

# Information synergy: adding unambiguous quality information rescues social information use in ants

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## Abstract

Animals have access to many alternative information sources when making decisions, such as private information (e.g. memory) and social information. Social insects make extensive use of social information. However, when intentional social information (e.g. pheromone trails in ants) conflicts with private information (e.g. route memories), insects often follow their private information. Why is this? We propose that it is an asymmetry in information content between these two information sources that drives the neglect of social information. In ants, workers with certain information about the quality of a food source (memory) ignore valuable social information (pheromone trails) because the pheromone trails encode only a very ambiguous measure of food quality. This leads to a testable hypothesis; the addition of unambiguous quality information should rescue social information following. To test this, we trained ants to a poor quality (0.25M) food source, and then provided an alternative path along with either 1) no information, 2) a pheromone trail, 3) a 0.2µl droplet of 1.5M sugar solution, providing unambiguous quality information, or 4) both a trail and a droplet. When either no or only one information source was provided (1-3), most ants (60-75%) continued following their own memory. However, the addition of unambiguous quality information to a trail (4) rescued trail following: when both a pheromone trail and a sugar droplet were provided, 75% of ants followed the trail. We propose that information content – what type of information a source can convey, and what is its ambiguity, is a strong driver of which type of information is attended to.

## Key words:

Information conflict; information use strategies; recruitment; social information; information asymmetry; Certainty Effect; ambiguity avoidance

## 32 Introduction

33 Animals have access to many types of information. These can be broadly separated into private  
34 information, which is available only to the individual animal, and public information, which is  
35 available to other animals as well <sup>1</sup>. Private information includes genetic information and non-genetic  
36 information such as internal states and, importantly, memories. Public information includes all  
37 observable cues, such as the colour of a flower. An important subset of public information is social  
38 information, which is information related in some way to other animals. These may be incidental  
39 cues, such as the presence of conspecifics at a resource, or intentionally produced signals, such as  
40 the waggle-dance of a honey bee.

41 Multiple information sources may provide information about the same thing. For example, both  
42 the colour and the odour of a flower patch, and whether other bees are dancing for that patch, might  
43 inform a bee about whether and where food is available in the environment [2,3]. These multiple  
44 information sources may interact in a variety of ways. Information may be used hierarchically, with  
45 one being used whenever it is available, and if it is not the next on the list is used [4]. When  
46 information sources agree, they may act additively or synergistically to improve behaviour. For  
47 example, ants which have private information about a food source (memory) which agrees with  
48 social information (a pheromone trail leading in the same direction) walk 25% faster than ants with  
49 either only one or none of these information sources [5]. These information sources also act  
50 additively by causing more ants to follow a pheromone trail [6]. Bumblebees which have experienced  
51 a novel flower odour in the nest (public information) are more likely to exploit the novel flowers, but  
52 only once they have tasted a flower scented with this novel odour (private information) [7].

53 A particularly interesting situation is when information sources conflict. One option in such  
54 situations is to weight information from different sources and produce an intermediate value  
55 [6,8,9]. An alternative is to rely on one type of information and ignore the others. In some situations,  
56 such as choosing a path at a trail bifurcation, an intermediate option is not available. Different  
57 strategies might be undertaken due to different ecological conditions or the state of individual  
58 animals, and understanding what strategies animals use to decide which information to follow is a  
59 very active field of research [10–14]. Information use strategies can be broadly divided into *when*  
60 strategies (when to use which information type) and *who* strategies (whose information to use) [15].

61 Evidence supporting various information use strategies has been described in wide array of taxa,  
62 including insects, fish, lizards, rats, and humans [16–19]. Information use strategies have been  
63 especially well researched in social insects such as ants and bees, as in these groups social

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<sup>1</sup> Our definition of private information deviates somewhat from that of Danchin et al. [1], who consider public information more-or-less synonymous with social information. We consider social information a subset of public information.

64 information has the potential to play a very large role [see 11,20 and references therein]. Social  
65 insects also represent a special case, since there are not usually expected to be any conflicts of  
66 interest in many situations requiring communication, such as foraging and nest-site selection. This  
67 should, at face value, strengthen the role of explicit social signals such as pheromone trails or  
68 waggle-dances. However, somewhat surprisingly, in most cases in which such intentionally produced  
69 social information is conflicted with private information, the ants and bees predominantly follow  
70 their own memories [21–29]. This was found not to be the case in only a few instances [23,30]. This  
71 preference could have strong implications for colony level behaviour, preventing colonies from  
72 optimally exploiting their environment.

