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

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Abstract

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 asocial cues (e.g. flower colour), hence affecting foraging decisions. Here, we investigated honeybees' (*Apis mellifera*) inspection and choices of unfamiliar flowers based on both natural colour preferences and simultaneous foraging information from conspecifics and heterospecifics. Individual honeybees' preferences for flowers were recorded when the reward levels of a learned flower type have declined and novel-coloured flowers were available where they would find either no social information or one conspecific and one heterospecific (*Bombus terrestris*), each foraging from a different coloured flower (either magenta or yellow). Honeybees were found to have a natural preference for magenta flowers. Social information affected honeybees' inspection time of both types of flowers, i.e., honeybees modified their approaching flights to yellow and magenta flowers in response to conspecific and heterospecific social information. The presence of either demonstrator on the less-preferred yellow

flower increased honeybees' inspection time of yellow flowers. Conspecific social information influenced observers' foraging choices of yellow flowers, thus outweighing their original preference for magenta flowers, such an influence was not elicited by heterospecific social information. Our results indicate that flower colour preferences of honeybees are rapidly adjusted in response to conspecific social information, which in turn is preferred over heterospecific information, thus favouring the transmission of adaptive foraging information within species.

Keywords: behavioural flexibility, decision making, innate colour bias, insects, intraspecific, interspecific, social information

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 (Stephens et al. 2007). Foraging decisions can be influenced in a context-dependant manner (Laland 2004; Kendal et al. 2009) by innate preferences (Raine et al. 2006), previous individual experience (Sclafani 1995), and the observation or interaction with another animals at a foraging resource, i.e., social information (Heyes 1994; Hoppitt and Laland 2013). For example, naïve individuals tend to rely more on social than individual information to gain familiarity about foraging sources (Galef and Giraldeau 2001; Galef and Laland 2005). Conversely, experienced individuals that have information on an advantageous foraging resource, will often ignore social cues. Thus, social information is only draw upon when individual information has become outdated and acquiring up to date information may be costly (Laland 2004; Galef and Laland 2005; Kendal et al. 2009). The influence of social information on foraging decisions is taxonomically widespread (Galef and Giraldeau 2001; Valone and Templeton 2002; Grüter and Leadbeater 2014). Social information allows animals to find profitable foraging resources efficiently, instead of iteratively sampling the environment through trial and error (Galef and Laland 2005).

In most animal communities, multiple species frequently 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 (Seppänen et al. 2007; Goodale et al. 2010; Avarguès-Weber et al. 2013; Parejo and Avilés 2016). Using social information indiscriminately is not adaptive but animals should be selective when acquiring information from other individuals (Laland 2004; Kendal et al. 2018). In a multi-species context, animals have access to social information from different sources, which may give rise to a trade-off between selecting

sources with a close ecological similarity, implying high competition, or 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 (Laland and Plotkin 1993; Leadbeater and Chittka 2007a; Jones et al. 2015) and existing individual information (van Bergen Yfke et al. 2004; Jones et al. 2015) to determine foraging decisions in a context-dependant manner (Laland 2004; Kendal et al. 2009).

Social bee workers forage for nectar and pollen from rapidly changing floral resources (Heinrich 1979; Chittka et al. 1999) within multi-species communities (Fægri and Van der Pijl 1979; Kevan and 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. For example, they test bees in relatively unnatural settings where a single source of social information is presented, e.g., a dead demonstrator pinned to simulated flowers (reviewed in Leadbeater and 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 and Van der pijl 1979; Kevan and Baker 1983) that may concur in time and space and diverge in their intrinsic relevance.

Honeybees and bumblebees are sympatric species that typically forage upon similar flowers due to their generalist diet (Rogers et al. 2013; Xie et al. 2016). Previous evidence indicates that bumblebees can acquire foraging information from dead demonstrator honeybees (Dawson and Chittka 2012). However, in more realistic

100 conditions, a bee forager whose known floral resources have decreased in reward levels,
101 will likely concur with other foragers, of their own and different species, feeding from
102 different types of flowers (Fægri and Van der Pijl 1979; Kevan and Baker 1983). It
103 remains unclear how bees respond to such divergent social information, and whether in
104 this context, social cues might modify bees' natural preferences for particular colours in
105 flowers (Chittka et al. 2004; Raine et al. 2006; Raine and Chittka 2007), hence affecting
106 foraging decisions. We address these questions by testing whether honeybees might
107 adjust their colour preferences in response to simultaneous sources of social
108 information, i.e., a conspecific and heterospecific, each foraging from either a preferred
109 or non-preferred flower type.

110 **MATERIALS AND METHODS**

111 *(a) Set-up*

112 We used free-flying honeybee foragers (*Apis mellifera*) of two different colonies
113 (Colonies A and B) for experiments. Over two consecutive summers (2017-2018), we
114 trained foragers (one colony per year) to collect 30% sucrose solution (w/w) from a
115 gravity feeder located 2 m away from their hive. The gravity feeder attracted foragers
116 from neighboring hives, thus individuals for experiments could have come from at least
117 three additional hives. In addition, we used bumblebee (*Bombus terrestris*) foragers
118 from two colonies (Biobest, Belgium N.V.) for the experiments. Bumblebee nests were
119 housed in bipartite wooden nest-boxes (l = 29.5 × w = 11.5 × h = 9.5 cm) connected to a
120 wooden flight arena (l = 77 cm, w = 52 cm, h = 30 cm) by a Plexiglas tunnel (l = 25 cm,
121 3.5 × 3.5 cm). The floor of the flight arena was covered in white laminated paper. Three
122 plastic sliding doors located along the corridor allowed controlled access to the arena.
123 Before and after experiments, bumblebees could freely feed upon 30% (w/w) sucrose

solution from a mass feeder in the middle of the arena. Bumblebee colonies were provided with 7 g of frozen pollen (Koppert B.V., The Netherlands) every two days.

(b) Training of honeybees

Training of demonstrators and observers took place over 18 daily sessions. Each day, five foraging honeybees (demonstrators) from the gravity feeder were lured to and trained to enter the wooden flight arena located outdoors. The five honeybees were group trained, i.e. allowed to enter the arena together at various times, to learn to forage upon an array of twelve plastic chips (2.4 × 2.4 cm, henceforth "flowers") placed on the top of transparent glass vials (h = 4 cm), 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 yellow flowers with 10 μL of rewarding 50% (w/w) sucrose solution, and four magenta and four transparent flowers with 10 μL of unrewarding water (Figure 1A). Flowers were refilled after they were depleted by foragers and the foragers left the flower. Half of the foragers experienced the opposite color-reinforcement contingency. We identified trained individuals by marking their thorax with a white paint mark (Posca Pen, Worcester, UK). Three hours after concluding the demonstrator's training, we selected a separate batch of five foragers (observers) that we trained them on a different set-up. Every day, observers were group trained to enter the same arena and forage upon a rectangular grid array of twelve transparent flowers (3 × 4) (Figure 1C). To encourage honeybee 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 after emptied and the forager left the flower, and the positions of all the flowers were changed every 10 minutes over 1 hour of training.

