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1 Bumblebees develop more efficient traplines than honey bees

2

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4

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9

10

11 **Abstract**

12 Central place foraging pollinators, such as bees, tend to learn multi-destination routes (traplines)
13 to efficiently visit known feeding locations and return to their nest. To what extent these routing
14 behaviours are shared across species is unknown. Here we ran laboratory experiments to compare
15 trapline formation and efficiency by foragers of two social bee species that differ in their collective
16 foraging strategies: the solo foraging bumblebee *Bombus terrestris* and the mass foraging honey
17 bee *Apis mellifera*. In a simple routing task with four artificial flowers, both bumblebees and honey
18 bees developed a stable route, although honey bees were slower and less efficient to do so. In a
19 more complex routing task with six flowers, only bumblebees developed a stable route. Honey bees
20 took a longer time to discover all flowers and never integrated them in a single route. Simulations
21 of a model of trapline formation show that these inter-specific differences can be replicated by
22 adjusting the strength of a single learning parameter. Comparing bumblebees and honey bees in
23 the same experimental conditions thus revealed key differences in their spatial foraging strategies,
24 potentially driven by social constraints.

25

26 **Keywords**

27 Honeybees; bumble bees; trapline foraging; navigation; comparative cognition.

28

29 **Introduction**

30 Central place foraging pollinators often develop multi-destination routes (or traplines) to efficiently
31 exploit patchily distributed feeding sites (Thomson et al. 1996). Trapline foraging is widespread in
32 nectar feeding insects (orchid bees: Janzen 1971; bumblebees: Thomson et al. 1997; honey bees:
33 Buatois and Lihoreau 2016; butterflies: Gilbert and Singer 1975) but also in birds (hummingbirds:
34 Tello-Ramos et al. 2015) and mammals (bats: Lemke 1984; opossums: Wooller et al 1999). This
35 routing behaviour is thought to optimize the exploitation of plants resources, by adjusting the
36 timing of nectar collection and deterring competitors (Possingham 1989; Ohashi and Thomson
37 2005).

38 Trapline formation has been best studied in bumblebees using arrays of artificial flowers
39 (i.e. feeders) in the lab and in the field (Ohashi and Thomson 2009; Lihoreau et al. 2013). Individual
40 bumblebees given an access to a small number of flowers for several hours often find and use the
41 shortest sequence to visit all flowers once and return to the nest (Ohashi et al. 2007; Lihoreau et al.
42 2010, 2012a). Analyses of the flight paths of bumblebees between visiting flowers, show that
43 insects also tend to optimize travel distances (Lihoreau et al. 2012b; Woodgate et al. 2017).
44 Trapline formation can be modelled using an iterative improvement heuristic of vector navigation
45 replicating trial-and-error learning by bees (Lihoreau et al. 2012b; Reynolds et al. 2013). In this
46 approach, the bumblebee compares the net length of all the route segments (i.e. straight movements
47 between two flowers or between a flower and the colony nest) composing the route it has just
48 experienced, and increases its probability to reuse these segments in future if the new route is
49 shorter (or of the same length) than the shortest route experienced before.

50 Recently, honey bees were also reported to be capable of developing traplines between four
51 artificial flowers (Buatois and Lihoreau 2016). The indirect comparison of the foraging patterns of
52 bumblebees and honey bees, using network statistics on data obtained in different studies, suggests
53 that honey bees develop less efficient routes and are less faithful to these routes than bumblebees
54 (Pasquaretta et al. 2017). This may be explained by major differences in the social ecology of these
55 bees. Bumblebees, as solo foragers, primarily rely on the acquisition of individual information to
56 locate and exploit plant resources (Dornhaus and Chittka 1999). By contrast, honey bee are mass
57 foragers and use social information to collectively exploit profitable food resources (e.g. they use
58 the waggle dance for recruiting nestmates to resources 100 m away from the nest, von Frisch 1967).
59 Honey bees may therefore invest less in individual sampling and spatial learning than bumblebees

60 (Buatois and Lihoreau 2016). Further understanding these behavioural differences could have
61 considerable implications for assessing the impact of foraging strategies and social structure on the
62 evolution of cognition in two major pollinators and model species in for insect behaviour (Farris
63 2016; Traniello et al. 2019). Such approach requires to study the animals in strictly identical setups
64 and make quantitative comparisons of their performances (Chittka et al. 2012).

65 Here, we tested the hypothesis that honey bees have poorer abilities to develop foraging
66 routes than bumblebees, by comparing the spatial patterns of individuals of both species in the
67 same arrays of artificial flowers in an indoor flight room. Since the number of possible routes to
68 visit each flower once and return to the nest increases factorially with the numbers of flowers to
69 visit (Lihoreau et al. 2013), we tested the influence of task complexity by observing bumblebees
70 and honey bees foraging in arrays of four flowers (24 possible routes) and six flowers (720 possible
71 routes). We then compared the performances of foragers of both species with numerical simulations
72 of a model of trapline formation.

73

74 **Materials and methods**

75 ***Bees***

76 We used a small colony (a queen and ca. 2000 workers) of honey bees (*Apis mellifera*, Buckfast)
77 originating from the experimental apiary of the University Paul Sabatier – Toulouse III (France).
78 We used a normal size colony (a queen and ca. 200 workers) of bumblebees (*Bombus terrestris*)
79 from Biobest (Belgium). Both honey bee and bumblebee hives were equipped with a transparent
80 entrance tube fitted with gates to precisely control the traffic of foragers. Colonies were provided
81 *ad libitum* defrosted pollen directly into the hives. Workers collected sucrose solution (40% w/w
82 in water) from artificial flowers in the flight room.

83

84 ***Flight room***

85 We conducted the experiments in an indoor flight room (length: 7 m, width: 5 m, height: 3 m;
86 **Fig.S1A**) equipped with 12 wide spectrum LED lights (6500K, Phillips, The Netherlands)
87 replicating natural sunlight and daily photocycle (15h Light/ 9h Dark). Four posters uniquely
88 characterized by a bicolored pattern were placed on the room walls to provide 2D visual landmarks
89 to the bees (**Fig.S2**).

90

91 ***Artificial flowers***

92 Each flower consisted of a 6 cm diameter blue landing platform sitting on a 10 cm high transparent
93 plastic cylinder. The cylinder was attached to a clamp stand 50 cm above ground (**Fig.S1B**, Buatois
94 and Lihoreau 2016). A yellow mark in the middle of the landing platform indicated the location of
95 a controlled volume of sucrose solution (40% w/w, range: min 20 μ l – max 140 μ l) dispensed using
96 an electronic micropipette (Brand Handystep 705000, Germany).

