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Honey bees adjust colour preferences in response to concurrent social information from conspecifics and heterospecifics

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Bees efficiently learn asocial and social cues to optimize foraging from fluctuating floral resources. However, it remains unclear how bees respond to divergent sources of social information, and whether such social cues might modify bees' natural preferences for nonsocial cues (e.g. flower colour), hence affecting foraging decisions. Here, we investigated honey bees', *Apis mellifera*, inspection and choices of unfamiliar flowers based on both natural colour preferences and simultaneous foraging information from conspecifics and heterospecifics. Individual honey bees' preferences for flowers were recorded when the reward levels of a learned flower type had declined and novel-coloured flowers were available where they would find either no social information or one conspecific and one heterospecific bumble bee, *Bombus terrestris*, each foraging from a different coloured flower (magenta or yellow). Honey bees showed a natural preference for magenta flowers. They modified their inspection of both types of flowers in response to conspecific and heterospecific social information. The presence of a conspecific demonstrator on the less-preferred yellow flower increased honey bees' inspection of yellow flowers and the likelihood of foraging on them, thus outweighing the original preference for magenta flowers. The presence of a heterospecific on a magenta flower increased honey bees' inspection of magenta flowers, but this effect was not observed when bumble bees fed on yellow flowers. Our results indicate that flower colour preferences of honey bees are rapidly adjusted in response to both conspecific and heterospecific presence, in different ways, with a preference for conspecific information possibly favouring the transmission of adaptive foraging information within species.

Foraging decisions are central to an animal's survival and reproduction; deciding where to forage in unpredictably changing environments is a major challenge that animals constantly encounter (Chittka, Thomson, & Waser, 1999; Stephens et al., 2007). Foraging decisions can be influenced in a context-dependent manner (Kendal, Coolen, & Laland, 2009; Laland, 2004) by innate preferences (Lunau, Wacht, & Chittka, 1996; Raine et al., 2006), previous individual experience (Sclafani, 1995) and the observation of, or interaction with, other animals at a foraging resource, i.e. social information (Heyes, 1994; Hoppitt & Laland, 2013; Leadbeater & Chittka, 2007b). For example, naïve individuals tend to rely more on social than individual information to gain familiarity about foraging sources (Galef & Giraldeau, 2001; Galef & Laland, 2005). Conversely, experienced individuals that have information on an advantageous foraging resource will often ignore social cues. Thus, social information is only drawn upon when individual information has become outdated and acquiring up to date information may be costly (Galef & Laland, 2005; Kendal et al., 2009; Laland, 2004). The influence of social information on foraging decisions is taxonomically widespread (Galef & Giraldeau, 2001; Grüter & Leadbeater, 2014; Valone & Templeton, 2002). Social information allows animals to find profitable foraging resources efficiently, instead of iteratively sampling the environment through trial and error (Galef & Laland, 2005).

In most animal communities, multiple species share the same foraging resources; thus members of the same (conspecific) and different (heterospecific) species can potentially act as sources and users of social information (Avarguès-Weber et al., 2013; Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Loukola, Gatto, Híjar-Islas, & Chittka, 2020; Parejo & Avilés, 2016; Seppänen, Forsman, Mönkkönen, & Thomson, 2007). Using social information indiscriminately is not adaptive and animals should be selective when acquiring information from other individuals (Kendal et al., 2018; Laland, 2004). In a multispecies context, animals have access to social information from different sources, which may give rise to a

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trade-off between selecting sources with a close ecological similarity, implying high competition, and sources whose ecological distance may involve less competition but a lower informative value (Seppänen et al., 2007). Furthermore, in a foraging context, social information has to be integrated with unlearned preferences (Jones, Ryan, & Chittka, 2015; Laland & Plotkin, 1993; Leadbeater & Chittka, 2007a) and existing individual information (Jones et al., 2015; van Bergen, Coolen, & Laland, 2004) to determine foraging decisions in a context-dependent manner (Kendal et al., 2009; Laland, 2004).

Social bee workers forage for nectar and pollen from rapidly changing floral resources (Chittka et al., 1999; Heinrich, 1979) within multispecies communities (Fægri & van der Pijl, 1979; Kevan & Baker, 1983) that might offer a wide spectrum of social information. This makes bees a valuable model to explore how different sources of social information can affect learned and unlearned preferences of individuals to shape foraging decisions. Traditionally, the laboratory paradigms that investigate the use of social information in bees tend to oversimplify the real field contexts where animals naturally acquire information from others. These paradigms usually test bees in relatively unnatural settings where a single source of social information is presented, for example a dead demonstrator pinned to simulated flowers (reviewed in Leadbeater & Dawson, 2017). Contrastingly, bees seeking nectar and pollen in the wild might encounter far more complex circumstances where they have access to multiple sources of social information (Fægri & van der Pijl, 1979; Kevan & Baker, 1983) that may coincide in time and space and diverge in their intrinsic relevance.

Honey bees and bumble bees of various species are, in many locations, sympatric and typically forage upon similar flowers due to their generalist diet (Rogers, Cajamarca, Tarpy, & Burrack, 2013; Xie, Pan, Teichroew, & An, 2016). Evidence indicates that bumble bees can acquire foraging information from demonstrator honey bees; in this case, the ‘demonstrators’ were dead individuals placed on artificial flowers (Dawson & Chittka, 2012). However, in more realistic conditions, a bee forager whose known floral resources have decreased in reward levels is likely to encounter other foragers, of their own and different species, feeding from different types of flowers (Fægri & van der Pijl, 1979; Kevan & Baker, 1983). It remains unclear how bees respond to such divergent social information, and whether, in this context, social cues might modify bees' natural preferences for particular colours in flowers (Chittka, Ings, & Raine, 2004; Raine & Chittka, 2007; Raine et al., 2006), hence influencing foraging decisions. We addressed these questions by testing whether honey bees might adjust their colour preferences in response to simultaneous sources of social information, that is, a conspecific and heterospecific, each foraging from either a preferred or a nonpreferred flower colour.

METHODS

Set-Up

We used free-flying honey bee, *Apis mellifera*, foragers from five hives located in an urban area of London, U.K. Over two consecutive summers (2017–2018), we trained foragers of one hive to collect 30% sucrose solution (w/w) from a gravity feeder (Von Frisch, 1965, Figure 16, p. 18), placed 2 m from one hive. The feeder in turn attracted foragers from the other four hives, which were then included in the experiments. The feeder was refilled every day at 0800 hours, but honey bees were also free to forage on local floral resources.

In addition, we used bumble bee, *Bombus terrestris*, foragers from two colonies (Biobest, Belgium N.V.) for the experiments. Bumble bee nests were housed in bipartite wooden nestboxes (29.5 × 11.5 cm and 9.5 cm high) connected to a wooden flight arena (77 × 52 cm and 30 cm high) by a Plexiglas tunnel (3.5 × 3.5 cm and 25 cm long). The floor of the flight arena was covered in white laminated paper. Three plastic sliding doors located along the corridor allowed controlled access to the arena. Before and after experiments, bumble bees could freely feed upon 30% (w/w) sucrose solution from a mass feeder in the middle of the arena. Bumble bee colonies were provided with 7 g of frozen pollen (Koppert B.V., The Netherlands) every 2 days.

