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ORIGINAL PAPER

Problem solving by worker bumblebees *Bombus impatiens* (Hymenoptera: Apoidea)

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Abstract During foraging, worker bumblebees are challenged by simple to complex tasks. Our goal was to determine whether bumblebees could successfully accomplish tasks that are more complex than those they would naturally encounter. Once the initial training to successfully manipulate a simple, artificial flower was completed, the bees were either challenged with a series of increasingly difficult tasks or with the most difficult task without the opportunity for prior learning. The first experiment demonstrated that the bees learned to slide or lift caps that prevented their access to the reinforcer sugar solution through a series of tasks with increasing complexity: moving one cap either to the right or to the left, or lifting it up. The second experiment demonstrated that the bees learned to push balls of escalating masses (diameters 1 and 1.27 cm) from the access to the hidden rewarding (sugar syrup) reservoir of artificial flowers. In both experiments, when bees with experience with only the simplest task (i.e. an artificial flower without a barrier to the reinforcer) were presented next with the most complex or difficult task, they failed. Only by proceeding through the series of increasingly difficult tasks were they able to succeed at the most difficult. We also noted idiosyncratic behaviours by individual bees in learning to succeed. Our results can be interpreted within the context of Skinnerian shaping and possibly scaffold learning.

Keywords Bumblebee · Bee · Apidae · *Bombus* · Learning · Cognition · Behaviour · Scaffold learning · Skinnerian shaping

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Introduction

Research on cognition and learning in bees (Hymenoptera: Apidae) has centred extensively on sensory discrimination of colours, colour patterns, shapes, sizes, scents, textures and combinations thereof. Another aspect of cognition and learning in bees has embraced navigation and communication (von Frisch 1967; Chittka and Thomson 2001; Kevan and Manzel 2012). Chittka and Thomson (2001) reviewed many aspects of learning and problem solving in bees, mostly with respect to sensory discrimination and responses to various cues. Little previous work has addressed gradual versus sudden exposure to complex tasks. Several researchers have tested honeybees (*Apis mellifera* L.) in mazes of varying complexity (Collett et al. 1993; Zhang et al. 1996, 1998, 2000) and found that increasing complexity of sensory cues and navigation could be learned but within the constraints of some level of confusion. There has been little research examining similar abilities in bumblebees. Laverty and co-workers (Laverty 1980, 1994; Laverty and Plowright 1988; Woodward and Laverty 1992; Gegear and Laverty 1998) challenged various species of bumblebees with simple to complex flowers. Flower complexity reflects how well the rewards (e.g. nectar or pollen) are hidden within the floral structure (Heinrich 1976, 1979; Laverty 1980). However, it can also be defined by the learning investment required in floral handling (Laverty 1994). In general, it has been shown that when faced with simple flowers, bees were immediately adept at foraging from them, but when faced with complex flowers, they required time and experience to learn how to manipulate them. Further, experience with simple flowers increases bees' handling efficiency and reduces the subsequent learning times on other simple flowers; however, it did not decrease handling times on more complex flowers when they were first encountered.

Problem solving, such as is demonstrated by maze-learning and by manipulation of simple to complex (problematic) flowers, can be invoked as part of how bees learn by sensory discrimination, navigation and communication (von Frisch 1967; Barth 1985; Chittka and Thomson 2001; Kevan and Manzel 2012; Mirwan and Kevan 2013). Age and size differences have been found to have little to no effect on learning in bumblebees (Raine et al. 2006; Muller and Chittka 2012; Raine and Chittka 2012). In the present experiments, we take the approach of challenging worker bumblebees, regardless of age and size, with increasingly difficult mechanical tasks, but outside the realm of floral structure, to test the bees' abilities solve problems in unnaturally complex circumstances. We avoid, as much as possible, problems that could be interpreted as variations on innate foraging activities.

Methods

We used standard methods (e.g. Laverty and Plowright 1988; Chittka 1998) to train our experimental subjects, adult worker bees of *Bombus impatiens* (Cresson, 1863) (Hymenoptera: Apoidea), to forage on artificial flowers in a screened flight cage (Fig. 1). The specific details of our training regimes for each series of tasks are described below.