73 Why do ants and bees so often underweight or ignore the directional information provided by  
74 their sisters? Explanations of information use strategies have been made in terms of the reliability of  
75 an information source – how often using one type of information is associated with a positive  
76 outcome, or how outdated the information is (e.g. [14,31]), or the cost of acquiring new information  
77 [32–34]. However, what has not been considered is the *information content* of different types of  
78 information.

79 Economists, and later behavioural ecologists, distinguish between two types of situations with an  
80 unknown outcome: risk and ambiguity (or uncertainty) [35–37]. The term ‘risk’ refers to a situation  
81 where the mean result or probabilities of a situation are known, but the precise value at any one  
82 time is not. A gamble on a six-sided die is thus a risky proposition: the average score is 3, the  
83 probability of any one side is 1/6, but the precise value on each roll is unknown. By contrast,  
84 ‘ambiguity’ or ‘uncertainty’ refers to a situation where neither the mean nor the variation is known; a  
85 gamble on a die with an unknown number of sides is thus gambling under ambiguity.

86 When faced with ambiguity, humans have been found to behave in a manner inconsistent with  
87 the predictions of expected utility theory, the standard economic theory of human behaviour.  
88 Specifically, humans are found to display *ambiguity aversion*. Given a choice between a risky and an  
89 ambiguous proposition, humans overwhelmingly prefer the risky proposition, although there is no *a*  
90 *priori* rational reason for them to do so [38,39], (but see [37] for a Bayesian perspective). This was  
91 famously described by the Ellsberg paradox [38]. He gives the example of a single choice, in which  
92 you are offered to pull one ball out of one of two urns. One urn contains an equal mix of red and  
93 black balls, the other contains an unknown ratio of red to black balls. Pulling out a red ball is  
94 rewarded with \$100, but the black ball is unrewarded. The urns are thus a risky and an ambiguous  
95 proposition, respectively. Most people choose the urn with the known distribution. Related to this,  
96 Kahneman and Tversky, in their famous Prospect Theory paper [40], describe *the Certainty Effect*.  
97 Here, subjects overweight certainty, and are willing to pay a premium to move from a risky to a

98 certain situation. For example, people usually prefer \$3000 with certainty to an 80% chance of  
99 \$4000, although the expected payoff of the gamble is \$3200. Effectively, subjects are willing to pay  
100 \$200 for certainty. Ambiguity aversion has also been documented in non-human primates [41,42].

101 A similar situation may be happening in social insects experiencing an information conflict.  
102 Imagine an ant which has found a poor quality food source. It is shuttling back and forth to this food  
103 source, and knows the quality of this resource with certainty. It then encounters a pheromone trail  
104 leading in a different direction. This pheromone trail was deposited by another ant, which had  
105 discovered a good food source. It would be in both of the ants' interests for the ant exploiting the  
106 poor food to follow the pheromone trail. However, this often does not happen, even if the  
107 recruitment to the alternative direction is very strong [21–29]. Why is this? We propose this is due  
108 the (lack of) information content of the social communication signal. The pheromone trail provides  
109 only very noisy, imprecise, and ambiguous information about the quality of a food source.  
110 Pheromone trail strength varies with resource quality, time since discovery, recruitment rates, and  
111 the individual pheromone depositions behaviour of ants: A strong trail may lead to a good food  
112 source exploited by a few ants, or to a poor one exploited by many ants; a weak trail may lead to a  
113 poor food source, or to a good one which has been unproductive for a while, or to a newly  
114 discovered food source. Importantly, there is a very large variation in the amount of pheromone  
115 deposited by individual ants to food sources of the same quality [43]. With no strong evidence that  
116 the new food source is better, the forager avoids paying the costs of attempting to find an advertised  
117 food source [32,44,45], and falls back on exploiting the food source she knows about.

118 This hypothesis leads to a testable prediction: If a worker foraging on a poor food source can be  
119 given unambiguous information about the quality of a better food source a pheromone trail  
120 advertises, she should follow the trail pheromone. Here, we set out to test this prediction.

