

RESEARCH ARTICLE

Flower constancy in honey bee workers (*Apis mellifera*) depends on ecologically realistic rewards

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SUMMARY

As first described by Aristotle, honey bee (*Apis mellifera*) workers show a strong tendency to visit flowers of only one type during a foraging trip. It is known that workers rapidly learn a flower colour when rewarded with artificial nectar (sucrose solution). However, some previous studies report that the degree of constancy after training is unaffected by reward quantity and quality when bees are tested in an array of artificial flowers of two easily distinguished colours, such as blue and yellow. One possible reason for this surprising result is that large reward volumes were compared. This is likely to mask the abilities of foragers to make adaptive decisions under more realistic conditions. To test this possibility, we offered untrained honey bee workers ecologically relevant rewards (0.5, 1 or 2 µl of 0.5 or 1 mol l⁻¹ sucrose solution) on one or two consecutive yellow or blue artificial flowers and then recorded which flowers the bees subsequently landed on in an array of 40 empty flowers. The results showed that an increase in all three factors (volume, concentration and number of rewards) significantly increased constancy (proportion of visits to flowers of the trained colour) and persistence (number of flowers visited) during the foraging bout. Constancy for the least rewarding situation was 75.9% compared with 98.6% for the most rewarding situation. These results clearly show that honey bee workers do become more constant to blue or yellow with increasing nectar rewards, provided that the rewards used are ecologically realistic. As the most rewarding conditions led to nearly 100% constancy, further reward increases during training would not have been able to further increase constancy. This explains why previous studies comparing large rewards found no effect of reward on constancy.

Key words: flower constancy, foraging, learning, honey bee, pollination.

INTRODUCTION

Foraging honey bee (*Apis mellifera*) workers are highly flower constant (Aristotle, ca. 340 B.C.; Darwin, 1876; Ribbands, 1949; Grant, 1950; Free, 1963; Waser, 1986), normally visiting only one type or species of flower during a foraging trip. Free, for example, found that 94% of all pollen foragers collected one pollen type during a foraging trip (Free, 1963). Flower constancy is possible because foragers quickly learn flower attributes such as colour, shape and odour and use this information to land selectively on particular flowers (von Frisch, 1914; von Frisch, 1919; Koltermann, 1969; Menzel, 1968; Menzel, 1990; Menzel, 1999). Flower constancy is of importance for plants because it prevents pollen loss to allospecific plants (Darwin, 1876; Waser, 1986; Chittka et al., 1999).

It has been reported that honey bee foragers fail to adjust the degree of constancy according to the energetic value of flowers in blue/yellow dimorphic patches (Wells and Wells, 1983; Wells and Wells, 1984; Wells and Wells, 1986; Hill et al., 1997; Hill et al., 2001; Sanderson et al., 2006) (but see Couvillon and Bitterman, 1993). Rather than choosing the flower colour that is most rewarding, foragers quickly became constant to one or the other colour ('spontaneous constancy') irrespective of the reward, suggesting that behavioural constraints are responsible for constancy (Wells and Wells, 1983; Wells and Wells, 1984; Wells and Wells, 1986; Hill et al., 1997; Hill et al., 2001; Sanderson et al., 2006). In these studies, differences in the energetic values of

flowers of particular colours were created by varying the amount of sucrose solution reward (2.5–5 µl for the less rewarding colour; 6–20 µl for the more rewarding colour) (Wells and Wells, 1983; Wells and Wells, 1986; Hill et al., 1997; Sanderson et al., 2006), the reward quality (e.g. 0.75 vs 2.5 mol l⁻¹ sucrose solution) (Wells and Wells, 1983; Wells and Wells, 1986), the distance between flowers (Hill et al., 2001) or handling time (Sanderson et al., 2006). Flower constancy may also be favoured by neurological constraints such as temporal limitations of information processing or interference sensitivity of short-term memory (Chittka et al., 1999; Raine and Chittka, 2007).