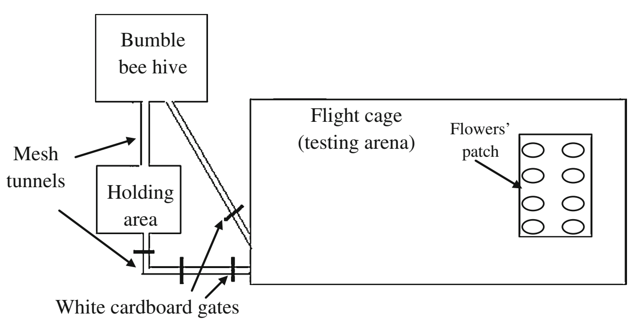

Fig. 1 Experimental set-up with *hive*, *holding area*, *flight cage testing arena*, *patch of artificial flowers* and *mesh tube routes* with gates by which the bees were allowed to enter and exit the flight cage. The bees, in training or as trained, exited from the hive and could take only one route 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 to let the tested bee enter her hive. Eight artificial flowers arranged in two rows were used in each experiment

Experimental set-up

Three experiments were carried out 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 from queen-right colonies of 30–40 workers/colony, supplied by Bio-Best Biological Systems Canada, Leamington, Ontario. Moveable screens on one side of the cages allowed experimenter access. Two colonies were used per experiment (six colonies in total). 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 supplies of pollen, and their diets were supplemented with sugar syrup (50 % sucrose in water). Each forager was marked on the thoracic dorsal surface by numbers and coloured Opalith tags (Plättchen, Christian Graze KG, Germany).

The experimental flower patch (Fig. 1) was placed in the flight cage 165 cm from where the bees entered and exited. It consisted of a green Styrofoam plate 45 × 35 × 5 cm with eight holes to hold artificial flowers made from centrifuge tubes (either 1.5 or 0.5 ml) and coloured surrounds (9 cm blue paper discs). The tubes, hidden from the bees, were supplied with 50 % sucrose solution (syrup) (1:1 w/w sucrose: water) as the reinforcer. The amount of syrup taken by the bees was not controlled, but it was replenished as soon as it was exhausted; eight artificial flowers of the same type were presented to the tested bees. During the experiments, the flowers were refilled and the barriers (caps or balls, see below) replaced.

Artificial flowers

Artificial flowers A (Fig. 2 and Table 1)

Six different types of artificial flowers were made from centrifuge tubes (1.5 ml) and 9 cm diameter blue paper disc surrounds. Each of the six types required different, but similar, handling by the bees for them to gain access to the syrup. In all six, the tubes' caps were cut off and attached to the sticks of cotton swabs, making the barrier to the tube 4.8 cm long (3 cm of the swab stick + 1.8 cm of the cap of the centrifuge tube). The cotton end of the swab was pinned down as the anchor/hinge at the edge of the blue paper disc allows the cap to be lifted or swung to the left or right. The ways the bees had to perform at the six different tasks were as follows: (a) cap (inverted to allow it to slide off the tube's opening) had to be moved in one of the three directions (right, left or up); (b) cap (inverted) had to be moved in one of the two directions (left or up: a pin

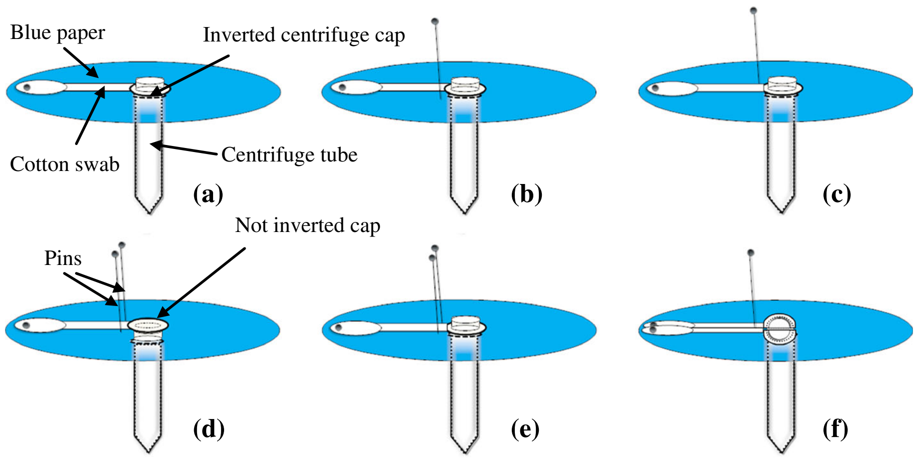

Fig. 2 Artificial flowers A and their increasing complexity. Sliding caps. Type **a** cap (inverted) had to be moved in one of the three directions *(right*, *left*, or *up*). Type **b** cap (inverted) had to be moved in one of the two directions (*left* or *up*: a pin prevented movement to the *right*). Type **c** cap (inverted) had to be moved in one of the two directions (*right* or *up*). Type **d** cap (not inverted) had to be moved only up. Type **e** cap (inverted) had to be moved only up. Type **f** cap was cut into halves, and the parts inverted had to be moved in one of the two ways (*left–right*, or up)

Table 1 Types of sliding and lifting artificial flowers occluded by caps, as used in Experiment 1