97

98 ***Flower arrays***

99 Bees were tested either in a four-flowers array or in a six-flowers array (see flower coordinates in
100 **Fig.S1A**). We used these two arrays to provide bees with spatial tasks of increasing complexity. In
101 the four-flowers arrays there was 24 possible sequences to visit all flowers once starting and ending
102 at the colony nest entrance (including the two optimal sequences F1-F2-F3-F4 or F4-F3-F2-F1;
103 Figs 1 and S1A). In the six-flowers array, there were 720 possible sequences (including the two
104 optimal sequences: F1-F2-F3-F4-F5-F6 or F6-F5-F4-F3-F2-F1; Figs 3 and S1B). Flower arrays
105 were generated using a computer program (R code available in Text S1) designed to maximize the
106 discrepancy between the two optimal flower visitation sequences minimizing travel distance to
107 visit all flowers (e.g. four-flowers array: F1-F2-F3-F4 or F4-F3-F2-F1) and the flower visitation
108 sequence linking all unvisited nearest neighbour flowers (e.g. four-flowers array: F1-F4-F5-F2)
109 given the dimensions of our flight room. The distance between neighbour flowers ranged from 1.48
110 m to 4.19 m in the four-flowers array, and 1.13 m to 4.22 m in the six-flowers array. Since bee
111 workers detect visual targets from a background subtending a minimum visual angle between ca.
112 3° (*B. terrestris*; Dyer et al. 2008) and 5° (*A. mellifera*; Giurfa et al. 1996; Kapustjansky et al.
113 2010), we assumed that bees could visually detect the 50 cm tall flowers from any location in the
114 flight room. The small spatial scale of the experimental arrays (i.e. the maximum length between
115 a flower and the nest was 6.41m) prevented any dance communication between the honey bees
116 (von Frisch 1967).

117

118 ***Traplining experiments***

119 We pre-trained the bees collectively on an artificial flower delivering *ad libitum* sucrose solution
120 (3.5cm petri dish full of sucrose solution on top of blue landing platform, 40% w/w) and marked

121 them with acrylic paint on the thorax for individual identification (von Frisch 1967). Once a bee
122 made regular foraging bouts (foraging trips starting and ending at the colony hive entrance), we
123 measured its nectar crop capacity (average \pm SE; bumblebees: 120 ± 20 μ L, N = 20; honey bees:
124 42.3 ± 10 μ L, N = 19) by estimating the average total amount of sucrose solution collected by that
125 bee over three foraging bouts (Lihoreau et al. 2010). We then tested the bee either for 30
126 consecutive foraging bouts in the four-flowers array or 50 consecutive foraging bouts in the six-
127 flowers array. The number of trials differed between the two arrays based on previous observations
128 that bees require more time to develop routes between six flowers than in a more simple array of
129 four flowers (Lihoreau et al. 2010, 2012a). Each flower provided either 1/4th (four-flowers array)
130 or 1/6th (six-flowers array) of the bee's nectar crop capacity and was refilled with sucrose solution
131 between each foraging bout. Between testing different bees, flowers were cleaned with ethanol
132 (70% w/w) to remove chemical cues that could influence the next foragers (Giurfa and Núñez
133 1992; Pearce et al. 2017). In total, 10 bumblebees and 10 honey bees were tested in the four-flowers
134 array, and another 10 bumblebees and 9 honey bees were tested in the six-flowers array (N = 39
135 bees in total). All data were collected by an experimenter using the software Ethom (Taiwanica
136 2000). For each foraging bout of each bee, we recorded the time when the bee left the hive, each
137 time it landed on a flower, took off, and the time when it returned to the nest.

138

139 ***Modeling***

140 We compared the observational data to numerical simulations of an agent-based model of trapline
141 development (see details in Lihoreau et al. 2012b; Reynolds et al., 2013). Briefly, in the model the
142 agent (bee) forages according to the following set of rules: (1) the bee has a probability of using
143 movement vectors joining two targets (two flowers, or the nest and a flower); (2) the initial
144 probability of using a vector depends on the distance between the two targets (probabilities are
145 inversely proportional to the squared distance between targets and are normalized with respect to
146 all targets); (3) the bee computes the net length of the route travelled by summing the lengths of all
147 vectors comprising the route; (4) if the route passed through all the flowers at least once (thus
148 filling the nectar crop capacity of the bee), the bee compares the net length of the current route to
149 the net length of the shortest route experienced so far that passes through all the flowers; (5) if the
150 length of the new route is inferior or equal, the probabilities of using the vectors comprising this
151 new route in the next foraging bout are multiplied by a common factor (learning factor, l_f) and all

152 probabilities are rescaled with respect to all flowers so that they sum to unity. (6) If the bee returns
153 to the nest, the foraging bout ends no matter the number of flowers visited. Revisits to flowers are
154 not taken into account in the learning process, so that vectors including revisits to any flower are
155 not reinforced through learning. We explored outputs of the model with values of learning factors
156 ranging between 1 and 2, as suggested by Reynolds et al. (2013) for simulations at small spatial
157 scales. A learning factor of 1.0 replicates situations where the bee does not learn (i.e. null model).
158 Increasing values of the learning factor should lead bees to converge faster towards a stable
159 optimized trapline. For each value of learning factor, we simulated 1000 times the execution of 30
160 foraging bouts (for the four-flowers array) or 50 foraging bouts (for the six-flowers array).

161

162 *Data analyses*

163 We ran all analyses in R (R Development Core Team 2016).

164

165 *Behavioural data*

166 From the behavioural data, we extracted raw sequences of flower visitation (see Table S1-4). We
167 calculated the total duration of a foraging bout (time between departure and arrival at the hive), the
168 number of different flowers visited per foraging bout, the number of foraging bouts for which each
169 flower has been visited during the whole experiment, and the number of immediate revisits to the
170 same flowers per foraging bout (no other flower visited in between). A bee was considered to use
171 a route (i.e., flower visitation sequence without immediate and non-immediate revisits)
172 significantly more often than expected by chance if the route was used at least four times in the
173 four-flowers array (24 possible routes in total), and two times in the six-flowers array (720 possible
174 routes in total). The ‘primary route’ for one bee was its most used one according to these previous
175 rules (Lihoreau et al. 2010).

