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The influence of past experience with flower reward quality on social learning in bumblebees

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Foraging decisions can be influenced by innate biases, previous individual experience and social information acquired from conspecifics. We examined how these factors interact to affect flower colour preference in the large earth bumblebee, *Bombus terrestris dalmatinus*. Individual bees with no experience foraging on coloured flowers were first tested for innate colour biases on an unrewarded array of blue and yellow artificial flowers. Depending on treatment, bees then acquired individual experience foraging on a colour (either blue or yellow) associated with high-quality sucrose rewards, or a colour with low-quality sucrose rewards, or they did not acquire any individual experience. Bees were then exposed to the alternative colour associated with conspecific demonstrator bees (social information) or the alternative colour with no social information. Bees that had no individual experience visited flower colours that were associated with conspecific demonstrators (social information) but only significantly if the socially demonstrated colour was one for which bees had an innate bias. When bees had individual experience foraging on a colour with high-quality rewards they continued foraging on that colour, and generally did not visit the socially demonstrated alternative colour, regardless of innate colour bias. Alternatively, when bees had individual experience foraging on colours with low-quality rewards, they made more visits to the socially demonstrated alternative flower colour, but only when the alternative colour was the colour for which they had an innate bias. Bees that had no access to social information continued to forage on low-reward coloured flowers. Thus we show that reward quality of resources with which bees have individual experience affects the use of social information but with an important role of innate biases.

When animals make decisions about which resources to consume they can be influenced by a number of different factors. Animals often have innate preferences, or biases, for particular foods (Birch, 1999). They also have previous individual experience with certain resources (Birch, 1999; Sclafani, 2007), and they often have access to information from other individuals, or social information (Avarguès-Weber & Chittka, 2014; Galef & Laland, 2005; Sherwin, Heyes, & Nicol, 2002). The use of social information in foraging decisions is taxonomically widespread, probably because social learning avoids the potentially costly mistakes of individual trial-and-error learning (Galef & Giraldeau, 2001). Social information, however, may not necessarily be relevant or accurate because it is acquired from others rather than by sampling the environment directly (Giraldeau, Valone, & Templeton, 2002). The costs and benefits of social information have led to the prediction that animals should use social information selectively in combination with information acquired from individual experience (Laland, 2004). Empirical research has confirmed that animals use social information only under certain conditions, following particular 'social learning strategies' (Kendal, Coolen, & Laland, 2009). For example, guppies (*Poecilia reticulata*) are more likely to use social information when they are uncertain (Kendal, Coolen, & Laland, 2004) and when acquiring individual information is costly (Laland & Williams, 1998); and nine-spined sticklebacks, *Pungitius pungitius*, are more likely to use social information when information acquired from individual experience is outdated (van Bergen & Coolen, 2004). These studies have provided important insights into how animals use social information when making foraging decisions.

Acquisition of information about novel foods has been proposed as a key advantage of social learning because testing novel foods carries inherent risks (Galef & Giraldeau, 2001). A substantial body

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of research on when animals use social information to learn about novel foods has been conducted in Norway rats, *Rattus norvegicus*; in which satisfaction, predation risk, uncertainty and environmental stability influence the use of social information about novel foods (Galef, 2009). This research is crucial to predict when foraging innovations will spread through social groups. One of the social learning strategies demonstrated in Norway rats is that of ‘copy when dissatisfied’ (Laland, 2004), in which rats that are fed on a low-quality diet are more likely to use social information than rats fed on a high-quality diet (Galef, Dudley, & Whisken, 2008). This social-learning strategy has also been demonstrated in the frog-eating bat, *Trachops cirrhosus*, for which individuals foraging using poorly rewarded prey cues are more likely to use social information to learn novel prey cues than bats foraging on well-rewarded cues (Jones, Ryan, Flores, & Page, 2013). ‘Copy when dissatisfied’ is a relatively simple social-learning strategy that is likely exhibited by many taxa. We tested whether large earth bumblebees, *Bombus terrestris dalmatinus*, exhibit this strategy.