Experienced (E) or inexperienced (INE)	Flower type Fig. 2	Flower description	Number of subjects tested: number that succeeded	Mean time (seconds ± SE) for bees to succeed on their first trial
INE	Type a)	Cap (inverted) had to be moved (right, left, or up)	13:12	43.9 ± 4
E	Type b)	Cap (inverted) had to be moved (left or up)	12:12	11.9 ± 1.6
E	Type c)	Cap (inverted) had to be moved (right or up)	12:12	21.9 ± 3.2
E	Type d)	Cap (not inverted) had to be moved only up	12:12	20.1 ± 2.5
E	Type e)	Cap (inverted) had to be moved only up	12:12	33.8 ± 2.4
E	Type f)	Cap was cut into halves, the parts inverted had to be moved (left—right, or up)	10:10	6.1 ± 0.5
INE	Type e)	Cap (inverted) had to be moved only up	14:4	450 ± 52.8

As the letters increase, the flower complexity increases to reach the most complex of type e) flowers, (type f) was easy to manipulate). Subject bees were inexperience except for foraging successfully on simple artificial flowers without barriers to the reinforcer (INE), or experienced (E), the mean time of the first trial ±SE

prevented movement to the right); (c) cap (inverted) had to be moved in one of the two directions (right or up: a pin prevented movement to the left); (d) cap (not inverted) had to be moved only up (two pins on the left and right prevented lateral movement), but there was a gap between the lip of the cap and the rim of the tube; (e) cap (inverted) had to be moved only up (two pins on the left and right prevented lateral movement), but the gap between the lip of the cap and the rim of the tube was eliminated; and (f) cap was cut into halves, the parts inverted and arranged on two swab sticks, each one or both of the half caps had to be moved in one of the two ways (left—right, or up: a pin prevented the two half caps from being moved across each other).

Artificial flowers B (Fig. 3 and Table 2)

These were made as above, but from 0.5-ml centrifuge tube with the same design of 7 cm blue paper surrounds. Precision plastic balls of six different masses and two different diameters were used to cover the entrances of the tubes: (a) 0.375 in. (1 cm) diameter, polystyrene ball at 0.47 g; (b) 0.375 in. (1 cm) diameter, acrylic ball, solid, clear at 0.54 g; (c) 0.375 in. (1 cm) diameter, Delrin ball acetal POM, at 0.62 g; (d) 0.375 in. (1 cm) diameter, Teflon ball PTFE acetal homopolymer, solid, natural at 0.97 g; (e) 0.5 in. (1.27 cm) diameter, polystyrene ball polypropylene, solid, natural at 1.13 g; (f) 0.5 in. (1.27 cm) diameter, acrylic ball, solid, clear at 1.27 g; and (g) 0.5 in.

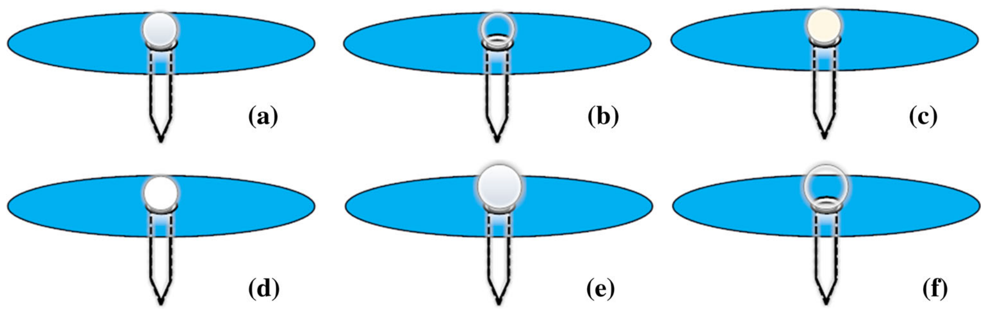

Fig. 3 Artificial flowers B and their increasing complexity. Balls of different massed occluding the syrup reservoir. Type **a** 1 cm diameter, polystyrene ball, *white grey* at 0.47 g. Type **b** 1 cm diameter, acrylic ball, clear at 0.54 g. Type **c** 1 cm diameter, Delrin ball white creamy at 0.62 g. Type **d** 1 cm diameter, Teflon ball white at 0.97 g. Type **e** 1.27 cm diameter, polystyrene ball *white grey* at 1.13 g. Type **f** 1.27 cm diameter, acrylic ball, clear at 1.27 g. Type **g** artificial flower with Teflon, *white* 1.27 cm diameter 2.32 g looked the same as type **d** but larger and is not depicted

Table 2 The types and diameters of balls used with their increasing masses and the numbers of bees tested versus those that succeeded