121

## 122 **Materials and methods**

123

### 124 *Study species and maintenance*

125 We used 8 queenless colony fragments of the black garden ant, *Lasius niger* (Linnaeus),  
126 collected from eight different colonies on the University of Regensburg campus. Colonies were  
127 housed in a plastic box (40×30×20cm) with a layer of plaster on the bottom. Each box contained a  
128 circular plaster nest (14cm diameter, 2cm high). Colonies contained c. 1000 workers and small  
129 amounts of brood. The ants were fed *ad libitum* on 1M sucrose solution supplemented with  
130 *Drosophila melanogaster* fruit flies. Colonies were deprived of food for four days prior to each trial to

131 give high and consistent motivation for foraging and pheromone deposition. Water was provided *ad*  
132 *libitum*.

133

### 134 *Experimental procedure*

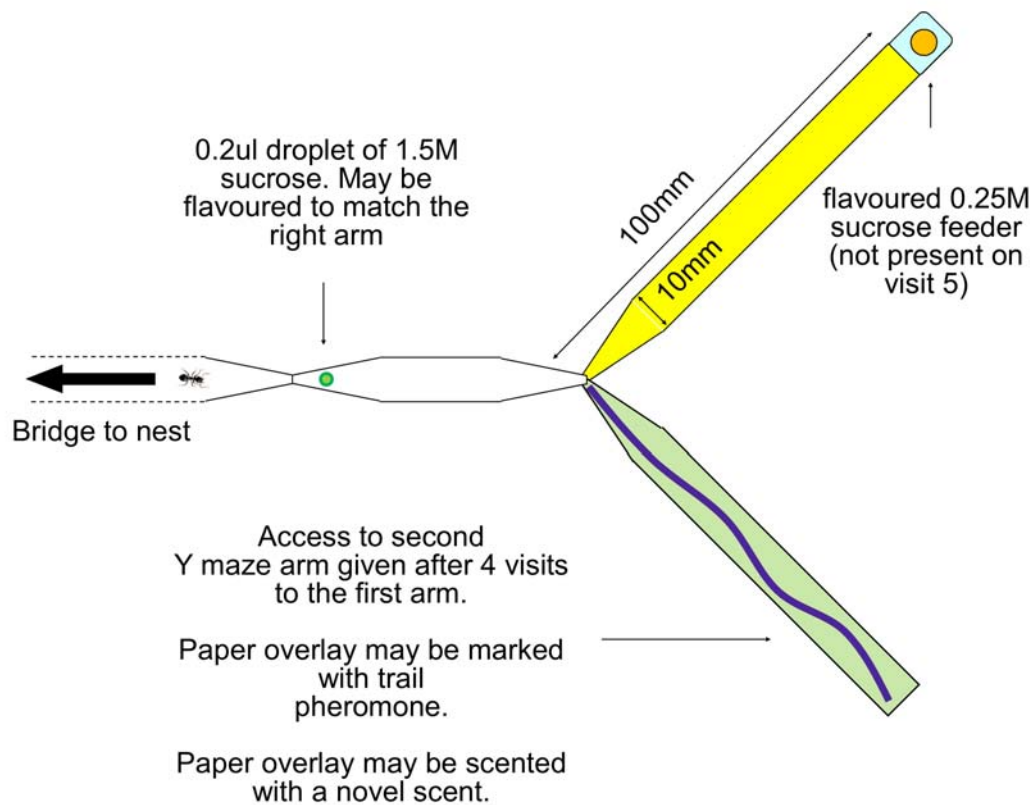
135 10 different experimental treatments were carried out in total, coded A-J. An overview of the  
136 different treatments is provided in table S4 in the supplement. All treatments were variations on a  
137 central design. The aim of the experiments was to test whether ants with a well-established memory  
138 of finding food on one arm of a Y maze can be induced to search a newly-presented alternate arm by  
139 the provision of various information sources. The information sources provided could be a  
140 pheromone trail, a small droplet of sucrose (simulating trophallaxis), a novel scent in either the  
141 droplet or on the newly presented path or both, or a combination of these. The scent treatments  
142 were added to test whether similar droplet and pathway odours cause a further increase in trail  
143 follow, as there could thus be an associative link between the quality of the droplet and the odour of  
144 the new runway. However, as there was no effect of the various odour treatments (see supplement  
145 S1 for details) we pooled our data into treatments groups for the final analysis, depending on the  
146 types of information presented to the ants, and the quality of the original feeder to which it was  
147 trained. This resulted in 5 treatment groups: i) no information (treatments A and B), ii) only a droplet  
148 of 1.5M sucrose just before the bifurcation (treatments C-E), iii) only a pheromone trail on the new  
149 path (treatment F), vi) both a pheromone trail and a droplet (treatments G-I), and finally v) a  
150 pheromone and a droplet for ants trained to 1.5M sucrose (treatment J).