Bumblebees can rapidly learn to associate particular colours (Menzel, 1985; Raine & Chittka, 2008) and scents (Guerrieri, Schubert, Sandoz, & Giurfa, 2005; Molet, Chittka, & Raine, 2009) with rewards, and to differentiate between flowers with different reward qualities (Heinrich, 2004; Waddington, 2001). Bumblebees also use social information in a variety of different contexts. Bumblebees are attracted to the presence of other bees on flowers (Leadbeater & Chittka, 2005, 2009), and they can even learn to associate flower colours with rewards by observing other bees through a screen (Avarguès-Weber & Chittka, 2014; Dawson, Avarguès-Weber, Chittka, & Leadbeater, 2013; Worden & Papaj, 2005). Bumblebees also learn to make nectar-robbing holes in flowers after encountering flowers in which other bees have made holes (Goulson, Park, Tinsley, Bussière, & Vallejo-Marin, 2013), and bumblebees learn to avoid flowers that have been scent-marked by previous visitors (Leadbeater & Chittka, 2011). Bumblebees additionally learn floral scents that they have been exposed to in the hive from nectar collected by other foragers (Dornhaus & Chittka, 1999). Bumblebees therefore have access to a wide range of social information with the potential to influence foraging decisions.

Recent studies have asked when bees use social information or rely on information from individual experience. One such study showed that bumblebees are more likely to associate with conspecifics when they are exposed to predation risk than when they are in predator-free environments (Dawson & Chittka, 2014). In addition, bumblebees are more likely to use scent marks from other bees as indicators that a flower's nectar has been depleted when the flowers are complex, and therefore individual sampling is more costly (Saleh, Ohashi, Thomson, & Chittka, 2006). In honeybees, individuals are also more likely to use social information when errors in individual experience are more costly (Wray, Klein, & Seeley, 2011). In both honeybees and bumblebees, however, use of social information is not ubiquitous (Grüter & Leadbeater, 2014). Bumblebees that have foraging experience with one rewarding floral scent do not use social information to switch to foraging on alternative scents encountered in the hive, even when the experienced scent is no longer rewarding (Leadbeater & Florent, 2014). Similarly, honeybees with experience foraging at feeders that become unrewarding are slow to switch to socially demonstrated rewarding alternatives, repeatedly revisiting the unrewarding feeders before switching (Grüter & Ratnieks, 2011). These studies emphasize the facultative but not obligate use of social information by bees.

Bees foraging in the wild have access to an array of different flower types with sucrose concentrations ranging from 10% to 75% (Kevan & Baker, 1983). To test whether bumblebees exhibit the social learning strategy of ‘copy when dissatisfied’ (Laland, 2004), we examined how variation in reward quality affects bumblebee social information use. We trained bees to associate a flower colour with either a low (20%) sucrose concentration or a high (50%) concentration. We then provided bees with social information about an alternative flower colour. We predicted that bees foraging on flowers with low sucrose concentrations would use social information to visit alternative, more highly rewarded, flower colours. In contrast, we predicted that bees already foraging on a flower colour associated with high sucrose rewards would continue to forage on that colour and not visit socially demonstrated alternatives.

Bumblebees also have adaptive innate biases for particular flower colours (especially in the violet–blue range; Chittka, Ings, & Raine, 2004; Gumbert, 2000; Lunau, Wacht, & Chittka, 1996; Raine & Chittka, 2007), but these biases are variable at the individual and colony level (Ings, Raine, & Chittka, 2009). The terms ‘innate colour biases’ or ‘innate colour preferences’ are used widely in the pollinator literature to refer to preferential approaches to certain colours by foraging-naïve individuals (Lunau & Maier, 1995). Even after learning, approaches to novel flower colours can be influenced by innate biases (Gumbert, 2000). There has been little investigation of the role of innate biases in the use of social information in any taxa, but one study with Norway rats showed that social transmission chains are more stable when they provide information about a preferred flavour (cinnamon) than a less preferred flavour (cocoa) (Laland & Plotkin, 1993). Many animals show innate foraging biases, but how they are integrated with acquired individual and social experience is not well understood. We therefore additionally investigated the role of innate colour biases in the use of social information by bumblebees.