149 We marked trained observers with a green dot to distinguish them from the
150 demonstrators. After each training session, we cleaned the flowers and the arena floor
151 with 70% ethanol.
152
153 *(c) Training of bumblebees*
154 In the same flight arena where honeybees were trained, bumblebee foragers
155 (demonstrators) from two colonies were separately trained in group. In this training, the
156 colour-reinforcement contingency was reversed so that bumblebees learned to forage on
157 flowers of the opposite colour that honeybees were trained on. Half of the bumblebees
158 experienced four magenta flowers with 40 µL of 50% (w/w) sucrose solution, and four
159 yellow and four transparent flowers with 40 µL of water (Figure 1B). The other half of
160 the bumblebees experienced the reverse color-reinforcement contingency. Rewarding
161 flowers were refilled after depleted by the foragers and the foragers left the flower.
162 Training took place for one day over 2 hours. We also carried out a refreshment bout
163 (20 min) each day before testing. We tracked demonstrator bees' identity with
164 individual number tags (Opalithplättchen, Warnholz & Bienenvoigt, Ellerau, Germany)
165 glued to the top of the thorax by means of Loctite Super Glue Gel (Loctite, Ohio, US).
166 The floor of the arena and flowers were cleaned with 70% ethanol after completing
167 training.
168
169 *(d) Testing the effect of color preference on honeybees' foraging decisions*
170 After each training session, we selected two honeybees trained on transparent
171 flowers, twenty-one subjects overall, and evaluate them individually in a control test
172 where transparent flowers were unrewarding to assess whether they might show a
173 preference to explore and forage from one flower type between two unfamiliar

alternatives, i.e., yellow and magenta. One honeybee was let in the arena to explore a rectangular grid array of twelve flowers (section b, 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, (Figure 1D). The test began once the individual inspected any flower. That is, the honeybee approached the flower with its head oriented towards it and displayed a slow side-to-side hover within at least one body length (Ings et al. 2009). Individuals were given up to 3 min to land and forage upon any unfamiliar flower, before the test concluded. As this test was designed to evaluate the influence of honeybees' 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 re-testing the same individuals, we captured honeybees, 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 honeybees' 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 (1,280 × 720 pixels). The camera was positioned 20 cm above the entrance of the bumblebee nest (Figure 1). Its field of view was adjusted such that it looked down into the arena at ~50° from a horizontal angle.

199 *(e) Testing the influence of social information on foraging decisions*

200 To evaluate the influence of simultaneous sources (conspecific and
201 heterospecific) of social information on honeybee's inspection of either yellow or
202 magenta flowers and their subsequent foraging decisions, we tested fifty-three
203 honeybees in the same context as individuals in the control group (section d), but in the
204 presence of one bumblebee and one honeybee demonstrator, each foraging upon either a
205 yellow or magenta flower. We introduced the demonstrators and observer in the arena
206 in the following order: 1) a honeybee demonstrator was let in through a sliding door on
207 the back wall of the arena (Figure 1D). Once she began to feed from a yellow flower
208 and started to forage, a bumblebee demonstrator was released from the Plexiglas tunnel
209 that connected the arena to the nest-box (Figure 1D). When she landed and began to
210 feed from a magenta flower, a honeybee observer was let into the arena through the
211 sliding door on the back wall. This color-reinforcement contingency was
212 counterbalanced for thirty-three observers. The test began once the observer inspected
213 (see section d) any occupied or unoccupied flower. Observers were given up to 3 min to
214 select and forage upon any unfamiliar flower before the test concluded. In the test,
215 demonstrators moved freely between flowers after depleting them, as they naturally do
216 within inflorescences. To prevent re-testing the same individuals, we caught tested
217 honeybees and marked them with a distinctive red paint mark. The flowers and arena
218 floor were cleaned with 70% ethanol between tests. To evaluate honeybees' inspection
219 of flowers and their interactions with the demonstrators before they made a foraging
220 decision, the test was recorded as described in section (d) above.

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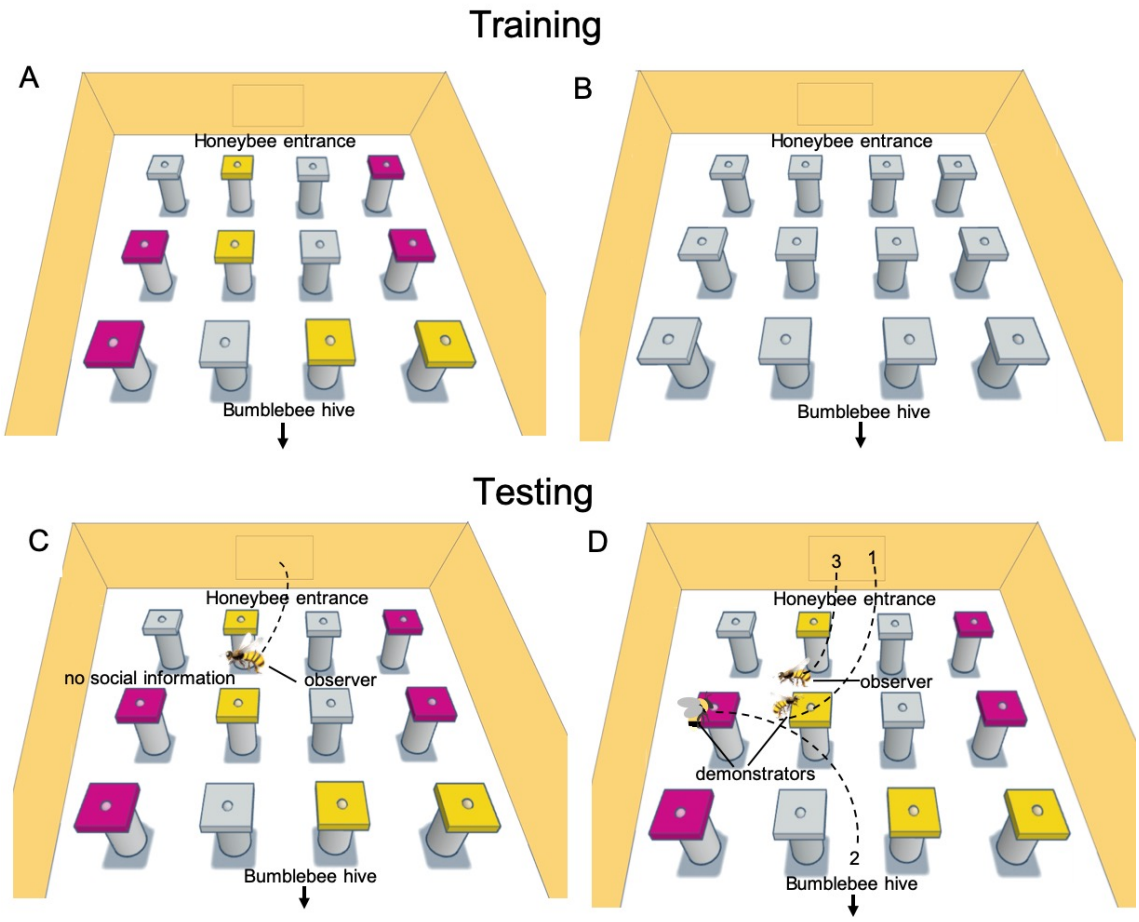

Figure 1. Training and testing protocols in the flight arena. (**A**) Honeybee foragers (demonstrators) were trained to find 50% sucrose solution on either four yellow or magenta flowers and water on four flowers of the alternative colour and four transparent flowers. Bumblebee foragers (demonstrators) were group trained using the same protocol (**C**) A different batch of honeybee foragers (observers) was group trained to find 50% sucrose solution on six of twelve transparent flowers and unrewarding water on the other six transparent flowers. (**D**) Honeybee 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. (**E**) Two demonstrators (one honeybee and one bumblebee) and one observer honeybee were sequentially introduced in the flight arena: (1) A honeybee demonstrator was let in the flight arena, once she foraged from a flower of her trained colour, (2) a bumblebee demonstrator was released into the arena and let to forage from a flower of her trained colour (different colour from the honeybee demonstrator), (3) an observer honeybee was then introduced to test her in a context where the flowers she was trained to associate with reward (transparent) were unrewarding and unfamiliar colored flowers were demonstrated by a conspecific and a heterospecific (bumblebee) demonstrator, each foraging from non-preferred (yellow) and preferred (magenta) flowers, this design was counterbalanced.