Training of Bumble Bees

We trained 30 bumble bee foragers (demonstrators) from two colonies (one colony per year) in a flight arena. In this group training, foragers were allowed to enter the arena together at various times, and bumble bees learned to forage on an array of 12 plastic chips (2.4 × 2.4 cm, henceforth ‘flowers’) placed on the top of transparent glass vials (4 cm high), positioned on the floor of the arena. The array was arranged in a rectangular grid formation (3 × 4) with a separation of 7.5 cm between the edges of the flowers. We filled four magenta and four transparent flowers with 100 μl of unrewarding water, and four yellow flowers with 100 μl of rewarding 50% (w/w) sucrose solution (Fig. 1a). Flowers were refilled after they were depleted by foragers and the foragers had left the flower. Volume was based on a rough estimation of *B. terrestris* crop load of 100 μl (Klein, Pasquaretta, Barron, Devaud, & Lihoreau, 2017). This volume of sucrose solution in flowers was simultaneously drained by various foragers, such that they were only able to fill their crop load by visiting multiple rewarding flowers per foraging bout. Half of the foragers experienced the opposite colour reinforcement contingency. Training took place over 2 h on 1 day. We carried out refreshment bouts (20 min) each day prior to testing. We tracked demonstrator identity with individual number tags (Opalithplättchen, Warnholz & Bienenvoigt, Ellerau, Germany) glued to the top of the thorax by means of Loctite Super Glue Gel (Loctite, Westlake, Ohio, U.S.A.). The floor of the arena and flowers were cleaned with 70% ethanol after completing training.

Training of Honey Bees

Once we completed bumble bees' training, we proceeded to train honey bee demonstrators and observers, over 18 daily sessions. Each day, we trained a set of five honey bees (demonstrators) foraging from the gravity feeder. In this group training, honey bees learned to enter the same flight arena (located outdoors) where bumble bees were trained. We reversed the colour reinforcement contingency so that honey bees learned to forage on flowers of the opposite colour that bumble bees were trained on. Half of the honey bees experienced four yellow and four transparent flowers with 40 μl of water, and four magenta flowers with 40 μl of 50% (w/w) sucrose solution (Fig. 1a). The other half of the honey bees experienced the reverse colour reinforcement contingency. Rewarding flowers were refilled after depletion by foragers and the foragers had left the flower. The volume in flowers was based on a crop load of 60 μl for *A. mellifera* (Snodgrass, 1984). This volume was simultaneously drained by various foragers during group training, such that foragers would visit multiple rewarding flowers per foraging bout. Training lasted 1 h, consisting of six bouts (10 min). We identified trained individuals by marking their thorax with a white paint mark (Posca Pen, Worcester, U.K.). We cleaned the floor of the arena and flowers with 70% ethanol after completing training.

Three hours after finalizing the demonstrator's training, we selected a separate batch of five foragers (observers) to train them

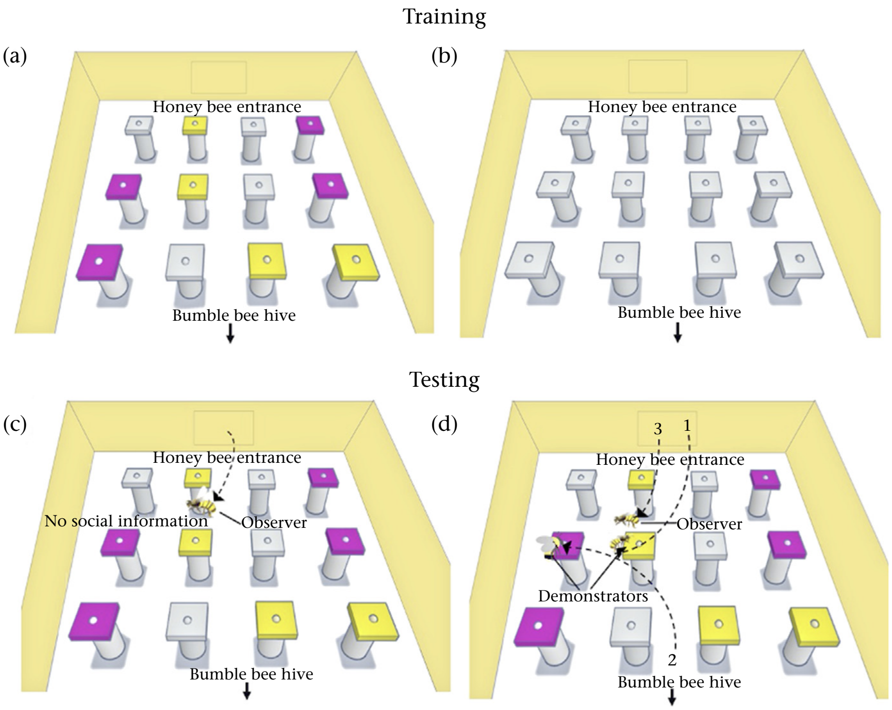


Figure 1. Schematic representation of training and testing protocols. (a) Honey bee foragers (demonstrators) were trained to find 50% sucrose solution on either four yellow or magenta flowers and water on four flowers of the alternative colour and four transparent flowers. Bumble bee foragers (demonstrators) were group trained using the same protocol. (b) A different batch of honey bee foragers (observers) was group trained to find 50% sucrose solution on six of 12 transparent flowers and unrewarding water on the other six transparent flowers. (c) Honey bee observers were tested on their preparedness to forage on an unfamiliar coloured flower type, depending on its colour (yellow or magenta), once their learned flower type (transparent) yielded no reward. (d) Two demonstrators (one honey bee and one bumble bee) and one observer honey bee were sequentially introduced into the flight arena. (1) A honey bee demonstrator was let into the flight arena. Once she had foraged from a flower of her trained colour, (2) a bumble bee demonstrator was released into the arena. Once she had also foraged from a flower of her trained colour (different colour from the honey bee demonstrator), (3) an observer honey bee was introduced to test her in a context where the flowers she previously associated with reward (transparent) were unrewarding and unfamiliar coloured flowers were demonstrated by a conspecific and a heterospecific (bumble bee) demonstrator, each foraging from nonpreferred (yellow) and preferred (magenta) flowers. This design was counterbalanced.

on a different set-up. Every day, observers were trained in a group to enter the same flight arena and forage upon a rectangular grid array of 12 transparent flowers (3 × 4; Fig. 1b). To encourage foragers to sample multiple flowers during their foraging trips, only half of the flowers contained 40 μl of 50% (w/w) sucrose solution, whereas the other half contained 40 μl of water. Rewarding flowers were replenished when empty and the forager had left the flower. The positions of all the flowers were changed every 10 min over 1 h of training. We marked trained observers with a green dot to distinguish them from the demonstrators. Already trained honey bees (demonstrators) were allowed to visit the set-up during this training, which did not interfere with the previous colour training, as shown in the Results. After training observers, we cleaned the flowers and the arena floor with 70% ethanol.

Effect of Colour Preference on Foraging Decisions

We carried out this control test every day after completing training. Only two to three individuals from the batch of five observer honey bees (trained on transparent flowers) regularly showed up at the set-up at the time of testing. Thus, we only tested two individuals per day. Overall, we tested 20 honey bees individually (control group) in a context where transparent flowers were unrewarding. We assessed whether they might show a natural preference to inspect and forage from one flower type between two unfamiliar alternatives, that is, yellow and magenta. One honey bee was let into the arena to explore a rectangular grid array of 12 flowers (described above), consisting of four familiar transparent flowers containing 20 μl of water and eight unfamiliar flowers, four yellow and four magenta, all filled with a scentless reward of 20 μl of 50% (w/w) sucrose solution, (Fig. 1c). This volume corresponds to the volume used in the test with live demonstrators (see section below). The test began once the individual inspected any flower. We defined ‘inspection’ as any time a honey bee displayed a slow side-to-side hover within one body length of a flower and with its head and body oriented towards the flower, for at least 500 ms (Ings, Raine, & Chittka, 2009). We based this definition on the established concept that honey bees orient towards what their attention is focused on (Spaethe, Tautz, & Chittka, 2006). The test concluded once the honey bee landed and foraged upon any unfamiliar flower, or 3 min after the test started. As this test was designed to evaluate the influence of honey bees' colour preferences on an actual foraging decision, rather than measuring their innate colour preferences, we regarded the flower type where the individual landed and foraged as preferred over the alternative type. To prevent retesting the same individuals, we captured honey bees, after concluding the test, to give them a distinctive red paint mark. The flowers and arena floor were cleaned with 70% ethanol between tests. To evaluate honey bees' inspection of flowers before they chose a flower to forage (foraging decision), we recorded the test with a sport camera (Yi, Xiaomi Inc. China) featuring a recording frame rate of 30 fps and a resolution of 720 p (1280 × 720 pixels). The camera was positioned 20 cm above the entrance of the bumble bee nest (Fig. 1). Its field of view was adjusted such that it looked down into the arena at ca. 50° from a horizontal angle.