176 We assessed route optimality using an index of route quality (i.e., the squared number of
177 different flowers visited divided by the length of the route). The index of each route was divided
178 by the route quality of the optimal route, so that its value varied between 0 (very poor route quality)
179 and 1 (quality equal to the optimal route). We assessed route repeatability using a determinism
180 index (DET; see details in Ayers et al., 2015). This index is set between 0 (no repeated visitation
181 patterns in a visitation sequence) and 1 (complete traplining). We computed the DET for groups of

182 10 successive foraging bouts, using a minimum length of recurrence of 4 and without considering
183 perpendicular diagonals.

184 We compared the behavioural performance (number of flowers visited, number of
185 immediate revisits and time flying per foraging bout) of bumblebees and honey bees using
186 generalized linear mixed models (GLMMs) with foraging bouts within bee identity as a random
187 factor using lme4 package (Bates et al., 2014). Regarding the first trial each flower was visited, as
188 well as the percentage of bout each flower was visited, the comparison between species within each
189 individual flower was done using a Wilcoxon Rank-test for independent data.

190

191 *Model simulations*

192 For each model simulation (set of 1000 stimulations), we extracted the visitation sequences, the
193 number of different flowers visited per foraging bout, the travel distance for each foraging bout,
194 the route quality and the DET. We compared the behavioural data to the model simulations using
195 GLMMs to check for significant differences in route quality and DET. We used the statistical
196 differences in slopes (seen in the model as the interaction between the bout and treatment effects)
197 to discriminate the experimental data and the models. A similar statistical comparison for treatment
198 effect alone can be found in the supplementary materials (Table S5).

199

200 **Results**

201 *Four-flowers array*

202 We first compared the flower visitation sequences of bumblebees and honey bees in an array of
203 four flowers (**Fig.1A**). Bumblebees and honey bees similarly increased the number of different
204 flowers visited per foraging bout as they gained experience with the array (**Fig.1B**; Poisson
205 GLMM; species, est=0.02, $z_{595}=0.19$, $p=0.85$; foraging bout: est=0.007, $z_{595}=2.12$, $p=0.03$; species
206 x foraging bout: est=0.002, $z_{595}=0.32$, $p=0.75$). Foragers of both species discovered the four flowers
207 during their first five foraging bouts, but honey bees were significantly slower to find the third
208 flower that was the closest to the door in the experimental room (**Fig.1C**; Wilcoxon test; $F3$:
209 $U=19.5$, $p=0.01$, $p>0.05$ for all other flowers). Bumblebees and honey bees visited all flowers in
210 more than $92.4\% \pm 2.5$ of their foraging bouts, although honey bees visited significantly less the
211 third flower (**Fig.1D**; Wilcoxon test; $F3$: $U=83.5$, $p=0.01$, $p>0.05$ for all other flowers).

212 Bumblebees and honey bees similarly decreased their number of immediate revisits to
213 flowers per foraging bout through time (**Fig.1E**; Poisson GLMM; foraging bout: $est=-0.1$, $z_{595}=-$
214 12.8 , $p<0.0001$). Foragers of both species also gradually decreased their flight duration (**Fig.1F**;
215 Poisson GLMM; foraging bout: $est=-0.01$ $z_{595}=-29.35$, $p<0.0001$). However, honey bees showed a
216 lower reduction of immediate revisits (**Fig.1E**; species x foraging bout: $est=0.05$, $z_{595}=6.43$,
217 $p<0.0001$) and spent consequently more time flying in search for the four flowers (**Fig.1F**; species
218 x foraging bout: $est=0.002$, $z_{595}=3.81$, $p=0.0001$) than bumblebees. As a result, honeybees showed
219 a significantly lower increase of route quality with time (Binomial GLMM; foraging bout:
220 $est=0.163$, $z_{595}=5.720$, $p<0.0001$, species x foraging bout: $est=-0.137$, $z_{595}=-4.353$, $p<0.0001$; Fig.
221 5A).

222 All bumblebees and honey bees used a primary route (i.e. most often used flower visitation
223 sequences excluding revisits) by the end of the experiment (**Fig.2A, B**). The optimal sequence (F1-
224 F2-F3-F4 or F4-F3-F2-F1) was used as a primary route by 30% of the bumblebees (3 out of 10)
225 and 80% of the honeybees (7 out of 10). On average, bumblebees used their primary route in 36.7
226 $\pm 4\%$ (SE) of their foraging bouts, and honeybees in $33 \pm 5\%$ (SE) (**Fig.2**). Foragers of both species
227 first used this route within their 10 first foraging bouts (bumblebees: 7 ± 1 bout, honeybees: 8 ± 1
228 bout; Wilcoxon-rank test; $U=42$, $p=0.56$) and showed a similar increase in route similarity (DET)
229 with time (Binomial GLMM; foraging bout: $est=0.223$, $z_{415}=2.493$, $p=0.013$; honey bee x foraging
230 bout: $est=0.301$, $z_{415}=0.782$, $p=0.4341$; Fig. 5A).

231 Thus, in the four-flowers array, all bumblebees and honey bees developed a route between
232 the four flowers. Honey bees were slower to locate all flowers and to reduce their revisits to empty
233 flowers, even though foragers of both species converged towards repeatable efficient routes
234 towards the end of the experiment.

235

236 *Six-flowers array*

237 To test whether the complexity of the spatial problem had an influence on the routing performances
238 of bees, we compared the flower visitation sequences of bumblebees and honey bees in an array of
239 six flowers (**Fig.3A**). Bumblebees and honey bees increased the number of different flowers visited
240 per foraging bout as they gained experience with the array (**Fig.3B**; Poisson GLMM; foraging bout:
241 $est=0.003$, $z_{945}=2.16$, $p=0.03$; species x foraging bout: $est=-0.001$, $z_{945}=-0.52$, $p=0.6$). However,
242 honey bees visited significantly less flowers per foraging bout (**Fig.3B**; species: $est=-0.18$, $z_{945}=-$

243 2.97, $p=0.003$). Honey bees also took significantly more foraging bouts to discover all flowers
244 (honey bees: 19 ± 5.7 (SE) foraging bouts; bumblebees: 4 ± 1.2 (SE) foraging bouts) (**Fig.3C**). The
245 flowers that were the farthest from the hive (flowers 2 and 4) were discovered significantly later
246 by honey bees (**Fig.3C**; Wilcoxon test; $F2$: $U=22.5$, $p=0.04$; $F4$: $U=16$, $p=0.02$; $p>0.05$ for all other
247 flowers). Moreover, all flowers, except flower 5, were visited in fewer foraging bouts by honey
248 bees than by bumblebees (**Fig.3D**; Wilcoxon test; $F1$: $U=71.5$, $p=0.03$; $F2$: $U=84$, $p=0.001$; $F3$:
249 $U=80.5$, $p=0.002$; $F4$: $U=80.5$, $p=0.004$; $F5$: $U=66$, $p=0.08$; $F6$: $U=76$, $p=0.01$).

