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 optimise 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 non-social 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 had 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 (magenta or yellow). Honeybees showed a natural preference for magenta flowers. Honeybees modified their inspection of both types of flowers in response to conspecific and heterospecific social information. The presence of either

demonstrator on the less-preferred yellow flower increased honeybees' inspection of yellow flowers. Conspecific social information influenced observers' foraging choices of yellow flowers, thus outweighing their original preference for magenta flowers. This effect 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, possibly favouring the transmission of adaptive foraging information within species.

Keywords: behavioural flexibility, decision making, innate colour bias, insects, interspecific, intraspecific, 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 (Chittka et al. 1999; Stephens et al. 2007). Foraging decisions can be influenced in a context-dependant manner (Laland 2004; Kendal et al. 2009) by innate preferences (Lunau et al. 1996; 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; Leadbeater and Chittka, 2007b; 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 drawn 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; Loukola et al. 2020). 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 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 of various species are in many locations sympatric and 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 demonstrator honeybees – in this study, the "demonstrators" were dead individuals placed on artificial flower types (Dawson and Chittka 2012). However, in more realistic conditions, a bee forager whose known floral resources have decreased in reward levels, will likely encounter other foragers, of their own and different species, feeding from different types of flowers (Fægri and van der Pijl 1979; Kevan and 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 et al. 2004; Raine et al. 2006; Raine and Chittka 2007), hence influencing foraging decisions. We address these questions by testing whether honeybees might adjust their colour preferences in response to simultaneous sources of social information, i.e., a conspecific and heterospecific, each foraging from either a preferred or non-preferred flower colour.

MATERIALS AND METHODS

101 *(a) Set-up*

102 We used free-flying honeybee foragers (*Apis mellifera*) from hives located in an
103 urban area of London, UK. Over two consecutive summers (2017-2018), we trained
104 foragers of one hive to collect 30% sucrose solution (w/w) from a gravity feeder (von
105 Frisch, 1965, Figure 16, p. 18), placed 2 m away from one the hive. The feeder in turn
106 attracted foragers from the other hives, which were then included in the experiments.
107 The feeder was refilled every day at 0800 hours, yet honeybees were also free to forage
108 on local floral resources.

109 In addition, we used bumblebee foragers from two colonies (Biobest, Belgium
110 N.V.) for the experiments. Bumblebee nests were housed in bipartite wooden nest-
111 boxes (l = 29.5 × w = 11.5 × h = 9.5 cm) connected to a wooden flight arena (l = 77 cm,
112 w = 52 cm, h = 30 cm) by a Plexiglas tunnel (l = 25 cm, 3.5 × 3.5 cm). The floor of the
113 flight arena was covered in white laminated paper. Three plastic sliding doors located
114 along the corridor allowed controlled access to the arena. Before and after experiments,
115 bumblebees could freely feed upon 30% (w/w) sucrose solution from a mass feeder in
116 the middle of the arena. Bumblebee colonies were provided with 7 g of frozen pollen
117 (Koppert B.V., The Netherlands) every two days.

118

119 *(b) Training of bumblebees*

120 We trained 30 bumblebee foragers (demonstrators) from two colonies (one
121 colony per year) in a flight arena. In this group-training, foragers were allowed to enter
122 the arena together at various times, and bumblebees learned to forage on an array of
123 twelve plastic chips (2.4 × 2.4 cm, henceforth "flowers") placed on the top of
124 transparent glass vials (h = 4 cm), positioned on the floor of the arena. The array was
125 arranged in a rectangular grid formation (3 × 4) with a separation of 7.5 cm between the

126 edges of the flowers. We filled four yellow flowers with 10 µL of rewarding 50% (w/w)
127 sucrose solution, and four magenta and four transparent flowers with 10 µL of
128 unrewarding water (Figure 1A). Flowers were refilled after they were depleted by
129 foragers and the foragers left the flower. Half of the foragers experienced the opposite
130 colour-reinforcement contingency. Training took place for one day over 2 hours. We
131 carried out refreshment bouts (20 min) each day prior to testing. We tracked
132 demonstrator bees' identity with individual number tags (Opalithplättchen, Warnholz &
133 Bienenvoigt, Ellerau, Germany) glued to the top of the thorax by means of Loctite
134 Super Glue Gel (Loctite, Ohio, US). The floor of the arena and flowers were cleaned
135 with 70% ethanol after completing training.

136 *(c) Training of honeybees*

137 Once we completed bumblebees' training, we proceed to train honeybee
138 demonstrators and observers, which took place over 18 daily sessions. Each day, we
139 trained a set of five honeybees (demonstrators) foraging from the gravity feeder. In this
140 group-training, honeybees learned to enter the same flight arena (located outdoors)
141 where bumblebees were trained. We reversed the colour-reinforcement contingency so
142 that honeybees learned to forage on flowers of the opposite colour that bumblebees
143 were trained on. Half of the honeybees experienced four magenta flowers with 40 µL of
144 50% (w/w) sucrose solution, and four yellow and four transparent flowers with 40 µL of
145 water (Figure 1A). The other half of the honeybees experienced the reverse colour-
146 reinforcement contingency. Rewarding flowers were refilled after depletion by the
147 foragers and the foragers left the flower. Training lasted 1 hour, consisting of six bouts
148 (10 min). We identified trained individuals by marking their thorax with a white paint
149 mark (Posca Pen, Worcester, UK). We cleaned the floor of the arena and flowers with
150 70% ethanol after completing training.