238 *(d) Analyses*

239 We analysed the behaviour of tested honeybees from video recordings, using the
240 BORIS behavioural observation software (Friard and Gamba, 2016). To assess
241 individuals' inspection of either yellow or magenta flowers and their preference to
242 forage upon one type of flower over the other, we analysed two main behavioural
243 categories, the frequency of inspecting transparent, yellow and magenta flowers (Ings et
244 al. 2009: 200; Balamurali et al. 2018) and individual's foraging choice, i.e., the yellow
245 or magenta flower where individuals landed and foraged. For honeybees in the control
246 group (no social information), we used a Chi-squared test to compare the proportion of
247 honeybees that foraged upon either a magenta or yellow flower, as well as the
248 likelihood of first inspecting one of these types of flower. Further, we compared the
249 proportion of instances that honeybees inspected a transparent, yellow or magenta
250 flower, using a Friedman test and a Wilcoxon signed rank test for *post hoc* comparisons.

251 For honeybees exposed to social information, we considered inspection of
252 occupied flowers as an indicator that observers detected the demonstrator's presence.
253 Thereby, four different scenarios were possible before honeybees made a foraging
254 decision: they could have detected both demonstrators, either the honeybee or
255 bumblebee demonstrator, or none of them. We compared the likelihood of each
256 situation against the expected probability with a Chi-Square Goodness of Fit Test. Nine
257 individuals that did not detect the presence of the demonstrators were not considered for
258 all analyses.

259 To contrast the influence of individual's color preferences and simultaneous,
260 conspecific and heterospecific, social information on foraging decisions of honeybees,
261 we compared the proportion of individuals that foraged on an unfamiliar flower
262 between the control group and the group exposed to social information. Further, to

263 evaluate the influence of social information on honeybees' readiness to forage on an
264 unfamiliar flower, we compared two measurements between the control group and the
265 group exposed to social information – the total number of flowers that individuals
266 inspected before choosing a flower to forage, and the time it took them to make such a
267 decision (latency to forage). To explore whether such readiness could be affected by the
268 species of the first demonstrator that the observers detected, we compared, with a
269 Wilcoxon rank sum test, the aforementioned measurements between the observers that
270 first detected the presence of either a honeybee or bumblebee foraging on a flower,
271 irrespective of whether they detected both or only one demonstrator during the test.
272 To determine whether observers that detected both demonstrators inspected the
273 flowers occupied by a honeybee and bumblebee at a similar frequency, we compared,
274 with a Wilcoxon signed rank test, the proportion of flowers occupied by each
275 demonstrator that observers inspected. We also analysed, with a Wilcoxon rank sum
276 test, whether the honeybees that only detected either a conspecific or heterospecific
277 demonstrator, differed in the proportion of occupied flowers that they inspected, in
278 relation to all the flowers they inspected during the test. To compare the specific
279 influence of conspecific and heterospecific social information on honeybees' foraging
280 decisions, we analysed, with a Chi-Squared test, the proportion of individuals that
281 selected the flower type demonstrated by either a honeybee or bumblebee, as well as the
282 likelihood that observers would select a flower occupied by either a honeybee or
283 bumblebee after inspecting it for the first time.
284 The instances in which observers inspected an occupied flower that did not
285 progress into landing and foraging were recorded as rejections. We evaluated whether
286 observers rejected the flowers occupied by a honeybee or bumblebee demonstrator at a
287 similar frequency. For observers that detected both demonstrators, we compared the

288 proportion of times that they rejected the flowers occupied by each demonstrator, using
289 a Wilcoxon signed rank test. We also compared, with a Wilcoxon rank sum test, the
290 total number of occupied flowers that observers rejected when they only detected either
291 the honeybee or bumblebee demonstrator.

292 To assess whether conspecific and heterospecific social information affected
293 honeybees' inspection of yellow or magenta flowers, we compared the proportion of
294 inspecting transparent, yellow and magenta flowers between honeybees in the control
295 group and the group that had access to social information.

296 To estimate whether the observers altered their inspection of flowers, after they
297 detected the presence of either a foraging honeybee or bumblebee, we adjusted the
298 frequency of observers' inspection of flowers by normalising the data through an index
299 calculation, with the following equation:

300 $$\text{Inspecting Index (II)} = \frac{i_m - i_y}{i_m + i_y}$$

301

302 , where, i_m and i_y are the frequency that the observer inspected magenta and yellow
303 flowers, respectively.

304 In the indices, a negative value (minimum -1) equates to a preference to inspect
305 yellow flowers, whereas a positive value (maximum +1) equates to a preference to
306 inspect magenta flowers, an index near equal to zero implies that the observers either
307 inspected both types of flowers equally, or they did not inspect the flowers at all. We
308 calculated inspecting indices (II) to represent the events that preceded the honeybees'
309 foraging decisions. That is, each approaching index (AI) represented observers'
310 inspection of flowers, before and after they detected either demonstrator (honeybee and
311 bumblebee) foraging on a flower . We compared indices against chance expectation
312 (Index = 0) with a Wilcoxon signed-rank test. A significant switch from a negative or

313 positive value, before the observer detected a demonstrator, to a positive or negative
314 value, after this occurred, indicates that observers modified their inspection of yellow or
315 magenta flowers in response to conspecific or heterospecific social information. All
316 analyses were conducted using R statistical software (R Core Team, 2019).
317
318 **RESULTS**
319 *Effect of color preference on honeybees' foraging decisions*
320 In a context where a familiar flower type ceases to yield reward, how does
321 colour preference influence honeybees' exploration of contiguous, novel flowers and
322 ultimate move to foraging from a new flower type? We carried out a control test to
323 assess whether honeybees preferentially inspect one unfamiliar flower type over
324 another, and whether this might be reflected in their ultimate foraging decision (move to
325 foraging on a new flower type). We trained honeybees (observers) to find either a food
326 reward (50% sucrose solution) or unrewarding water on transparent flowers (Materials
327 and Methods), then we tested them in a context where transparent flowers were
328 unrewarding, and two unfamiliar yellow and magenta flower types, delivered an
329 undetectable food reward. The majority of individuals (77%) did not inspect the familiar
330 transparent flowers at all; rather, they inspected the magenta flowers more frequently
331 than the other types of flower (Friedman; X^2 (2) = 19.07, df = 2, N = 18, p = 7.231e-05;
332 *post hoc*, Wilcoxon signed rank; comparison between flower types: magenta *versus*
333 transparent: p = 0.002; magenta *versus* yellow: p = 0.0008; yellow *versus* transparent: p
334 = 0.67; figure 2A).
335 Similarly, honeybees were more likely to first inspect a magenta than a yellow
336 flower (Chi-square; chi = 14.23, N = 18, p = 1.6132e-04; figure 2B), and a higher
337 proportion of individuals selected magenta over yellow flowers to forage (Chi-square;