250 Bumblebees and honey bees similarly decreased their number of immediate revisits to
251 flowers with experience (**Fig.3E**; Poisson GLMM; foraging bout: $est=-0.03$, $z_{945}=-12.8$, $p<0.0001$;
252 species x foraging bout: $est=0.006$, $z_{945}=1.88$, $p=0.06$). Foragers of both species gradually
253 decreased their flight duration (**Fig.3F**; Poisson GLMM; foraging bout: $est=-0.006$, $z_{945}=-29.26$,
254 $p<0.0001$). However, once again, honey bees spent significantly more time flying than bumblebees
255 (**Fig.3F**; species: $est=0.26$, $z_{945}=2.6$, $p=0.01$; species x foraging bout: $est=-0.005$, $z_{945}=-16.63$,
256 $p<0.0001$). Thus overall, honey bees showed a lower increase in route quality with time (Binomial
257 GLMM; foraging bout: $est=0.064$, $z_{945}=7.953$, $p<0.0001$; species x foraging bout: $est=-0.043$,
258 $z_{945}=-3.087$, $p=0.002$; Fig. 5B).

259 All bumblebees developed a primary route between the six flowers ($n = 10$; **Fig.4A**). On
260 average, bumblebees used it in $14 \pm 2\%$ (SE) of their foraging bouts, which is higher than expected
261 by chance (binomial test, $p<0.0001$). The optimal route (F1-F2-F3-F4-F5-F6) was used as primary
262 route by 40% of the bumblebees (4 out of 10 individuals). By contrast, only two honey bees
263 developed a primary route between the six flowers and they used it in $12 \pm 2\%$ (SE) of their foraging
264 bouts. The seven remaining honey bees only developed primary routes between five flowers ($n=4$),
265 four flowers ($n=2$), or three flowers ($n=1$; **Fig.4B**). Irrespective of the number of flowers visited,
266 both species showed a similar increase in route similarity (DET) over successive foraging bouts
267 (Binomial GLMM; foraging bout: $est=0.265$, $z_{774}=2.817$, $p=0.005$; honey bee x foraging bout:
268 $est=4.583e+01$, $z_{774}=0.000$, $p=1.000$; Fig. 5B).

269 Thus, foragers of both species increased their foraging efficiency with experience.
270 However, while bumblebees developed a route between the six flowers, honey bees hardly found
271 all flowers and used routes between less flowers.

272

273 ***Model simulations***

274 To test whether the model of trapline formation proposed in previous studies (Lihoreau et al. 2012b;
275 Reynolds et al. 2013) could explain the observed differences in routing behaviour between
276 bumblebees and honey bees, we compared observed flower visitation sequences to simulated
277 flower visitation sequences, using route quality and route similarity (DET). In each case, we
278 compared the binomial fit of the experimental data to that of the simulations with different values
279 of learning factor (Lf), and rejected all models that showed a significant difference, ultimately
280 providing a set of Lf relevant for each species. The results are summarized in Table 1 (comparisons
281 of slopes) and Table S2 (comparisons of intercepts).

282 We first compared observational and simulated data in the four-flowers array. For
283 bumblebees, the increase of route quality was replicated with Lf ranging from 1.3 to 1.7 (**Fig.5A**;
284 Table 1) and the increase in route similarity (DET) with Lf ranging from 1.1 to 1.2 (**Fig.5B**;
285 Table 1). For honey bees, the increase of route quality was replicated with Ln ranging from 1.1 to 1.5
286 (**Fig.5A**; Table 1) and the increase of route similarity with Ln ranging from 1.0 to 1.2 (**Fig.5B**;
287 Table 1). Results followed a similar pattern in the six-flowers array. For bumblebees, the increase
288 of route quality was replicated with Lf 1.5, 1.6, 1.7 and 1.9 (**Fig.5C**; Table 1) and the increase of
289 route similarity with Lf ranging from 1.1 to 1.6, and 1.8 and 2.0. (**Fig.5D**; Table 1). For honey bees,
290 route quality was replicated with a Lf ranging from 1.3 to 1.5 (**Fig.5C**; Table 1) and route similarity
291 with a Lf ranging from 1.0 to 1.3 and 1.5 (**Fig.5D**; Table 1). Similar observations were made by
292 comparing the intercepts of experimental data and models (Table S2). Thus overall, the behaviour
293 of honey bees was replicated with lower values of Lf than that of bumblebees in both arrays of
294 flowers. This indicates that honey bees were generally slower to develop a route and that their
295 routes were also less efficient.

296

297 **Discussion**

298 We compared the routing behaviour of two naturally co-occurring generalist pollinators foraging
299 in the same arrays of artificial flowers. While bumblebees and honey bees established routes
300 between four flowers, only bumblebees did so between six flowers. In these conditions, honey bees
301 took a longer time to discover all the flowers and never integrated them all in a single stable
302 visitation sequence.

303 Many animals develop foraging routes (or traplines) to efficiently exploit multiple familiar
304 feeding sites that replenish over time (Janzen 1971; Thomson et al. 1997; Buatois and Lihoreau

305 2016; Gilbert and Singer 1975; Tello-Ramos et al. 2015; Lemke 1984; Wooller et al 1999). Most
306 experiments on trapline foraging have been designed to test whether animals could optimise overall
307 travel distances and to explore the cognitive mechanisms involved in route formation (Ohashi and
308 Thomson 2009; Lihoreau et al. 2013). However, comparing these behaviours across individuals
309 and species can bring important insights into the evolution of spatial cognition and its impact on
310 pollination. Recently, Klein et al. (2017) compared the spatial patterns of bumblebee foragers in
311 different arrays of flowers, showing consistent inter-individual variations in speed and efficiency
312 for route development. Here we adopted a similar strategy to compare the routing behaviour of
313 bumblebees and honey bees, and demonstrated that honey bees are generally slower in developing
314 routes, and that their routes are less efficient than those of bumblebees. This result is consistent
315 with indirect comparisons of semi field data (Pasquaretta et al. 2017). Importantly, this key
316 behavioural difference between honey bees and bumblebees was well-captured by changing a
317 single parameter value (the learning factor) in simulations of a previously proposed model of
318 trapline formation (Lihoreau et al. 2012b, Reynolds et al. 2013). Overall, the behaviour of honey
319 bees was best-replicated with lower learning factors than that of bumblebees.