Effect of Social Information on Foraging Decisions

To evaluate the influence of simultaneous sources (conspecific and heterospecific) of social information on honey bee's inspection of either yellow or magenta flowers and their subsequent foraging decisions, we tested 45 honey bees in the same context as individuals in the control group (see section above) but in the presence of one bumble bee and one honey bee demonstrator, each foraging upon either a yellow or a magenta flower. We filled flowers with 20 μl of either water or sucrose solution. This volume ensured demonstrators stayed long enough on each flower so that the observers had enough time to notice and inspect them. Additionally, demonstrators moved freely between flowers after depleting them, mimicking what they would naturally do within inflorescences to fill their crop load. Flowers were not refilled after being depleted.

We introduced the demonstrators and observer in the arena in the following order. (1) A honey bee demonstrator was let in through a sliding door on the back wall of the arena (Fig. 1d). Once she began to feed from a flower of her trained colour, (2) a bumble bee demonstrator was released from the Plexiglas tunnel that connected the arena to the nestbox (Fig. 1d). When she started to forage from a flower of her trained colour (opposite colour to the honey bee demonstrator), (3) a honey bee observer was let into the arena through the sliding door on the back wall. Both demonstrators swiftly landed and foraged exclusively on flowers of their trained colour. We tested 19 observer honey bees with a conspecific demonstrator foraging on magenta flowers and a heterospecific foraging on yellow flowers and 26 observers with the reversed colour reinforcement contingency. The test began once the observer honey bee inspected (see section above) any occupied or unoccupied flower. The test concluded once the observer landed and foraged upon any unfamiliar flower, or 3 min after the test started. In the test, demonstrators moved freely between flowers after depleting them, as they naturally do within inflorescences. Thus, we only considered that observers foraged on an unfamiliar flower when they fed upon the sucrose solution reward from unemptied flowers. To prevent retesting the same individuals, we caught tested honey bees and marked them with a distinctive red paint mark. The flowers and arena floor were cleaned with 70% ethanol between tests. To evaluate honey bees' inspection of flowers and their interactions with the demonstrators before they made a foraging decision, the test was recorded as described above.

Analyses

We analysed the behaviour of tested honey bees from video recordings, using the BORIS behavioural observation software (Friard & Gamba, 2016). To assess individuals' inspection of either yellow or magenta flowers and their preference to forage upon one type of flower over the other, we analysed two main behavioural categories: the frequency of inspecting transparent, yellow and magenta flowers (Balamurali, Nicholls, Somanathan, & Hempel de Ibarra, 2018; Ings et al., 2009) and the individual's foraging choice, that is, the yellow or magenta flower on which individuals landed and foraged. We used logistic analysis to explore the influence of flower colour on the likelihood of honey bees inspecting a flower for the first time, the likelihood of foraging on a flower type and the proportion of transparent, yellow and magenta flowers they inspected. For the latter two variables, we took underdispersion into account via a quasibinomial model (Wilson & Hardy, 2002).

For honey bees exposed to social information, we considered inspection of occupied flowers as an indicator that observers detected the demonstrator's presence. Here, we also applied the concepts from spatial attention research (Spaethe et al., 2006) to determine when observers detected the presence of either foraging demonstrator, that is, attentional focus was given to a demonstrator for the first time while inspecting an occupied flower, under the criteria described above. Detection of demonstrators was confirmed by observers' measurable behavioural response to demonstrators' presence (see Results). Four different scenarios were possible before honey bees made a foraging decision: they could have detected both demonstrators, either the honey bee or bumble bee demonstrator, or neither. We compared the likelihood of each situation against the expected probability with a chi-square goodness-of-fit test. Nine individuals did not detect the presence of the demonstrators and were thus not considered for all analyses.

We used logistic analysis to determine whether colour preferences and concurrent conspecific and heterospecific social information had a similar influence on foraging decisions of honey bees. Social information was included as a predictor variable (binary: 1 = present, 0 = absent) for the likelihood of honey bees landing on either an unfamiliar yellow or magenta flower.

Further, to evaluate the influence of social information on honey bees' readiness to forage on an unfamiliar flower, we compared two measurements between the control group and the group exposed to social information: the total number of flowers that individuals inspected before they chose a flower to forage on and the time it took them to make this decision (latency to forage). We analysed both measurements to explore whether observers' readiness to forage was influenced by the first foraging demonstrator they detected in the test (i.e. honey bee or bumble bee). This was irrespective of whether they detected only one or both demonstrators. These analyses were conducted with a Wilcoxon rank sum test.

To determine whether observers that detected both demonstrators inspected the flowers occupied by a honey bee and bumble bee at a similar frequency, we compared, with a Wilcoxon signed-rank test, the proportion of flowers occupied by each demonstrator that observers inspected. We also analysed, with a Wilcoxon rank sum test, whether honey bees that only detected either a conspecific or heterospecific demonstrator differed in the proportion of occupied flowers that they inspected, relative to all the flowers they inspected during the test. We used logistic analysis to explore the influence of flower colour and demonstrator's species on the likelihood of honey bee observers selecting the demonstrated type of flower and the likelihood that observers would forage on a flower occupied by either a honey bee or bumble bee, after approaching it for the first time. For the latter variable, we took underdispersion into account via a quasibinomial model (Wilson & Hardy, 2002).

The instances in which observers inspected an occupied flower that did not progress into landing and foraging were recorded as rejections. We evaluated whether observers rejected the flowers occupied by a honey bee or bumble bee demonstrator at a similar frequency. For observers that detected both demonstrators, we compared the proportion of times that they rejected the flowers occupied by each demonstrator, using a Wilcoxon signed-rank test. We also compared, with a Wilcoxon rank sum test, the total number of occupied flowers that observers rejected when they only detected either the honey bee or bumble bee demonstrator.

To assess whether observers altered their inspection of flowers after they initially detected the presence of either a foraging honey bee or bumble bee, we adjusted the frequency of observers' inspection of flowers by normalizing the data through an index calculation, with the following equation:

$$\text{inspecting index} = \frac{i_\text{m} - i_\text{y}}{i_\text{m} + i_\text{y}}$$

where i_m and i_y are the frequency with which the observer inspected magenta and yellow flowers, respectively.