151 Three hours after finalising the demonstrator's training, we selected a separate
152 batch of five foragers (observers) to train them on a different set-up. Every day,
153 observers were trained in group to enter the same flight arena and forage upon a
154 rectangular grid array of twelve transparent flowers (3 × 4) (Figure 1B). To encourage
155 foragers to sample multiple flowers during their foraging trips, only half of the flowers
156 contained 40 µL of 50% (w/w) sucrose solution, whereas the other half contained 40 µL
157 of water. Rewarding flowers were replenished after emptied and the forager left the
158 flower. The positions of all the flowers were changed every bout (10 min) over 1 hour
159 of training. We marked trained observers with a green dot to distinguish them from the
160 demonstrators. Original honeybees trained (demonstrators) were allowed to visit the
161 setup during this training, which did not interfere with the previous colour training, as
162 shown in the results section. After training observers, we cleaned the flowers and the
163 arena floor with 70% ethanol.
164
165 *(d) Testing the effect of colour preference on honeybees' foraging decisions*
166 We carried out this control test every day after completing training. Only two to
167 three individuals from the batch of five observer honeybees (trained on transparent
168 flowers) regularly showed up at the setup at the time of testing. Thus, we only tested
169 two daily individuals. Overall, we tested 20 honeybees individually (control group) in a
170 context where transparent flowers were unrewarding. We assessed whether they might
171 show a natural preference to inspect and forage from one flower type between two
172 unfamiliar alternatives, i.e., yellow and magenta. One honeybee was let in the arena to
173 explore a rectangular grid array of twelve flowers (section b, above), consisting of four
174 familiar transparent flowers containing 20 µL of water and eight unfamiliar flowers,
175 four yellow and four magenta, all filled with a scentless reward of 20 µL of 50% (w/w)

176 sucrose solution, (Figure 1D). The test began once the individual inspected any flower.
177 That is, the honeybee approached the flower by displaying a slow side-to-side hover,
178 with its head oriented towards it and within at least one body length (Ings et al. 2009).
179 The test concluded once the honeybee landed and foraged upon any unfamiliar flower,
180 or 3 minutes after the test started. As this test was designed to evaluate the influence of
181 honeybees' colour preferences on an actual foraging decision, rather than measuring
182 their innate colour preferences, we regarded the flower type where the individual landed
183 and foraged as preferred over the alternative type. To prevent re-testing the same
184 individuals, we captured honeybees, after concluding the test, to give them a distinctive
185 red paint mark. The flowers and arena floor were cleaned with 70% ethanol between
186 tests. To evaluate honeybees' inspection of flowers before they chose a flower to forage
187 (foraging decision), we recorded the test with a sport camera (Yi, Xiaomi Inc. China)
188 featuring a recording frame rate of 30 fps and a resolution of 720 p (1,280 × 720 pixels).
189 The camera was positioned 20 cm above the entrance of the bumblebee nest (Figure 1).
190 Its field of view was adjusted such that it looked down into the arena at ~50° from a
191 horizontal angle.
192
193 *(e) Testing the influence of social information on foraging decisions*
194 To evaluate the influence of simultaneous sources (conspecific and
195 heterospecific) of social information on honeybee's inspection of either yellow or
196 magenta flowers and their subsequent foraging decisions, we tested 45 honeybees in the
197 same context as individuals in the control group (section d) but in the presence of one
198 bumblebee and one honeybee demonstrator, each foraging upon either a yellow or
199 magenta flower. We introduced the demonstrators and observer in the arena in the
200 following order: 1) a honeybee demonstrator was let in through a sliding door on the

201 back wall of the arena (Figure 1D). Once she began to feed from a flower of her trained
202 colour, 2) a bumblebee demonstrator was released from the Plexiglas tunnel that
203 connected the arena to the nest-box (Figure 1D). When she started to forage from a
204 flower of her trained colour (opposite colour as the honeybee demonstrator), 3) a
205 honeybee observer was let into the arena through the sliding door on the back wall. Due
206 to training, both demonstrators swiftly landed and foraged exclusively on flowers of
207 their trained colour. We tested 19 observer honeybees with a conspecific demonstrator
208 foraging on magenta flowers and a heterospectific foraging on yellow flowers and 26
209 observers with the reversed colour-reinforcement contingency.
210 The test began once the observer honeybee inspected (see section d) any
211 occupied or unoccupied flower. The test concluded once the observer landed and
212 foraged upon any unfamiliar flower, or 3 minutes after the test started. In the test,
213 demonstrators moved freely between flowers after depleting them, as they naturally do
214 within inflorescences. Thus, we only considered that observers foraged on an unfamiliar
215 flower when they actually fed upon the sucrose solution reward from unemptied
216 flowers. To prevent re-testing the same individuals, we caught tested honeybees and
217 marked them with a distinctive red paint mark. The flowers and arena floor were
218 cleaned with 70% ethanol between tests. To evaluate honeybees' inspection of flowers
219 and their interactions with the demonstrators before they made a foraging decision, the
220 test was recorded as described in section (d) above.
221

