cognition" in honeybees," *IETE Journal of Research*, vol. 49, no. 2-3, pp. 127–134, 2003.