338 chi = 28.44, N = 18, p = 9.6426e-08; figure 2C). These results indicate that tested
339 individuals had a common preference for magenta over yellow flowers, which
340 influenced their inspection of flowers and foraging decisions.
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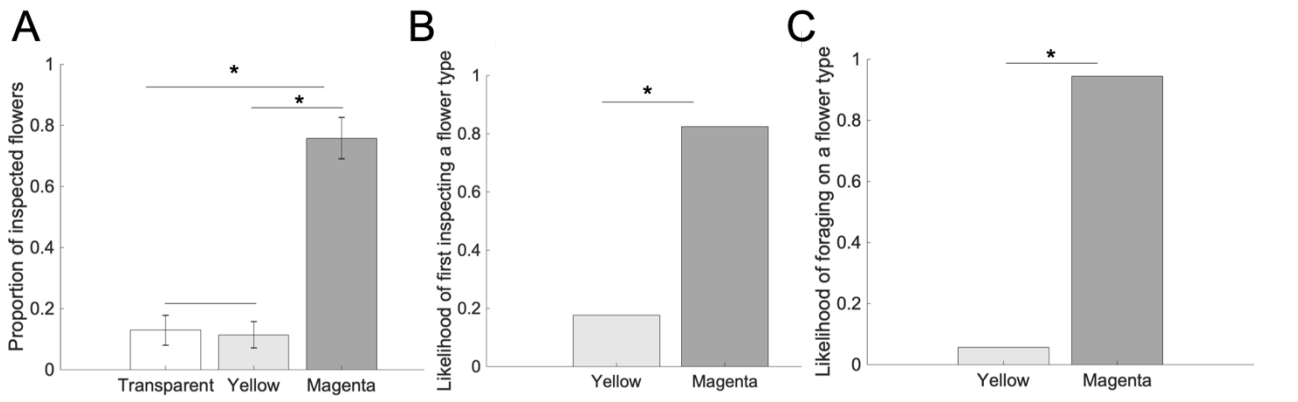

342
343
344 **Figure 2.** Honeybees prefer magenta over yellow flowers **(A)** Honeybees inspected magenta flowers
345 more frequently than yellow and transparent flowers. **(B)** The likelihood of honeybees inspecting an
346 unfamiliar flower for the first time was higher for magenta compared to yellow flowers. **(C)** A higher
347 proportion of honeybees preferred to forage on magenta than yellow flowers. Bars = mean. Horizontal
348 lines = standard error. Asterisks = $p < 0.05$. n.s. = not significantly different.
349
350 *Influence of social information on honeybees' foraging decisions*
351 In a field-like context, including simultaneous and divergent conspecific and
352 heterospecific social information, we investigated how this social information might
353 affect honeybees' inspection of flower types and ultimate foraging decisions. We
354 considered that observers detected the demonstrators' presence once they inspected an
355 occupied flower for the first time. We found no difference in the proportion of observers
356 that detected both demonstrators, only the honeybee or bumblebee demonstrator, or
357 none of them (Chi-Square Goodness of Fit Test; χ^2= 2.2, df= 3, N = 45, p = 0.312;
358 Figure 3A). The proportion of observer honeybees that detected the foraging

demonstrators and then selected an unfamiliar flower to forage was not different from individuals that selected unfamiliar flowers in the control group (Chi-square; χ^2 = 1.022, N = 56, p = 0.312; Figure 3B). Similar to the control group, the vast majority of observers (90%) did not inspect the transparent flowers at all. These results suggest that both individual colour bias and social information similarly influenced honeybees when locating a new foraging resource. Interestingly, honeybees in the control group whose foraging decisions were solely influenced by their color preference, inspected a similar number of flowers (Wilcoxon rank-sum; W = 125, N = 30, p= 0.447; Figure 3D and made equally swift foraging decisions (Wilcoxon rank-sum; W = 133, N = 30, p= 0.299; Figure 3C) as honeybees exposed to social information that in the test, initially detected the conspecific demonstrator foraging. However, when observer honeybees first detected the heterospecific demonstrator foraging, they made slower foraging decisions and inspected more flowers compared to both the control group (Wilcoxon rank-sum; latency: W = 71, N = 35, p = 0.007; Figure 3C, number of flowers inspected: W = 77, N = 35, p = 0.011; Figure 3D) and those honeybees that detected the conspecific demonstrator first (Wilcoxon rank-sum; latency: W = 184, N = 29, p = 0.0003; Figure 3C, number of flowers inspected: W = 176.5, N = 29, p = 0.0009; Figure 3D). These results suggest that individual preference for magenta flowers and conspecific social information similarly influenced honeybees' foraging choices which allowed them to make fast decisions. This did not occur in response to heterospecific social information as observers inspected the flowers extensively before making a foraging decision.

Observer honeybees similarly inspected flowers occupied by a honeybee and bumblebee demonstrator, regardless whether in the test they detected only one demonstrator (Wilcoxon rank-sum; W = 34.5, N= 16; p-value = 0.449; Figure 3F) or both demonstrators (Wilcoxon signed-rank; V = 22.5, N = 13, p = 1; Figure 3E). However, a significantly higher proportion of honeybees selected and foraged on the type of flowers demonstrated by conspecifics over the flowers demonstrated by heterospecifics (Chi-square; χ^2 = 17.15, N = 29, p = 3.4516e-05; Figure 3G). Further, observer honeybees that inspected an occupied flower for the first time, were considerably more likely to forage on it if the occupier was a conspecific demonstrator (Chi-square; χ^2 = 15.6508, N = 41, p = 7.6181e-05; Figure 3H). This evidence demonstrates that foraging conspecifics had a strong influence on honeybees' foraging decisions. Contrastingly, observer honeybees rejected flowers occupied by a bumblebee more frequently than the flowers occupied by a conspecific in both situations, when they detected either one (Wilcoxon rank-sum; W = 2, N = 16, p = 0.002; Figure 3I) or both demonstrators (Wilcoxon signed-rank; V = 3, N = 13, p = 0.008; Figure 3J).