Test subjects	Flower type	Ball material	Diameter cm	Mass, gram	Number of subjects tested versus succeeded	Mean time to finish the first trial, seconds ± SE
Experiment 2a						
INE	Type a)	Polystyrene	1	0.47	15:13	113 ± 25
E	Type b)	Acrylic	1	0.54	13:13	32 ± 5
E	Type c)	Delrin	1	0.62	13:13	33 ± 6
E	Type d)	Teflon	1	0.97	12:12	24 ± 7
E	Type e)	Polystyrene	1.27	1.13	12:12	19 ± 4
E	Type f)	Acrylic	1.27	1.27	9:9	43 ± 15
INE	Type f)	Acrylic	1.27	1.27	15:6	239 ± 19
Experiment 2b						
INE	Type a)	Polystyrene	1	0.47	19:15	407 ± 59
E	Type d)	Polystyrene	1.27	1.13	14:14	29 ± 8
E	Type g)	Teflon	1.27	2.32	14:10	103 ± 35
INE	Type g)	Teflon	1.27	2.32	14:0	∞

Subject bees were inexperienced, except for foraging successfully on simple artificial flowers without barriers to the reinforcer (INE) or experienced (E) for Experiment 2a and Experiment 2b

(1.27 cm) diameter, Teflon acetal, solid, homopolymer, natural white at 2.32 g. The balls were obtained from K-mac plastic (K-mac Plastics & Distribution, Wyoming, Michigan).

Experimental procedure

The first step was to allow naïve bees to encounter simple artificial flowers (no occluding ball or barrier). Once they were accustomed to foraging at those artificial flowers for a week to 10 days, they were marked individually and then challenged with learning tasks as described for each experiment (below). Each experiment started with the simplest flower type (a) at which single marked bees were allowed to forage. The time that the each bee spent to get the syrup was recorded for ten of its foraging bouts in sequence. The time to complete the task was measured from when the bee landed on the flower until it inserted its proboscis into the sucrose solution using a stop watch. The techniques that bees used to get access to the syrup were recorded descriptively. All marked bees which succeeded at taking syrup from the initial, simplest flower were challenged in subsequent experimental stages, but those that failed were eliminated.

Experiment 1: sliding and lifting caps (Fig. 2)

Our first experiment involved the bees learning to solve a relatively complex problem after first being confronted with a simple, but related, problem using capped centrifuge tubes in artificial flowers A (see Fig. 2). After experience with single caps which the bees could displace in any direction (left, right or up), the bees were challenged with single caps that they had to displace in either of two directions (including up) and then in only one direction (up). To succeed in obtaining the reinforcer syrup, the bees had to displace the cap that occluded the opening to the centrifuge tube. The experiment involved trials with bees that had never encountered the challenge of type a) flowers, the simplest. Then, each bee was challenged through the series of flower types to type f), the most complex of the series in which the occluding cap needed to be moved upwards. The times the bees took to obtain the reinforcer syrup were recorded. To compare between the abilities of bees that had learned to manipulate a series of artificial flowers of increasing complexity (above) and the abilities of 'inexperienced' bees that had learned to forage at only the simplest artificial flowers (centrifuge tube without occluding cap), inexperienced bees were confronted with type e) flowers (Fig. 2), the most complex flowers.

Experiment 2: pushing balls (Fig. 3)

Our next experiment paralleled Experiment 1, but the task given to the bees was to displace occluding balls from the opening of the centrifuge tubes in the centres of artificial flowers B shown in Fig. 3. Bees were allowed to experience and learn the task through being confronted with a series of increasingly massive balls (Experiments 2a and b). In Experiment 2b, we also challenged bees that had learned to forage from flowers with open centrifuge tubes immediately with the most massive ball (type g of Fig. 3).

Experiment 2a: increasing of the mass of the ball (six balls of increasing masses)

To succeed in obtaining the reinforcer syrup, the bees had to remove the ball. The experiment involved trials with bees that had never encountered the challenge of type a) with the lightest ball. Then, each bee was challenged through the series of types to type f) with the heaviest ball blocking the entrance to the tubes. The times the bees took to obtain the reinforcer syrup were recorded. Those that succeeded with the lightest ball were then challenged with the heavier balls (including, eventually, the heaviest). To compare inexperienced and experienced bees, inexperienced bees were given type f) flowers (Fig. 3), the heaviest ball, after they had learnt to forage only at the simplest (no occluding ball or barrier) flowers. The length of time each subject took to remove the ball from the artificial flowers and start to forage was recorded for ten trials on each artificial flower type. The subjects that gave up were observed, and we recorded how many of them gave up and in which trial.

Experiment 2b: Increasing of the mass of the ball (three balls of increasing masses)

In this experiment, we used the artificial flowers as in Experiment 2a but with flower types type a), type e) and an additional flower type (type g) with the heaviest ball available to us at twice the mass of type e), i.e. Teflon acetal, solid, homopolymer, natural white 1.27 cm, 2.32 g.