The energetic returns of flowers differ greatly between plant species and change rapidly over time (Butler, 1945; Vogel, 1983). Assessing these differences between rewards and responding to them is vital for efficient foraging and, ultimately, to colony survival and reproduction (Seeley and Visscher, 1985; Real, 1991; Seeley, 1995; Raine et al., 2006). Hence, even if constraints contribute to flower constancy, natural selection should have favoured flower choice behaviours that take the energetic returns of flowers into account (Real, 1991). It is, therefore, surprising that foragers did not respond to the energetic value (i.e. volume or sugar concentration) of flowers of distinctive colours, like yellow and blue. One potential problem in the studies that found spontaneous colour constancy in blue/yellow patches is that flower reward quantities were unnaturally high, between 2 and 20 µl per flower (Wells and Wells, 1983; Wells and

Wells, 1986; Hill et al., 1997; Hills et al., 2001; Sanderson et al., 2006). Individual *A. mellifera* foragers collect up to ca. 50 µl of nectar per foraging trip (Núñez, 1966; Seeley, 1995), which means that, depending on the experimental condition, foragers were full after only 2–25 flower visits. However, foragers visiting natural flowers need to visit many more flowers. Ribbands, for example, found that nectar foragers visited between 250 and 1446 flowers per trip (Ribbon, 1949). The large rewards per flower used in previous experiments might have masked the bees' ability to respond to energetic returns and led to the impression that behavioural constraints are mainly responsible for colour constancy in blue/yellow patches.

The aim of this study was to investigate the effect of the magnitude of sucrose reward on flower constancy and persistence using an ecologically realistic range of volumes and concentrations in an array of blue and yellow artificial flowers. We used monochromatic artificial flowers and unscented sucrose solution in order to avoid the confounding effects of food odours and dichromatic flowers (Hill et al., 2001). In experiment 1, bees were trained on a single flower colour using varying reward volumes (0.5, 1.0 and 2 µl), concentrations (0.5, 1 mol l⁻¹) and either one or two training flowers. Experiment 2 used similar training conditions except that the bees were trained on two consecutive flowers of different colours to investigate the effect of 'contradictory' information (see also Menzel, 1979) on flower choice. Our results show that the degree of colour constancy increases with increasing reward quality, quantity and reward number. In addition, the higher the reward, the more empty flowers a forager bee visited afterwards (i.e. persistence).

MATERIALS AND METHODS

Study site and organism

We studied free flying honey bee workers *Apis mellifera mellifera* Linnaeus 1758. The artificial flower array was located 10 m from the apiary at the Laboratory of Apiculture and Social Insects, University of Sussex. Data were collected on sufficiently warm days (temperature range: ca. 10–20°C) from 18 October to 9 December 2008 using naturally flying bees.

Experimental design

We used an artificial flower patch of 20 blue and 20 yellow artificial flowers, alternating in an 8×5 grid with 5 cm between flowers. Each flower was mounted on a 10 cm plastic 'stalk' attached at the base to a green plastic table. Individual flowers were eight-pointed 4×4 cm radially symmetrical stars with a black cross (two stripes, each 0.1×2 cm) at the centre to simulate a nectar guide (Fig. 1). The flowers were laser printed on white paper and laminated. A glass-jar feeder (see von Frisch, 1967) containing 2 mol l⁻¹ sucrose solution was set up next to the flower patch in order to attract and maintain a steady supply of naive bees to the area. Ten white flowers of the same design were also set up next to the patch; these contained weak solution (0.5 mol l⁻¹ sucrose). These flowers were continually refilled to train naive bees to the shape, but not to the colour, of the experimental flowers and thereby to encourage bees to land on the experimental flowers during experimental periods. The glass-jar feeder was removed once a sufficient number of bees were attracted to the area. This prevented switching from the experimental flowers back to the feeder. No bee other than a test bee was ever rewarded on a blue or yellow artificial flower, and each test bee was marked with a small dot of paint on its notum whilst being trained in order to avoid using the same bee twice.