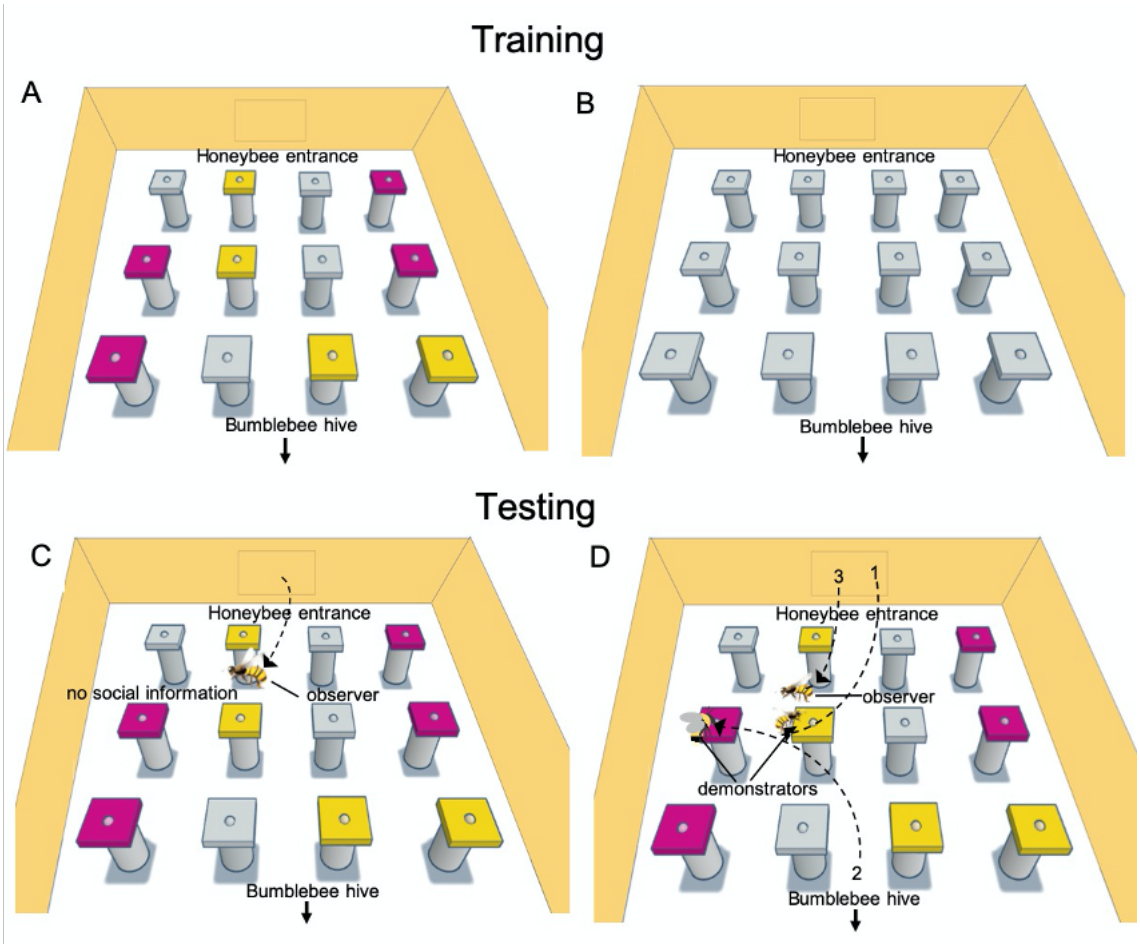

Figure 1. Training and testing protocols in the flight arena. (**A**) Honeybee foragers (demonstrators) were trained to find 50% sucrose solution on either four yellow or magenta flowers and water on four flowers of the alternative colour and four transparent flowers. Bumblebee foragers (demonstrators) were group trained using the same protocol (**B**) 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. (**C**) 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. (**D**) 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 previously associated with reward (transparent) were unrewarding and unfamiliar coloured

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.

(d) Analyses

We analysed the behaviour of tested honeybees from video recordings, using the BORIS behavioural observation software (Friard and 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. That is, the frequency of inspecting transparent, yellow and magenta flowers (Ings et al. 2009; Balamurali et al. 2018) and individual's foraging choice, i.e., the yellow or magenta flower where individuals landed and foraged. We used logistic analysis to explore the influence of flower colour on the likelihood of honeybees inspecting a flower for the first time, the likelihood of foraging on a flower type, as well as the proportion of transparent, yellow and magenta flowers they inspected. For the latter two variables, we took underdispersion into account via a quasinomial model.

For honeybees exposed to social information, we considered inspection of occupied flowers as an indicator that observers detected the demonstrator's presence. Thus, four different scenarios were possible before honeybees made a foraging decision: they could have detected both demonstrators, either the honeybee or bumblebee demonstrator, or none of them. We compared the likelihood of each situation against the expected probability with a Chi-Square Goodness of Fit Test. Nine individuals that did not detect the presence of the demonstrators were 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 honeybees. Social information was included as a predictor

variable (binary: 1= present, 0= absent) for the likelihood of honeybees landing on either an unfamiliar yellow or magenta flower.