320 Why do honey bees and bumblebees do not behave the same? The two species greatly differ
321 in social organization and it is possible that their behavioural strategies are influenced by social
322 constraints. Honey bees use the waggle dance to recruit foragers on profitable sites (von Frisch
323 1967) and may thus invest less in individual sampling and learning than bumblebees that do not
324 exhibit dance communication (Dornhaus and Chittka 1999). At the collective level, unperfect
325 traplining and dance communication may be more efficient in tropical environments dominated by
326 densely aggregated resources such as blooming trees where honey bees are expected to originate
327 (Dyer and Seeley 1989), whereas perfect traplining may be an efficient strategy to maximize
328 collective foraging in environments dominated by spatially distributed resources such as small
329 flower patches. The size of colonies are also dramatically different in the two species. While a
330 honey bee colony can contain thousands of workers, a bumblebee colony only contains hundreds.
331 The foraging workforce of honey bees is therefore highly superior, resulting in a potentially more
332 intense activity of exploration to find new resources and exploit them rapidly, than individual
333 learning to monopolize specific resources for long period of times. Recent studies indicate that
334 honey bee foragers are less accurate than bumblebee foragers in many aspects of foraging, for
335 instance when selecting pollen of different qualities (Leonhard and Bluthgen 2012) or searching

336 for a target in an arena (Morawetz and Spaethe 2012). Our results are consistent with these
337 observations since, even in the most complex array of six flowers, bumblebees managed to find
338 every flower, while honey bees never visited them all during the same foraging bout.

339 These different spatial behaviours between honey bees and bumblebees may also result
340 from differences in bio-energetics. In addition to an obvious difference of body size, foragers of
341 the two species have a very different nectar crop capacities. While it is well accepted that the usual
342 crop capacity of honey bees is about 60 μ L (Nunez 1966), the crop of bumblebees is typically
343 around 120 μ L (Lihoreau et al. 2010,2012a,b). In contrast to bumblebees that often return home
344 with a full crop, honey bees often abandon non-depleting food sources with a partially filled crop
345 (Schmid-Hempel et al. 1985). This behaviour does not maximize the net rate of energy extraction
346 from the food sources but appears to maximize energetic efficiency (net energetic gain/unit energy
347 expenditure) (Schmid-Hempel et al. 1985). This may explain why honey bees in the six-flowers
348 array rarely visited all flowers during a given foraging bout. Note however that honey bees tested
349 both on the four- and six-flowers arrays did significantly more immediate revisits to empty flowers
350 than bumblebees, as well as flew significantly longer, suggesting that they were searching for
351 additional food. It remains relatively unclear why bumblebees have a crop capacity way more
352 stable than honeybees during a foraging flight. Different studies have shown that metabolic rates
353 tested in bumblebees and honey bees during flight were not so different (Kammer and Heinrich
354 1974, Heinrich 1975a,b, Schaffer et al. 1979, Harrison and Fewell 2002, Darveau et al. 2014).
355 Consequently, the flight energy could not be an explanation for the differences observed during
356 our experiments. In addition to potential physical constraints, it is more likely that the difference
357 regarding the crop capacity is triggered by the difference in colony size, as well as the number of
358 recruited foragers for both species. Indeed, the low number of foragers in bumblebees, as well as a
359 poor communication about food, have to be balanced by an optimal individual foraging and
360 therefore a fully filled crop to ensure a maximal transport of resources. However, in honeybees,
361 with a very large number of foragers, as well as a very sophisticated system of recruitment, the
362 individual foraging does not have to be as efficient since other bees will come to help foraging the
363 resources.

364 The morphological differences between the two species are also accompanied with size
365 differences in sensory organs and brains that could influence routing behaviour. For instance, the
366 bumblebee eye surface is 2 times larger (Streinzer et al. 2013, Streinzer and Spaethe 2014) and its

367 resolution is about 25% better than that of the honey bee eye (Macuda et al. 2001). Consequently,
368 bumblebees are more likely to identify a small object at a long distance. In our experiments,
369 although artificial flowers were designed to be detectable by both bumblebees and honey bees,
370 differences in visual acuity may explain why bumblebees were more efficient at finding all flowers.
371 Beyond visual perception, honey bees and bumblebees can notoriously perform a rich diversity of
372 elemental and non-elemental learning tasks (Giurfa 2013, Perry et al. 2017). Despite these
373 elaborated cognitive abilities in both species, the different body size of the two insects also comes
374 with an obvious difference of brain size (Mares et al. 2005). Although it is still quite debated
375 (Chittka and Niven 2009, Lihoreau et al. 2012c), some studies conducted in different species has
376 shown that a larger brains could be associated with better cognitive performances (Buechel et al.
377 2018; Herculano-Houzel 2017). For instance, when tested on the same learning task, large-brained
378 females guppy performed better than the small-brain females (Kotrschal et al. 2013). Such
379 observations have also been performed in bees and allowed to highlight correlation between brain
380 size and some specific behaviour. Sayol et al. (2020) showed an association between larger brain
381 could be associated with ecologically specialized bee species when compared with generalist or
382 multi-generation species. More recently, this question has been explored by comparing 32 different
383 bee species brain size after a colour discrimination task. Regardless of the species, bees with a
384 larger brain were more likely to learn the association between the reward and the colour (Collado
385 et al. 2020). It is therefore reasonable to hypothesise that with a larger brain, bumblebees would be
386 cognitively more efficient, explaining their best performance in our experiments.

387 Our study focused on route development by bees at small spatial scales in the lab. Although
388 bees can forage in these conditions, route optimization is faster and more pronounced at larger
389 spatial scales, where feeding sites are visually isolated from each other and the cost of flying long
390 suboptimal routes is magnified (Lihoreau et al. 2012b, Buatois and Lihoreau 2016; Woodgate et
391 al. 2017). Future studies should therefore explore whether the differences between bumblebees and
392 honey bees are maintained at larger spatial scales. Honey bees and bumblebees can fly to up to ca.
393 10 kms (Goulson and Stout 2001; Pahl et al. 2011). In the field, the difference in relative energetic
394 cost of flight in the two species, due body size differences, may lead honey bees to invest more in
395 route optimization between distant feeding sites. Ultimately, a more systematic analysis and
396 comparisons of the spatial behaviours of key pollinators will help clarify their impact on pollen

397 transfer and potential complementarity or redundancy for plant reproduction and crop yield
398 (Garibaldi et al. 2016).