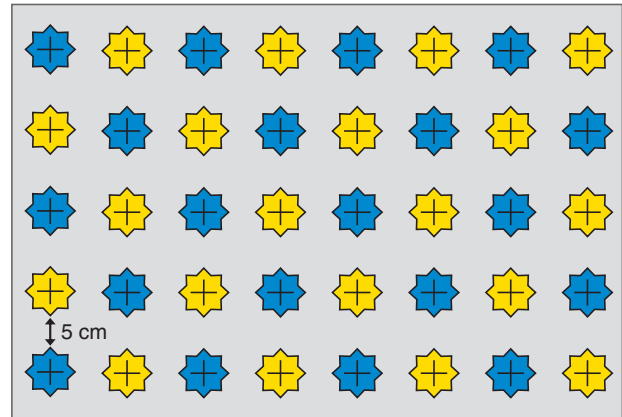


Fig. 1. Diagram showing the shape of the artificial flowers and their arrangement in the artificial patch. We used 20 blue and 20 yellow 4 cm diameter flowers, each on a 10 cm stalk, with 5 cm between flower edges.

Experiment 1: effect of volume, sugar concentration and number of rewards

Couvillon and Bitterman, using an array of blue and yellow flowers, found that reward quantity had an effect on flower choice (Couvillon and Bitterman, 1993). It has been argued, however, that pre-training on the two colours and 'forced' sampling between these two flower types [e.g. bees were trained to both colours in Couvillon and Bitterman (Couvillon and Bitterman, 1993)] were responsible for the lack of constancy (Hill et al., 1997). To avoid this, our test bees were allowed to freely choose either colour. To reward and train a test forager bee, we hand-fed an individual bee that had landed on an artificial flower in the array with sucrose solution from a micropipette. Hand feeding made work with small reward sizes easier and also prevented bees from estimating the amount of reward by the size of the droplet. Each bee was rewarded on the flower she had landed on, either blue or yellow. Rewards were 0.5, 1 or 2 µl of either 0.5 or 1 mol l⁻¹ sucrose solution. This corresponds to 0.09–0.68 mg sucrose (dry mass) and is similar to the standing crop in *Silene latifolia*, *Silene dioica* or *Saponaria officinalis*, but higher than in *Lychnis flos-cuculi*, *Stachys palustris* or *Malva moschata* (Comba et al., 1999), which are visited by honey bees and other bee species. Each bee was trained on either one or two consecutive flowers of the same colour. The test bee was then allowed to forage freely on the patch of unrewarding flowers, and the sequence of colour landings was noted. We worked in pairs so that the person recording a test bee's behaviour did not know the reward volume or concentration given. Flowers were frequently wiped clean with water to avoid scent marks from previous bees affecting choice behaviour (Giurfa and Núñez, 1992).

In total, there were 24 different training combinations for experiment 1 [three reward amounts × two concentrations × two colours × two training paradigms (i.e. one or two rewards)]. We used nine bees for each combination, totalling 216 bees. We carried out all 24 training combinations on one day to reduce the effect of uncontrolled variables such as daily change in weather or temperature or longer-term changes in nectar conditions. In addition, we randomized the order of combination testing per experimental day.

Although we could not be sure that our naive test bees did not already have some colour preferences, this would not have compromised our results as our experimental design was based on comparisons. Thus, each bee that landed initially on a blue flower (and may therefore have had a preference for blue) was trained using

