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1 **A model of resource partitioning between foraging bees**

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27 **Statement of authorship**

28 CP, TD and ML designed the study. TD and JG developed the models. CP and TD performed the
29 analyses. CP, TD and ML wrote the first draft of the manuscript. All authors contributed substan-
30 tially to revisions.

31

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40 **Abstract**

41 Central place foraging pollinators tend to develop multi-destination routes (traplines) to exploit several
42 patchily distributed plant resources. While the formation of traplines by individual pollinators has been stud-
43 ied in details, how populations of individuals exploit resources in a common area is an open question diffi-
44 cult to address experimentally. Here we explored conditions for the emergence of resource partitioning
45 among traplining bees using agent-based models built from experimental data of bumblebees foraging on
46 artificial flowers. In the models, bees learn to develop routes as a consequence of feedback loops that change
47 their probabilities of moving between flowers. While a positive reinforcement of route segments leading to
48 rewarding flowers is sufficient for the emergence of resource partitioning when flowers are evenly distribut-
49 ed, a negative reinforcement of route segments leading to unrewarding flowers is necessary when flowers are
50 patchily distributed. In these more complex environments, the negative experiences of individual bees favour
51 the spatial segregation of foragers and high levels of collective foraging efficiency.

52

53 **Keywords:** bumblebees; competition; resource partitioning; trapline foraging; vector navigation

54 **Introduction**

55 Animals competing for food resources are expected to self-distribute on feeding sites in order to maximize
56 their individual energy gain (Fretwell and Lucas 1969; Giraldeau and Caraco 2000). Resource partitioning
57 between individuals of different species is well documented, and often results from functional (Fründ *et al.*
58 2010; 2013) or behavioral (Nagamitsu and Inoue 1997; Valdovinos *et al.* 2016) differences. By contrast, how
59 individuals of the same species optimally interact to exploit resources in a common foraging area is less un-
60 derstood (Johst *et al.* 2008; Tinker *et al.* 2012).

61 For pollinators, such as bees that individually exploit patchily distributed floral resources in envi-
62 ronments with high competition pressure, efficient resource partitioning appears a prodigious problem in-
63 volving the quality of food resources, their spatial distribution, their replenishment rate, and the activity of
64 other pollinators. As central place foragers, bees often visit familiar feeding sites in a stable sequence or
65 trapline (Janzen 1971; Thomson *et al.* 1997). Individual bees with exclusive access to an array of artificial
66 flowers tend to develop traplines minimizing travel distances to visit all the necessary flowers to fill their
67 nectar crop and return to the nest (e.g. bumblebees: Ohashi *et al.* 2008, Lihoreau *et al.* 2012a, Woodgate *et al.*
68 2017; honey bees: Buatois and Lihoreau 2016). This routing behavior involves spatial memories that can
69 persist several days or weeks (Thomson *et al.* 1996; Lihoreau *et al.* 2010).

70 How bees partition resources, when several conspecifics exploit a common foraging area, is however
71 still an open question. Experimentally the problem is challenging to address as it requires monitoring the
72 movements of several bees simultaneously over large spatial and temporal scales. In theory, bees should
73 develop individualistic traplines that minimize travel distances and spatial overlap with other foragers, there-
74 by improving their own foraging efficiency and minimizing the costs of competition (Ohashi and Thomson
75 2005; Lihoreau *et al.* 2016). Best available data supporting this hypothesis come from observations of small
76 numbers of bumblebees foraging on potted plants (e.g. Makino and Sakai 2005, Makino 2013) or artificial
77 flowers (Lihoreau *et al.* 2016, Pasquaretta *et al.* 2019) in large flight tents. In these rather simple foraging
78 conditions, bees tended to avoid spatial overlaps as a consequence of competition by exploitation (when bees
79 visited empty flowers) and interference (when bees interacted on flowers) (Pasquaretta *et al.* 2019).

80 Computational modeling is a powerful approach to further explore how such partitioning might
81 emerge from spatial learning and competitive interactions. At the individual level, trapline formation has

82 been modeled using an iterative improvement algorithm by which a bee compares the net length of the route
83 it has just traveled (sum of the lengths of all movement vectors comprising the flower visitation sequence) to
84 the length of the shortest route experienced so far (Lihoreau *et al.* 2012b). If the new route is shorter (or
85 equivalent), the bee increases its probability of using all the movement vectors composing the new route in
86 its subsequent foraging bout. After several iterations, this route-based learning algorithm typically leads to
87 the discovery and selection of a short (if not the shortest possible) trapline. While this approach can accurately
88 replicate observations across a wide range of experimental conditions (Reynolds *et al.* 2013), it makes the
89 strong assumption that bees can compute, memorize and compare the lengths of multi-leg routes upon return
90 to their nest. Recently, it was proposed that such behavior could also emerge from vector-based learning (Le
91 Moël *et al.* 2019), which is more parsimonious and plausible considering the current understanding of spatial
92 computation in the insect brain (Stone *et al.* 2017). So far, however, none of these traplining models have
93 accounted for social interactions and current models of pollinator populations do not take into account indi-
94 vidual specificities of movements based on learning and memory (Becher *et al.* 2014; 2016; 2018). Thus
95 presently, there has been no realistic exploration of how resource partitioning between interacting bees might
96 form.