399

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405

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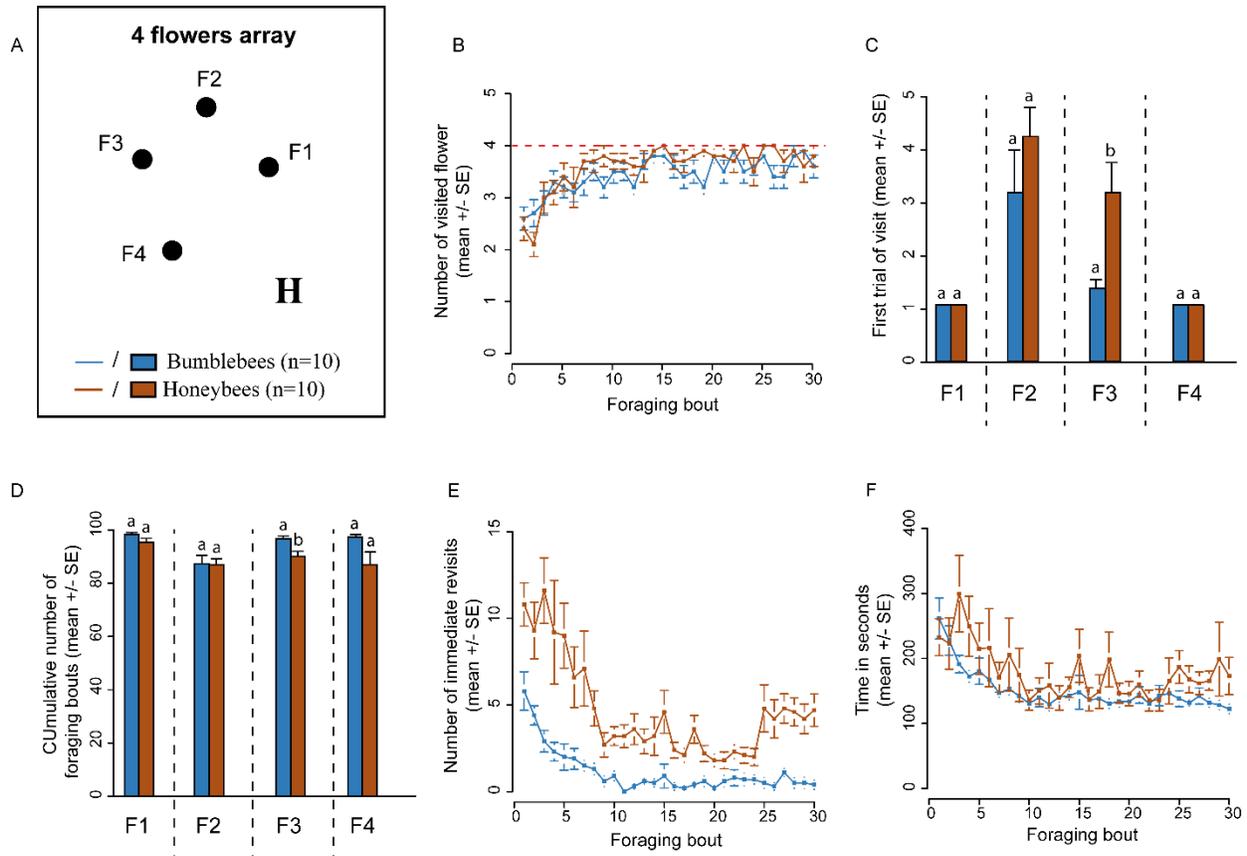
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548 **Figures and figure legends**

549 **Figure 1**

550



551

552 **Figure 1: Route formation in the four-flowers array.** (A) Schematic representation of the flower

553 array. Flowers are labelled F1-F4. H is the colony hive location. (B) Number of flowers visited per

554 foraging bout. (C) Cumulated number of foraging bouts before the flower was first visited. (D)

555 Percentage of foraging bouts for which each flower was visited. (E) Number of immediate revisits

556 to flowers per foraging bout. (F) Flight duration per foraging bout. The mean \pm standard error is

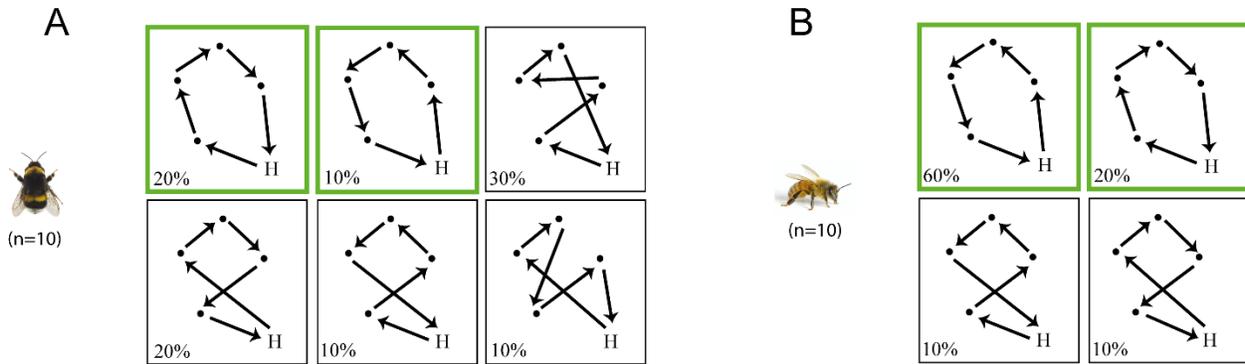
557 presented for each graph. Different letters indicate a significant difference in (C) and (D)

558 (Wilcoxon Rank-test for independent data).