METHODS

Experimental Overview

For each bee we first tested innate bias for two colours, blue and yellow, in an unrewarded initial test. Bees were then randomly assigned to one of four treatments, which differed in the availability of individual experience with a coloured flower, the quality of rewards acquired during this individual experience, and access to social information about an alternative flower colour (Fig. 1, Table 1). The four treatments were as follows: (1) No training – Social, in which bees had no individual experience and were provided with social information about a flower colour; (2) Training to high-quality flower – Social, in which bees acquired individual experience with a coloured flower with high-quality (50% v/v sucrose solution) rewards and social information about an alternative

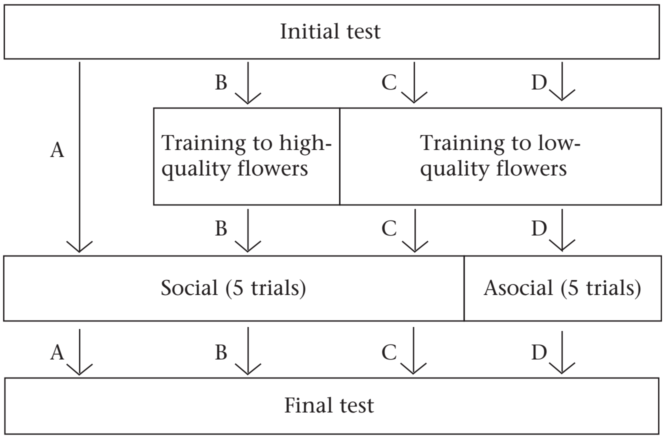

Figure 1. Experimental procedures for each of the four treatments are indicated by letters. A: No training – Social; B: Training to high-quality flower – Social; C: Training to low-quality flower – Social; D: Training to low-quality flower – Asocial.

Table 1
Experimental treatments

Treatment	Reward of trained flower colour	Reward of alternative flower colour	Social information?	Predicted to approach alternative flower?
No training – Social	NA	High (50% v/v)	Yes	Yes
Training to high-quality flower – Social	High (50% v/v)	High (50% v/v)	Yes	No
Training to low-quality flower – Social	Low (20% v/v)	High (50% v/v)	Yes	Yes
Training to low-quality flower – Asocial	Low (20% v/v)	High (50% v/v)	No	No

flower colour; (3) Training to low-quality flower – Social, in which bees acquired individual experience with a coloured flower with low-quality (20% v/v sucrose solution) rewards and were exposed to social information about an alternative flower colour; and (4) Training to low-quality flower – Asocial, in which bees acquired individual experience with a flower with low quality rewards and then were exposed to an alternative flower colour but no social information.

Each bee was then tested in an unrewarded final test in which we again examined preferences for blue and yellow. We predicted that bees would rely on social information when they had no previous experience (No training – Social) (Leadbeater & Chittka, 2005). We also predicted that bees would use social information to learn about flower colours when their previous experience was with flowers with low-quality rewards (Training to low-quality flower – Social), whereas they would not use social information when their previous experience was with highly rewarded flowers (Training to high-quality flower – Social). Finally, we predicted that when bees had no access to social information (Training to low-quality flower – Asocial), they would continue to forage on flowers with low rewards and not risk individual exploration of an alternative resource.

Experimental Animals and Arena

Bumblebee, *B. terrestris dalmatinus*, colonies ($N = 3$) were obtained from Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands. Bees had no prior experience foraging from coloured flowers. Colonies were transferred to nestboxes (28 × 16 × 11 cm) and attached to a flight arena (117 × 72 × 30 cm) by a clear Plexiglas tube with sliding doors to control which bees could enter and exit the arena. The floor of the flight arena was covered in laminated green paper. Bees were allowed to forage together in the flight arena from 16 colourless transparent artificial flowers arranged in a grid provisioned with 50% v/v sucrose solution. Naïve bees are attracted to other bees on flowers (Leadbeater & Chittka, 2009), but allowing bees to forage together and associate the presence of other bees with rewards strengthens this attraction (Avarguès-Weber & Chittka, 2014; Dawson et al., 2013). Foragers were individually marked with numbered, coloured bee tags (Opalith, Christian Graze KG, Germany). Bees that were consistently seen foraging were then selected for the experiment and randomly assigned to one of the four treatments. Twenty bees were tested individually in each of the treatments with the exception of one treatment in which 19 bees were tested; therefore, a total of 79 bees were tested. Each treatment contained bees from all three colonies. Within each treatment half of the bees were assigned to receive blue as the socially demonstrated (or the alternative, in the absence of social information) flower colour and the other half were assigned yellow.