97 Here, we investigated the behavioral mechanisms underpinning resource partitioning among
98 traplining bees by comparing predictions of agent-based models integrating route learning and social interac-
99 tions. First, we developed models implementing biologically plausible vector navigation based on positive
100 and negative reinforcements of route segments leading to flowers. We used different models to test the indi-
101 vidual and combined influences of these feedback loops on route learning. Next, we explored how these
102 simple learning rules at the individual level can promote complex patterns of resource partitioning at the
103 collective level, using simulations with multiple foragers in environments with different resource distribu-
104 tions.

105

106 **METHODS**

107 *Model overview*

108 We developed two agent-based models in which bees learn to develop routes in an array of flowers (Fig. 1).
109 In both models, all flowers contain the same quality and volume of nectar that is refilled between foraging

110 bouts (flower visitation sequence, beginning and ending at the colony nest entrance). In simulations with
111 multiple bees, all bees start their foraging bout synchronously and the flowers are filled after the last bee has
112 returned to the nest. At each foraging bout, each bee attempts to collect nectar from five different flowers in
113 order to fill its nectar crop (stomach) to capacity. For simplicity, this rule was set constant across all
114 simulations. For each bee, flower choice is described using movement vectors (orientated jump between two
115 flowers or between the nest and a flower). The initial probability of using each possible movement vector is
116 based on movement vector length. This probability is then modulated through learning when the bee uses a
117 vector for the first time. The learning rule varied depending on the model. If the ending flower of the vector
118 contains nectar, it is rewarding and the probability to reuse the vector later increased (positive reinforcement,
119 models 1 and 2). If the flower is empty, it is not rewarding and the probability to reuse the vector is either
120 left unchanged (model 1) or decreased (negative reinforcement, model 2). A flower is empty if it has
121 previously been visited in the same foraging bout by the same bee or another bee (exploitation competition).
122 If two bees visit a flower at the same time, a fight to secure the possible reward occurs (interference
123 competition). Only one bee can stay on the flower and access the potential nectar reward with a random
124 probability. The winner bee takes the reward if there is one. The loser reacts as for an empty flower. Both
125 bees update their probabilities to reuse the vector accordingly. Route learning thus depends on the experience
126 of the bee and its interactions with other foragers. For simplicity, we restricted our analysis to two bees, but
127 the same models can be used to simulate interactions among more bees (see examples with five bees in
128 Video S1, Appendix S1). The complete R code is available at
129 <https://gitlab.com/jgautrais/resourcepartitioninginbees/-/releases>.

130

131 ***Environment***

132 *Simulations with one foragers*

133 To calibrate our models, we ran simulations in environments replicating published experimental studies in
134 which individual bumblebees (*Bombus terrestris*) were observed developing traplines between five equally
135 rewarding artificial flowers in a large open field (Lihoreau *et al.* 2012b; Woodgate *et al.* 2017). To our
136 knowledge, these studies provide the most detailed available datasets on trapline formation by bees. Lihoreau
137 *et al.* (2012b) used a positive array of flowers (regular pentagon, Fig. S1A) in which the distance and
138 direction between flowers were positively linked, i.e. nearest neighbor flowers could be visited using lowest

139 angular deviation between consecutive vectors. The authors tracked seven bumblebees, which we judged
140 enough to run quantitative comparisons with model simulations (raw data are available in Table S1 of
141 Lihoreau *et al.* 2012b). Woodgate *et al.* (2017) used a negative array of flowers (narrow pentagon, Fig. S1B)
142 in which the distance and direction between flowers were negatively linked. Here, however, the small sample
143 size of the original dataset (three bumblebees, data shared by J. Woodgate) only enabled a qualitative
144 comparison with the model simulations (Appendix S2).

145

146 *Simulations with two foragers*

147 We explored conditions leading to resource partitioning by running model simulations with two foragers.
148 Here we simulated environments containing 10 flowers (each bee had to visit five rewarding flowers to fill
149 its crop to capacity). To test whether model predictions were robust to variations in resource spatial
150 distribution, we simulated three types of environments characterized by different levels of resource
151 patchiness: (i) a patch of 10 flowers, (ii) two patches of five flowers each, and (iii) three patches of five,
152 three and two flowers respectively (see examples in Fig. S2). We generated flower patches into a spatial
153 range comparable to the one used in both experimental setups (Lihoreau *et al.* 2012b; Woodgate *et al.* 2017):
154 about 500 m² with a minimum distance of 160 m between each patch center. Within a patch, flowers were
155 randomly distributed according to two constraints: (i) flowers were at least 20 m apart from each other, (ii)
156 the maximum distance of each flower from the center of the patch was 40 m. This ensured that each patch
157 had a maximum diameter of 80 m and inter-flower distances were smaller between all flowers of the same
158 patch than between all flowers of different patches.