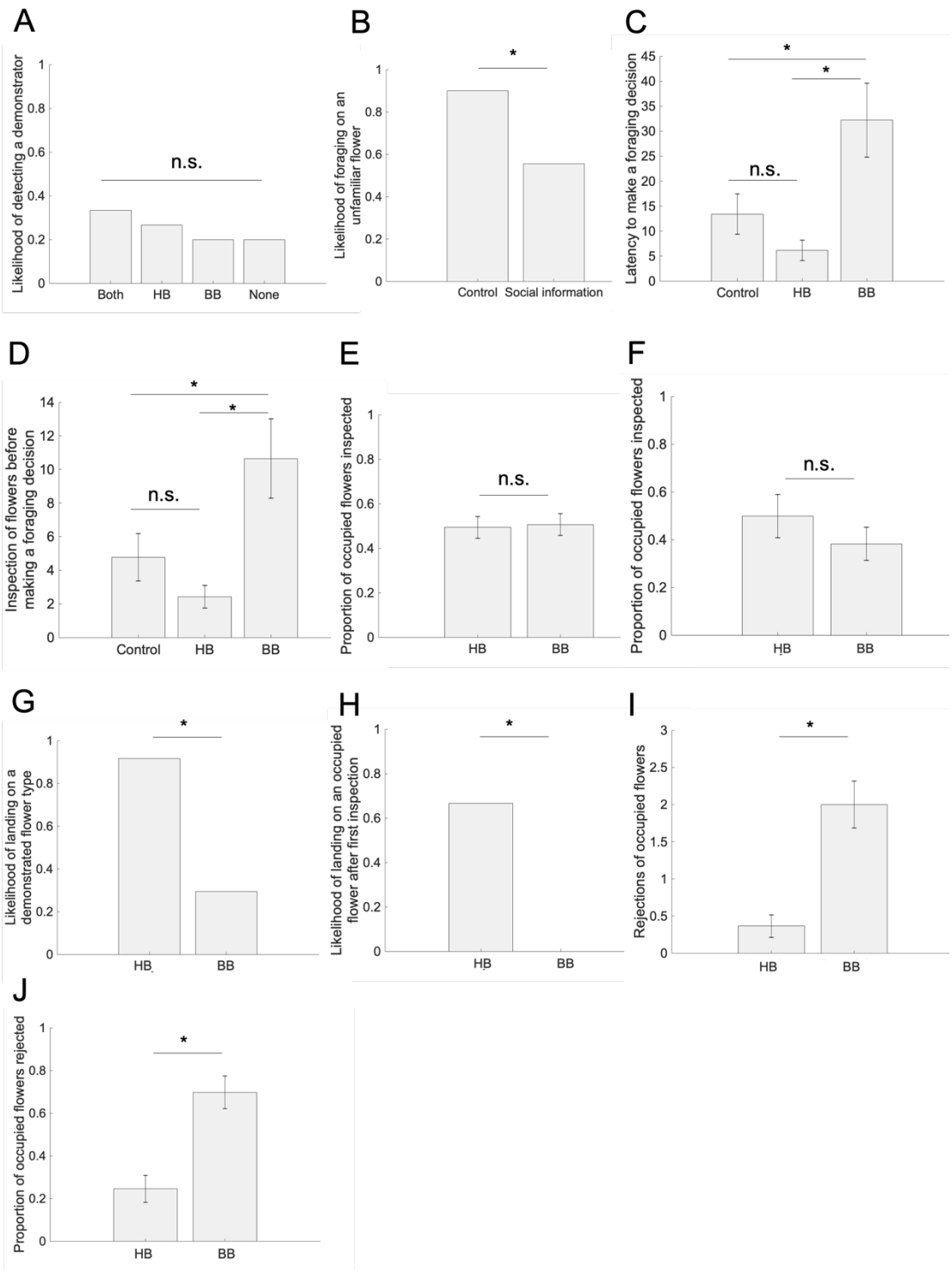

Figure 3. Concurrent conspecific and heterospecific social information influences foraging behaviour of honeybees differently **(A)** Observer honeybees were equally likely to detect both demonstrators, only the honeybee or bumblebee demonstrator, and none of them. **(B)** The proportion of honeybees that foraged on unfamiliar flowers was not different between observers that detected the presence of demonstrators and individuals in the control group (no social information). **(C)** Honeybees in the control group and those that first detected a foraging conspecific made faster foraging decisions than observers that first

415 detected a foraging heterospecific. **(D)** Honeybees in the control group and those that first detected a
416 foraging conspecific inspected fewer flowers before making a foraging decision than observers that first
417 detected the presence of a foraging heterospecific. **(E)** Observers that detected both demonstrators during
418 the test inspected occupied flowers irrespective of the demonstrator's species. **(F)** Observers that only
419 detected either the conspecific or heterospecific demonstrator showed a similar proportion of inspecting
420 occupied flowers. **(G)** A higher proportion of observers preferred to forage on the type of flowers
421 demonstrated by conspecifics compared to the type of flowers demonstrated by heterospecifics. **(H)** Once
422 observers detected the presence of a conspecific demonstrator foraging on an unfamiliar flower type, they
423 were more likely to land and forage on this flower, but they never chose a flower occupied by a
424 heterospecific demonstrator. **(I)** Observers that only detected either a conspecific or heterospecific
425 demonstrator, rejected flowers occupied by a bumblebee more frequently than flowers occupied by a
426 conspecific. **(J)** Observers that detected both demonstrators rejected the flowers occupied by a bumblebee
427 at a higher proportion than the flowers occupied by a conspecific. HB = honeybee, BB = bumblebee. Bars
428 = mean. Horizontal lines = standard error. Asterisks = $p < 0.05$. n.s. = not significantly different.
429

430 *Adjustment of honeybees' colour preference in response to social information*

431 Our results indicate that social information can influence honeybee's foraging
432 decisions. But how does such information interact with an individual's colour
433 preference to shape honeybees' flower choices? Compared to individuals in the control
434 group, observers that detected a honeybee foraging on magenta flowers, and a
435 bumblebee on the yellow ones, inspected a similar proportion of magenta flowers
436 (Wilcoxon rank-sum test; W = 96, N = 29, p = 0.9029; Figure 4A) but they inspected
437 more yellow flowers (Wilcoxon rank-sum; W = 137.5, N = 29, p = 0.002; Figure 4B).
438 In the alternative scenario, where honeybees observed a conspecific and heterospecific
439 demonstrator, respectively foraging on a yellow and magenta flower, the proportion of
440 yellow flowers that observers inspected was markedly higher than individuals in the
441 control group (Wilcoxon rank-sum; W = 221.5, N = 29, p = 1.499e-05; Figure 4B);
442 hence they tended to inspect fewer magenta flowers, compared to the control group

443 (Wilcoxon rank-sum; W = 49, N = 29, p = 0.095; Figure 4A). These results
444 demonstrate that individuals in the control group and those exposed to social
445 information similarly inspected magenta flowers, regardless the species of the
446 demonstrator foraging on these flowers. Contrastingly, the presence of either
447 demonstrator foraging on yellow flowers, scarcely explored by honeybees in the control
448 group, attracted observers' attention to such type of flowers. Particularly, observers that
449 detected a conspecific foraging on a yellow flower, focused on inspecting these flowers,
450 so that their preference for magenta flowers was overridden. This evidence confirms
451 that even though honeybees' foraging decisions was determined by their preference for
452 magenta flowers in the absence of social information, this colour preference was clearly
453 outweighed by conspecific social information.
454 The inspecting indexes (II), described in (d), allowed us analysing honeybees'
455 inspection of flowers as a flexible process that culminated in a foraging decision, and
456 whose variation in response to social information was measurable in terms of an index
457 value. Observer honeybees showed no preference to inspect magenta or yellow flowers
458 before they detected the bumblebee demonstrator foraging on either a magenta
459 (Wilcoxon signed-rank test; V = 20, N = 9, p = 0.149; Figure 4D) or yellow flower
460 (Wilcoxon signed-rank test; V = 12, N = 9, p = 0.112; Figure 4D). After honeybees
461 detected a bumblebee demonstrator foraging on a magenta flower, they preferentially
462 inspected this type of flower (Wilcoxon signed-rank; V = 26, N = 9, p = 0.026; Figure
463 4A). However, after honeybees observed a bumblebee foraging on a yellow flower, they
464 showed no preference to inspect either type of flower (Wilcoxon signed-rank; V = 18.5,
465 N = 9, p = 0.5; Figure 4D). Honeybees did not prefer to inspect neither type of flower
466 before they detected a conspecific foraging upon either a magenta (Wilcoxon signed-
467 rank; V = 16.5, N = 11, p = 0.612; Figure 4E) or yellow flower (Wilcoxon signed-rank;

V = 23, N = 11, p = 0.261; Figure 4E). Honeybees responded to the presence of a conspecific foraging on either a magenta or yellow flower by increasing their inspection of demonstrated flowers (Wilcoxon signed-rank; magenta: V = 52, N = 11, p = 0.006471; yellow: V = 1, N = 13, p = 0.002; Figure 4E). These results show that honeybees' inspection of the different types of flowers underwent a sequential adjustment in response to conspecific and heterospecific social information, which ultimately affected foraging decisions.