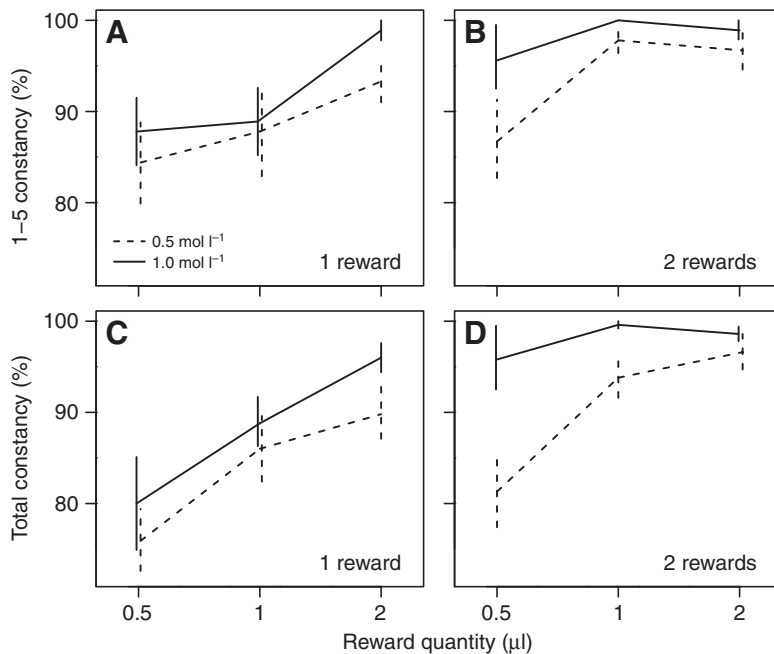


Fig. 2. Degree of constancy of honey bees in experiment 1. (A) Constancy for the first five flower landings after training on one flower offering 0.5, 1 or 2 μl of 0.5 or 1 mol l^{-1} sucrose solution. (B) Constancy for the first five landings after training on two flowers (blue/blue or yellow/yellow). (C) Total constancy (all flower landings) after training on one flower. (D) Total constancy after training on two flowers (blue/blue or yellow/yellow). Values are means \pm s.e.m.

one of the 12 reward combinations for blue, allowing us to compare the level of constancy among these combinations. In addition, our results showed that there was no overall preference of naive bees for either yellow or blue (see Results).

Experiment 2: effect of two different training colours

The sucrose rewards were the same as for experiment 1. However, each test bee was rewarded on two consecutive flowers of different colours. Because bees are usually reluctant to land on a different colour from the one on which they have just been rewarded (see Results), each bee was coaxed onto the second flower after being fed on the first flower colour. To do this, the second flower was held next to the first and the tip of the pipette was made to come into contact with the bee's antenna (Menzel and Erber, 1978). There were 12 training combinations (three reward amounts \times two concentrations \times two training paradigms). Again, we used nine bees for each combination, totalling 108 bees. Half were first rewarded on blue and half on yellow.

In both experiments, constancy was defined as the proportion of landings on the colour on which a bee was first trained, and was quantified in two slightly different ways, based on the first five landings (1–5 constancy) or all the landings (total constancy) after training. All bees visited a minimum of five artificial flowers after training, hence the choice of five visits. Most bees visited more than five flowers (mean \pm s.d. = 11.97 \pm 4.77). Additionally, we tested the effect of training paradigm, reward amount and concentration on the number of landings or persistence.

In addition to these reward paradigms, we allowed one naive bee per data collection day to land freely on any artificial flower in the blue and yellow flower array without being given any reward. The sequence of colours on which these bees alighted was noted. Again, constancy was defined as the proportion of landings on the colour on which a bee first landed. This data provided information about constancy of naive bees in our patch that received zero reward on either colour.

Data analysis

All tests were performed in R 2.9 (R Development Core Team, 2009). For 1–5 constancy, we found only four different constancies (0.4,

0.6, 0.8 and 1); that is, each bee landed on two to five flowers of the trained colour. Therefore, we used ordinal logistic regression models with multinomial response to analyse the effect of sucrose solution quantity, concentration, flower colour and training paradigm on flower constancy (Dobson and Barnett, 2008). We used ordinal models because there is a natural order in the categories (Dobson and Barnett, 2008). The models were performed using the *polr*-function of the MASS package of R. Because the total constancy of bees was neither normal nor Poisson distributed we created seven different categories, which allowed us to analyse total constancy with the same ordinal logistic regression models. The seven categories were 0.3–0.4, >0.4–0.5, >0.5–0.6, >0.6–0.7, >0.7–0.8, >0.8–0.9 and >0.9–1. The effects of sucrose solution concentration, quantity and training paradigm on the number of landings were tested with standard generalized linear models (GLMs) with Poisson distribution (Faraway, 2006). Non-significant interactions were removed from the models.