159

160 **Movements**

161 At each step, a bee chooses to visit a target location (flower or nest) based on a matrix of movement
162 probabilities (Fig. 1). This matrix is initially defined using the inverse of the square distance between the
163 current position of the bee and all possible target locations (Lihoreau *et al.* 2012b; Reynolds *et al.* 2013). The
164 probability of moving from location *i* to the location *j* among *n* possible targets, is initially set to:

165

$$166 \quad (1) \quad P(i \rightarrow j) = \frac{1}{d_{ij}^2} / \sum_{k \neq j} \frac{1}{d_{ik}^2}$$

167

168 Where d_{ij} is the distance between locations i and j . Before choosing its destination, the bee lists all possible
169 target locations. For simplicity, the bee excludes its current location, thus preventing looping flights to and
170 from the same flower or nest, which are rare in experienced bumblebee foragers (Ohashi *et al.* 2007; Saleh
171 and Chittka 2007; Lihoreau *et al.* 2010; Lihoreau *et al.* 2012a; Lihoreau *et al.* 2012b; Woodgate *et al.* 2017).
172 The bee also excludes the location it had just come from. This simulates the tendency of bumblebees to avoid
173 recently visited (and thus depleted) flowers (Ohashi *et al.* 2007; Saleh and Chittka 2007; Lihoreau *et al.* 2010;
174 Lihoreau *et al.* 2012a; Lihoreau *et al.* 2012b; Woodgate *et al.* 2017). The foraging bout ends if: (i) the bee
175 fills its crop to capacity, (ii) the bee chooses the nest as a target destination, or (iii) the bee reaches a
176 maximum travelled distance of 3000 m. The latest was added to avoid endless foraging trips in the model. Its
177 value was chosen based on the observation that bumblebees typically forage within a distance of less than 1
178 km from their nest (Osborne *et al.* 1999; Wolf and Moritz 2008; Woodgate *et al.* 2016).

179

180 **Learning**

181 Learning modulates the probability of using movement vectors as soon as the bee experiences the chosen
182 target (online learning) and only once within a foraging bout (the first time the movement vector is used; Fig.
183 1). This approach has the advantage of implementing vector navigation (Stone *et al.* 2017; Le Moël *et al.*
184 2019) and thus avoids unrealistic assumptions about computation and comparison of complete routes
185 (Lihoreau *et al.* 2012b; Reynolds *et al.* 2013). Positive reinforcement was implemented in models 1 and 2. It
186 occurs when a bee uses a vector leading to a rewarding flower. The probability of using this vector is then
187 multiplied by 1.5 (other vectors probabilities are scaled accordingly to ensure that all sum up to 1). This
188 positive reinforcement is based on the well-known tendency of bumblebees to return to nectar rewarding
189 places through appetitive learning (Goulson 2010). Negative reinforcement was implemented in model 2
190 only. It occurs when a bee uses a vector leading to a non-rewarding flower. The bee reduces the probability
191 of using that vector by multiplying it by 0.75 (here also rescaling the other ones). This negative
192 reinforcement rule is based on the tendency of bumblebees to reduce their frequency of revisits to
193 unrewarded flowers with experience (Pasquaretta *et al.* 2019). We applied a lower value to negative
194 reinforcement because bees are much more effective at learning positive stimuli (visits to rewarding flowers)

195 than negative stimuli (visits to non-rewarding flowers) (review in Menzel 1990). Sensitivity analyses of these
196 two parameters show that increasing positive and/or negative reinforcement increases the speed and level of
197 resource partitioning (see Appendix S1).

198

199 *Competitive interactions*

200 We implemented competitive interactions between foragers in the form of exploitation and interference (Fig.
201 1). Exploitation competition occurs when a bee lands on a flower whose nectar reward has already been
202 collected by another bee. If the flower is empty, the probability to reuse the vector is either left unchanged
203 (model 1) or decreased (negative reinforcement, model 2). Interference competition occurs when two bees
204 encounter on a flower. Only one bee can stay on the flower and access the potential nectar reward with a
205 random probability ($p=0.5$). After the interaction, the winner bee takes the reward if there is one. The loser
206 bee reacts as for an empty flower.

207

208 *Statistical Analyses*

209 All analyses were performed in R version 3.3 (R Development Core Team 2018).

210

211 *Simulations with one forager*

212 For each model, we compared the results of the simulations to the reference observational data, either
213 quantitatively (for Lihoreau *et al.* 2012b) or qualitatively (for Woodgate *et al.* 2017; see Appendix S2). We
214 stopped the simulations after 50 foraging bouts to match the experimental conditions of the published data
215 (22-37 foraging bouts in Lihoreau *et al.* 2012b; 47-61 foraging bouts in Woodgate *et al.* 2017). We run 500
216 simulations for each model (without and with negative reinforcement) and we estimated how models fitted
217 the experimental data using two main measures:

218

219 (i) the quality of each route QL , calculated as:

220

$$221 \quad (2) \quad QL = \frac{F^2}{d} * 1 \\ QL_{opt}$$

222

223 Where F is the number of rewarding flowers visited during a foraging bout and d is the net length of all
224 vectors traveled during the foraging bout. QL is standardized in $[0 ; 1]$ by the quality of the optimal route in
225 each array QL_{opt} (shortest possible route to visit all flowers).

226

227 (ii) a similarity index SI_{ab} between flower visitation sequences experienced during two consecutive foraging
228 bouts a and b as follows:

229

$$230 \quad (3) \quad SI_{ab} = \frac{s_{ab}}{2l_{ab}}$$

231

232 Where s_{ab} represents the number of vectors between two flowers found in both sequences, and l_{ab} the
233 length of the longest flower visitation sequence between i and j multiplied by 2 to make sure that $SI_{ab} = 1$
234 occurs only when two consecutive sequences sharing the same vectors also have the same length.

235 We applied generalized linear mixed effect models (GLMM) with binomial error, using the *glmer*
236 function in 'lme4' package (Bates *et al.* 2014), to assess whether the estimated trends across foraging bouts
237 for QL and SI_{ab} obtained from model simulations with one forager differed from trends obtained from
238 observational data. In each model, we used a random structure to account for the identity of bees.