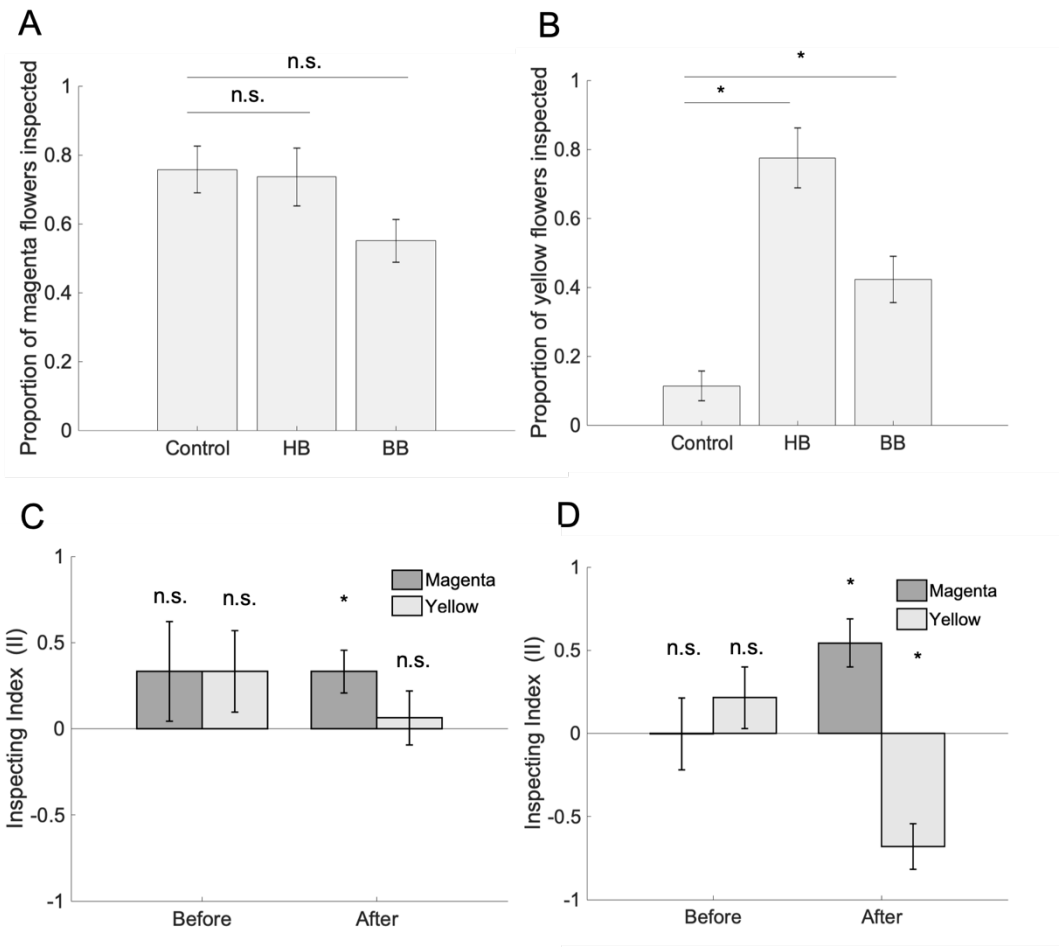

Figure 4. Honeybees adjust their exploration of flowers and foraging preferences in response to simultaneous conspecific and heterospecific social information **(A)** Observer honeybees, previously trained on transparent flowers, similarly inspected unfamiliar magenta flowers in the absence of social information (control group) and when these flowers were demonstrated by either a conspecific or a

heterospecific (bumblebee) demonstrator. **(B)** In comparison to individuals in the control group, observers inspected more yellow flowers in response to the presence of either a conspecific or heterospecific demonstrator foraging on this flower type. **(C)** and **(D)** Inspecting indices (II) compare to chance level (Index = 0) the inspection of magenta (dark gray bars) and yellow (light gray bars) flowers that observers displayed before and after detecting either a conspecific or heterospecific demonstrator foraging on either a magenta or yellow flower. **(C)** Before observers detected a bumblebee demonstrator foraging on either a magenta or yellow flower, they showed no preference to inspect neither of these flower types. After observers detected a bumblebee demonstrator foraging on a magenta flower, they inspected more frequently this type of flowers, but when observers detected the bumblebee demonstrator foraging on a yellow flower, they did not alter their inspection of yellow or magenta flowers. **(D)** Before observers detected a conspecific foraging upon either a yellow or magenta flower, they did not preferentially inspect magenta or yellow flowers. After observers detected a conspecific demonstrator foraging on either a yellow or magenta flower, they increased their inspection of the demonstrated flower type. HB = honeybee, BB = bumblebee. Index = 0. Bars = mean. Horizontal lines = standard error. Asterisks = $p < 0.05$. n.s. = not significantly different between groups or from chance level.

DISCUSSION

The results presented here provide evidence that honeybees'colour preferences can be adjusted in response to simultaneous social information from conspecific and heterospecific sources, with conspicuous effects on honeybees' exploration of flowers and consequent foraging decisions. Unexpectedly, honeybees payed little attention to the transparent flowers on which they were trained, instead prior to making a foraging decision, they inspected more frequently the magenta flowers (control group) or the type of flower demonstrated by a conspecific.

Despite inspection of flowers provide foragers with no information on the reward status of a flower, they are important in the process of choosing a flower (Lunau et al. 1996). In the absence of social information, honeybees' natural preference for magenta flowers influenced inspection and choices of flowers . Magenta is actually a

510 mixture of blue and red, since the red component is not fully perceived by bees (Menzel
511 and Shmida 1993), they perceive magenta flowers as blue (Waser and Chittka 1998).
512 Honeybees and bumblebees usually have innate biases for colours in the violet to blue
513 range of the spectrum (Giurfa et al. 1995; Chittka et al. 2004), which adaptively
514 correlates with the nectar production of local flowers (Giurfa et al. 1995; Chittka et al.
515 2004). Although colour biases can somewhat be overridden by individual learning
516 (Raine et al., 2006), they potentially govern foraging decisions in bees when selecting
517 among novel flower types (Gumbert 2000). In the absence of social information, flower
518 choices of tested honeybees conceivably resulted from either their innate colour
519 preferences or previous experience in the field with local flower species as both factors
520 can be linked with the likelihood of finding a profitable food reward (Giurfa et al. 1995;
521 Chittka et al. 2004).
522 In the wild, honeybee foragers are likely to encounter members of the same and
523 different species foraging concurrently in a flower patch from distinct flower types
524 (Fægri and Van der Pijl 1979; Kevan and Baker 1983). Our results demonstrate that
525 such social information is certainly integrated with honeybees' colour preferences
526 during the process of making a foraging decision. In this realistic scenario, with two
527 simultaneous sources of conspecific and heterospecific social information, when the
528 first foraging demonstrator that honeybees detected was a member of the same species,
529 they promptly responded to social information by joining the demonstrator on the
530 unfamiliar flower type. This evidence is consistent with previous findings in
531 bumblebees (reviewed in Leadbeater and Dawson 2017) and supports the notion that the
532 use of conspecific social information in bees may be mediated by local enhancement,
533 with foragers being attracted to flowers occupied by members of the same species
534 (Leadbeater and Chittka 2007a). Such a response potentially optimises the foraging

efficiency of bees by facilitating their movements between different flower types (Leadbeater and Chittka 2005; Kawaguchi et al. 2007).