In the indices, a negative value (minimum -1) equates to a preference to inspect yellow flowers, whereas a positive value (maximum $+1$) equates to a preference to inspect magenta flowers, an index close to zero implies that the observers either inspected

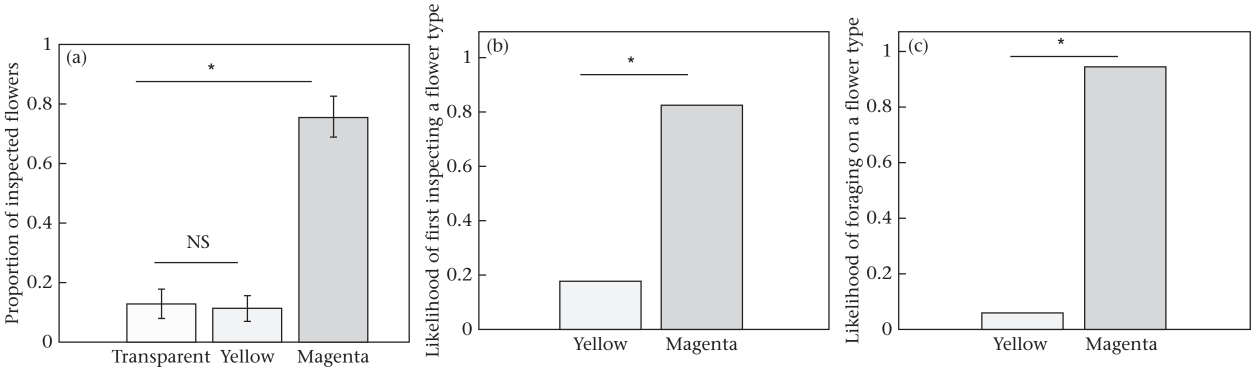


Figure 2. Colour preferences of honey bees. (a) Proportion of transparent, yellow and magenta flowers inspected. (b) The likelihood of honey bees inspecting an unfamiliar yellow or magenta flower first. (c) The likelihood of honey bees foraging on a yellow or magenta flower. Means are shown ± SEM. *$P < 0.05$.

both types of flowers equally or they did not inspect the flowers at all. We calculated inspecting indices based on the sequence of events that preceded the honey bees' foraging decisions. That is, each inspecting index represented observers' inspection of flowers, before and after they detected either demonstrator (honey bee or bumble bee) foraging on a flower. We compared indices against chance expectation (index = 0) with a Wilcoxon signed-rank test. A significant switch from a negative or positive value, before the observer detected a demonstrator, to a positive or negative value, after this occurred, indicates that observers modified their inspection of yellow or magenta flowers in response to conspecific or heterospecific social information. All analyses were conducted using R statistical software (R Core Team, 2019).

Ethical Note

The research described here aligns with the ASAB/ABS Guidelines for the Use of Animals in Research. No licences or permits were required for this study. Bees were kept in their natural colony environment in unaltered dark conditions. The gravity feeder from which honey bees foraged was only filled when no individuals were present to avoid disturbance. Bumble bees were fed with minimal disturbance under red light, which is poorly visible to bees. Colonies were not food deprived during experiments. Only bee foragers that freely engaged in foraging behaviour were trained and tested. Honey bees were tagged with a dot of paint on the thorax while feeding and bumble bees were carefully handled with dissection forceps to glue number tags on their thoraxes. These tags did not alter their natural behaviour.

RESULTS

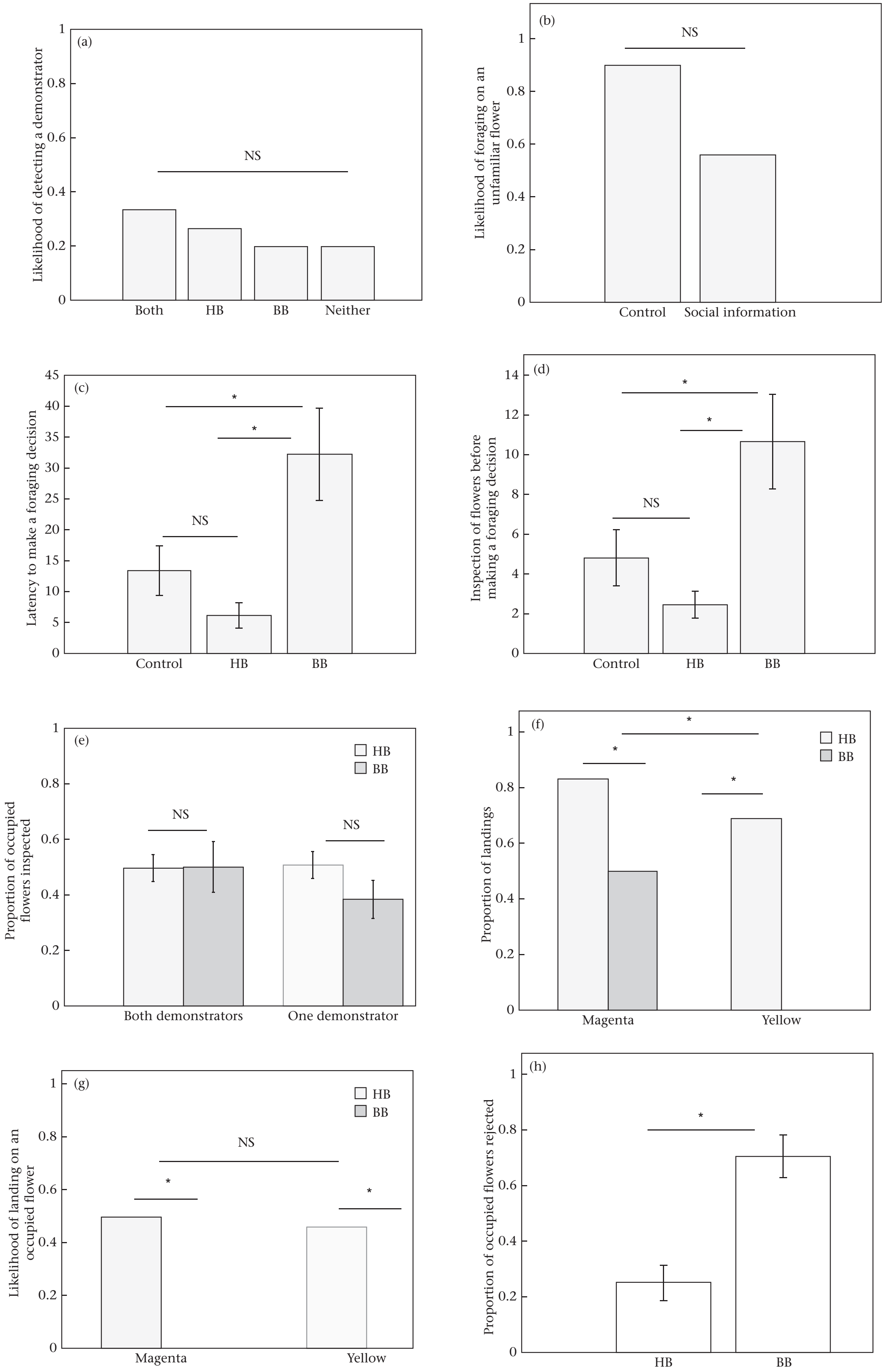
Effect of Colour Preference on Foraging Decisions

The majority of individuals (77%) did not inspect the familiar transparent flowers at all; rather, honey bees preferred to inspect and forage on magenta flowers. The proportion of flowers inspected by honey bees was influenced by flower colour (logistic regression: $F = 35.86$, $N = 20$, $P < 0.001$; Fig. 2a). Flower colour also influenced the likelihood of honey bees first exploring a flower type (logistic regression: $\chi^2_1 = 15.44$, $N = 20$, $P < 0.001$; Fig. 2b) and the likelihood of selecting a flower to forage (logistic regression: $F = 30.04$, $N = 20$, $P < 0.001$; Fig. 2c). This shows that honey bees had a colour preference for magenta over yellow flowers.