239

240 *Simulations with two foragers*

241 We generated 10 arrays of flowers for each of the three types of environment, and ran 100 simulations for
242 each of the two models (6000 simulations in total). We compared the simulation outcomes of both models
243 using four measures:

244

245 i) the frequency at which each bee experienced exploitation competition (i.e. flower visits when the reward
246 has already been collected by another bee) and interference competition (i.e. flower visits when two bees
247 encounter);

248

249 *ii*) the similarity index SI_{ab} between successive foraging bouts by the same bee;

250

251 *iii*) the degree of resource partitioning among bees, based on network modularity Q (Pasquaretta and Jeanson

252 2018; Pasquaretta *et al.* 2019). Q is calculated using the *computeModules* function implemented in the R

253 package ‘bipartite’ (Dormann *et al.* 2008) using the DIRTLP Awb+ algorithm recently developed by Beckett

254 (2016). Although Q ranges between 0 (the two bees visit the same flowers) and 1 (the two bees do not visit

255 any flower in common), the comparison of modularity between networks requires normalization because the

256 magnitude of modularity depends on network configuration (e.g., total number of flower visits) (Dormann

257 and Strauss 2014; Beckett 2016). For each network, we computed :

258

259 (4)
$$Q_{norm} = \frac{Q}{Q_{max}}$$

260

261 where Q_{max} is the modularity in a rearranged network that maximizes the number of modules (Pasquaretta

262 and Jeanson 2018).

263

264 *iv*) an index of collective foraging efficiency, QL_{group} , computed for each foraging bout i , to estimate the

265 cumulated efficiency of all foraging bees, as:

266

267 (5)
$$QL_{group,i} = \frac{\sum_{j=1}^n QL_{j,i}}{QL_{optimal}}$$

268

269 where $QL_{j,i}$ is the route quality of the individual j during bout i , n the number of bees and $QL_{optimal}$ is the

270 maximum value of all the possible sums of individual route qualities.

271

272 To assess whether the trends across foraging bouts obtained from simulations with two bees

273 differed between models (Fig. 1) and type of environments (Fig. S2), we applied GLMMs for each of the

274 following response variables: *(i)* frequency of competition types (Poisson error distribution), *(ii)* SI_{ab}

275 (Binomial error distribution), (iii) Q_{norm} (Binomial error distribution) and (iv) QL_{group} (Binomial error
276 distribution). In each model, we used a random structure to account for bee identity nested in flower arrays
277 (i.e. 100 simulations of each spatial array for each model). To statistically compare the trends across foraging
278 bouts we estimated the marginal trends of the models, as well as their 95% confident intervals using the
279 *emtrends* function in ‘emmeans’ package (Lenth 2018). When the 95% confidence intervals of the estimated
280 trends included zero, the null hypothesis was not rejected. Statistical models were run using the *glmer*
281 function in ‘lme4’ package (Bates *et al.* 2014).

282

283 **RESULTS**

284 *Simulations with one forager*

285 We first tested the ability of our models to replicate trapline formation by real bees, by comparing
286 simulations with one forager to published experimental data. In the positive array of flowers (Fig. S1A), real
287 bees developed routes of increasing quality and similarity with experience (GLMM_{route quality}: *Estimate* =
288 0.128 ± 0.021 , $P < 0.001$; GLMM_{route similarity}: *Estimate* = 0.148 ± 0.027 , $P < 0.001$). Simulated bees with
289 positive and negative reinforcements (model 2) or positive reinforcement only (model 1) developed routes of
290 similar qualities as real bees (Fig. 2A; GLMM_{model 1}: *Estimate* = 0.024 ± 0.021 , $P = 0.244$; GLMM_{model 2}:
291 *Estimate* = 0.017 ± 0.021 , $P = 0.416$). In both models, the simulated bees also increased route similarity as
292 much as real bees (Fig. 2B; GLMM_{model 1}: *Estimate* = 0.048 ± 0.027 , $P = 0.074$; GLMM_{model 2}: *Estimate* =
293 0.044 ± 0.027 , $P = 0.105$). In the negative array of flowers (Fig. S1B), a qualitative match between the
294 simulations of both models and the experimental data was also observed (Fig. S5; see Appendix S2). Thus,
295 overall, positive reinforcement was sufficient to replicate the behavioral observations. The addition of
296 negative reinforcement had no major effect on route quality and similarity.

297

298 *Simulations with two foragers*

299 *Exploitation and interference competition*

300 Having calibrated our models with one forager, we next explored conditions for the emergence of resource
301 partitioning within pairs of foragers. Here experimental data are not available for comparison. We first
302 analyzed exploitation competition by quantifying the frequency of visits to non-rewarding flowers by each

303 bee during each foraging bout. Simulated bees with positive and negative reinforcements (model 2)
304 decreased their frequency of visits to non-rewarding flowers with time, irrespective of the type of
305 environment (Fig. 3A; GLMM_{one patch}: *Estimate* = -8.94e-03, 95%CI = -9.16e-03 | -8.71e-03; GLMM_{two patches}:
306 *Estimate* = -1.88e-02, 95%CI = -1.91e-02 | -1.86e-02; GLMM_{three patches}: *Estimate* = -1.05e-02, 95%CI = -
307 1.07e-02 | -1.03e-02). However, with positive reinforcement only (model 1), bees behaved differently in the
308 different environments. In the one patch environment, bees decreased their visits to non-rewarding flowers
309 (Fig. 3A; GLMM_{one patch}: *Estimate* = -4.26e-03, 95%CI = -4.47e-03 | -4.05e-03), whereas in the two and three
310 patch environments, bees tended to increase their visits to non-rewarding flowers (Fig. 3A; GLMM_{two patches}:
311 *Estimate* = 6.27e-03, 95%CI = 6.09e-03 | 6.44e-03; GLMM_{three patches}: *Estimate* = 6.65e-03, 95%CI = 6.46e-
312 03 | 6.84e-03).