559

560 **Figure 2**

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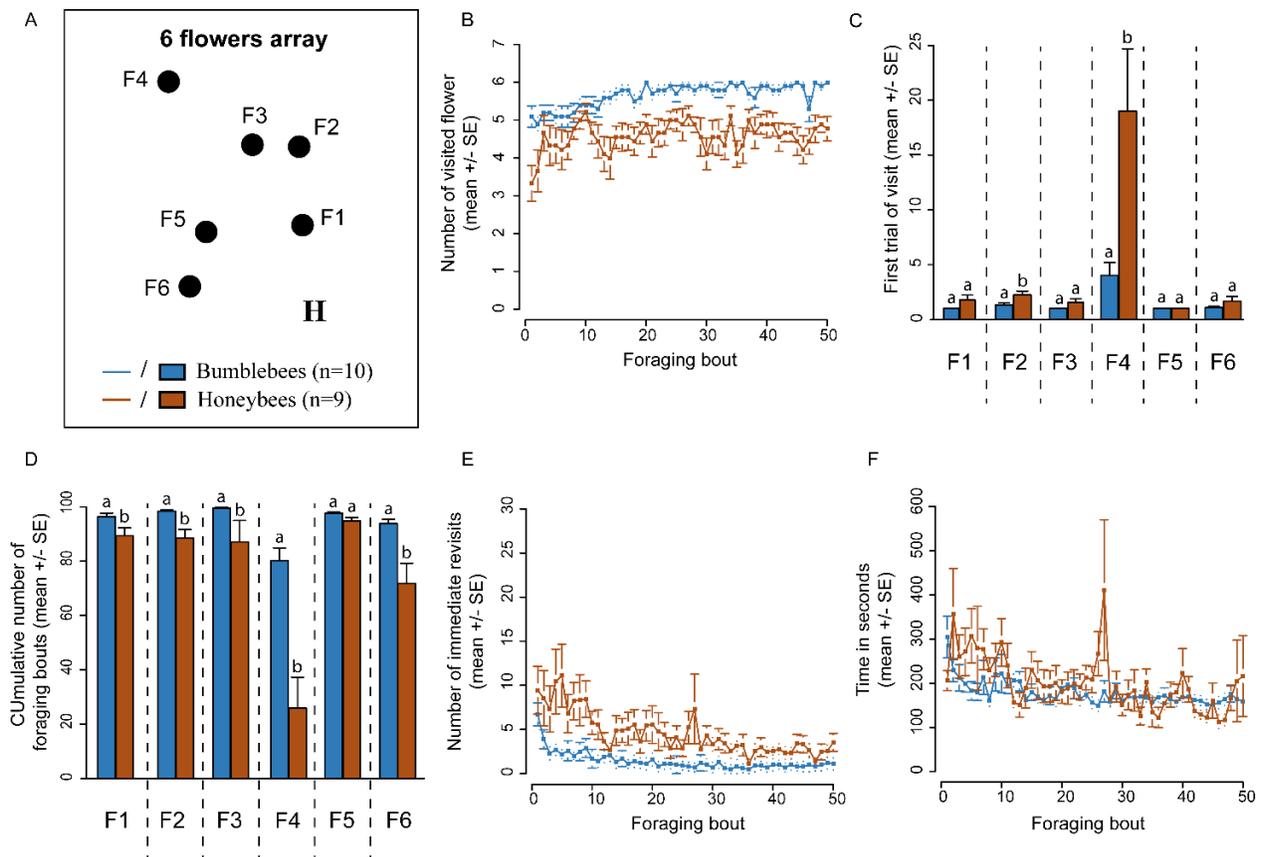
562

563 **Figure 2: Primary routes in the four-flowers array. (A)** Primary route used by bumblebees. **(B)**
564 Primary route used by honeybees **(B)**. Black dots represent flower locations. H is the colony hive
565 location. Arrows indicate the direction in which the bee moved. The percentage indicates the
566 proportion of bees that used this route pattern. Optimal routes are highlighted in green.

567

568 **Figure 3**

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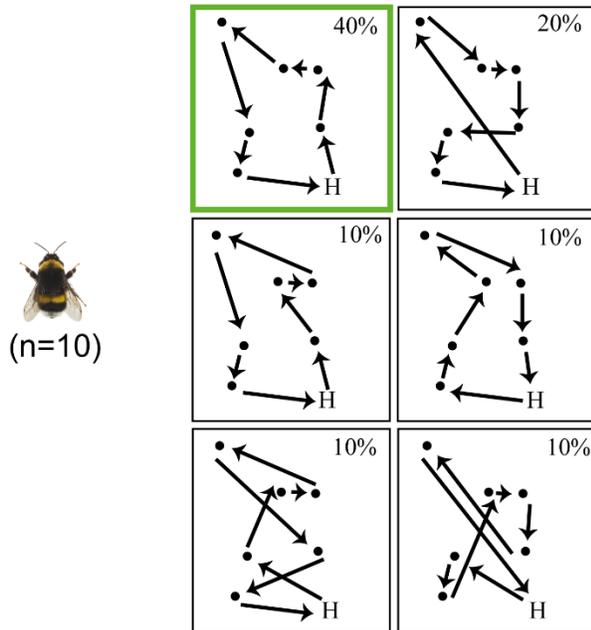
571 **Figure 3: Route formation in the six-flowers array.** (A) Schematic representation of the flower
 572 array. Flowers are labelled F1-F6. H is the colony hive location. (B) Number of flowers visited per
 573 foraging bouts. (C) Cumulated number of foraging bouts before the flower was first visited (D)
 574 Percentage of foraging bouts for which each flower was visited. (E) Number of immediate revisits
 575 to flowers per foraging bout. (F) Flight duration per foraging bout. The mean \pm standard error is
 576 presented for each graph. Different letters indicate a significant difference in (C) and (D)
 577 (Wilcoxon Rank-test for independent data).

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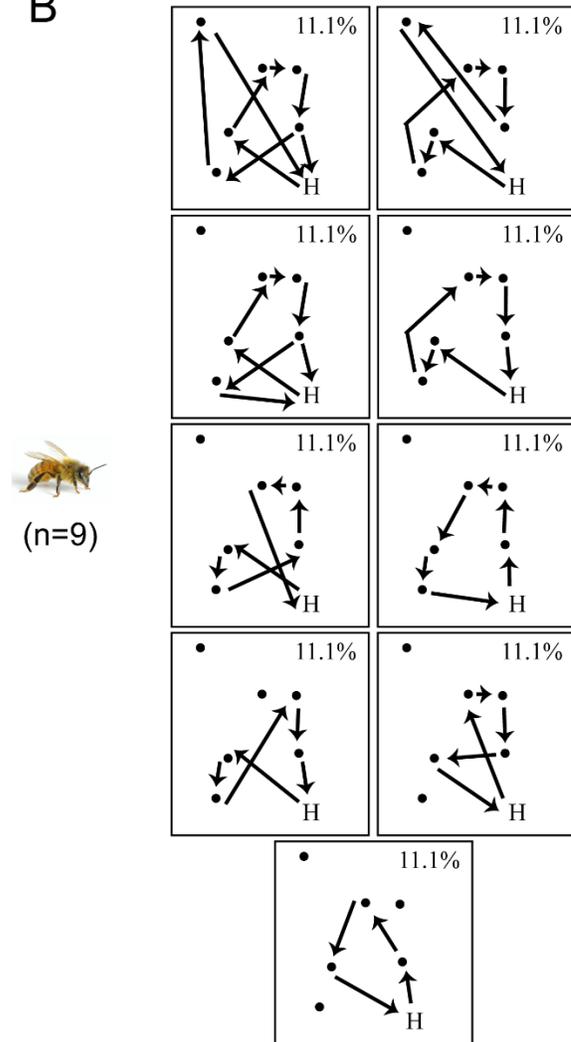
579 **Figure 4**