Effect of Social Information on Foraging Decisions

In a field-like context, including simultaneous and divergent conspecific and heterospecific social information, we investigated how such social information might affect honey bees' inspection of flower types and ultimate foraging decisions. We found no difference in the proportion of observers that detected both demonstrators, only the honey bee or bumble bee demonstrator or neither (chi-square goodness-of-fit test: $\chi^2_3 = 2.2$, $N = 45$, $P = 0.31$; Fig. 3a). The likelihood of foraging on an unfamiliar flower type was not influenced by the presence of social information (logistic regression: $\chi^2_1 = 0.9$, $N = 56$, $P = 0.34$; Fig. 3b). That is, similar to the control group, the majority of observers (90%) did not inspect the transparent flowers at all. These results suggest that both social information and natural colour preference for magenta flowers similarly affected honey bees' exploration of flowers and foraging decisions. That is, honey bees in the control group (no social information) and those exposed to social information both devoted little exploration to the transparent flowers they were trained on, and both groups were equally likely to forage on an unfamiliar flower type. Compared to observer honey bees that first detected a foraging bumble bee in the test, individuals in the control group, whose foraging decisions were solely influenced by colour preference, made faster choices (Wilcoxon rank sum: $W = 71$, $N = 35$, $P = 0.007$; Fig. 3c) and inspected fewer flowers (Wilcoxon rank sum: $W = 77$, $N = 35$, $P = 0.011$; Fig. 3d). However there was no difference between the control group and those observers that first detected the presence of a foraging conspecific (Wilcoxon rank sum: latency: $W = 133$, $N = 30$, $P = 0.29$; Fig. 3c; number of flowers: $W = 125$, $N = 30$, $P = 0.45$; Fig. 3d). Furthermore, when observers first detected the conspecific demonstrator, they made faster foraging decisions (Wilcoxon rank sum: $W = 184$, $N = 29$, $P < 0.001$; Fig. 3c), preceded by less inspection of flowers (Wilcoxon rank sum: $W = 176.5$, $N = 29$, $P < 0.001$; Fig. 3d), than when they first detected the heterospecific bumble bee. These results suggest that both colour preference for magenta flowers and conspecific social information similarly enabled honey bees to make swift foraging decisions, whereas observers that first detected a foraging heterospecific explored the flowers extensively before making a foraging decision.

Honey bee observers that detected either one or both demonstrators equally inspected flowers occupied by either the honey bee or bumble bee demonstrator (one demonstrator: Wilcoxon rank sum: $W = 34.5$, $N = 16$; $P = 0.45$; both demonstrators: Wilcoxon signed-rank: $V = 22.5$, $N = 13$, $P = 1$; Fig. 3e). However, the likelihood that an observer would forage on an unfamiliar flower type


(a)
Likelihood of detecting a demonstrator
NS
Both
HB
BB
Neither
0
0.2
0.4
0.6
0.8
1
(b)
Likelihood of foraging on an unfamiliar flower
NS
Control
Social information
0
0.2
0.4
0.6
0.8
1
(c)
Latency to make a foraging decision
*
*
NS
Control
HB
BB
0
5
10
15
20
25
30
35
40
45
(d)
Inspection of flowers before making a foraging decision
*
*
NS
Control
HB
BB
0
2
4
6
8
10
12
14
(e)
Proportion of occupied flowers inspected
☐ HB
▨ BB
NS
NS
Both demonstrators
One demonstrator
0
0.2
0.4
0.6
0.8
1
(f)
Proportion of landings
☐ HB
▨ BB
*
*
*
Magenta
Yellow
0
0.2
0.4
0.6
0.8
1
(g)
Likelihood of landing on an occupied flower
☐ HB
▨ BB
NS
*
*
Magenta
Yellow
0
0.2
0.4
0.6
0.8
1
(h)
Proportion of occupied flowers rejected
*
HB
BB
0
0.2
0.4
0.6
0.8
1

was influenced by the demonstrator's species (logistic regression: $\chi^2_1 = 11.78$, $N = 45$, $P < 0.001$; Fig. 3f) and flower colour (logistic regression: $\chi^2_1 = 5.08$, $N = 45$, $P = 0.024$; Fig. 3f) but was only marginally influenced by the statistical interaction between these main effects (logistic regression: $\chi^2_1 = 3.17$, $N = 45$, $P = 0.07$; Fig. 3f). Further, the demonstrator's species influenced the likelihood of observers foraging on an occupied flower after approaching it for the first time (logistic regression: $\chi^2_1 = 20.51$, $N = 51$, $P < 0.001$; Fig. 3g). That is, observers readily responded to the presence of a foraging conspecific by joining this demonstrator on the unfamiliar flower type. This response was not affected by flower colour (logistic regression: $\chi^2_1 = 0.03$, $N = 51$, $P = 0.82$; Fig. 3g) nor by any statistical interaction between the main effects (logistic regression: $\chi^2_1 = 0$, $N = 51$, $P = 1$; Fig. 3g). In contrast, observer honey bees rejected a higher proportion of the flowers occupied by a bumble bee demonstrator (Wilcoxon signed-rank: $V = 3$, $N = 13$, $P = 0.008$; Fig. 3h) than the flowers occupied by a conspecific. These results show that the observer's exploration of flowers and foraging decisions were separately affected by their colour preference and the demonstrator's species.

Effect of Social Information on Colour Preference

The inspecting indices, described in the analyses section, allowed us to analyse honey bees' inspection of flowers as a flexible process that culminated in a foraging decision, and whose variation in response to social information was measurable in terms of an index value. Observer honey bees showed no preference to inspect magenta or yellow flowers before they detected the bumble bee demonstrator foraging on either a magenta (Wilcoxon signed-rank test: $V = 20$, $N = 9$, $P = 0.15$; Fig. 4a) or yellow flower (Wilcoxon signed-rank test: $V = 12$, $N = 9$, $P = 0.11$; Fig. 4a). After honey bees detected a bumble bee foraging from a magenta flower, they preferentially inspected this type of flower (Wilcoxon signed-rank: $V = 26$, $N = 9$, $P = 0.026$; Fig. 4a). This effect was not evident after they observed a bumble bee demonstrator foraging on a yellow flower; instead honey bees showed no preference to inspect either type of flower (Wilcoxon signed-rank: $V = 18.5$, $N = 9$, $P = 0.5$; Fig. 4a). Honey bees showed no preference to inspect either type of flower before they detected a conspecific foraging on either a magenta (Wilcoxon signed-rank: $V = 16.5$, $N = 11$, $P = 0.61$; Fig. 4b) or yellow flower (Wilcoxon signed-rank: $V = 23$, $N = 11$, $P = 0.26$; Fig. 4b). However, observer honey bees did respond to the presence of a conspecific foraging on either flower type by increasing their inspection of demonstrated flowers (Wilcoxon signed-rank: magenta: $V = 52$, $N = 11$, $P = 0.006$; yellow: $V = 1$, $N = 13$, $P = 0.002$; Fig. 4b). These results show that honey bees' inspection of unfamiliar flowers underwent a sequential adjustment in response to conspecific and heterospecific social information, which ultimately affected their foraging decisions.

DISCUSSION

The results presented here provide evidence that honey bees' colour preferences can be adjusted in response to simultaneous social information from conspecifics and heterospecifics. Thus, specific social information may differently influence honey bees' exploration of flowers and consequent foraging decisions. Unexpectedly, honey bees payed little attention to the transparent flowers on which they were trained. Instead, prior to making a foraging decision, they more frequently inspected the magenta flowers (control group) or the type of flower demonstrated by a conspecific.

Even though inspecting flowers from a close distance does not provide foragers with information on the reward status of a flower, it is important in the process of choosing a flower (Lunau et al., 1996). In the absence of social information, honey bees' natural preference for magenta flowers influenced inspection and choices of flowers. Magenta is a mixture of blue and red; since the red component of this colour is not fully perceived by bees (Menzel & Shmida, 1993), they perceive magenta flowers as blue (Chittka & Waser, 1997; Waser & Chittka, 1998). Honey bees and bumble bees usually have innate biases for colours in the violet to blue range of the spectrum (Chittka et al., 2004; Giurfa, Núñez, Chittka, & Menzel, 1995), which correlates with the nectar production of local flowers (Chittka et al., 2004; Giurfa et al., 1995). Although colour biases may be overridden by individual learning (Raine et al., 2006), they potentially govern foraging decisions in bees when selecting among novel flower types (Gumbert, 2000). In the absence of social information, flower choices of tested honey bees conceivably resulted from either their innate colour preferences or previous field experience with local flower species, as both factors can be linked with the likelihood of finding a profitable food reward (Chittka et al., 2004; Giurfa et al., 1995).