313 We analyzed interference competition by quantifying the number of interactions on flowers at each
314 foraging bout between the two bees. Bees with positive and negative reinforcements (model 2) decreased
315 their frequency of encounters on flowers with time irrespective of the type of environment (Fig. 3B; GLMM
316 _{one patch}: *Estimate* = -1.53e-02, 95%CI = -1.61e-02 | -1.45e-02; GLMM_{two patches}: *Estimate* = -1.66e-02, 95%CI
317 = -1.73e-02 | -1.59e-02; GLMM_{three patches}: *Estimate* = -1.01e-02, 95%CI = -1.07e-02 | -0.94e-02). Here again,
318 bees with positive reinforcement only (model 1) behaved differently in the different environments. In the one
319 patch environment, bees decreased their frequency of encounters on flowers (Fig. 3B; GLMM_{one patch}:
320 *Estimate* = -4.57e-03, 95%CI = -5.29e-03 | -3.85e-03), whereas in the two and three patch environments,
321 bees increased their frequency of interactions (Fig. 3B; GLMM_{two patches}: *Estimate* = 1.05e-02, 95%CI =
322 1.01e-02 | 1.10e-02; GLMM_{three patches}: *Estimate* = 9.16e-03, 95%CI = 8.64e-03 | 9.68e-03).

323 Thus overall, negative reinforcement was necessary for reducing exploitation and interference
324 competition. By allowing bees to avoid empty flowers, negative reinforcement facilitated the discovery of
325 new flowers and thus gradually relaxed competition. In the absence of negative reinforcement, both types of
326 competition increased in environments with several flower patches.

327

328 *Route similarity*

329 We analyzed the tendency of bees to develop repeated routes by comparing the similarity between flower
330 visitation sequences of consecutive foraging bouts for each individual (Fig. 3C). In the two models, bees
331 increased route similarity through time in all types of environments (Fig. 3C model 1; GLMM_{one patch}:

332 $Estimate = 8.68e-02$, $95\%CI = 8.56e-02 | 8.80e-02$; GLMM_{two patches}: $Estimate = 8.07e-02$, $95\%CI = 7.96e-$
333 $02 | 8.19e-02$; GLMM_{three patches}: $Estimate = 6.77e-02$, $95\%CI = 6.66e-02 | 6.88e-02$; Fig. 3C model 2;
334 GLMM_{one patch}: $Estimate = 6.80e-02$, $95\%CI = 6.69e-02 | 6.91e-02$; GLMM_{two patches}: $Estimate = 5.40e-02$,
335 $95\%CI = 5.29e-02 | 5.50e-02$; GLMM_{three patches}: $Estimate = 3.56e-02$, $95\%CI = 3.46e-02 | -3.65e-02$). Note
336 however that the presence of negative reinforcement (model 2) reduced the final level of route similarity. In
337 these conditions bees learned to avoid revisits to empty flowers and showed greater variation in their
338 visitation sequences, as a result of searching for new flowers.

339

340 *Resource partitioning*

341 We analyzed the level of resource partitioning by quantifying the tendency of the two bees to use different
342 flowers. With positive and negative reinforcements (model 2), pairs of bees showed a significant increase of
343 resource partitioning with time for all types of environments (Fig. 3D; GLMM_{one patch}: $Estimate = -3.82e-02$,
344 $95\%CI = 3.69e-02 | 3.95e-02$; GLMM_{two patches}: $Estimate = 2.91e-02$, $95\%CI = 2.78e-02 | 3.04e-02$; GLMM_{three patches}:
345 $Estimate = 2.66e-02$, $95\%CI = 2.53e-02 | 2.78e-02$). With positive reinforcement only (model 1),
346 bees showed an increase of resource partitioning in environments with one patch (Fig. 3D; GLMM_{one patch}:
347 $Estimate = 3.24e-02$, $95\%CI = 3.11e-02 | -3.36e-02$), and a decrease in environments with two or three
348 patches (Fig. 3D; GLMM_{two patches}: $Estimate = -1.06e-02$, $95\%CI = -1.19e-02 | -0.93e-02$; GLMM_{three patches}:
349 $Estimate = -8.08e-03$, $95\%CI = -9.40e-03 | -6.77e-03$). In these patchy environments, negative reinforcement
350 facilitates the movements of bees between more distant flowers in different patches and thus the
351 establishment of spatially segregated routes.