Further, to evaluate the influence of social information on honeybees' readiness to forage on an unfamiliar flower, we compared two measurements between the control group and the group exposed to social information. That is, the total number of flowers that individuals inspected before they chose a flower to forage, and the time it took them to make such 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., honeybee or bumblebee). 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 honeybee and bumblebee 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 honeybees 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 honeybee observers selecting the demonstrated type of flower and the likelihood that observers would forage on a flower occupied by either a honeybee or bumblebee, after approaching it for the first time. For the latter variable, we took underdispersion into account via a quasinomial model.

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 honeybee or bumblebee 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 honeybee or bumblebee demonstrator.

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

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

, where, i_m and i_y are the frequency that 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 near equal to zero implies that the observers either inspected both types of flowers equally, or they did not inspect the flowers at all. We calculated inspecting indices (II) based on the sequence of events that preceded the honeybees' foraging decisions. That is, each inspecting index (II) represented observers' inspection of flowers, before and after they detected either demonstrator (honeybee or bumblebee) 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

Bees were kept in their natural colony environment in unaltered dark conditions. The gravity feeder where honeybees foraged from, was only filled when no individuals were present to avoid disturbance. Bumblebees were fed with a minimum 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. Honeybees were tagged with a dot of paint on the thorax while feeding and bumblebees were carefully handled with dissection forceps to glue number tags on their thoraxes.

RESULTS

Effect of colour preference on honeybees' foraging decisions

In a context where a familiar flower type ceases to yield reward, how does colour preference influence honeybees' exploration of contiguous, novel flowers and ultimate move to foraging upon a new flower type? We carried out a control test to assess whether honeybees preferentially inspect one unfamiliar flower type over another, and whether this might affect their ultimate foraging decision (move to foraging upon a new flower type). We trained honeybees (observers) to find either a food reward (50% sucrose solution) or unrewarding water on transparent flowers (Materials and Methods). We then we tested bees in a context where transparent flowers were unrewarding and two unfamiliar yellow and magenta flower types delivered a food

reward (scentless 50% sucrose solution). The majority of individuals (77%) did not inspect the familiar transparent flowers at all; rather honeybees preferred to inspect and forage on magenta flowers. The proportion of flowers inspected by honeybees was influenced by flower colour (Logistic regression: $F = 35.86$, $N = 20$, $P < 0.001$; Fig. 3.2A). Flower colour also influenced the likelihood of honeybees first exploring a flower type (Logistic regression: $\chi^2_1 = 15.44$, $N = 20$, $P < 0.001$; Fig.3.2B) and the likelihood of selecting a flower to forage (Logistic regression: $F = 30.04$, $N = 20$, $P < 0.001$; Fig. 3.2C). This shows that honeybees had a colour preference for magenta over yellow flowers.

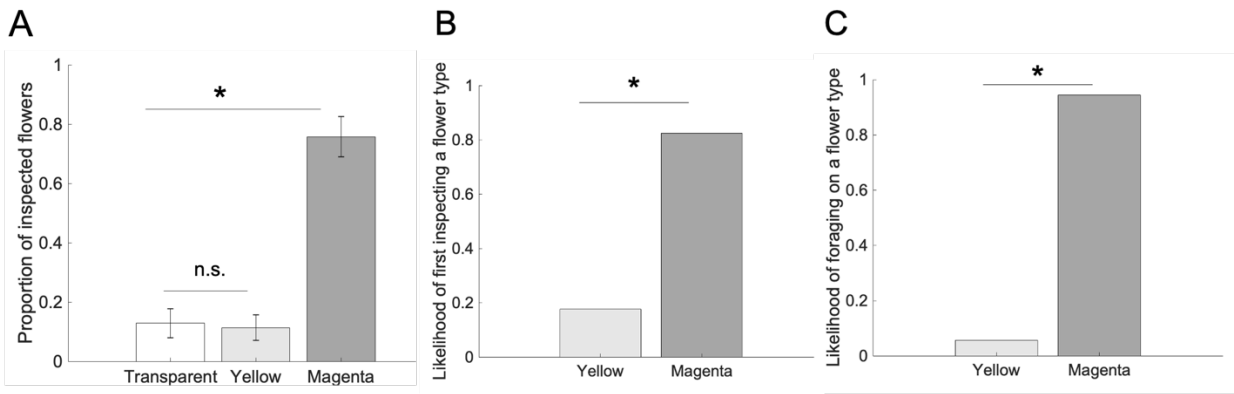

Figure 3.2. Honeybees prefer magenta over yellow flowers **(A)** Honeybees inspected magenta flowers at a higher proportion than yellow and transparent flowers. **(B)** The likelihood of honeybees inspecting an unfamiliar flower for the first time was higher for magenta compared to yellow flowers. **(C)** A higher proportion of honeybees preferred to forage on magenta than yellow flowers. Bars = mean. Horizontal lines = standard error. Asterisks = $p < 0.05$.