The experiment started by training bees (already familiar with artificial flowers without any barriers to the syrup reservoir) to forage from artificial flowers with entrances to the reinforcer syrup reservoir occluded by the lightest ball (type a). We recorded how long it took the bees to remove the ball from the artificial flower and start to forage. The subject bees that succeeded in feeding on the syrup were used in further tests, but the ones which gave up were eliminated. The successful subject bees then were tested for pushing ability with type e) flowers and then type g) flowers (with the heaviest balls). The length of time each subject took to remove the ball from the artificial flowers and start to forage was recorded for ten trials on each artificial flower type. The subjects that gave up were observed, and we recorded how many of them gave up and in which trial.

Data analysis

Our behavioural hypothesis that worker bumblebees can solve complex problems is tested through the statistical hypotheses that the mean durations taken by the bees, after landing, to slide or lift the caps or to remove the ball from the artificial flower and start to forage differed between flower complexity types. One-way ANOVA for repeated measures was used. Following that, relevant pair-wise comparisons were made by Multiple Comparison Procedures (Holm-Sidak method) to refine the comparisons while maintaining an overall significance level of 0.05. Fisher's exact test was used to analyse the number of subjects that succeeded in manipulating the flower and to obtain the reinforcer versus the number that failed.

Results

All the bees that had experience with sliding and lifting caps with increasing complexity or with pushing balls of increasing masses from the artificial flowers performed the tasks up to the most complex capped-flowers (Table 1) or the heaviest balls (Table 2). However, many (Tables 1, Experiment 1 and Table 2, Experiment 2a), or all (Table 2, Experiment 2b), of the inexperienced bees presented with the most complex tasks gave up. Throughout our experiments, the time it took the experienced bees to perform the