352

353 *Collective foraging efficiency*

354 To quantify the collective foraging efficiency of bees, we analyzed the capacity of the two foragers to reach
355 the most efficient combination of route qualities (i.e. minimum distance traveled by a pair of bees needed to
356 visit the 10 flowers). With positive and negative reinforcements (model 2), pairs of bees increased their
357 cumulated foraging efficiency with time in all types of environments (Fig. 3E; GLMM_{one patch}: $Estimate =$
358 $3.05e-02$, $95\%CI = 2.91e-02 | 3.19e-02$; GLMM_{two patches}: $Estimate = 3.05e-02$, $95\%CI = 2.91e-02 | 3.19e-02$;
359 GLMM_{three patches}: $Estimate = 1.85e-02$, $95\%CI = 1.73e-02 | 1.98e-02$). With positive reinforcement only
360 (model 1), bees increased their cumulated foraging efficiency in environments with one patch (Fig. 3E;

361 GLMM_{one patch}: *Estimate* = 3.24e-02, 95%*CI* = 3.11e-02 | 3.37e-02), but decreased or maintained low levels
362 in environments with two or three patches (Fig. 3E; GLMM_{two patches}: *Estimate* = -5.05e-03, 95%*CI* = -6.33e-
363 03 | -3.76e-03; GLMM_{three patches}: *Estimate* = 3.07e-03, 95%*CI* = -1.42e-03 | 4.32e-03). Cumulated foraging
364 efficiency thus follows the same pattern as resource partitioning. Note that bees can reach higher levels in
365 environments with one patch than in environments with two or three patches because the probability to
366 encounter new flowers within a patch is higher in environments with one patch.

367

368 **Discussion**

369 Central place foraging animals exploiting patchily distributed resources that replenish over time are expected
370 to develop foraging routes minimizing travel distances and interactions with competitors (Possingham 1989;
371 Ohashi and Thompson 2005; Lihoreau *et al.* 2016). Here we developed a cognitively plausible agent-based
372 model to explore the behavioral mechanisms leading to resource partitioning between traplining bees. In the
373 model, bees learn to develop routes as a consequence of feedback loops that modify the probabilities of
374 moving between flowers. While a positive reinforcement of route segments leading to rewarding flowers is
375 sufficient for resource partitioning to develop when resources are evenly distributed, a negative
376 reinforcement of route segments leading to unrewarding flowers is necessary in environments with patchily
377 distributed resources.

378 When considering bees foraging among uniformly distributed plant resources (one patch), the initial
379 probabilities to encounter each resource are similar (Fig. S6), and the likelihood of bees to discover new
380 rewarding resources after encountering unrewarding ones is high. Consequently, two bees are very likely,
381 over time, to learn non-overlapping foraging routes and show resource partitioning. However, in
382 environments with non-uniformly distributed resources (two or three patches), the added spatial complexity
383 can interfere with this process. The initial likelihood of moving between distant patches is relatively low.
384 Thus, the only implementation of positive reinforcement for route segments to rewarded flowers, often does
385 not enable bees to explore all possible patches, so that the paths of competing bees overlap and interfere
386 within a subset of the available patches. Adding a negative reinforcement for route segments to unrewarded
387 flowers increases aversion for these flowers, the spatial segregation of foraging paths between competing
388 bees and the collective exploitation of all available patches, even if the initial probabilities of moving to

389 distant patches are low. This interplay between the influences of positive and negative experiences at flowers
390 on the spatial and competitive decisions of bees is in accordance with behavioral observations (Lihoreau *et al.*
391 2016; Pasquaretta *et al.* 2019).

392 The need of negative reinforcement rules to enhance discrimination between different options or
393 stimuli is well known in both learning theory and behavioral studies (Beshers and Fewell 2001; Garrison *et al.*
394 *al.* 2018; Kazakova *et al.* 2020). This is especially notable in collective decisions making by groups of
395 animals and robots (Sumpter 2010), where negative feedbacks enable individuals to make fast and flexible
396 decisions in response to changing environments (Robinson *et al.* 2005; Seeley *et al.* 2012). At the individual
397 level, negative experiences also modulate learning. For both honey bees and bumblebees, adding negative
398 reinforcement to a learning paradigm (e.g. quinine or salt in sucrose solution) enhances fine scale color
399 discrimination (Avarguès-Weber *et al.* 2010) and performances in cognitive tasks requiring learning of rules
400 of non-elemental associations (Giurfa 2004). The insect brain contains multiple distinct neuromodulatory
401 systems that independently modulate negative and positive reinforcement (Schwaerzel *et al.* 2003) and the
402 ability of bees to learn negative consequences is well-established (Vergoz *et al.* 2007). Even so, the utility of
403 negative reinforcement to enhance efficient route learning and the consequences of this for the emergence of
404 effective resource partitioning has not been commented on previously. It may be that this is a general
405 phenomenon with applicability to other resource partitioning systems.

406 Our study implies that some very simple learning and interaction rules are sufficient for trapline
407 formation and resource partitioning to emerge in bee populations. Several improvements of the model could
408 be considered for future theoretical and experimental investigations of bee spatial foraging movements and
409 interactions, for instance by implementing documented inter-individual variability in cognitive abilities and
410 spatial strategies of bees (Chittka *et al.* 2003; Raine and Chittka 2012; Klein *et al.* 2017), the variability in
411 the nutritional quality of resources (Wright *et al.* 2018; Hendriksma *et al.* 2019) and the specific needs of
412 each colony (Kraus *et al.* 2019), or the well-known ability of bees to use chemical (Leadbeater and Chittka
413 2005) and visual (Dunlap *et al.* 2016) social information to decide whether to visit or avoid flowers. For
414 instance, it is well-known that foragers of many species of bees leave chemical cues as footprints on the
415 flowers they have visited (bumblebees and honeybees: Stout and Goulson 2001; several species of solitary
416 bees: Yokoi and Fujisaki 2009). Bees learn to associate the presence or absence of a reward to these
417 footprints and to revisit or avoid scented flowers (Leadbeater and Chittka 2011). Such a pheromone system is

418 an advantageous signal for all participants in the interaction (Stout and Goulson 2001). Our model suggests
419 that this additional information could significantly enhance the negative value experienced by a bee thus
420 increasing resource partitioning to the benefit of all bees coexisting in the patch (Appendix S3), even of
421 different species that learn to use these cues (Stout and Goulson 2001; Dawson and Chittka 2013).