In the wild, honey bee foragers are likely to encounter members of the same as well as different species foraging concurrently in a flower patch including distinct flower types (Fægri & van der Pijl, 1979; Kevan & Baker, 1983). Our results demonstrate that such social information is integrated with honey bees' colour preferences during the process of making a foraging decision. In this realistic scenario, with two simultaneous sources of conspecific and heterospecific social information, when the first foraging demonstrator that honey bees detected was a member of the same species, they promptly responded to social information by joining the demonstrator on the unfamiliar flower type. This evidence is consistent with previous findings in bumble bees (reviewed in Leadbeater & Dawson, 2017) and supports the notion that the use of conspecific social information in bees may be mediated by local enhancement, with foragers being attracted to flowers occupied by members of the same species (Leadbeater & Chittka, 2007a). Because, in our experiments, we used free-flying honey bees, we were unable to determine whether observers and demonstrators belonged to the same or different colonies. However, observers' behavioural response to conspecific demonstrators varied little, and further experiments would be required to determine whether or not nestmates and non-nestmates might differently affect observers' behaviour.

Honey bees and bumble bees often forage upon similar floral resources; it is thus conceivable that they may be in the same flower patches at the same time (Rogers et al., 2013; Xie et al., 2016). In our experiments, we used freely moving bumble bee demonstrators to elucidate how social information might flow

Figure 3. Effects of concurrent conspecific and heterospecific social information on honey bees' colour preferences. (a) Likelihood of honey bees detecting both demonstrators, only the honey bee or bumble bee demonstrator, or neither. (b) The likelihood of honey bees foraging on unfamiliar flowers in the control group (no social information and in the presence of demonstrators (social information). (c) Latency (s) to start foraging of honey bees in the control group and in those with a foraging conspecific or heterospecific (bumble bee) present. (d) Number of flowers inspected before foraging by honey bees in the control group and in those with a foraging conspecific or heterospecific (bumble bee) present. (e) Proportion of flowers occupied by a demonstrator that were inspected by honey bees when only one or both demonstrators were detected. (f) Proportion of landings on magenta or yellow flowers when a foraging conspecific or heterospecific (bumble bee) was present. (g) Likelihood of landing on a magenta or yellow flower when a foraging conspecific or heterospecific (bumble bee) was occupying it. (h) Proportion of flowers rejected when a foraging conspecific or heterospecific (bumble bee) was occupying it. HB = honey bee, BB = bumble bee. Means are shown ± SEM. $^*P < 0.05$.

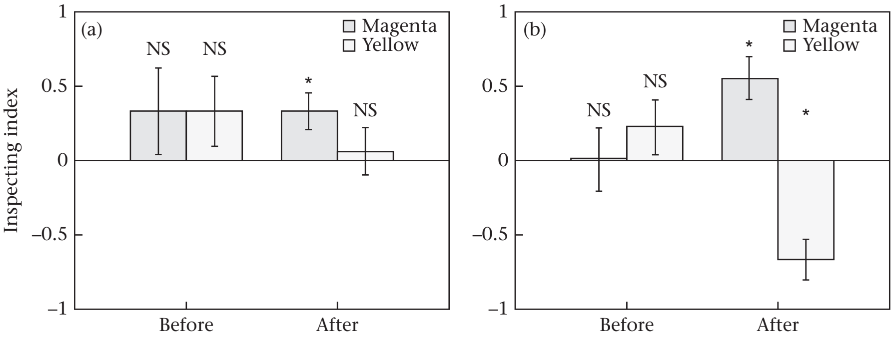


Figure 4. Inspecting indices compared to chance level (index = 0) of honey bees' inspection of unfamiliar flowers, before and after they detected either (a) a heterospecific (bumble bee) or (b) a conspecific demonstrator, each foraging on either a preferred or nonpreferred flower colour. Means are shown ± SEM. *$P < 0.05$.

between these species. Our results indicate that in the likely scenario of a honey bee exploring a flower patch and encountering both a conspecific and a heterospecific (bumble bee) individual foraging from different flower types, its readiness to use social information and make a foraging decision might depend on the first observed species providing social information. That is, observer honey bees that detected a conspecific demonstrator before a heterospecific bumble bee made swifter foraging decisions than those observers that first detected the bumble bee demonstrator, which spent more time exploring the flowers before making a foraging decision. This evidence suggests that in a foraging context, honey bees’ discrimination of conspecifics and heterospecifics might determine the selective use of social information. Theory predicts that using social information from heterospecifics should be favourable when there is a large niche overlap (Seppänen et al., 2007); yet, on adaptive grounds, when animals can select between social information from conspecifics and heterospecifics, they should typically favour the former as this naturally reflects their ecological needs (Jaakkonen, Kivelä, Meier, & Forsman, 2015). In line with this, honey bees consistently selected the type of flowers demonstrated by conspecifics, even though they attended to the presence of both demonstrators while exploring the set-up. Prioritizing conspecific over heterospecific choices can be explained by its high fitness value (Jaakkonen et al., 2015; Seppänen et al., 2007) but it can also serve to transmit novel behavioural traits or preferences that may be adaptively valuable for a particular species (Alem et al., 2016; Danchin et al., 2018; Jaakkonen et al., 2015; Laland & Plotkin, 1993; Leadbeater & Chittka, 2005).

Floral reward levels differ strongly between plant species and constantly change over time in an unpredictable manner (Heinrich, 1979). To achieve efficient foraging, bees can rapidly learn to associate floral traits such as colour, shape and scent with reward quality in flowers (Chittka et al., 1999). Bees can be initially attracted to forage from an unfamiliar flower species via either innate and learned colour preferences (Chittka et al., 2004; Giurfa et al., 1995; Gumbert, 2000; Raine & Chittka, 2007) or social information (Grüter & Leadbeater, 2014; Leadbeater & Chittka, 2007b; Leadbeater & Dawson, 2017). In the wild, bees seeking floral resources are unlikely to experience asocial and social cues in isolation; rather, they may frequently be exposed to a complex combination of cues potentially affecting their flower choices. Our findings demonstrate that simultaneous conspecific and heterospecific social information affects honey bees’ colour preferences, which may in turn shape the acquisition of new information and resulting foraging decisions.

Compared to honey bees in the control group (i.e. no social information), the exploration behaviour of honey bees that observed a conspecific or heterospecific demonstrator foraging on the less preferred yellow flowers reflected a more evenly distributed inspection of magenta and yellow flowers. That is, the presence of either demonstrator on a yellow flower increased the ‘attractiveness’ of this flower type for honey bees, possibly via stimulus enhancement, an effect widely described in the social learning literature (Heyes, 2012). Remarkably, honey bees' inspection of flowers, naturally biased towards magenta flowers, underwent a sequential and flexible adjustment prior to the bees making a foraging decision. This adjustment was modulated by visual foraging information from members of the same and different species.