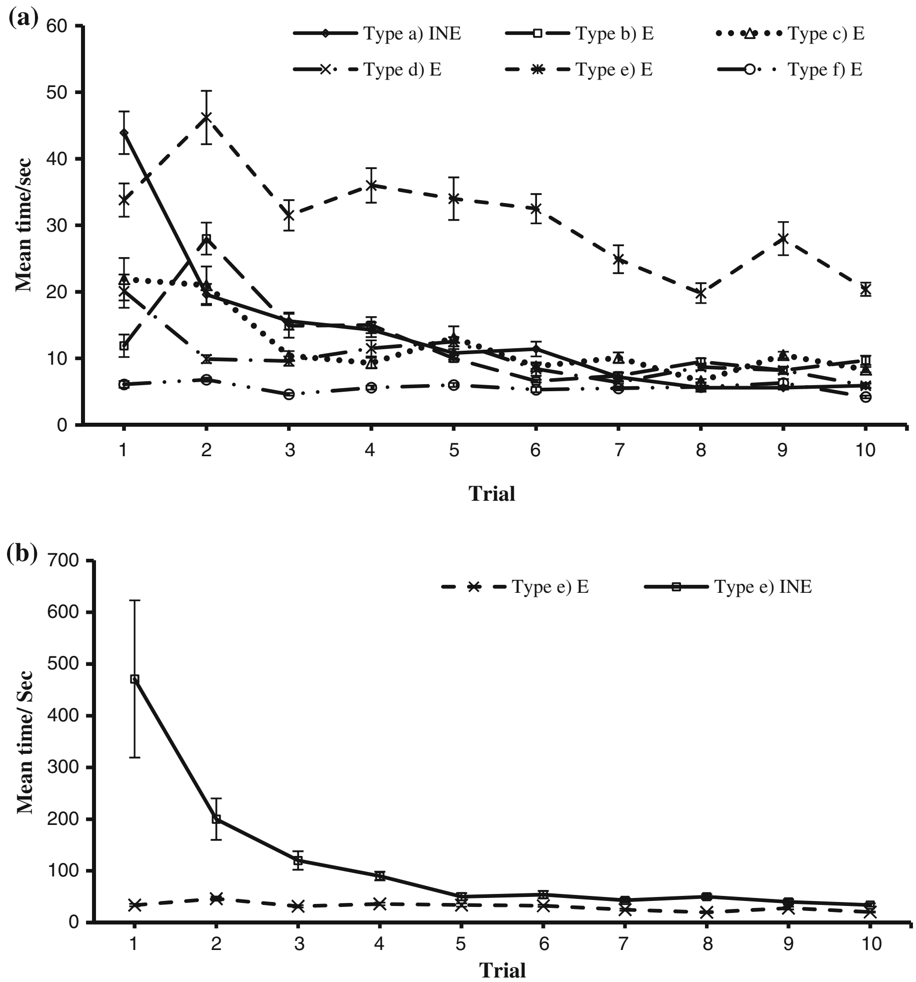

Fig. 4 Sliding and lifting caps. **a** Shows the mean time of sliding and lifting caps ±(SE) for ten trials on artificial flowers (Fig. 2) *type a)* on which caps could be moved three ways (*right*, *left* and *up*) IEN: inexperienced bees ($N = 12$). *Type b)* caps could be moved two ways (*left* and *up*) E: experienced bees ($N = 12$). *Type c)* caps could be moved two ways (*right* and *up*) E: experienced bees ($N = 12$). *Type d)* caps in right position and could be lift E: experienced bees ($N = 12$). *Type e)* caps upside down and could be lifted but with difficulty because of the lack of anywhere to gain purchase E: experienced bees ($N = 12$). *Type f)* caps divided and could be slid to left or right or lifted E: experienced bees ($N = 10$). **b** Shows the mean time of lifting caps ±(SE) for ten trials on *type e)* artificial flowers IEN inexperienced bees ($N = 4$) and caps upside down and could be lifted but with difficulty because of the lack of anywhere to gain purchase E: experienced bees ($N = 12$)

tasks did not increase as the complexity increased (Table 1; Fig. 4 and Table 2; Figs. 5, 6).

In sliding and lifting caps experiment bees that did not have the opportunity for experience in experiments with sliding and lifting caps, some succeeded (4 of 14 bees vs. 12 of 13 experienced bees; $P < 0.01$ by Fisher's exact test) but took statistically longer times to succeed that those bees that had experience (<34 vs. 471 s (Table 1; Fig. 4) ($F_{2,9} = 5.48$; $P = 0.02$); the others gave up. A statistical pair-wise comparison of the data indicates that the first encounter with the task (type a flower) took significantly longer than subsequent encounters with the same or similar tasks (type b to type d, and type f flowers, Fig. 2) and that the bees working with type e flowers always took statistically longer to accomplish their task (Fig. 4a, b).

In the experiments with pushing balls, 6 of 15 bees without experience in Experiment 2a and without shaping experience actually succeeded in obtaining the syrup with the less massive of the two most massive balls (vs. 9 of 9 that succeeded with shaping experience: a statistically significant difference $P < 0.01$ by Fisher's exact test) (Table 2 Experiment 2a). Even so, those bees that succeeded took much longer to succeed than did those bees that had the opportunity for learning (18 vs. 69 s (Table 2 Experiment 2a) ($F_{2,9} = 7.64$; $P = 0.004$); some struggled for as much as 20 min and gave up. None the bees that succeeded (6 of 15) showed any observed consistency of technique in how to push these balls, unlike the experienced bees, which had developed idiosyncratic techniques throughout their training (see below). In Experiment 2b (pushing balls), some bees did give up even though they had previous experience, even so they did not give up at the first or second trial, only in later trials (3rd and 5th), after some learning (Table 2, Experiment 2b). All the bees that had never experienced moving any ball at all, gave up when challenged with the most massive ball, versus 10 of 14 experienced bees that succeeded ($P < 0.01$ by Fisher's exact test; Table 2 Experiment 2b).

In the experiment with pushing balls, statistical pairwise comparisons of the data indicate that the first encounter with the task (type a flower) took significantly longer than subsequent encounters with the same or similar