RESULTS

Experiment 1: effect of volume, sugar concentration and number of rewards

Overall, 1–5 and total constancies were high, between 0.76 and 1.0 across the different treatments (Fig. 2). Total constancy after one reward decreased by 20.1% (from 96 to 75.9%) from the energetically most rewarding (1 mol l^{-1} , 2 μl) to the least rewarding treatment (0.5 mol l^{-1} , 0.5 μl ; Fig. 2C). After two rewards, total constancy decreased by 17.3% from the energetically most rewarding to the least rewarding treatment (from 98.6 to 81.3%; Fig. 2D). By contrast, total constancy of the nine unrewarded and untrained control bees was 58% (data not shown). For 1–5 constancy, the reductions in constancy from the most rewarding to the least rewarding treatments were slightly smaller, decreasing by 14.5% after one reward (from 98.9 to 84.4%) and by 12.2% after two rewards (98.9 to 86.7%). Overall, both measures of constancy show that greater reward volume, sucrose concentration and number of training visits all result in greater constancy. There was no effect of training colour (Table 1).

We found a significant interaction between reward molarity and the number of training rewards in the case of total constancy (see Fig. 2C,D). This is because after two rewards of 1 mol l^{-1} , sucrose solution constancy plateaus at almost 100%.

Table 1. Effects of flower colour [blue (B) or yellow (Y)], reward (sucrose solution) volume (0.5, 1 or 2 μl) and molarity (0.5 or 1 mol l^{-1}), number (1 or 2) of rewards and colour sequence (BB, YY, BY or YB) on colour constancy of forager honey bees in experiments 1 and 2

	1–5 constancy			Total constancy		
	d.f.	Likelihood ratio	<i>P</i>	d.f.	Likelihood ratio	<i>P</i>
Experiment 1						
Colour	1	0.07	0.79	1	0.092	0.76
Reward volume	2	12.8	<i>0.0017</i>	2	27.87	<i><0.0001</i>
Molarity	1	5.33	<i>0.021</i>	1	17.68	<i><0.0001</i>
Reward number	1	13.9	<i>0.0002</i>	1	29.25	<i><0.0001</i>
Molarity \times Reward number	1	1.91	0.17	1	7.02	<i>0.0081</i>
Experiment 2						
Colour sequence	1	1.71	0.19	1	3.66	0.056
Reward volume	2	0.14	0.93	2	1.76	0.41
Molarity	1	2.40	0.12	1	3.30	0.069
Reward volume \times Molarity	2	10.4	<i>0.0055</i>	2	3.76	0.15

Non-significant interactions are not shown. Results are shown for both 1–5 constancy (constancy for the first 5 visits on unrewarded flowers after training) and total constancy (constancy for all visits on unrewarded flowers after training; mean \pm s.d.=11.97 \pm 4.77). Values in italic are significant ($P<0.05$).

Experiment 2: effect of two different training colours

Of 108 bees, 83 made more landings on the colour they were trained on first, 19 on the second, and six visited both colours equally. This shows that the first training event had a stronger effect on subsequent landing decisions ($\chi^2=40.16$, d.f.=1, $P<0.0001$; Fig. 3). However, colour constancies were lower than in experiment 1 at only 66%. There was no significant effect of colour sequence, molarity or reward volume on constancy (Table 1). However, we found a significant interaction between volume and molarity during the first five visits after training (Fig. 3A).

Number of landings before giving up (persistence)

Trained bees made more landings on unrewarding flowers, i.e. they were more persistent after (1) being rewarded with 1 vs 0.5 mol l^{-1} sucrose solution, (2) experiencing two rewards vs one and (3) receiving 1 or 2 μl vs 0.5 μl (GLM; concentration: $z=4.13$, $P<0.0001$; reward number: $z=5.03$, $P<0.0001$; reward quantity: 0.5 vs 1 μl , $z=4.09$, $P<0.0001$; 0.5 vs 2 μl , $z=2.81$, $P=0.005$; 1 vs 2 μl , $z=-1.29$, $P=0.20$; Fig. 4A–C).