It has been demonstrated that bees are attracted to the presence of foraging conspecifics when presented with unfamiliar flowers which may lead them to identify new rewarding flower species (Jones et al., 2015; Leadbeater & Chittka, 2005; Leadbeater & Chittka, 2007a). Our results indicate that the presence of a foraging conspecific not only influenced honey bee observers to select flowers that matched their colour preference (magenta) but this conspecific social information also outweighed the observers' colour preference so that they selected the normally nonpreferred yellow flowers. Whereas intraspecific social transmission of foraging information may be more stable when it reinforces a prior preference (Laland & Plotkin, 1990), such preferences may be adjusted and potentially overridden in response to conspecific social information about a novel foraging resource (Jones et al., 2015). This may enable bees to reasonably adapt to wildly varying floral reward levels. Thus, if the presence of a foraging conspecific can reliably be associated with a rewarding outcome, the use of this social cue should be reinforced to consistently influence bees' flowers choices across foraging contexts (Leadbeater & Chittka, 2009). Interestingly, in our experiments the presence of a foraging heterospecific also increased honey bees' attraction to the demonstrated flower types; yet, heterospecific social information did not influence honey bees' foraging choices. In fact, honey bee observers never landed on the flowers occupied by the bumble bee demonstrator, in contrast to the flowers occupied by the conspecific demonstrator. Even though heterospecific social information is predictably valuable when there is a large niche overlap (Seppänen et al., 2007), conspecifics’ choices might offer a more predictable social cue, decreasing the risk of acquiring maladaptive information (Giraldeau, Valone, & Templeton, 2002) as conspecifics share the same ecological needs (Goodale et al., 2010; Seppänen et al., 2007).

Multiple social and asocial cues can potentially affect animals’ foraging decisions in different circumstances (Galef & Giraldeau, 2001; Grüter & Leadbeater, 2014; Sclafani, 1995). The effect of social information on previous, innate or learned preferences influences the foraging decision of a particular individual and may also promote the transmission of adaptive information about food sources (Galef & Giraldeau, 2001; Laland & Plotkin, 1990). Despite the fact that social information offers a clear advantage to individuals exploring novel foraging resources (Galef & Giraldeau, 2001), its use should not be indiscriminate but should respond to particular circumstances in order to lead to adaptive choices (Kendal et al., 2018; Laland, 2004). Our results extend previous evidence showing that conspecific social information is commonly used in situations of uncertainty (Galef, Dudley, & Whiskin, 2008; Kendal, Coolen, & Laland, 2004; Smolla, Alem, Chittka, & Shultz, 2016; van Bergen Yfke et al., 2004), such that it can outweigh both predetermined individual preferences (Dugatkin, 1996; Jones et al., 2015) and heterospecific social information (Jaakkonen et al., 2015) to influence ecologically relevant decisions in animals.

It is conceivable that natural selection should favour the salience of social stimuli with high ecological relevance (Leadbeater & Dawson, 2017; Seppänen et al., 2007), conspecifics in our experiments. Whether such salience can similarly operate to select information from heterospecific sources, based on their relative informative value, deserves further consideration. We provide an ecologically relevant picture of the process by which multiple nonsocial and social cues may shape foraging decisions of bees. Thus, the findings presented here contribute to our understanding of the flexibility of individual preferences and their adjustment in response to different sources of social information. Our results in turn shed light on the selectivity of animals for conspecific over heterospecific information as a possible mechanism to facilitate the social transmission of foraging information within species.

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References

Alem, S., Perry, C. J., Zhu, X., Loukola, O. J., Ingraham, T., Søvik, E., et al. (2016). Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. *PLoS Biology, 14*(10), Article e1002564. https://doi.org/10.1371/journal.pbio.1002564

Avarguès-Weber, A., Dawson, E. H., & Chittka, L. (2013). Mechanisms of social learning across species boundaries. *Journal of Zoology, 290*(1), 1–11. https://doi.org/10.1111/jzo.12015

Balamurali, G. S., Nicholls, E., Somanathan, H., & Hempel de Ibarra, N. (2018). A comparative analysis of colour preferences in temperate and tropical social bees. *Science of Nature, 105*(1), 8. https://doi.org/10.1007/s00114-017-1531-z

van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B: Biological Sciences, 271*(1542), 957–962. https://doi.org/10.1098/rspb.2004.2684

Chittka, L., Ings, T. C., & Raine, N. E. (2004). Chance and adaptation in the evolution of island bumblebee behaviour. *Population Ecology, 46*(3), 243–251. https://doi.org/10.1007/s10144-004-0180-1

Chittka, L., Thomson, J. D., & Waser, N. M. (1999). Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften, 86*(8), 361–377. https://doi.org/10.1007/s001140050636

Chittka, L., & Waser, N. M. (1997). Why red flowers are not invisible to bees. *Israel Journal of Plant Sciences, 45*(2–3), 169–183. https://doi.org/10.1080/07929978.1997.10676682

Danchin, E., Nöbel, S., Pocheville, A., Dagaeff, A.-C., Demay, L., Alphand, M., et al. (2018). Cultural flies: Conformist social learning in fruitflies predicts long lasting mate-choice traditions. *Science, 362*(6418), 1025–1030. https://doi.org/10.1126/science.aat1590

Dawson, E. H., & Chittka, L. (2012). Conspecific and heterospecific information use in bumblebees. *PloS One, 7*(2), Article e31444. https://doi.org/10.1371/journal.pone.0031444

Dugatkin, L. A. (1996). Interface between culturally based preferences and genetic preferences: Female mate choice in *Poecilia reticulata*. *Proceedings of the National Academy of Sciences, 93*(7), 2770–2773. https://doi.org/10.1073/pnas.93.7.2770

Fægri, K., & van der Pijl, L. (1979). Animals as pollinators. In K. Fægri, & L. van der Pijl (Eds.), *Principles of pollination ecology* (3rd ed., pp. 96–133). Pergamon.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution, 7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Galef, B. G., Dudley, K. E., & Whiskin, E. E. (2008). Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. *Animal Behaviour, 75*(2), 631–637. https://doi.org/10.1016/j.anbehav.2007.06.024

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour, 61*(1), 3–15. https://doi.org/10.1006/anbe.2000.1557

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience, 55*(6), 489–499. https://doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2

Giraldeau, L., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical transactions of the Royal Society Series B, Biological Sciences, 357*(1427), 1559–1566. https://doi.org/10.1098/rstb.2002.1065

Giurfa, M., Núñez, J., Chittka, L., & Menzel, R. (1995). Colour preferences of flower naive honeybees. *Journal of Comparative Physiology, 177*(3), 247–259. https://doi.org/10.1007/BF00192415

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution, 25*(6), 354–361. https://doi.org/10.1016/j.tree.2010.01.002

Grüter, C., & Leadbeater, E. (2014). Insights from insects about adaptive social information use. *Trends in Ecology & Evolution, 29*(3), 177–184. https://doi.org/10.1016/j.tree.2014.01.004

Gumbert, A. (2000). Color choices by bumble bees (*Bombus terrestris*): Innate preferences and generalization after learning. *Behavioural Ecology and Sociobiology, 48*(1), 36–43. https://doi.org/10.1007/s002650000213

Heinrich, B. (1979). Resource heterogeneity and patterns of movement in foraging bumblebees. *Oecologia, 40*(3), 235–245. https://doi.org/10.1007/BF00345321

Heyes, C. M. (1994). Social-learning in animals–categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society, 69*(2), 207–231. https://doi.org/10.1111/j.1469- 185X.1994.tb01506.x

Heyes, C. M. (2012). What's social about social learning? *Journal of Comparative Psychology, 126*(2), 193–202. https://doi.org/10.1037/a0025180

Hoppitt, W., & Laland, K. N. (2013). *Social learning: An introduction to mechanisms, methods, and models*. Princeton University Press. https://doi.org/10.2307/j.ctt2jc8mh

Ings, T. C., Raine, N. E., & Chittka, L. (2009). A population comparison of the strength and persistence of innate colour preference and learning speed in the bumblebee *Bombus terrestris*. *Behavioural Ecology and Sociobiology, 63*(8), 1207–1218. https://doi.org/10.1007/s00265-009-0731-8