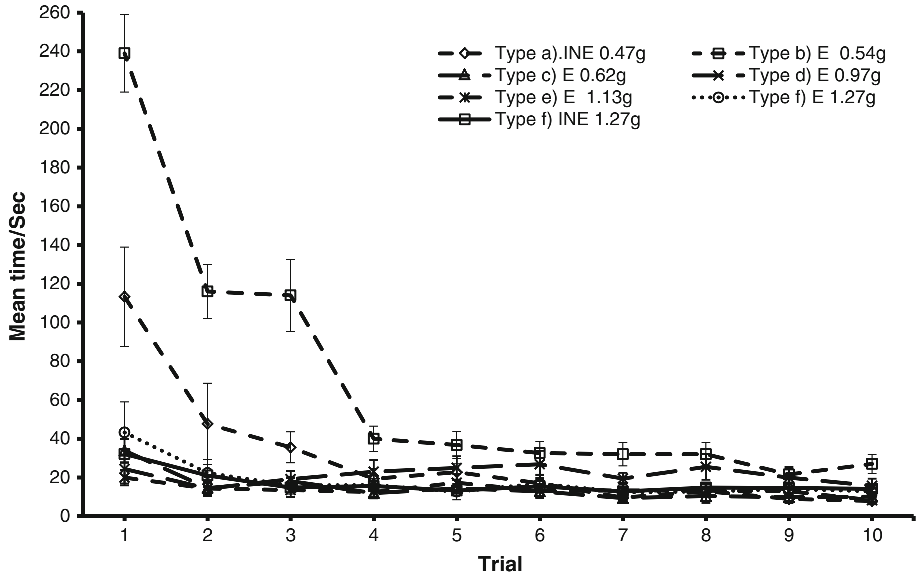

Fig. 5 The mean (±SE) of the duration (seconds) taken by the bees, after landing, to push balls away from the centrifuge tube entry. The data are for ten trials by between 6 and 13 individual bumblebees tested, ($N \times 10$) observations: *Type a)* polystyrene ball 1 cm diameter at 0.47 g, INE (inexperienced bees) ($N = 13$). *Type b)* acrylic ball 1 cm diameter at 0.54 g, E (experience with the previous ball) ($N = 13$). *Type c)* Delrin ball 1 cm diameter at 0.62 g, E (experience with the previous balls) ($N = 13$). *Type d)* Teflon ball 1 cm diameter at 0.97 g, E (experience with the previous balls) ($N = 12$). *Type e)* polystyrene ball 1.27 cm diameter at 1.13 g, E (experience with the previous ball) ($N = 12$). *Type f)* acrylic ball 1.27 cm diameter at 1.27 g, E (experience with the previous balls) ($N = 9$). *Type f)* acrylic ball 1.27 cm diameter at 1.27 g, INE (inexperienced bees) ($N = 6$)

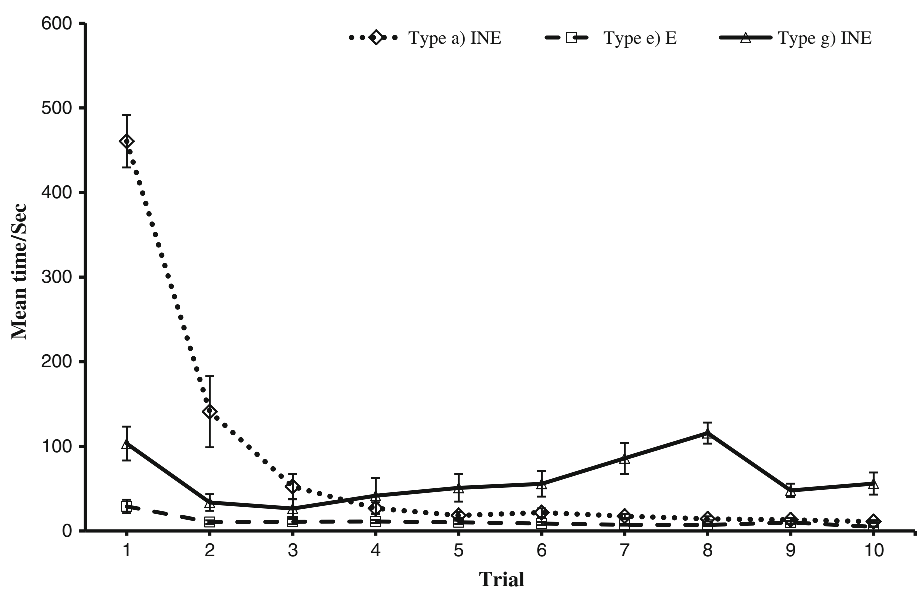

Fig. 6 The mean (±SE) of the durations (seconds) taken by the bees, after landing, to push balls away from the centrifuge tubes entry. The data are for first trial by between 6 and 13 individual bumblebees tested maximum allowable giving up time was set at 20 min. Labels on the horizontal axis are explained as follows, for (10) observations: *Type a)* polystyrene ball 1 cm diameter at 0.47 g, INE: inexperienced bees ($N = 15$). Type e) polystyrene ball 1.27 cm diameter at 1.13 g, E (experience with the previous ball) ($N = 14$). *Type g)* Teflon ball 1.27 cm diameter at 2.32 g, E (experienced bees) ($N = 10$)

(type b to type e, Fig. 3; Table 2 Experiment 2a) or (type e, Fig. 3; Table 2 Experiment 2b) and that the bees working with type f or type g flowers always took statistically longer to accomplish their task (Figs. 5, 6).

As our experiments proceeded, we noted that individual bees developed their own techniques to solve the problems of pushing the ball from the entrance of the artificial flowers that they encountered. We did not attempt to quantify those idiosyncrasies. The following techniques were observed: (a) bees landing on the ball: from above, the individual landed on the ball, inserted its proboscis beneath it and then it put its head between its mid-legs on the flower then pushed against the base of the flower to lever the ball off. (b) Same as above (a), but the bee used both middle legs without putting its head on the flower. (c) Same as above (b), but the bee used both middle legs and did not insert its proboscis beneath the ball. (d) Same as above (a), but the bee used one middle leg and used one hind leg to push the ball aside. (e) As (d) but without inserting the proboscis. (f) Landing on the flower, inserting the proboscis underneath the ball then pushing with both middle legs. (g) Landing on the flower, using the head to butt the ball while pushing with both middle legs. Once an individual bee had developed its own technique, it did not seem to change thereafter.