DISCUSSION

Our results show that both the concentration and quantity of sucrose solution reward affect flower constancy in honey bees foraging in a blue/yellow flower patch. From the most rewarding to the least rewarding treatment (Fig. 2C), respectively, total and 1–5 constancies decreased by 20 and 15% with one training visit and by 17 and 12% with two training visits. The two measures of constancy gave very similar results.

These findings are in sharp contrast to previous studies that found no effect of reward size on constancy in a blue/yellow flower patch (Wells and Wells, 1983; Hills et al., 1997; Hills et al., 2001; Sanderson et al., 2006) and support the hypothesis that the lack of effect was caused by the use of sucrose solution rewards that were larger than the nectar rewards that occur commonly in flowers. In these previous studies, foragers quickly became constant to either blue or yellow (spontaneous constancy) even if the reward of the preferred colour was inferior in quantity or quality, or associated with higher costs in terms of handling time or flight distance. However, several previous studies have also shown that forager honey bees do respond to energetic returns in adaptive ways. If blue (or violet) and white are used as flower colours instead of blue and yellow, foragers often chose flowers based on their energetic value, handling time (Sanderson et al., 2006; Cakmak et al., 2009), flow rate (Greggers and Menzel, 1993) or flight distance between flowers (Marden and Waddington,

1981; Hill et al., 2001). Sugar concentration affected flower choice in a patch with two different types of dichromatic flowers (blue/white and yellow/white flowers) (Banschbach, 1994) [see Hill et al. (Hill et al., 2001) for discussion]. Hence, there seems to be a striking difference in choice behaviour depending on whether experiments used a flower patch with blue and white flowers or a patch with blue and yellow flowers (Hill et al., 2001; Sanderson et al., 2006). This led some authors to speculate that constraints elicit colour constancy when the two colours are sufficiently separate in the bee colour space

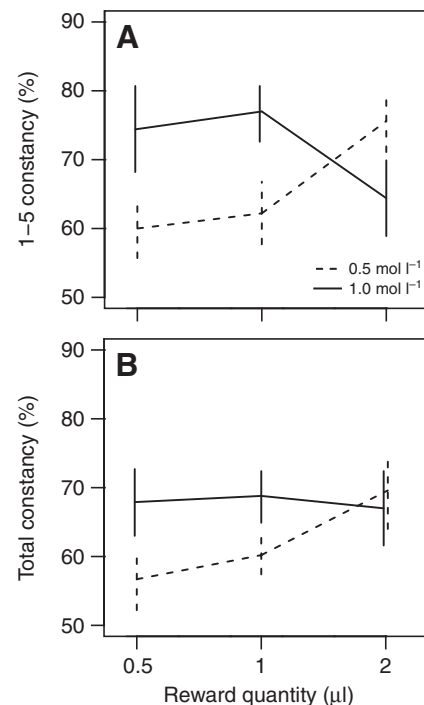


Fig. 3. Degree of constancy to the first training colour in experiment 2, in which individual bees were trained in the sequence yellow/blue (YB) or blue/yellow (BY). (A) Constancy for the first five landings after training on two flowers (YB or BY) offering 0.5, 1 or 2 μl of 0.5 or 1 mol l^{-1} sucrose solution. (B) Total constancy for the first five landings after training on two flowers (BY or YB) offering 0.5, 1 or 2 μl of 0.5 or 1 mol l^{-1} sucrose solution. All constancies were $>50\%$, which means that, overall, the first training event had a stronger effect on flower choice than the second training event.