Influence of social information on honeybees' foraging decisions

In a field-like context, including simultaneous and divergent conspecific and heterospecific social information, we investigated how this social information might affect honeybees' inspection of flower types and ultimate foraging decisions. We

360 considered that observers detected the demonstrators' presence once they inspected an
361 occupied flower for the first time. We found no difference in the proportion of observers
362 that detected both demonstrators, only the honeybee or bumblebee demonstrator, or
363 none of them (Chi-Square Goodness of Fit Test: $\chi^2_3 = 2.2$, $N = 45$, $P = 0.31$; Fig. 3A).
364 The likelihood of foraging on an unfamiliar flower type was not influenced by the
365 presence of social information (Logistic regression: $\chi^2_1 = 0.9$, $N = 56$, $P = 0.34$; Fig.
366 3.2B). Similar to the control group, the vast majority of observers (90%) did not inspect
367 the transparent flowers at all. These results suggest that both individual colour
368 preference and social information similarly influenced honeybees when locating a new
369 foraging resource. Compared to observer honeybees that first detected a foraging
370 bumblebee in the test, individuals in the control group, whose foraging decisions were
371 solely influenced by colour preference, made faster choices (Wilcoxon rank-sum: $W =$
372 71, $N = 35$, $P = 0.007$; Fig. 3.3C) and inspected fewer flowers (Wilcoxon rank-sum: W
373 $= 77$, $N = 35$, $P = 0.011$; Fig. 3.3D). However there was no difference between the
374 control group and those observers that first detected the presence of a foraging
375 conspecific (Wilcoxon rank-sum: latency: $W = 133$, $N = 30$, $P = 0.29$; Fig. 3.3C;
376 number of flowers: $W = 125$, $N = 30$, $P = 0.45$; Fig. 3.3D). Further, when observers
377 first detected the conspecific demonstrator, they made faster foraging decisions
378 (Wilcoxon rank-sum: $W = 184$, $N = 29$, $P < 0.001$; Fig. 3.3C), preceded by less
379 inspection of flowers (Wilcoxon rank-sum: $W = 176.5$, $N = 29$, $P < 0.001$; Fig. 3.3D),
380 than when they first detected the heterospecific bumblebee. These results suggest that
381 both individual preference for magenta flowers and conspecific social information
382 similarly affected honeybees' foraging choices, enabling swift decisions. Conversely,
383 observers that initially detected a foraging heterospecific, explored the flowers
384 extensively before making a foraging decision.

385 Honeybee observers that detected either one or both demonstrators, similarly
386 inspected flowers occupied by either the honeybee or bumblebee demonstrator
387 (Wilcoxon rank-sum; one demonstrator: $W = 34.5$, $N = 16$; $P = 0.45$; both
388 demonstrators: Wilcoxon signed-rank: $V = 22.5$, $N = 13$, $P = 1$; Fig. 3.3E). However, the
389 likelihood that an observer would forage on an unfamiliar flower type was influenced
390 by the demonstrators' species (Logistic regression: $\chi^2_1 = 11.78$, $N = 45$, $P < 0.001$; Fig.
391 3.3F) and flower colour (Logistic regression: $\chi^2_1 = 5.08$, $N = 45$, $P = 0.024$; Fig. 3.3F)
392 but was only marginally influenced by the statistical interaction between these main
393 effects (Logistic regression: $\chi^2_1 = 3.17$, $N = 45$, $P = 0.07$; Fig. 3.3F). Further,
394 demonstrators' species influenced the likelihood of observers foraging on an occupied
395 flower after approaching it for the first time (Logistic regression: $\chi^2_1 = 20.51$, $N = 51$, P
396 < 0.001; Fig. 3.3G). That is, observers readily responded to the presence of a foraging
397 conspecific by joining such demonstrator on the unfamiliar flower type. This response
398 was not affected by flower colour (Logistic regression: $\chi^2_1 = 0.03$, $N = 51$, $P = 0.82$;
399 Fig. 3.3G) nor by any statistical interaction between main effects (Logistic regression:
400 $\chi^2_1 = 0$, $N = 51$, $P = 1$; Fig. 3.3G). In contrast, observer honeybees rejected the flowers
401 occupied by a bumblebee demonstrator at a higher proportion (Wilcoxon signed-rank: V
402 $= 3$, $N = 13$, $P = 0.008$; Fig. 3.3H) than the flowers occupied by a conspecific.
403