Jaakkonen, T., Kivelä, S. M., Meier, C. M., & Forsman, J. T. (2015). The use and relative importance of intraspecific and interspecific social information in a bird community. *Behavioral Ecology, 26*(1), 55–64. https://doi.org/10.1093/beheco/aru144

Jones, P. L., Ryan, M. J., & Chittka, L. (2015). The influence of past experience with flower reward quality on social learning in bumblebees. *Animal Behaviour, 101*, 11–18. https://doi.org/10.1016/j.anbehav.2014.12.016

Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, & M., & Jones, P. L. (2018). Social learning strategies: Bridge-building between fields. *Trends in Cognitive Sciences, 22*(7), 651–665. https://doi.org/10.1016/j.tics.2018.04.003

Kendal, R. L., Coolen, I., & Laland, K. N. (2004). The role of conformity in foraging when personal and social information conflict. *Behavioral Ecology, 15*(2), 269277. https://doi.org/10.1093/beheco/arh008

Kendal, R. L., Coolen, I., & Laland, K. N. (2009). Adaptive trade-offs in the use of social and personal information. In R. Dukas, & J. M. Ratcliffe (Eds.), *Cognitive ecology* (2nd ed., pp. 249–271). The University of Chicago Press.

Kevan, P. G., & Baker, H. G. (1983). Insects as flower visitors and pollinators. *Annual Review of Entomology, 28*(1), 407–453. https://doi.org/10.1146/annurev.en.28.010183.002203

Klein, S., Pasquaretta, C., Barron, A. B., Devaud, J.-M., & Lihoreau, M. (2017). Inter-individual variability in the foraging behaviour of traplining bumblebees. *Scientific Reports, 7*(1). https://doi.org/10.1038/s41598-017-04919-8

Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior, 32*(1), 414. https://doi.org/10.3758/BF03196002

Laland, K. N., & Plotkin, H. C. (1990). Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Animal Learning & Behavior, 18*(3), 246–251. https://doi.org/10.3758/BF03205282

Laland, K. N., & Plotkin, H. C. (1993). Social transmission of food preferences among Norway rats by marking of food sites and by gustatory contact. *Animal Learning & Behavior, 21*(1), 35–41. https://doi.org/10.3758/BF03197974

Leadbeater, E., & Chittka, L. (2005). A new mode of information transfer in foraging bumblebees? *Current Biology, 15*(12), R447–R448. https://doi.org/10.1016/j.cub.2005.06.011

Leadbeater, E., & Chittka, L. (2007a). The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behavioural Ecology and Sociobiology, 61*(11), 1789–1796. https://doi.org/10.1007/s00265-007-0412-4

Leadbeater, E., & Chittka, L. (2007b). Social learning in insects — from miniature brains to consensus building. *Current Biology, 17*(16), R703–R713. https://doi.org/10.1016/j.cub.2007.06.012

Leadbeater, E., & Chittka, L. (2009). Bumble-bees learn the value of social cues through experience. *Biology Letters, 5*(3), 310–312. https://doi.org/10.1098/rsbl.2008.0692

Leadbeater, E., & Dawson, E. H. (2017). A social insect perspective on the evolution of social learning mechanisms. *Proceedings of the National Academy of Sciences, 114*(30), 7838–7845. https://doi.org/10.1073/pnas.1620744114

Loukola, O. J., Gatto, E., Híjar-Islas, A. C., & Chittka, L. (2020). Selective interspecific information use in the nest choice of solitary bees. *Animal Biology, 70*(2), 215–225. https://doi.org/10.1163/15707563-20191233

Lunau, K., Wacht, S., & Chittka, L. (1996). Colour choices of naive bumble bees and their implications for colour perception. *Journal of Comparative Physiology, 178*(4). https://doi.org/10.1007/BF00190178

Menzel, R., & Shmida, A. (1993). The ecology of flower colours and the natural colour vision of insect pollinators: The Israeli flora as a study case. *Biological Reviews, 68*(1), 81–120. https://doi.org/10.1111/j.1469-185X.1993.tb00732.x

Parejo, D., & Avilés, J. M. (2016). Social information use by competitors: Resolving the enigma of species coexistence in animals? *Ecosphere, 7*(5), Article e01295. https://doi.org/10.1002/ecs2.1295

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/.

Raine, N. E., & Chittka, L. (2007). The adaptive significance of sensory bias in a foraging context: Floral colour preferences in the bumblebee *Bombus terrestris*. *PloS One, 2*(6), Article e556. https://doi.org/10.1371/journal.pone.0000556

Raine, N. E., Ings, T. C., Dornhaus, A., Saleh, N., & Chittka, L. (2006a). Adaptation, genetic drift, pleiotropy, and history in the evolution of bee foraging behavior. *Advances in the Study of Behavior, 36*, 305–354. https://doi.org/10.1016/S0065-3454(06)36007-X. Academic Press.

Raine, N. E., Ings, T. C., Ramos-Rodriguez, O., & Chittka, L. (2006b). Unterschiede im Lernverhalten zwischen Kolonien einer freilebenden Britischen Hummelpopulation (Hymenoptera: Apidae: *Bombus terrestris audax*). *Entomologia Generalis, 28*(4), 241–256. https://doi.org/10.1127/entom.gen/28/2006/241

Rogers, S. R., Cajamarca, P., Tarpy, D. R., & Burrack, H. J. (2013). Honey bees and bumble bees respond differently to inter- and intra-specific encounters. *Apidologie, 44*(6), 621–629. https://doi.org/10.1007/s13592-013-0210-0

Sclafani, A. (1995). How food preferences are learned: Laboratory animal models. *Proceedings of the Nutrition Society, 54*(2), 419–427. https://doi.org/10.1079/PNS19950011

Seppänen, J.-T., Forsman, J. T., Mönkkönen, M., & Thomson, R. L. (2007). Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology, 88*(7), 1622–1633. https://doi.org/10.1890/06-1757.1

Smolla, M., Alem, S., Chittka, L., & Shultz, S. (2016). Copy-when-uncertain: Bumblebees rely on social information when rewards are highly variable. *Biology Letters, 12*(6), 20160188. https://doi.org/10.1098/rsbl.2016.0188

Snodgrass, R. E. (1984). *Anatomy of the honey bee*. Cornell University Press.

Spaethe, J., Tautz, J., & Chittka, L. (2006). Do honeybees detect colour targets using serial or parallel visual search? *Journal of Experimental Biology, 209*(6), 987–993. https://doi.org/10.1242/jeb.02124

Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (Eds.). (2007). *Foraging: Behavior and ecology*. University of Chicago Press.

Valone, T. J., & Templeton, J. J. (2002). Public information for the assessment of quality: A widespread social phenomenon. *Philosophical Transactions of the Royal Society B: Biological Sciences, 357*(1427), 1549–1557. https://doi.org/10.1098/rstb.2002.1064

Von Frisch, K. (1965). *Tanzsprache und Orientierung der Bienen*. Springer. https://doi.org/10.1007/978-3-642-94916-6_2

Waser, N., & Chittka, L. (1998). Bedazzled by flowers. *Nature, 394*(6696), 835–836. https://doi.org/10.1038/29657

Wilson, K., & Hardy, I. C. W. (2002). Statistical analysis of sex ratios: An introduction. In I. C. W. Hardy (Ed.), *Sex ratios* (pp. 48–92). Cambridge University Press. https://doi.org/10.1017/CBO9780511542053.004.

Xie, Z., Pan, D., Teichroew, & J., & An, J. (2016). The potential influence of bumble bee visitation on foraging behaviors and assemblages of honey bees on squash flowers in highland agricultural ecosystems. *PloS One, 11*(1), Article e0144590. https://doi.org/10.1371/journal.pone.0144590