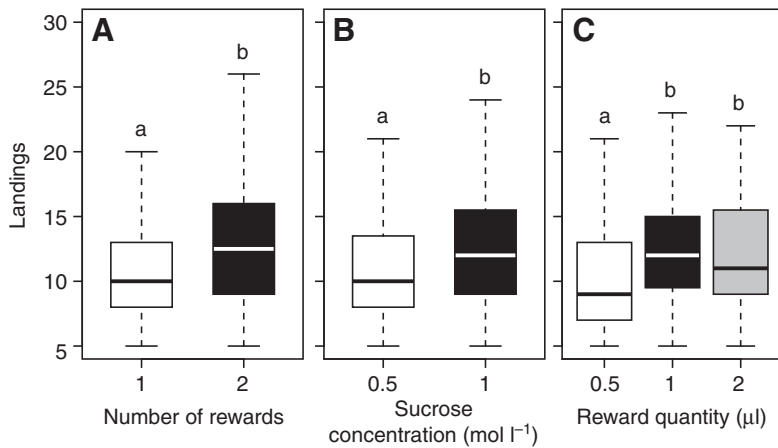


Fig. 4. Number of landings, i.e. persistence, on empty flowers after training. (A) Number of landings after being rewarded either on one flower (blue or yellow) or on two flowers (blue/blue or yellow/yellow) ($N=108$ for each reward number). (B) Number of landings after being rewarded on one or two flowers offering either 0.5 or 1 mol l⁻¹ sucrose solution ($N=108$ for each concentration). (C) Number of landings after being rewarded on one or two flowers offering either 0.5, 1 or 2 µl sucrose solution ($N=72$ for each reward quantity). The box plots show medians, quartiles, 5th and 95th percentiles, and number of bees tested. Different lowercase letters indicate statistically significant differences, $P < 0.05$.

(Hill et al., 2001; Sanderson et al., 2006). Following this hypothesis, colours that are sufficiently separate in the bee's colour space elicit 'spontaneous' colour constancy (Hill et al., 1997; Hill et al., 2001). As white and blue are close to each other in the colour space (Chittka, 1992), the difference in colour does not elicit strong constancy (Hill et al., 2001; Sanderson et al., 2006). The idea that colour differences between types of flowers affect the likelihood of changing from one type to the other is supported by observations of naturally foraging honey bees that switched most readily between blue, violet, pink and white forms of *Centaurea cyanus* (Grant, 1950) and bumblebees that switched between flower species that are visually more similar (Chittka et al., 1997; Raine and Chittka, 2007).

From a more functional perspective, efficient harvesting of carbohydrate sources is crucial for the survival of honey bee colonies during winters in temperate habitats, when as much as 20 kg of stored honey is needed for survival (Seeley and Visscher, 1985). Hence, we expect that natural selection will favour foraging strategies of individual foragers that take the energetic value of the currently visited food type into account (Raine et al., 2006). As the energetic value of the currently exploited flower species drops, foragers should allocate more time to the acquisition of information about profitable alternatives, even if alternatives are of distinctive colour. Our results provide clear support for this idea. In our experiment, foragers experienced empty flowers after training. This can occur, but in a less extreme way, in a natural situation. Wetherwax, for example, found that 73% of the *Lotus corniculatus* flowers visited by honey bees were empty (Wetherwax, 1986). Experiencing one or several flowers with zero or minimal reward is, therefore, natural.

The natural situation and our experimental conditions with small rewards differ from the studies that found spontaneous constancy, in which the energetic value of the different flower types did not affect the constancy of worker honey bees. The rewards given in these experiments were very large (between 2 and 20 µl per flower) (Wells and Wells, 1983; Wells and Wells, 1986; Hill et al., 1997; Hill et al., 2001; Sanderson et al., 2006) in relation to ecologically realistic rewards (e.g. Wetherwax, 1986; Comba et al., 1999). Natural selection might not have led to a fine-tuning of flower choice behaviour in the range of rewards used in these experiments (see also Waddington and Gottlieb, 1990). The reward amounts used in the present study (0.5–2 µl of 0.5 or 1 mol l⁻¹ sucrose; ~0.09–0.68 mg sucrose per flower) are still relatively high compared with what can be expected in several species of flowering plants (Comba et al., 1999), but bees were able to adjust their choices based on the energetic value of the experienced rewards. In the most rewarding situation in our experiment, colour constancy approached 100%, so

that any further increase in reward would not have resulted in increased constancy. This supports our hypothesis for why previous studies that used large rewards found no effect on flower constancy.