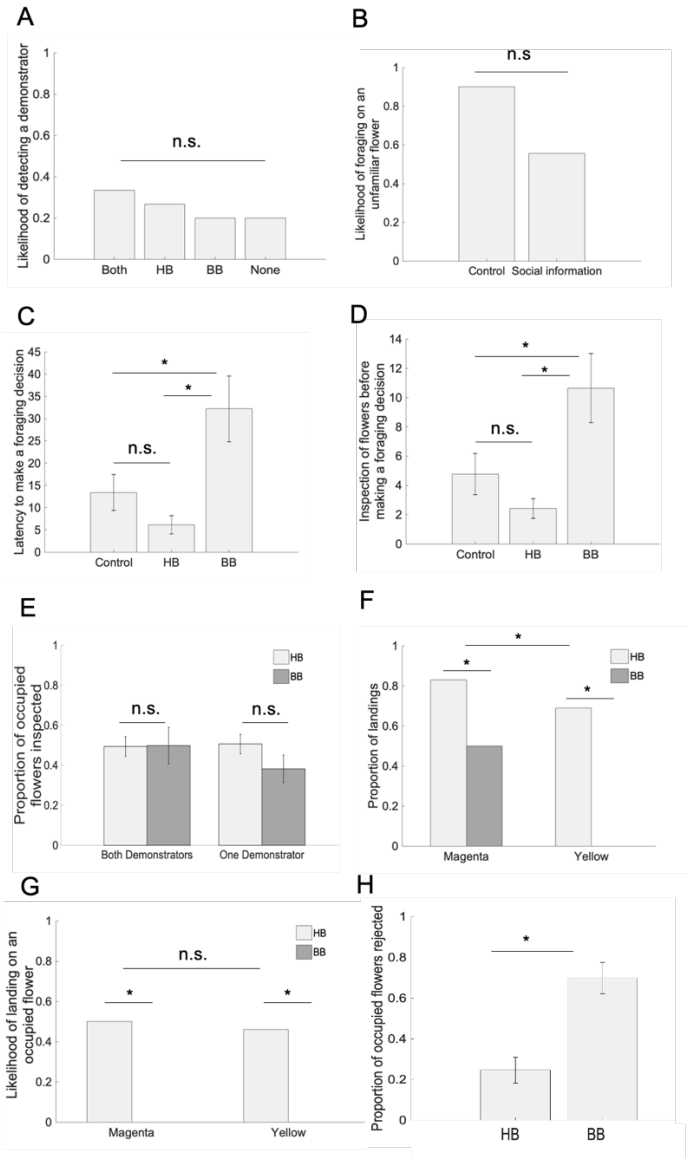

Figure 3. Concurrent conspecific and heterospecific social information influences foraging behaviour of honeybees **(A)** Observer honeybees were equally likely to detect both demonstrators, only the honeybee or bumblebee demonstrator, and none of them. **(B)** The proportion of honeybees that foraged 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 detected a foraging heterospecific. **(D)** Honeybees in the control group and those that first detected a foraging conspecific inspected fewer flowers before making a foraging decision than observers that first detected the presence of a foraging heterospecific. **(E)** Honeybee observers that detected only one or both demonstrators during the test; similarly inspected flowers occupied by the honeybee and bumblebee demonstrator. **(F)** Demonstrators' species and flower colour had an effect on the proportion of honeybees

that foraged on unfamiliar flowers, yet no interaction of main effects was found. **(G)** Once observers detected a conspecific demonstrator foraging on an unfamiliar flower type, they were more likely to land and forage on such a flower, but they never foraged on a flower occupied by a heterospecific demonstrator. **(H)** Observers rejected flowers occupied by a bumblebee at a higher proportion than flowers occupied by a conspecific. HB = honeybee, BB = bumblebee. Bars = mean. Horizontal lines = standard error. Asterisks = $p < 0.05$. n.s. = not significantly different.

Adjustment of honeybees' colour preference in response to social information

The inspecting indexes (II), described in (d), allowed us to analyse honeybees' 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 honeybees showed no preference to inspect magenta or yellow flowers before they detected the bumblebee 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 honeybees detected a bumblebee foraging from a magenta flower, they preferentially inspected this type of flower (Wilcoxon signed-rank: $V = 26$, $N = 9$, P = 0.026; Fig. 3.4A). This preference did not occur after they observed a bumblebee demonstrator foraging on a yellow flower, and instead they showed no preference to inspect either type of flower (Wilcoxon signed-rank: $V = 18.5$, $N = 9$, $P = 0.5$; Fig. 3.4A). Honeybees showed no preference to inspect either type of flower before they detected a conspecific foraging upon either a magenta (Wilcoxon signed-rank: $V = 16.5$, $N = 11$, $P = 0.61$; Fig. 3.4B) or yellow flower (Wilcoxon signed-rank: $V = 23$, $N = 11$, $P = 0.26$; Fig. 3.4B). However, observer honeybees 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 honeybees' inspection of unfamiliar flowers underwent a sequential

adjustment in response to conspecific and heterospecific social information, which ultimately affected their foraging decisions.

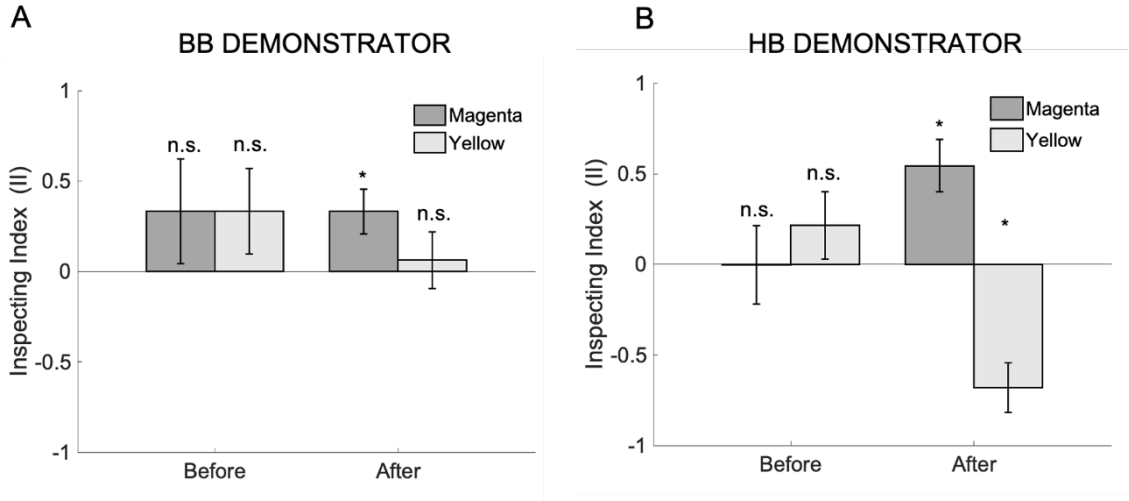

Figure 4. Honeybees adjust their exploration of flowers and foraging preferences in response to concurrent conspecific and heterospecific social information. Inspecting indices (II) compare to chance level (Index = 0) the inspection of magenta (dark grey bars) and yellow (light grey bars) flowers that honeybee observers had before and after they detected either a conspecific or heterospecific demonstrator foraging on either type of flower. **(A)** 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 this type of flowers more frequently. However, when observers detected the bumblebee demonstrator foraging on a yellow flower, this did not affect their inspection of yellow or magenta flowers. **(B)** Before observers detected a conspecific foraging upon either a yellow or magenta flower, they showed no preference to 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 type of flower. 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