Initial Tests

Bees were first given an initial test of their response to blue and yellow artificial flowers. Artificial flowers were 2.4 × 2.4 cm plastic tiles with a well (2 mm diameter and 2 mm deep) in the centre. We randomly arranged 16 flowers (eight yellow and eight blue) in a grid spaced with the centre wells 9.5 cm apart in each row or column. All flowers contained 20 μl of water (unrewarded). We recorded all the choices that the bee made in 3 min. A choice was scored when the bee landed on a flower. After 3 min the test ended and the bee was trapped in a plastic cup. Bees that did not make a choice in 3 min were returned to the colony and retested at a later point.

Training

For the training phase all of the 16 artificial flowers were the same colour, either blue or yellow. Artificial flowers were provisioned with 20 μl of either 20% v/v or 50% v/v sucrose solution depending on the treatment. The test bee was released from the plastic cup into the arena. After a bee drained a flower and moved away, the flower was immediately reprovisioned with 20 μl of solution. The training phase concluded when the test bee exited the arena and returned to the colony. If the bee did not approach a flower within the first 10 min of the training phase, they were placed on an artificial flower to encourage them to forage. Bees that did not continue to forage were excluded from the experiment. Bees in the No training – Social treatment did not receive the training trials.

Social Trials

The test bee was then given five social trials (or asocial trials for the Training to low-quality flower – Asocial treatment). Each trial was a foraging bout on a spatially randomized array of eight yellow and eight blue flowers provisioned with 20 μl of sucrose solution with concentrations depending on treatment. For the social trials, demonstrator bees were attached to the flowers of the alternative colour (e.g. blue if the trained colour was yellow). Demonstrator bees were adult bees from the same colony as the test bee that were freeze-killed (Dawson et al., 2013). To our knowledge freezing is the most humane method for killing bumblebees because bumblebees' natural response to cold temperatures is to enter torpor, a common experience for bumblebees in the wild (Heinrich, 1993). Bees maintained below freezing for an extended period die while torpid. The freeze-killed bees were pinned through the thorax using entomology pins. The pins were then attached to the flowers with white clay (Fimo Soft, Staedtler, Germany). To control for any effect of the presence of the clay, clay was attached to the flowers with and without demonstrators (Fig. 2). New clay was used for each tested bee. Trials began when the bee entered the arena and ended when the bee exited to return to the colony. Bees had to visit at least one artificial flower in order to count the social trial. We recorded all of the flowers visited during the social trials and refilled flowers with 20 μl of the appropriate sucrose solution after the bee drained them. All of the artificial flowers were cleaned with 50% ethanol between trials to ensure that the foraging behaviour of the bees was not affected by scent marks (Schmitt & Bertsch, 1990).

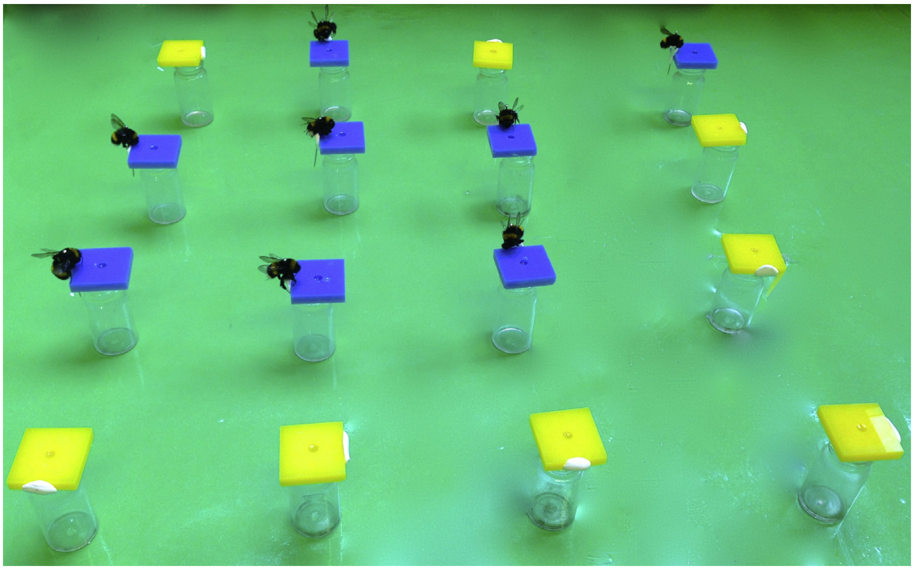

Figure 2. Photograph of the experimental arena set-up for a social trial with demonstrator bees pinned to the blue flowers.