151

152 A trial began by allowing an ant onto the apparatus via a drawbridge. The drawbridge led to a  
153 Y maze with one arm drawn out just out of reach of the ants, to form an L maze (Figure 1). The arm  
154 that was out of reach (left or right) was systematically varied. The arms of the maze were 10cm long  
155 and 1cm wide, narrowing to 2mm wide at the junction. The arms of the maze were covered with  
156 paper overlays. The overlay on the stem of the maze was unscented, while the overlay on the arm of  
157 the maze was scented with either rosemary or lemon essential oil – the odour used was  
158 systematically varied between trials. Odour impregnation was achieved by storing the paper overlays  
159 in a sealed plastic container containing one 0.1ml drop of essential oil on a glass petri dish for at least  
160 24 hours. An acetate sheet affixed to the end of the L maze arm acted as a feeder. A large drop of  
161 0.25M sucrose solution (1.5M in treatment J), flavoured similarly to the L maze arm leading to it, was  
162 placed onto the feeder. Sucrose solutions were flavoured by adding 10 $\mu$ l essential oil per 100ml  
163 sucrose solution, following Czaczkes *et al.* [46]. Once the ant found the feeder it was marked with a  
164 dot of acrylic paint on the abdomen, and allowed to return to the nest. While the ant was in the nest,

165 unloading her sucrose load, the paper overlays on the stem and arm were replaced by fresh overlays,  
166 to remove any trail pheromone the ant might have laid. The ant was then allowed to make 3 further  
167 return visits to the same feeder, resulting in 4 visits to the original feeder in total. This is sufficient to  
168 ensure that, even given the relatively low quality of food, most ants will return to this arm of the  
169 maze given a choice (Oberhauser, Koch and Czaczkes, **submitted**, see also data below).

170           While the ant was in the nest prior to its fifth return to the feeder, the feeder from the  
171 original arm of the Y maze was removed, and access to the second arm was given. The new arm was  
172 either marked with a pheromone trail (treatments F - J) or not (treatments A-E). This pheromone trail  
173 was produced by immersing 8 worker hindgut glands in 2ml of dichloromethane (DCM), following  
174 von Thienen *et al.* [47]. 5.6µl of this mixture was applied in an even line along the paper overlay  
175 covering the arm, using a capillary tube (Servoprax GmbH, Germany). This amount was calculated to  
176 produce a pheromone trail of a realistic strength [47], and in control trials elicited a trail following  
177 accuracy of 82% (594 / 715), which is indistinguishable from those recorded from naïve ants  
178 following a reasonably strong naturally-deposited trails as reported by Czaczkes *et al.* [48] (82-83%  
179 accuracy). See supplement S1 for detailed methods and results regarding the artificial pheromone  
180 trail.



181

182 **Figure 1** – experimental setup. Ants are first trained for 4 visits on a Y maze with access to only one  
183 arm (here the top arm, in yellow in the figure but not coloured in the experiment), leading to a 0.25M  
184 sucrose feeder flavoured with lemon or rosemary (1.5M in treatment J). On the 5<sup>th</sup> outward journey the  
185 second arm of the Y maze (here bottom, green) is added, and the feeder removed. The new arm may  
186 be marked with a pheromone trail and/or scented with a novel scent (lemon or rosemary).  
187 Additionally, a small (0.2µl) droplet of 1.5M sucrose may be placed after a narrowing of the stem  
188 before the bifurcation, which the ant can drink but will not become satiated from. The droplet may be  
189 flavoured to match the new Y maze arm scent or may be unflavoured.