Discussion

It is well known that bumblebees quickly learn to manipulate simple natural and artificial flowers, but take longer to handle more complex ones (Laverty 1980; Laverty and Plowright 1988; Gegear and Laverty 1995, 2005). Thus, increasing speed and accuracy in handling a given complex task indicate that experience and memory are important components of worker bumblebees' learning to manipulate objects that they encounter in their natural lives. Although Laverty (1980, 1994) tested experienced and inexperienced bees for their abilities to manipulate complex flowers, he did not increase complexity in serial order. Moreover, he compared different species of bees that differed in size and tongue length and differed in behaviour from generalists to specialists. Our experiments show that those abilities in increasing speed and accuracy in handling complex tasks extend to the bees' abilities to solve problems in unnaturally complex circumstances where innate reactions would seem unlikely to apply (as could be involved with flower visitation). Although Laverty (1978) reports that the behaviour of experienced bees was relatively consistent, when inexperienced bees landed on complex flowers, they needed to search for the floral access to the rewards. He concluded that even small changes in floral form had large effects on the bees' learning to manipulate them (Laverty 1978).

Worker bumblebees learn through experience and solving problems. That learning is presumably an outcome of shaping and scaffold learning.

In shaping (Skinner 1953, pp 92–93), animals can be, for example, trained to perform tasks of increasing difficulty. Those range from rewarding naïve animals' positive responses to simple tasks to more and more involved responses in more and more difficult tasks, just as we have shown in these experiments, especially in the experiments with the bees' removing the increasingly massive balls occluding access to the reinforcer in which the task is the same, but becomes more difficult as the balls' masses increase.

The related notion of scaffold learning is used in human psychology to refer to increasing sophistication and complexity of a set of tasks that at first are simple when the task is introduced, and then are used to teach learners through increasing sophistication in such subjects as reading, writing, mathematics, music, use of tools and social interactions (Sawyer 2006; Olson and Platt 2000). It assumes that the subject may spend longer or give up if first given overly complex tasks they can solve well if presented with gradually increasing set of difficulties of the tasks by which to learn. Vygotsky (1987) proposed a means of quantifying learning rates through the Zone of Proximal Development (ZPD) which is the difference between (a) the actual development as determined by independent problem solving and (b) the potential development as determined through problem solving under guidance—or incremental experience including problem solving (our addition to the concept originally restricted to scaffolding). The experiments with the bees sliding and lifting caps to access the reinforcer sugar syrup could be considered scaffolding in which the experimenters coached the bees through a series of incrementally complex tasks. The tasks presented involved the complexity of moving caps to the left or right or above to allow access to the reinforcer.

The ZPD values we obtained from our experiments are as follows: Experiment 1 with floral complexity from type a to type e flowers (Fig. 2), ZPD = 113.1–29.1 = 84 s; Experiment 2a with difficulty from lightest to most massive ball used (Fig. 3) ZPD = 69.1–17.9 = 51.2 s; and Experiment 2b with difficulty from the lightest to the most massive ball available (Fig. 3) ZPD = ∞–103 = ∞ s (the inexperienced bees never pushed the most massive ball from the artificial flower). The ZPD values indicate that skill acquisition in bumblebees can be measured as it is for human learning (Bransford et al. 2000).

Thus, through experience, worker bumblebees become able to solve new problems they encounter rather just giving up, as bees that have had no previous experience do. Experiences provide bumblebees advantages in both qualitative (time) (Figs. 4, 5, 6) and quantitative (strategy) modes.

Through solving problems, learners may invent specific, sometimes idiosyncratic, techniques to solve their problems. Additional studies are required to quantify and analyse the kinds of different behaviours we noted, as Thorndike did with domestic cats (*Felis catus*) (see Chance 1999). Other, more refined studies using our techniques and concepts may elucidate the issues of age and individual differences in learning in bees, including honeybees (*A. mellifera*) (Ray and Ferneyhough 1997; Pankiw and Page 1999; Raine et al. 2006; Muller and Chittka 2012) and between species (Ray and Ferneyhough 1997; Laverty and Plowright 1988; Amaya-Marquez et al. 2008; Amaya Marquez 2009). Also, neurotoxins, such as some insecticides in sublethal doses, change the capacities of bees to perform tasks (Thompson 2003; Alston et al. 2007; Gill et al. 2012), and our approach could be applicable to such research.

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