Final Tests

Final tests were conducted to examine the bees' preferences for the trained and alternative colours following the social trials. Final tests were identical to initial tests with a spatially randomized array of eight blue and eight yellow flowers all filled with 20 μl of water. We recorded all the flower choices made by bees for the first 3 min after they entered the arena. The tested bee was then removed and the floor of the arena and flowers were cleaned with 50% ethanol before testing the next bee.

Statistical Analyses

All statistical analyses were conducted with R version 3.0.2 (R Core Team., 2013). We examined whether there were overall innate colony biases for blue by testing whether the proportion of landings that bees made on blue flowers significantly differed from 50% (random) for each colony using one-sample Wilcoxon signed-ranks tests. As there were no overall colony biases for blue but individuals showed biases for one colour or the other (see Results), we determined how many landings each bee made on the colour that was assigned to be its alternative (socially demonstrated) colour. This enabled us to assign bees within each treatment to a group in which the alternative colour was the one for which they had shown an innate bias or a group in which the bees were innately biased towards the trained colour. We categorized innate bias two ways: as more than 55% of landings on that colour in initial test, or as 100% of landings on that colour in the initial test. We conducted two different analyses of the results using these two criteria for innate bias (see Analyses Using Bees That Made 100% of Visits to One Colour in the Initial Tests).

For the final tests we examined whether there were colony differences in the proportion of the landings that bees made on the alternative colour using a Kruskal–Wallis two-sample test. To examine effect of groups to which bees were assigned on the proportion of landings on the alternative colour in the final test we used mixed-effects models with the lme4 package in R (Bates, Maechler, & Bolker, 2013) with colony as a random effect. Within each group we analysed whether preference for the alternative colour (proportion of landings) in the final tests significantly differed from 50% (random) using one-sample Wilcoxon signed-ranks tests.

RESULTS

Initial Tests

Within each colony the proportion of visits by naïve bees to blue flowers did not significantly differ from random (Wilcoxon signed-ranks tests: colony 1: $V = 211$, $N = 28$, $P = 0.176$; colony 2: $V = 392.5$, $N = 35$, $P = 0.099$; colony 3: $V = -52$, $N = 16$, $P = 0.410$). Most (95%) bees, however, made at least 55% of their visits to one flower colour; with 45 individuals (57%) biased towards blue flowers and 30 individuals (38%) biased towards yellow flowers (Fig. 3). Four bees (5%) showed no such bias in visiting patterns and were eliminated from further analyses.

Colony Effects

There was no significant effect of colony identity on the proportion of landings bees made on the alternative (socially demonstrated) colour in the final test (Kruskal–Wallis two-sample test: $\chi^2_2 = 0.758$, $P = 0.685$).

Final Tests

There was a significant effect of the different groups to which bees were assigned on the proportion of landings bees made on the alternative colour in the final tests (linear mixed-effect model: $\chi^2_7 = 80.122$, $P < 0.001$).

No Training – Social

Bees with no previous individual experience (training) predominantly landed on the socially demonstrated alternative colour in the final tests. This preference was significant when the socially demonstrated colour was the colour for which bees showed an innate bias (Wilcoxon signed-ranks test: $V = 21$, $N = 6$, $P = 0.031$). When the socially demonstrated alternative colour was not the bias

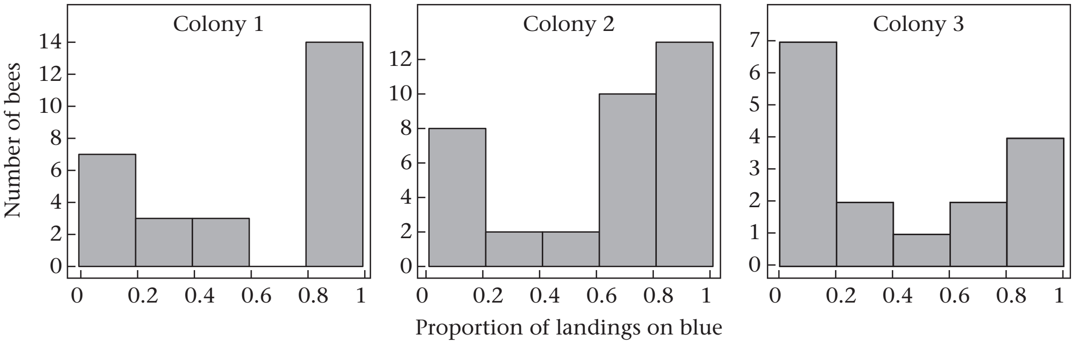

Figure 3. Results from initial tests for bees from each colony. Values of 1 indicate bees that only landed on blue flowers in the initial test. Values of 0 indicate bees that only landed on yellow flowers in the initial test.