190

191 The new arm was also either scented (treatments B, D, E, H, I, J) with a different scent to that  
192 of the original arm, or was not (treatments A, C, F, G). Lastly, a small (c. 0.2µl) droplet of sucrose  
193 either was (treatments C, D, E, G, H, I, J) or was not (treatments A, B, F) placed on the stem of the Y  
194 maze, before the bifurcation but just after a narrowing of the stem. This ensured that the ant  
195 contacted the droplet as it walked towards the bifurcation. This droplet was either flavoured similarly  
196 to the scent on the newly presented runway (treatments E, I, J) or was unscented (treatments C, D,

197 G, H). The droplet was large enough for the ant to detect and drink, but not enough to satiate the ant  
198 [49], which proceeded onwards after drinking the droplet. This droplet was designed to simulate  
199 trophallaxis. Trophallaxis is used in the nest to unload food, and also provides ants with information  
200 about the food available in the environment [50–53]. This information is attended to very strongly  
201 [51,54]. *L. niger* ants can often be observed performing trophallaxis away from the nest, and  
202 recipients of these trophalactic interactions usually continue on their outwards journey afterwards  
203 (TJC, personal observation). Unfortunately, we could not reliably achieve such on-trail trophallaxis  
204 with the trained ant under controlled experimental conditions.

205 We then noted which arm of the Y maze the ant chose. We took two choice measurements:  
206 the initial decision, as defined by the ant crossing a line 2cm from the bifurcation, and the final  
207 decision, as defined by the antennae of the ant reaching the end of the Y maze arm. As the ant  
208 reached the end of the Y maze, it was allowed to walk onto a piece of paper and replaced on the  
209 path leading to the Y maze, before the location of the sugar droplet. This allowed us to make 10  
210 repeated measures of each ant. After 10 such measurements the ant was permanently removed  
211 from the colony. The number of ants tested in each treatment is given in table S7 in the supplement.

212

### 213 *Statistical analysis*

214 Since the initial decision (crossing a line 2cm from the bifurcation) and the final decision (reaching  
215 the end of the arm) rarely differed (<5% of cases), we analysed only the final decision. While we  
216 collected 10 data points per ant to increase the potential power of our experiments, we finally  
217 decided to perform a conservative analysis by only considering the first decision made by the ants.  
218 This avoids the possibility of ants becoming frustrated in later trials. Initial data exploration revealed  
219 a leftward side bias, which is not uncommon in the behaviour of ants or other animals [55], and so  
220 training side was also added to the model. Finally, colony identity was added as a random effect. This  
221 resulted in the following model:

222 
$$\text{Decision} \sim \text{treatment.group} + \text{training.side}$$
  
223 
$$+ (\text{colony as a random effect})$$

224 As the data is binomial we used a binomial error structure. Data were analysed in R v.3.4.1 [56] using  
225 generalised linear mixed models from the LME4 package [57]. Model fit was checked using the  
226 DHARMA package [58].

227 We also tested whether the decisions of each group differed significantly from random using two  
228 tailed exact binomial tests.



229 Following Benjamin et al. [59] we set significance level for hypothesis testing at  $p = 0.005$ , terming  $p$ -  
230 values greater than that but smaller than 0.05 'suggestive'. However, due to the limitations of using  
231  $p$ -values alone, we provide estimates and confidence intervals for all effects.