Honeybees and bumblebees often forage upon similar floral resources; it is then conceivable that they may concur in the same flower patches (Rogers et al. 2013; Xie et al. 2016). In our experiments, we used freely moving bumblebee demonstrators to elucidate how social information might flow between these species. Our results indicate that in the likely scenario of a honeybee exploring a flower patch and encountering both a conspecific and heterospecific (bumblebee) individual foraging from different flower types, its foraging decisions might depend on the species identity of the first source of social information that is observed. That is, foraging decisions of observer honeybees that detected a bumblebee before a conspecific demonstrator were characteristically preceded by an extensive exploration of the flowers. This evidence suggests that in a foraging context, honeybees' discrimination of conspecifics and heterospecifics might determine their readiness to use social information in making foraging decisions. 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, animals should typically favour conspecific over heterospecific social information when they can select between both sources (Jaakkonen et al. 2015). In line with this, honeybees consistently selected the type of flowers demonstrated by conspecifics, even though they attended to the presence of both demonstrators whilst exploring the set-up. Prioritizing conspecific over heterospecific choices can be explained due to its high fitness value (Seppänen et al. 2007; Jaakkonen et al. 2015) but it can also serve to the transmission of novel behavioural traits or preferences that may be adaptively valuable for a particular species (Laland and Plotkin 1993; Jaakkonen et al. 2015; Alem et al. 2016; Danchin et al. 2018).

560 Floral reward levels differ strongly among plant species and constantly change
561 over time in an unpredictable manner (Heinrich 1979). To achieve efficient foraging,
562 bees can rapidly learn to associate floral traits such as colour, shape and scent with
563 reward quality in flowers (Chittka et al. 1999). Bees can be initially attracted to forage
564 from an unfamiliar flower species via either innate and learned colour preferences
565 (Giurfa et al. 1995; Gumbert 2000; Chittka et al. 2004; Raine and Chittka 2007) or
566 using social information (Leadbeater and Chittka 2007b; Grüter and Leadbeater 2014;
567 Leadbeater and Dawson 2017). In the wild, bees seeking floral resources are unlikely to
568 experience asocial and social cues separately, rather they may frequently be exposed to
569 a complex combination of cues potentially affecting their flower choices. Our findings
570 demonstrate a clear interplay between colour preferences and social information
571 simultaneously delivered by conspecifics and heterospecifics. This may underlie the
572 process of gathering new information that shapes honeybees' foraging decisions.
573 Compared to honeybees in the control group (i.e., no social information) the exploration
574 behaviour of honeybees that observed a conspecific or heterospecific demonstrator
575 foraging upon the less preferred yellow flowers, reflected a more evenly distributed
576 inspection of magenta and yellow flowers. That is, the presence of either demonstrator
577 on a yellow flower increased the 'attractiveness' of such flower type for honeybees,
578 possibly via stimulus enhancement, an effect widely described in social learning
579 literature (Heyes 2012). Remarkably, honeybees' inspection of flowers, naturally biased
580 towards magenta flowers, underwent a sequential and flexible adjustment before they
581 made a foraging decision. Such adjustment was modulated by visual foraging
582 information from members of the same and different species, and resulting foraging
583 decisions reflected the selective use of conspecific over heterospecific social
584 information. It has been demonstrated that bees are attracted to the presence of foraging

585 conspecifics when presented with unfamiliar flowers which may lead them to
586 identifying new rewarding flower species (Leadbeater and Chittka 2007a; Jones et al.
587 2015). Our results indicate that conspecific social information not only directed
588 honeybees' foraging choices to flowers that matched their colour preference (magenta),
589 but it also outweighed this colour preference, such that honeybees selected the
590 originally less preferred yellow flowers. Whereas intraspecific social transmission of
591 foraging information may be more stable when it reinforces a prior preference (Laland
592 and Plotkin 1990), such preferences may be adjusted and potentially overridden in
593 response to conspecific social information about a novel foraging resource (Jones et al.
594 2015). Thus, enabling a fast adaptation to varying floral reward levels. If the presence of
595 a foraging conspecific can reliably be associated with a rewarding outcome, the use of
596 such social cue should be reinforced to continuously influence bees' flowers choices
597 across foraging contexts (Leadbeater and Chittka 2009). Interestingly, in our
598 experiments the presence of a foraging heterospecific attracted honeybees' attention to
599 the demonstrated flower types, yet this effect did not influence honeybees' foraging
600 decisions as they selectively used social information from conspecifics. Even though,
601 heterospecific social information is predictably valuable when there is a large niche
602 overlap (Seppänen et al. 2007), conspecifics choices might offer a more predictable
603 social cue that lowers the risk of acquiring maladaptive information (Giraldeau et al.
604 2002) as conspecifics share the same ecological needs (Seppänen et al. 2007; Goodale
605 et al. 2010).
606 Multiple social and asocial cues can potentially affect animals' foraging
607 decisions in different circumstances (Sclafani 1995; Galef and Giraldeau 2001; Grüter
608 and Leadbeater 2014). The interaction between social information and previous, innate
609 or learned preferences possibly not only influences the foraging decision of a particular

individual but may also promote the transmission of adaptive information about food sources (Laland and Plotkin 1990; Galef and Giraldeau 2001). Despite social information offers a clear advantage to individuals exploring novel foraging resources (Galef and Giraldeau 2001), its use should not be indiscriminate but respond to particular circumstances in order to lead to adaptive choices (Laland 2004; Kendal et al. 2018). Our results extend previous evidence showing that conspecific social information is commonly used in situations of uncertainty (Kendal et al. 2004; van Bergen Yfke et al. 2004; Galef et al. 2008; Smolla et al. 2016), 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 (Seppänen et al. 2007; Leadbeater and Dawson 2017), 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. By depicting in depth, the plausible ecological process, thereby multiple sensory inputs may shape foraging decisions in bees, findings presented here contribute to our current knowledge about the flexibility of individual preferences and their adjustment in response to different types 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 CJ, Zhu X, Loukola OJ, Ingraham T, Søvik E, Chittka L. 2016. Associative Mechanisms Allow for Social Learning and Cultural Transmission of String Pulling in an Insect. PLOS Biol. 14(10):e1002564. doi:10.1371/journal.pbio.1002564.

Avarguès-Weber A, Dawson EH, Chittka L. 2013. Mechanisms of social learning across species boundaries. J Zool. 290(1):1–11. doi:10.1111/jzo.12015.

Balamurali GS, Nicholls E, Somanathan H, Hempel de Ibarra N. 2018. A comparative analysis of colour preferences in temperate and tropical social bees. Sci Nat. 105(1):8. doi:10.1007/s00114-017-1531-z.

Chittka L, Ings TC, Raine NE. 2004. Chance and adaptation in the evolution of island bumblebee behaviour. Popul Ecol. 46(3):243–251. doi:10.1007/s10144-004-0180-1.

Chittka L, Thomson JD, Waser NM. 1999. Flower Constancy, Insect Psychology, and Plant Evolution. Naturwissenschaften. 86(8):361–377. doi:10.1007/s001140050636.

Dugatkin LA. 1996. Interface between culturally based preferences and genetic preferences: female mate choice in Poecilia reticulata. Proc Natl Acad Sci. 93(7):2770–2773. doi:10.1073/pnas.93.7.2770.

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

Dawson EH, Chittka L. 2012. Conspecific and Heterospecific Information Use in Bumblebees. PLOS ONE. 7(2):e31444. doi:10.1371/journal.pone.0031444.

Fægri K, Van der Pijl L. 1979. Chapter 11 - Animals as pollinators. In: Fægri K, Van der Pijl L, editors. Principles of Pollination Ecology (Third Edition). Amsterdam: Pergamon. p. 96–133.

Galef BG, Dudley KE, Whiskin EE. 2008. Social learning of food preferences in ‘dissatisfied’ and ‘uncertain’ Norway rats. Anim Behav. 75(2):631–637. doi:10.1016/j.anbehav.2007.06.024.