colour, the preference was not statistically significant ($V = 58.5$, $N = 12$, $P = 0.092$; Fig. 4).

Training to High-quality Flower — Social

Bees that had individual experience with an artificial flower colour associated with high-quality rewards (50% v/v sucrose solution) showed a significant preference for the trained flower colour whether the alternative was the colour for which they had shown an innate bias (Wilcoxon signed-ranks test: $V = 0$, $N = 9$, $P = 0.005$) or not ($V = 0$, $N = 10$, $P = 0.003$; Fig. 4).

Training to Low-quality Flower — Social

Bees that had individual experience with artificial flowers associated with poor-quality rewards (20% v/v sucrose solution) showed a significant preference for the trained flower colour only when the trained colour was the colour for which they had an innate bias (Wilcoxon signed-ranks test: $V = 0$, $N = 7$, $P = 0.012$). When the socially demonstrated alternative flower colour was the colour for which they had shown an innate bias, they did not show a significant preference for the trained colour due to bees visiting the socially demonstrated alternative ($V = 24$, $N = 12$, $P = 0.233$; Fig. 4).

Training to Low-quality Flower — Asocial

When bees acquired individual experience with colours associated with poor-quality rewards and were provided access to alternative flower colours but no social information, they predominantly did not investigate the alternative flowers but showed a significant preference for the trained flower colour whether they had an innate bias for the alternative colour (Wilcoxon signed-ranks test: $V = 3$, $N = 12$, $P = 0.003$), or not ($V = 1$, $N = 7$, $P = 0.028$; Fig. 4).

Analyses Using Bees That Made 100% of Visits to One Colour in the Initial Tests

In a separate analysis we only included bees that exclusively visited one colour (100%) in the initial tests; 32 (41% of the tested bees) were eliminated and we retained 21 bees (27% of tested bees) that exclusively visited blue flowers and 26 bees (33% of tested bees) that exclusively visited yellow flowers. When we analysed only these bees we found very similar results. There was no significant effect of colony identity on the proportion of landings on the alternative colour in the final test (Kruskal–Wallis two-sample test: $\chi^2_2 = 0.582$, $P = 0.748$). There was a significant effect of the group to which the bees were assigned on the proportions of visits that bees made to the alternative colour in the final tests (linear