232

## 233 **Results**

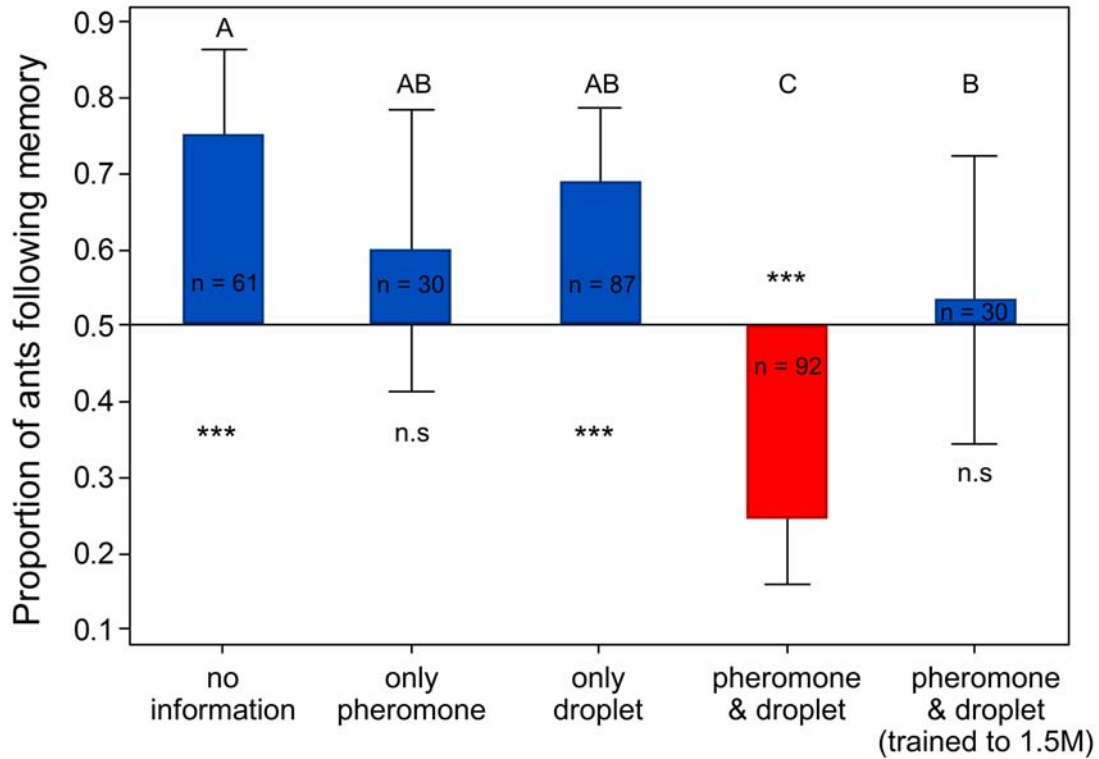
234 The type of information available to a forager strongly influenced her decision of whether or  
235 not to follow her memory. For ants trained to 0.25M sucrose, given just an unmarked novel path on  
236 the Y maze, most ants (75%) choose to follow their own memory (figure 2), significantly more than  
237 chance (two tailed binomial exact test, 46/61 followed their memory, mean = 0.75, 95% C.I. range =  
238 0.63 – 0.86,  $p < 0.0001$ ). The addition of a small 1.5M sucrose droplet does not significantly change  
239 the choices made by the ants, who still preferentially follow their memory (binomial test, 60/87,  
240 mean = 0.69, 95% C.I. = 0.58 – 0.78,  $P = 0.0005$ ). The addition of a pheromone trail on the novel arm  
241 still resulted in most ants (60%) following their memory, but this result was not different from  
242 random choice (binomial test, 18/30, mean = 0.6, 95% C.I. = 0.41 – 0.77,  $p = 0.36$ ). These three  
243 groups do not differ significantly from each other (GLMM,  $z \leq 1.90$ ,  $p \geq 0.057$ , for details of all  
244 pairwise comparisons, including estimates for each comparison, see table S1 in supplement S1).

245 However, a striking synergistic effect of presenting a pheromone trail and a sucrose droplet  
246 was found. If both were presented, only 25% of ants chose to follow their memory, with 75%  
247 choosing to follow the novel path. This is significantly fewer than chance (binomial test, 23/92, mean  
248 = 0.25, 95% C.I. = 0.17 – 0.35,  $p < 0.0001$ ) and differs significantly from all other groups provided with  
249 less information (GLMM,  $Z \geq 2.97$ ,  $P \leq 0.0029$ ).

250 The effect of presenting both information sources depends on the relative quality of the  
251 droplet presented and the food quality the ant was trained on. If ants were trained on 1.5M sucrose,  
252 53% of ants chose to follow their memory, which does not differ from random choice (binomial test,  
253 16/30, mean = 0.53, 95% C.I. = 0.34-0.72,  $p = 0.86$ ). This is a non-significantly, but suggestively,  
254 greater than for the ants receiving the same information, but trained on poorer food (GLMM,  $z =$   
255 0.23,  $p = 0.020$ ), and also suggestively less than the ants receiving no information (GLMM,  $z = -2.56$ ,  $p$   
256 = 0.011). It is not significantly different from the ants receiving either one information source (GLMM  
257 vs only droplet,  $z = 1.95$ ,  $p = 0.051$ , vs only pheromone  $z = 0.60$ ,  $p = 0.55$ ).

258 The entire dataset on which these results are based in provided in online supplement S2.

259



260

261 **Figure 2** – proportion of ants following their memory down the original Y-maze arm as a  
262 function of what other information was available to them. Ants may have had either no  
263 information about the new Y-maze arm, a pheromone trail on the new arm, a small 1.5M  
264 sucrose droplet before the bifurcation, or a pheromone trail and a droplet. In most groups ants  
265 were trained to 0.25M sucrose, but in one group they were trained to 1.5M sucrose. Whiskers  
266 are 95% C.I. for the mean. Letters indicate groups that are significantly ( $P < 0.005$ ) different  
267 from each other. “\*\*\*” and “n.s.” signify groups that are either significantly different from  
268 0.5 (exact binomial test,  $P < 0.0001$ ), or not different from 0.5 ( $P > 0.05$ ), respectively.  
269 Sample sizes per group are show in the bars. Detailed statistical analysis results are presented  
270 in tables S1 and S2 in online supplement S1.