Galef BG, Giraldeau L-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav. 61(1):3–15. doi:10.1006/anbe.2000.1557.

Galef BG, Laland KN. 2005. Social Learning in Animals: Empirical Studies and Theoretical Models. BioScience. 55(6):489–499. doi:10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2.

Giraldeau L, Valone TJ, Templeton JJ. 2002. Potential disadvantages of using socially acquired information. Johnstone RA, Dall SRX, editors. Philos Trans R Soc Lond B

Biol Sci. 357(1427):1559–1566. doi:10.1098/rstb.2002.1065.

Giurfa M, Núñez J, Chittka L, Menzel R. 1995. Colour preferences of flower-naive honeybees. J Comp Physiol A. 177(3):247–259. doi:10.1007/BF00192415.

Goodale E, Beauchamp G, Magrath RD, Nieh JC, Ruxton GD. 2010. Interspecific information transfer influences animal community structure. Trends Ecol Evol. 25(6):354–361. doi:10.1016/j.tree.2010.01.002.

Grüter C, Leadbeater E. 2014. Insights from insects about adaptive social information use. Trends Ecol Evol. 29(3):177–184. doi:10.1016/j.tree.2014.01.004.

Gumbert A. 2000. Color choices by bumble bees (Bombus terrestris): innate preferences and generalization after learning. Behav Ecol Sociobiol. 48(1):36–43. doi:10.1007/s002650000213.

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

Heyes C. 2012. What's social about social learning? J Comp Psychol. 126(2):193–202. doi:10.1037/a0025180.

Heyes CM. 1994 Social-learning in animals–categories and mechanisms. Biol. Rev. Camb. Phil. Soc. 69, 207–231. doi:10.1111/j.1469- 185X.1994.tb01506.x

Hoppitt W, Laland KN. 2013. Social Learning: An Introduction to Mechanisms, Methods, and Models. Princeton University Press.

Ings TC, Raine NE, Chittka L. 2009. A population comparison of the strength and persistence of innate colour preference and learning speed in the bumblebee Bombus terrestris. Behav Ecol Sociobiol. 63(8):1207–1218. doi:10.1007/s00265-009-0731-8.

Jaakkonen T, Kivelä SM, Meier CM, Forsman JT. 2015. The use and relative importance of intraspecific and interspecific social information in a bird community. Behav Ecol. 26(1):55–64. doi:10.1093/beheco/aru144.

Jones PL, Ryan MJ, Chittka L. 2015. The influence of past experience with flower reward quality on social learning in bumblebees. Anim Behav. 101:11–18. doi:10.1016/j.anbehav.2014.12.016.

Kawaguchi Lina G, Ohashi Kazuharu, Toquenaga Yukihiko. 2007. Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers. Proc R Soc B Biol Sci. 274(1626):2661–2667. doi:10.1098/rspb.2007.0860.

Kendal RL, Boogert NJ, Rendell L, Laland KN, Webster M, Jones PL. 2018. Social Learning Strategies: Bridge-Building between Fields. Trends Cogn Sci. 22(7):651–665. doi:10.1016/j.tics.2018.04.003.

Kendal RL, Coolen I, Laland KN. 2004. The role of conformity in foraging when personal and social information conflict. Behav Ecol. 15(2):269–277. doi:10.1093/beheco/arh008.

Kendal, RL, Coolen, I, Laland, KN. Adaptive trade-offs in the use of social and personal information. In: Dukas R, Ratcliffe JM, editors. Cognitive ecology II. Chicago: The University of Chicago Press. p. 249-271.

Kevan PG, Baker HG. 1983. Insects as Flower Visitors and Pollinators. Annu Rev Entomol. 28(1):407–453. doi:10.1146/annurev.en.28.010183.002203.

Laland KN. 2004. Social learning strategies. Anim Learn Behav. 32(1):4–14. doi:10.3758/BF03196002.

Laland KN, Plotkin HC. 1990. Social learning and social transmission of foraging information in Norway rats (Rattus norvegicus). Anim Learn Behav. 18(3):246–251. doi:10.3758/BF03205282.

Laland KN, Plotkin HC. 1993. Social transmission of food preferences among norway rats by marking of food sites and by gustatory contact. Anim Learn Behav. 21(1):35–41. doi:10.3758/BF03197974.

Leadbeater E, Chittka L. 2005. A new mode of information transfer in foraging bumblebees? Curr Biol. 15(12):R447–R448. doi: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). Behav Ecol Sociobiol. 61(11):1789–1796. doi:10.1007/s00265-007-0412-4.

Leadbeater E, Chittka L. 2007b. Social Learning in Insects — From Miniature Brains to Consensus Building. Curr Biol. 17(16):R703–R713. doi:10.1016/j.cub.2007.06.012.

Leadbeater E, Dawson EH. 2017. A social insect perspective on the evolution of social learning mechanisms. Proc Natl Acad Sci. 114(30):7838–7845. doi:10.1073/pnas.1620744114.

Leadbeater Ellouise, Chittka Lars. 2009. Bumble-bees learn the value of social cues through experience. Biol Lett. 5(3):310–312. doi:10.1098/rsbl.2008.0692.

Lunau K, Wacht S, Chittka L. 1996. Colour choices of naive bumble bees and their implications for colour perception. J Comp Physiol A. 178(4). doi: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. Biol Rev. 68(1):81–120. doi:10.1111/j.1469-185X.1993.tb00732.x.

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

Raine NE, 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):e556. doi:10.1371/journal.pone.0000556.

Raine Nigel E., Ings TC, Dornhaus A, Saleh N, Chittka L. 2006. Adaptation, Genetic Drift, Pleiotropy, and History in the Evolution of Bee Foraging Behavior. In: Advances in the Study of Behavior. Vol. 36. Academic Press. p. 305–354.

Raine Nigel E, Ings TC, Ramos-Rodriguez O, Chittka L. 2006. Unterschiede im Lernverhalten zwischen Kolonien einer freilebenden Britischen Hummelpopulation (Hymenoptera: Apidae: Bombus terrestris audax). Entomol Gen. 28(4):241–256. doi:10.1127/entom.gen/28/2006/241.

Rogers SR, Cajamarca P, Tarpy DR, Burrack HJ. 2013. Honey bees and bumble bees respond differently to inter- and intra-specific encounters. Apidologie. 44(6):621–629. doi:10.1007/s13592-013-0210-0.

Sclafani A. 1995. How food preferences are learned: laboratory animal models. Proc Nutr Soc. 54(2):419–427. doi:10.1079/PNS19950011.

Seppänen J-T, Forsman JT, Mönkkönen M, Thomson RL. 2007. Social Information Use Is a Process Across Time, Space, and Ecology, Reaching Heterospecifics. Ecology. 88(7):1622–1633. doi: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. Biol Lett. 12(6):20160188. doi:10.1098/rsbl.2016.0188.

Stephens DW, Brown JS, Ydenberg RC, editors. 2007. Foraging: behavior and ecology. Chicago: University of Chicago Press.

Valone TJ, Templeton JJ. 2002. Public information for the assessment of quality: a widespread social phenomenon. Johnstone RA, Dall SRX, editors. Philos Trans R Soc Lond B Biol Sci. 357(1427):1549–1557. doi:10.1098/rstb.2002.1064.

van Bergen Y, Coolen I, Laland KN. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. Proc R Soc Lond B Biol Sci. 271(1542):957–962. doi:10.1098/rspb.2004.2684.

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

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):e0144590. doi:10.1371/journal.pone.0144590.