580

A



B



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582 **Figure 4: Primary routes on the six-flowers assay. (A)** Primary route used by bumblebees. **(B)**

583 Primary route used by honeybees **(B)**. Black dots represent flower locations. H is the colony hive

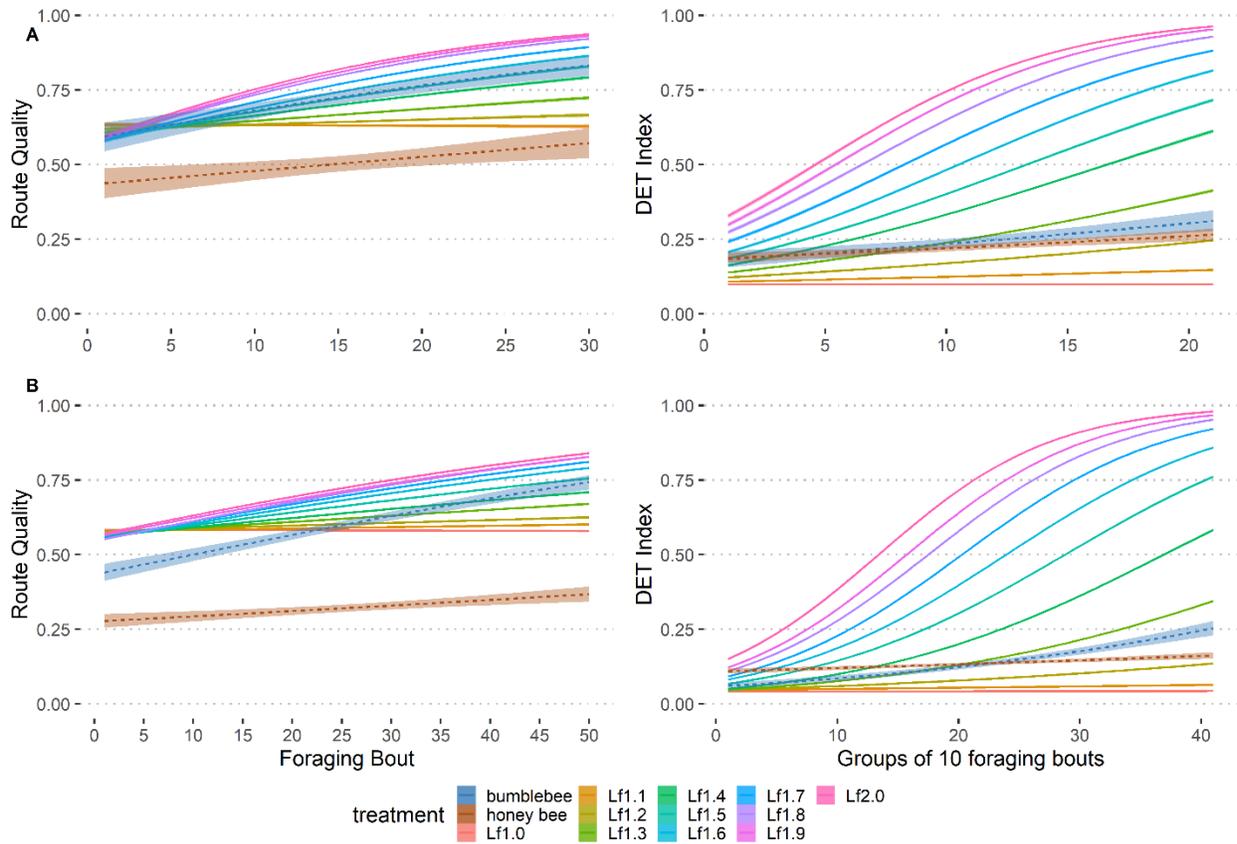
584 location. Arrows indicate the direction in which the bee moved. The percentage indicates the

585 proportion of bees that used this route pattern. Optimal routes are highlighted in green.

586

587 **Figure 5**

588



595 **Table**

596

Array	Variable	Species	Lf1.0	Lf1.1	Lf1.2	Lf1.3	Lf1.4	Lf1.5	Lf1.6	Lf1.7	Lf1.8	Lf1.9	Lf2.0
4F	Quality	Bumblebee	0.001	0.005	0.029	0.084	0.306	0.832	0.432	0.155	0.005	9.00e-04	2.89e-05
4F	Quality	Honey bee	0.014	0.070	0.054	0.577	0.332	0.070	2.92e-04	4.13e-06	3.42e-12	6.77e-12	9.70e-14
4F	Similarity (DET)	Bumblebee	0.046	0.351	0.557	0.046	0.035	0.007	7.04e-05	0.008	2.77e-05	2.91e-05	1.26e-04
4F	Similarity (DET)	Honey bee	0.667	0.222	0.324	0.029	0.001	0.003	0.001	0.002	4.35e-06	1.25e-05	3.52e-05
6F	Quality	Bumblebee	1.42e-06	2.05e-07	1.20e-06	1.22e-04	8.72e-04	0.154	0.743	0.154	0.018	0.059	6.78e-05
6F	Quality	Honey bee	8.59e-04	0.001	0.003	0.084	0.525	0.106	0.012	3.01e-08	4.03e-08	2.21e-06	2.25e-07
6F	Similarity (DET)	Bumblebee	0.007	0.339	0.978	0.064	0.052	0.343	0.225	0.040	0.077	0.033	0.064
6F	Similarity (DET)	Honey bee	0.077	0.453	0.800	0.077	0.019	0.091	0.005	9.69e-04	3.18e-04	0.003	6.16e-04

597

598 **Table 1: Statistical comparison between observed and simulated data.** Summary of all the p-
 599 values obtained when comparing the models to the experimental data, using the route quality and
 600 route similarity (DET Index). The p-values displayed are for the slope comparisons. The color code
 601 for p-values is ‘green’ <1; ‘yellow’ <0.1; ‘orange’ <0.05; ‘light red’ <0.01; ‘red’ <0.001.

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