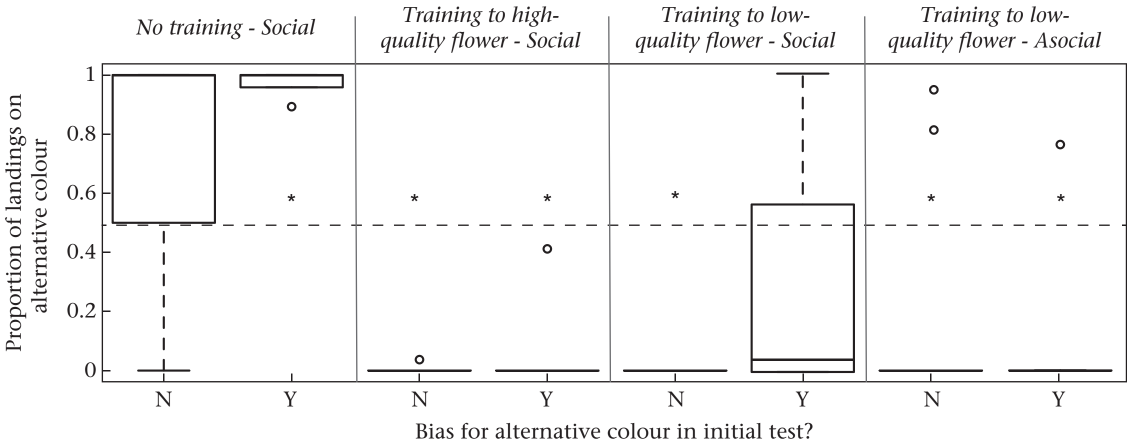

Figure 4. Box plot of proportion of visits bees made to the alternative (or socially demonstrated) flower colour in the final tests by bees that made more than 55% of their visits to one colour in the initial test. A value of 0 would indicate a bee that only visited the colour that it was trained to in the final test. A value of 1 would indicate a bee that only visited the alternative colour in the final test. Within each treatment the results are divided into bees for which the alternative (or socially demonstrated) colour was the colour for which they showed an innate bias (>55% of landings on that colour in the initial test) (Y) and bees for which the alternative colour was not the colour for which they showed a bias (N). The edges of the boxes indicate the first and third quartiles. Whiskers extend to the lowest datum that was 1.5 times the interquartile range from the lower quartile and the highest datum within 1.5 times the interquartile range from the upper quartile. Open circles indicate outliers. Asterisks designate significant differences from 0.5, indicated by the dotted line.

mixed-effect model: $\chi^2{}_7 = 52.662$, $P < 0.001$). Bees with no training that were exposed to social information about an alternative colour (No training − Social) all preferentially visited the socially demonstrated colour when it was the colour for which they had an innate bias, but due to the small sample size this result was not statistically significant (Wilcoxon signed-ranks test: $V = 6$, $N = 4$, $P = 0.174$; Fig. 5). There was no significant preference for the socially demonstrated colour when it was not the bias colour ($V = 30$, $N = 9$, $P = 0.351$; Fig. 5). Bees that received individual experience with a high-quality rewarded colour and then social information about an alternative colour (Training to high-quality flower − Social) significantly preferred the trained colour whether they had an innate bias for the alternative colour ($V = 0$, $N = 6$, $P = 0.026$) or not ($V = 0$, $N = 6$, $P = 0.026$; Fig. 5). Bees with individual experience foraging on a colour with low-quality rewards and social information about an alternative (Training to low-quality flower − Social) showed a significant preference for the trained colour when it was the colour for which they had an innate bias ($V = 0$, $N = 6$, $P = 0.020$), but when the socially demonstrated colour was the colour for which bees had an innate bias, there was not a significant preference for the trained colour due to bees visiting the socially demonstrated alternative ($V = 9$, $N = 7$, $P = 0.416$; Fig. 5). Finally, for bees with individual experience foraging on a colour associated with low-quality rewards and no social information (Training to low quality flower − Asocial), all of the bees continued to forage on the trained colour even when they were innately biased towards the alternative colour, but this was not statistically significant ($V = 0$, $N = 4$, $P = 0.089$). Bees with innate biases for the trained colour did show a significant preference for the trained colour ($V = 0$, $N = 6$, $P = 0.020$; Fig. 5).

DISCUSSION

Our study shows a clear interaction between individual experience (training), social information and innate biases when bumblebees make foraging decisions: social information is more often used when the individual experience is with flowers with low-quality rewards and when the social information directs the bees to flowers that match the bees' innate bias. We found similar results when we used either a low (55% of visits to one of the colours) or a high (100%, i.e. exclusive) criterion for innate bias. The few discrepancies between these two analyses were due to the smaller number of bees that showed exclusive biases in the initial tests. The criterion used for identifying bias, therefore, does not appear to have a large influence on the pattern of results in our study. Individuals of many species have innate biases for particular types of food (Birch, 1999; Rozin & Vollmecke, 1986), and research with rats has shown that innately preferred flavours increase the stability of social transmission chains (Laland & Plotkin, 1993). Previous studies, however, have not examined the interaction between the three factors: innate biases, individual experience and social learning. The foraging decisions of wild bees are likely influenced by all of these sources of information. We therefore show that this is one more domain in which there are complex interactions between nature and nurture (Haldane, 1946; Pigliucci, 2001).

We predicted that when bees were foraging on high-quality flowers, they would not approach socially demonstrated alternative flower colours. Our results confirm this prediction and agree with other studies showing that animals foraging on highly rewarding resources are less likely to be influenced by social information (e.g. Jones et al., 2013). Animals that are foraging on resources with low rewards, in contrast, should benefit more from investigating socially demonstrated alternatives. We found evidence for this in the bees that had individual experience with a colour associated with low reward and approached the socially demonstrated alternative, supporting the social learning strategy of ‘copy when dissatisfied’ (Laland, 2004).