271

272

## 273 **Discussion**

274 By providing unambiguous information about the quality of other resources in the environment  
275 the information asymmetry in a communication system was rebalanced. This rescued pheromone  
276 following behaviour in our experiment. When ants had no information about alternative food  
277 sources in the environment, they predominantly (75%) chose to continue exploiting their private  
278 information, returning to the sure but poor quality (0.25M) feeder. When ants were provided with  
279 the information that better food exists in the environment (a small 1.5M sucrose droplet), they  
280 nonetheless predominantly (69%) returned to the poor quality feeder they knew about. Even when a  
281 strong pheromone trail led in the opposite direction, 60% of the ants continued to exploit the known,  
282 poor quality feeder. However, when social information (a pheromone trail) and unambiguous quality  
283 information (the sugar droplet) was provided, the behaviour of the ants completely reversed, with  
284 75% of choices made for the unknown, but advertised, route.

285 Information use strategies have been divided into ‘*when*’ and ‘*who*’ strategies – when should  
286 information be used, and who should one listen to [15]. Here, we propose considering information  
287 use in terms of a ‘*what*’ strategy – what is the information content of an information type, and what  
288 is its’ level of ambiguity? Social information sources such as pheromone trails and honey bee waggle-  
289 dances do not provide unambiguous quality information, while private sensory information does.  
290 While pheromone trails and waggle-dances do encode some information about food quality, this  
291 information is extremely imprecise and noisy, both due to individual variation in responses to fixed  
292 food quality [43,60] and due to the effect of time and foraging patterns on these information sources  
293 (see introduction for details). We propose that is it this ambiguity in social information, or the  
294 certainty of the private information, which causes otherwise valuable social information to be  
295 neglected. Our data supports this claim.

296 Understanding information use strategies in terms of information asymmetry can explain  
297 previously puzzling findings. Leadbeater and Florent [7] unexpectedly found that bumblebees do not  
298 rate social information above personal experience, even when their personal experience becomes  
299 outdated. Bumblebees which had experienced a novel odour in the nest (social information) were  
300 just as unlikely to sample novel flowers scented with this odour as bees which did not experience the  
301 novel odour in the nest. Both groups continued choosing known-odour flowers, even when those  
302 flowers became unproductive. However, once the bees with the social information did, eventually,  
303 sample the novel flowers, they were much more likely to switch to the novel flowers than the group  
304 without social information. This is directly analogous to the situation we report: neither private  
305 sensory information providing reliable quality information (sampling the novel flowers), nor social  
306 information (smelling the novel odour in the nest) is sufficient to make bees change their choices.

307 However, when both are provided together (here, after the first sampling of the novel flower), bees  
308 are willing to switch.

309 Similarly, understanding information use in terms of information quality can explain situations in  
310 which social information does override personal information. This is because in such cases, the social  
311 information is actually based on personal, sensory information, which provides unambiguous quality  
312 information. For example, Dunlap et al. [14] and Smolla et al. [61] find that social information alone  
313 can drive decision making during flower choice in bumblebees, and that social information even  
314 outweighs private information when the two compete [14]. This result could be understood through  
315 the psychological concept of blocking [20]. However, differences in information content between the  
316 two information sources can also explain these results: in these studies the social information is  
317 actually private information, based on making associations between a social cue (the presence of a  
318 conspecific) and the direct personal experience of the forager with the flower [20]. There is thus no  
319 quality ambiguity. Indeed, if ambiguity exists, it is lower in the social information: the forager not  
320 only has her own experience of finding the flower acceptable, but also the presence of a conspecific  
321 suggests that the conspecific also finds the flower acceptable, resulting in more weight of  
322 information about quality for the socially advertised flower. Likewise, Josens et al. [54] describe how  
323 trophallactic interactions with a forager providing scented, untainted food can cause foragers to  
324 accept similarly scented food tainted with poison, which they would otherwise avoid. Here again, the  
325 social information component is based in direct sensory experience of the food (trophallaxis), and  
326 the reason the ants overweigh this information over their own later sensory information are similar  
327 to those described for the bumblebee examples above.