422 Our agent-based model thus builds on previous attempts to simulate trapline foraging by individual
423 bees (Lihoreau *et al.* 2012b, Reynolds *et al.* 2013; LeMoël *et al.* 2019) and fills a major gap of current
424 pollinator population dynamic models (Becher *et al.* 2014; 2016; 2018). As such, it constitutes a unique
425 theoretical modeling framework to explore the spatial foraging movements and interactions of bees in
426 ecologically relevant conditions within and between plant patches. This holds considerable promising tool to
427 guide novel experiments in a wide range of pollinators exhibiting routing behavior. It can readily be used to
428 test predictions with more than two bees (see examples Video S1 and Appendix S3), several colonies, or
429 even different species of bees (e.g. honey bees) and may be used to complement current predictions about
430 pollinator population dynamics (Becher *et al.* 2014; 2016; 2018). Ultimately, the robust predictions of the
431 spatial movements and interactions of bees over large spatio-temporal scales, through experimental
432 validations of the model, has the potential to help illuminate the influence of bees on plant reproduction
433 patterns and pollination efficiency (Ohashi and Thomson 2009).

434

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438

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444

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446

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600

601

602 **Figure legends**

603 **Figure 1.** Flowchart summarizing the agent-based models (1 and 2). Rectangles represent actions performed
604 by a bee. Diamonds indicate conditional statements. Arrows connect the different modules. Colored
605 rectangles describe the negative reinforcement rule specific to model 2. R code is available in GitLab:
606 <https://gitlab.com/jgautrais/resourcepartitioninginbees/-/releases>

607

608 **Figure 2.** Comparisons of route qualities (A) and similarities (B) between simulations and experimental data
609 for one forager (positive array of flowers as in Lihoreau *et al.* 2012b). Model 1: positive reinforcement only.
610 Model 2: positive and negative reinforcements. For each dataset, we show the estimated average trends
611 across foraging bouts (colored curves), along with their 95% CI (gray areas). For the sake of eye comparison,
612 in the simulation plot we represent estimated 95% confidence intervals for a random subsample of 7
613 simulated bees ($N = 7$ bees in Lihoreau *et al.* 2012b). Average trends were estimated over 100 simulation
614 runs, using GLMM Binomial model with bee identity as random effect (bee identity nested in simulation
615 identity for simulated data).

616

617 **Figure 3.** Results of simulations with two foragers in environments with 10 flowers. Light blue: simulations
618 with positive reinforcement only (model 1). Dark blue: simulations with positive and negative reinforcement
619 (model 2). The x axis is the number of completed foraging bouts by the two foragers. The y axis represents
620 respectively: A) the estimated mean frequency of visits to empty flowers; B) the estimated mean frequency
621 of encounters on flowers; C) the similarity index SI_{ab} between two successive flower visitation sequences;
622 D) the index of resource partitioning Q_{norm} (0: both bees visit the same set of flowers; 1: bees do not visit
623 any flower in common); E) the collective foraging efficiency index QL_{group} . Average trends for each model
624 are estimated across all types of environments (one patch, two patches and three patches; see Fig S2).

625

626

627

628

629 **Supplementary materials**

630

631 **Appendix S1.** *Sensitivity analysis of positive and negative reinforcements.*

632 We ran a sensitivity analyses for the two main parameters: the positive and negative reinforcement. As we
633 had no a priori understanding of how the model behaved with different values of the two main parameters of
634 the model (positive and negative reinforcement), we explored the spectrum of potential outcomes with
635 different sets of parameters. We ran simulations on ranges of positive (1, 1.2, 1.4, 1.6, 1.8, 2) and negative (0,
636 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1) reinforcement factors for a total of 66 sets of parameters, for each
637 environment type explored (one, two and three patches, Fig. S2). We simulated 10 environments for each
638 environment type and computed 100 simulations of 50 foraging bouts per iteration (i.e. 1000 simulations per
639 environment type and set of parameters).

640 Since our observations focused on resource partitioning, we extracted the Q_{norm} index values for
641 these simulations and compared them. We plotted a heatmap showing the value of the mean Q_{norm} index at
642 the last foraging bout for each set of parameters and environment type (Fig. S3). In all types of environments,
643 the positive reinforcement has a strong effect on the final Q_{norm} index value. High values of resource parti-
644 tioning are obtained for positive reinforcement values > 1.5 . For the negative reinforcement factor, however,
645 it appears that high values of resource partitioning were obtained for negative reinforcement values larger
646 than 0.75. Negative reinforcement has little to no impact on the environment type with only one patch.