463 The results presented here provide evidence that honeybees' colour preferences
464 can be adjusted in response to simultaneous social information from conspecifics and
465 heterospecifics. Thus, specific social information differently influences honeybees'
466 exploration of flowers and consequent foraging decisions. Unexpectedly, honeybees
467 payed little attention to the transparent flowers on which they were trained. Instead,
468 prior to making a foraging decision, they inspected more frequently the magenta flowers
469 (control group) or the type of flower demonstrated by a conspecific.
470 Even though inspecting flowers from a close distance does not provide foragers
471 with information on the reward status of a flower, it is important in the process of
472 choosing a flower (Lunau et al. 1996). In the absence of social information, honeybees'
473 natural preference for magenta flowers influenced inspection and choices of flowers.
474 Magenta is actually a mixture of blue and red, since the red component is not fully
475 perceived by bees (Menzel and Shmida 1993), they perceive magenta flowers as blue
476 (Chittka and Waser, 1997; Waser and Chittka 1998). Honeybees and bumblebees
477 usually have innate biases for colours in the violet to blue range of the spectrum (Giurfa
478 et al. 1995; Chittka et al. 2004), which adaptively correlates with the nectar production
479 of local flowers (Giurfa et al. 1995; Chittka et al. 2004). Although colour biases may be
480 overridden by individual learning (Raine et al., 2006), they potentially govern foraging
481 decisions in bees when selecting among novel flower types (Gumbert 2000). In the
482 absence of social information, flower choices of tested honeybees conceivably resulted
483 from either their innate colour preferences or previous experience in the field with local
484 flower species as both factors can be linked with the likelihood of finding a profitable
485 food reward (Giurfa et al. 1995; Chittka et al. 2004).
486 In the wild, honeybee foragers are likely to encounter members of the same and
487 different species foraging concurrently in a flower patch including distinct flower types

488 (Fægri and van der Pijl 1979; Kevan and Baker 1983). Our results demonstrate that
489 such social information is integrated with honeybees' colour preferences during the
490 process of making a foraging decision. In this realistic scenario, with two simultaneous
491 sources of conspecific and heterospecific social information, when the first foraging
492 demonstrator that honeybees detected was a member of the same species, they promptly
493 responded to social information by joining the demonstrator on the unfamiliar flower
494 type. This evidence is consistent with previous findings in bumblebees (reviewed in
495 Leadbeater and Dawson 2017) and supports the notion that the use of conspecific social
496 information in bees may be mediated by local enhancement, with foragers being
497 attracted to flowers occupied by members of the same species (Leadbeater and Chittka
498 2007a). Such a response potentially optimises the foraging efficiency of bees by
499 facilitating their movements between different flower types (Leadbeater and Chittka
500 2005; Kawaguchi et al. 2007).

501 Honeybees and bumblebees often forage upon similar floral resources; it is then
502 conceivable that they may concur in the same flower patches (Rogers et al. 2013; Xie et
503 al. 2016). In our experiments, we used freely moving bumblebee demonstrators to
504 elucidate how social information might flow between these species. Our results indicate
505 that in the likely scenario of a honeybee exploring a flower patch and encountering both
506 a conspecific and heterospecific (bumblebee) individual foraging from different flower
507 types, its readiness to use social information and make a foraging decision might
508 depend on the first observed species providing social information. That is, observer
509 honeybees that detected a conspecific demonstrator before a heterospecific bumblebee
510 made swifter foraging decisions than those observers that first detected the bumblebee
511 demonstrator, which spent more time exploring the flowers before making a foraging
512 decision. This evidence suggests that in a foraging context, honeybees' discrimination

513 of conspecifics and heterospecifics might determine the selective use of social
514 information. Theory predicts that using social information from heterospecifics should
515 be favourable when there is a large niche overlap (Seppänen et al. 2007) yet, on
516 adaptive grounds, when animals can select between social information from
517 conspecifics and heterospecifics, they should typically favour the former as this
518 naturally reflects its ecological needs (Jaakkonen et al. 2015). In line with this,
519 honeybees consistently selected the type of flowers demonstrated by conspecifics, even
520 though they attended to the presence of both demonstrators whilst exploring the set-up.
521 Prioritising conspecific over heterospecific choices can be explained due to its high
522 fitness value (Seppänen et al. 2007; Jaakkonen et al. 2015) but it can also serve to the
523 transmission of novel behavioural traits or preferences that may be adaptively valuable
524 for a particular species (Laland and Plotkin 1993; Jaakkonen et al. 2015; Alem et al.
525 2016; Danchin et al. 2018).
526 Floral reward levels differ strongly among plant species and constantly change
527 over time in an unpredictable manner (Heinrich 1979). To achieve efficient foraging,
528 bees can rapidly learn to associate floral traits such as colour, shape and scent with
529 reward quality in flowers (Chittka et al. 1999). Bees can be initially attracted to forage
530 from an unfamiliar flower species via either innate and learned colour preferences
531 (Giurfa et al. 1995; Gumbert 2000; Chittka et al. 2004; Raine and Chittka 2007) or
532 using social information (Leadbeater and Chittka 2007b; Grüter and Leadbeater 2014;
533 Leadbeater and Dawson 2017). In the wild, bees seeking floral resources are unlikely to
534 experience asocial and social cues separately, rather they may frequently be exposed to
535 a complex combination of cues potentially affecting their flower choices. Our findings
536 demonstrate that simultaneous conspecific and heterospecific social information