328 Also supportive of the information content hypothesis is the response of ants whose receive  
329 unambiguous information that alternative food qualities are *not* better – the ants trained to a high  
330 quality 1.5M feeder in our experiment. Both paths (apparently) led to equally good food sources, so  
331 there was no particular reason to prefer either, and indeed ants chose both feeders equally often.

332 Finding drops of liquid honeydew lying around on a trail is not a common situation in nature.  
333 However, we argue that our results are analogous to an ant receiving a trophallactic interaction,  
334 either on the trail or in the nest. Returning ants often perform trophallaxis with multiple partners on  
335 returning to the nest, and these partners are then themselves likely to go out to forage. Similarly,  
336 dancing honeybees often engage in trophallaxis with followers. Ants receiving trophallaxis may even  
337 respond as if they have themselves successfully foraged, depositing trail pheromone when otherwise  
338 only successful ants do so [62]. Ants can also occasionally be seen to perform trophallactic  
339 interactions on the trail, with receivers continuing on their outwards journey afterwards (TC, pers.  
340 obs.). Information gained during trophallactic interactions seems to be particularly well attended to –

341 even more so than information gained while foraging [51,54]. This information, gained in the nest or  
342 on the trail, can then drive information use. Indeed, provision of unambiguous quality information,  
343 may well be a major role of most trophallactic interactions, especially those occurring on a trail.  
344 Provision of information about food associated cues such, as the odour of the shared food [50,54], is  
345 also no doubt important, although we could not find any role for food odour in the current  
346 experiment (see supplement S1).

347 Trophallactic networks within a nest are complex [63]. Social insect colonies contain a high  
348 proportion of apparently taskless individuals ([64] and references therein), which can be divided into  
349 inactives and interactives [65]. Interactives have a more central place in interaction networks within  
350 the colony [64,65]. If they also receive trophallactic interactions from many foragers and food  
351 receivers, they may act to homogenise the various food qualities being returned to the nest,  
352 providing a reading of the average food being brought into the colony. Foragers interacting with  
353 these ants may then compare this reading to their current exploited food source. If they find their  
354 own food source to be worse, they may begin to follow social information. It has already been shown  
355 that ants which receive high quality food via trophallaxis are less willing to accept medium quality  
356 food, and vice versa for ants receiving poor quality food [Wendt & Czaczkes, in prep]. It is also known  
357 that ants which have experienced higher quality food source avoid exploiting poorer but otherwise  
358 acceptable food source discovered en-route [66]. Using newly developed imaging technologies  
359 allows the flow of food via trophallaxis in a colony to be tracked and quantified [67], opening the  
360 possibility to empirically test these suggestions. Such an information use pattern would correspond  
361 to the strategy “copy if better”, a strategy normally ignored, as direct quality comparison is not  
362 usually considered possible.

363 Finally, we note that while our results are consistent with ambiguity aversion or the Certainty  
364 Effect playing a role in insect behaviour, they do not constitute a direct test of either of these related,  
365 but distinct, effects. The memory of the ants can be considered certain, while the pheromone trails  
366 ambiguous. Thus, the ants may be following their memory due to its certainty, or avoiding the  
367 pheromone trail due to its ambiguity. Moreover, our different treatments likely affected the  
368 subjective probabilities of receiving a particular reward each ant assigned to each path. Only by  
369 repeatedly testing the same ant in both a risky and an ambiguous situation could one demonstrate  
370 that the behaviour of the ants truly deviates from standard economic behaviour, as described by  
371 expected utility theory. It is intriguing that the results of this study are in line with the ‘Certainty  
372 Effect’ from Prospect theory, while ants also perceive value relative to a reference point – another  
373 key aspect of Prospect theory [Wendt & Czaczkes, in prep].

374 Here, we explored how three different information sources, one private and two public,  
375 interacted. In doing so, we found evidence that the information content of an information source is a  
376 key driver in whether it will be heeded or not. Uncertainty avoidance or the Certainty Effect [38,40]  
377 could be the driver behind the repeated findings that social insects often preferentially follow their  
378 own memory over the communications of their nestmates. We propose that as well as considering  
379 ‘when’ and ‘who’ strategies for information use, ‘what’ is an important question to ask: what type of  
380 information can be provided. Social insects, and animals in general, demonstrably use complex  
381 mechanisms to decide which information to attend to, and integrate information from a wide variety  
382 of sources in order to do so.

383

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389

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