Bees that had no social information showed significant preferences for the colour to which they were trained even though it was associated with low-quality rewards. Only a few bees investigated the alternative colour in the absence of social information. Bees are known to exhibit ‘flower constancy’, in which individuals show strong preferences for one particular flower type from which they have received rewards (Free, 1970; Grant, 1950; Heinrich, 1976; Waser, 1986). Extensive research has examined the costs and benefits of flower constancy (Chittka, Thomson, & Waser, 1999; Cnaani, Thomson, & Papaj, 2006; Gegear & Laverty, 2005; Goulson & Cory, 1993). The presence of other bees on flowers may overcome a persistence in foraging from particular low-reward flowers, perhaps by decreasing the costs of investigating alternative flower colours. Even in the treatment in which the bees had access to social information, not all of the bees used it, and many of the bees continued to forage on the flower colour with which they had individual experience. Recent research has shown that demonstrator motion enhances social learning in bumblebees (Avarguès-Weber & Chittka, 2014). It is possible, therefore, that moving demonstrators might have increased the use of social information in our study. Absence of social learning, however, even in conditions when it is predicted to be advantageous, has been found in other studies with bumblebees (Leadbeater & Florent, 2014) as well

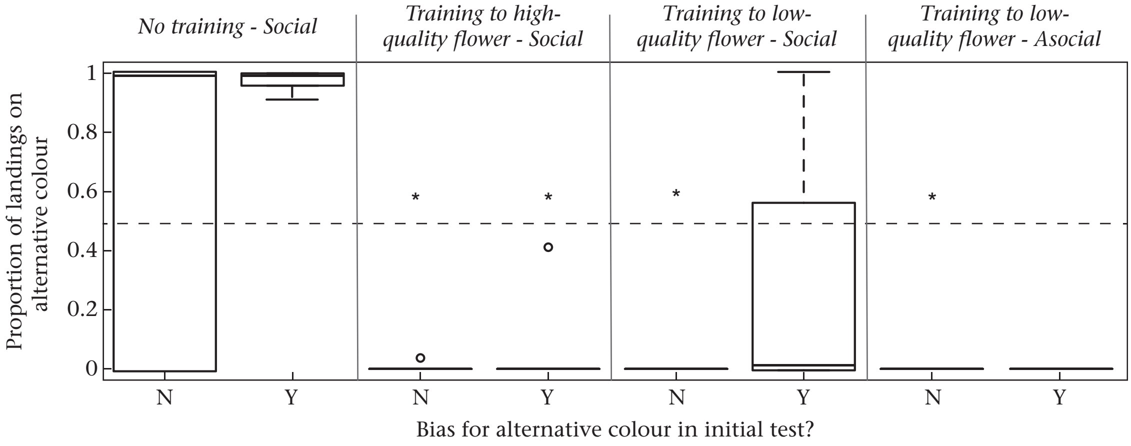

Figure 5. Box plot of proportion of visits bees made to the alternative (or socially demonstrated) flower colour in the final tests only by bees that made 100% of their visits to one colour in the initial tests.

as with honeybees (Grüter & Ratnieks, 2011). These studies have led to the proposal that predictions about social information use should be different for eusocial insects in which individuals forage to feed the colony as well as themselves (Grüter & Leadbeater, 2014). The colony as a whole may be more successful through environmental changes when individuals are collecting food from a variety of sources rather than converging through social learning.

Conclusions

We show that foraging decisions by bumblebees are affected by multiple sources of information. When bees had no individual experience, they made more visits to flower colours about which they had social information. When bees had individual experience foraging on a flower colour associated with high-quality rewards, they continued to forage on that colour. In contrast, when bees had individual experience foraging on a flower colour associated with low-quality rewards, they did not show a preference for that colour due to more bees investigating alternative flower colours, but only when there was social information available and the alternative colours were the colours for which they had an innate bias. Our study therefore integrates multiple factors that are likely to influence foraging behaviour. Bumblebees foraging in the wild are faced with an even broader array of options and additional sensory cues such as different flower shapes and scents. All of these sources of information likely affect bee foraging decisions with potential fitness consequences for both the pollinators and the plants.

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