Our results also showed that greater energetic rewards increased the total number of unrewarding flowers visited by a trained bee before it ceased foraging in the experimental array of artificial flowers. Hence, honey bees not only show higher levels of constancy after visiting relatively more profitable flowers but they also are more persistent before giving up when experiencing a series of empty flowers. Our findings link well with numerous studies that show that foragers adjust various behaviours, such as flight speed (von Frisch and Lindauer, 1955), waggle dancing (reviewed in von Frisch, 1967; Seeley, 1995), trophallactic behaviour (reviewed in Farina and Grüter, 2009), crop filling (Núñez, 1966) and body temperature regulation (Stabentheiner, 1996) according to food profitability.

Flower constancy is an intriguing behaviour and constraints certainly play a role (see Chittka et al., 1999). Foragers might visit the same type of flower again and again because information about this type of flower is readily available in short-term memory. Information about profitable alternatives might be stored in long-term memory, but retrieving this information takes more time and, therefore, leads to time costs (Chittka et al., 1999). There is also evidence that flower constancy helps to avoid short-term memory interference (Laverty, 1994). Short-term memories last up to a few minutes in honey bee workers and are relatively unstable (Menzel, 1999). Indeed it has been shown that switching increases handling time and handling errors (Chittka and Thomson, 1997; Chittka et al., 1999). Bees might also stay constant to a flower species if switching involves a period of learning to correctly handle the flower to extract nectar, leading to a reduced rate of energetic return (Chittka et al., 1999). This, however, would not have been the case in our experiment as the rewards were directly fed to the bee *via* a pipette. If bees have to learn two different types of flowers in short succession, the second experience might erase the first one because of the relative instability of short-term memory (Menzel, 1979; Menzel, 1999; Chittka et al., 1999). We simulated this situation in experiment 2. Our bees more strongly responded to the first training event, in agreement with Menzel (Menzel, 1979), who found that bees responded preferentially to the first of two training colours for periods of 1–2 min between the two learning events. Only one of 108 of our test bees exclusively visited flowers of the second training colour. Hence, the different colour of the second flower did not erase the information of the first flower, although it did lead to a reduction in individual constancy of tested bees. Our results indicate that, at least with small food amounts (0.5–1 µl), reward quality has a positive effect on the probability to

respond to the colour that was first rewarded (Table 1, Fig. 3). Hence, if a flower offers a reward of higher quality, memory might be less altered by subsequent contradicting information in the same reward range. However, if the currently experienced reward is even higher (as in the case of 2 µl and 1 mol l⁻¹ rewards), the second or subsequent experience will gain some more influence on choice compared with the first or previously experienced reward (Fig. 3).

Compared with other bees, honey bees appear to have high levels of constancy (Grant, 1950; Free, 1963; Free, 1970; Slaa et al., 2003). One reason for this may be their sophisticated communication system (Chittka et al., 1999). Many foragers use information from waggle dances performed by successful foragers inside the hive to find a food source (von Frisch, 1967; Seeley, 1983; Biesmeijer and Seeley, 2005). The waggle dance provides information about the presence, location and odour of good food sources (von Frisch, 1967; Riley et al., 2005; Grüter and Farina, 2009). Only foragers that collect from high quality food sources perform dances (von Frisch, 1967; Seeley, 1995). In this way, they filter food quality information for their nestmates (Seeley 1995; Grüter et al., 2010). This might reduce the incentive for honey bee foragers to sample alternative food types.

It has been pointed out that there need not be a single explanation for flower constancy (Chittka et al., 1999). Constancy might be the best option if flower rewards are above a certain threshold (Greggers and Menzel, 1993). This threshold seems to be different for different pairs of colours because constraints for constancy play a more important role with certain pairs of colours, depending on how different they are in the bee colour space (Hill et al., 1997; Hill et al., 2001). However, our results show that even in the presence of information processing limitations, honey bees are able to quickly learn about the value of flowers with a particular colour in arrays of blue and yellow flowers and use this information to adjust the degree of constancy in a way that is adaptive to the reward levels that occur in nature.

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