537 influences honeybees' colour preferences, which may in turn shape the process of
538 acquiring new information underlying foraging decisions.
539 Compared to honeybees in the control group (i.e., no social information), the
540 exploration behaviour of honeybees that observed a conspecific or heterospecific
541 demonstrator foraging upon the less preferred yellow flowers, reflected a more evenly
542 distributed inspection of magenta and yellow flowers. That is, the presence of either
543 demonstrator on a yellow flower increased the 'attractiveness' of such flower type for
544 honeybees, possibly via stimulus enhancement, an effect widely described in social
545 learning literature (Heyes 2012). Remarkably, honeybees' inspection of flowers,
546 naturally biased towards magenta flowers, underwent a sequential and flexible
547 adjustment prior to make a foraging decision. Such adjustment was modulated by visual
548 foraging information from members of the same and different species.
549 It has been demonstrated that bees are attracted to the presence of foraging
550 conspecifics when presented with unfamiliar flowers which may lead them to identify
551 new rewarding flower species (Leadbeater and Chittka 2007a; Jones et al. 2015). Our
552 results indicate that the presence of a foraging conspecific not only influenced honeybee
553 observers to select flowers that matched their colour preference (magenta) but such
554 conspecific social information also outweighed observers' colour preference so that
555 they selected the normally non-preferred yellow flowers. Whereas intraspecific social
556 transmission of foraging information may be more stable when it reinforces a prior
557 preference (Laland and Plotkin 1990), such preferences may be adjusted and potentially
558 overridden in response to conspecific social information about a novel foraging resource
559 (Jones et al. 2015). This may enable bees to reasonably adapt to wildly varying floral
560 reward levels. Thus, if the presence of a foraging conspecific can reliably be associated
561 with a rewarding outcome, the use of such social cue should be reinforced to

562 consistently influence bees' flowers choices across foraging contexts (Leadbeater and
563 Chittka 2009). Interestingly, in our experiments the presence of a foraging
564 heterospecific also increased honeybees' attraction to the demonstrated flower types, yet
565 heterospecific social information did not influence honeybees' foraging choices. In fact,
566 honeybee observers never landed on the flowers occupied by the bumblebee
567 demonstrator, in contrast to the flowers occupied by the conspecific demonstrator. Even
568 though, heterospecific social information is predictably valuable when there is a large
569 niche overlap (Seppänen et al. 2007), conspecifics choices might offer a more
570 predictable social cue, decreasing the risk of acquiring maladaptive information
571 (Giraldeau et al. 2002) as conspecifics share the same ecological needs (Seppänen et al.
572 2007; Goodale et al. 2010).

573 Multiple social and asocial cues can potentially affect animals' foraging
574 decisions in different circumstances (Sclafani 1995; Galef and Giraldeau 2001; Grüter
575 and Leadbeater 2014). The effect of social information on previous, innate or learned
576 preferences influences the foraging decision of a particular individual and may also
577 promote the transmission of adaptive information about food sources (Laland and
578 Plotkin 1990; Galef and Giraldeau 2001). Despite the fact that social information offers
579 a clear advantage to individuals exploring novel foraging resources (Galef and
580 Giraldeau 2001), its use should not be indiscriminate but respond to particular
581 circumstances in order to lead to adaptive choices (Laland 2004; Kendal et al. 2018).
582 Our results extend previous evidence showing that conspecific social information is
583 commonly used in situations of uncertainty (Kendal et al. 2004; van Bergen Yfke et al.
584 2004; Galef et al. 2008; Smolla et al. 2016), such that it can outweigh both
585 predetermined individual preferences (Dugatkin 1996; Jones et al. 2015) and

586 heterospecific social information (Jaakkonen et al. 2015) to influence ecologically
587 relevant decisions in animals.
588 It is conceivable that natural selection should favour the salience of social
589 stimuli with high ecological relevance (Seppänen et al. 2007; Leadbeater and Dawson
590 2017), conspecifics in our experiments. Whether such salience can similarly operate to
591 select information from heterospecific sources, based on their relative informative
592 value, deserves further consideration. We provide an ecologically relevant picture of the
593 process thereby multiple non-social and social cues may shape foraging decisions of
594 bees. Thus, findings presented here contribute to our understanding of the flexibility of
595 individual preferences and their adjustment in response to different sources of social
596 information. Our results in turn shed light on the selectivity of animals for conspecific
597 over heterospecific information as a possible mechanism to facilitate the social
598 transmission of foraging information within species.
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