647 We also looked at how this same index evolved over successive foraging bouts, for each pair of
648 bees. Fig. S4 shows the dynamics of mean Q_{norm} index across 50 foraging bouts for each combination of
649 positive reinforcement (1.0, 1.2, 1.4, 1.6, 1.8, 2.0) and negative reinforcement (0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6,
650 0.7, 0.8, 0.9, 1) parameters, and each environment type (one patch, two patches, three patches). Higher val-
651 ues of both positive and negative reinforcement factors most often lead to faster resource partitioning (with
652 some uncertainty due to the probabilistic nature of the model). Combinations of values in which the negative
653 reinforcement factor is missing (violet gradient curves) led to a decrease in partitioning.

654

655

656 **Appendix S2.** *Qualitative analysis for the negative array case.*

657 We ran simulations with one forager to compare model outcomes to observational data using a second
658 reference field study (Woodgate *et al.* 2017). In this study, the authors used a ‘negative array’ (narrow
659 pentagon, Fig. S1B) in which the distance between flowers and the directionality of movement were
660 negatively linked, i.e. moving between nearest neighbor flowers required bees to make sharp deviations
661 between consecutive vectors. Four bumblebees were tested during 27 to 61 foraging bouts each (flower
662 visitation sequences were provided by Joe Woodgate). One of these bumblebees was tested over different
663 days and was therefore removed from the analyses. In these conditions, none of the bumblebees developed a
664 stable trapline, although all individuals significantly increased their foraging efficiency with time (e.g.
665 reduced travel distance and duration, increased similarity between two consecutive flower visitation
666 sequences).

667 The addition of a negative reinforcement had no major effect on route quality nor on route
668 similarity trends (Fig. S5). Model simulations showed good qualitative fit the traplining behavior observed in
669 real bees exploiting a negative array of flowers – i.e. there is a trend of increasing route similarities across
670 foraging bouts. Note however that the model tends to overestimate the bee ability to develop stable routes in
671 arrays of flowers where proximity and directionality are negatively linked (Woodgate *et al.* 2017). This
672 imperfect match could be due to the low amount of available experimental data (three individuals in
673 Woodgate *et al.* 2017). Alternately, the model does not integrate any kind of stochastic exploration so that at
674 each new step, bees do not provide the possibility to choose unknown spatial targets. Real bees, on the
675 contrary, show phases of stochastic explorations during and after trapline formation (Woodgate *et al.* 2017;
676 Kembro *et al.* 2019). Future experiments with more bees in a larger diversity of arrays of flowers will be
677 useful to further quantitatively calibrate the model.

678

679 **Appendix S3. Predictions with more than two bees.**

680 Here we explored the emergence of resource partitioning in groups of 5 bees, and how this varies as a
681 consequence of number of available flowers and number of foraging bees in environments of 20, 25, 30, 40,
682 50, 70 and 100 flowers, thus encompassing a gradient of competition pressures from conditions where there
683 is not enough flowers for all bees (20) to conditions where there is four times more flowers than necessary
684 for all bees (100). For simplicity, in all these environments, flowers were evenly distributed (i.e. environment
685 with one patch). The positive reinforcement factor was set at 1.5, and the negative reinforcement factor was

686 set at 0.75. For each flower density, we generated 10 environments, and ran 100 simulations of 100 foraging
687 bouts, for a total of 1000 simulations per density value. We extracted the resource partitioning index (Q_{norm})
688 at each foraging bout. Unsurprisingly, the mean final Q_{norm} was higher in environments with most flowers
689 (Fig. S7). Plotting the mean final Q_{norm} (final foraging bout) as a function of the number of available
690 flowers confirms that bees converge to a plateau where increasing the number of flowers only provokes
691 increase of partitioning (i.e. around 50 flowers) (Fig. S7).

692

693

694 **Figure S1.** Arrays of artificial flowers for the experimental dataset. A. ‘Positive array’ (regular pentagon) in
695 which the distance between flowers and the directionality of movement are positively linked, i.e. nearest
696 neighbor flowers can be linked using lowest angular deviation between consecutive vectors. Modified from
697 Lihoreau *et al.* (2012b). B. ‘negative array’ (narrow pentagon) in which the distance between flowers and the
698 directionality of movement are negatively linked, i.e. moving between nearest neighbor flowers requires bees
699 to make sharp deviations between consecutive vectors. Modified from Woodgate *et al.* (2017)

700

701 **Figure S2.** Examples of simulated environments. Distribution of 10 flowers (gray circles) and a nest (black
702 pentagon) in three environments defined by different levels of resource patchiness. A flower patch was
703 characterized by: 1) a uniform distribution of flowers, 2) a lower distance between flowers within the patch
704 than between all flowers from different patches.

705

706 **Figure S3** Heatmap showing the mean Q_{norm} Index value after 50 foraging bouts (mean over 1000 simula-
707 tions on 10 arrays of the same environment type), for each combination of positive reinforcement (1.0, 1.2,
708 1.4, 1.6, 1.8, 2.0) and negative reinforcement (0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1) parameters, and
709 for each environment type (one patch, two patches, three patches). For simplicity we inverted the values of
710 negative reinforcement here. 0 being models without negative reinforcement.

711

712 **Figure S4.** Dynamic of the mean Q_{norm} Index across foraging bouts for each combination of positive (1.0,
713 1.2, 1.4, 1.6, 1.8, 2.0) and negative (0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1) reinforcement factors and

714 for each environment type (one patch, two patches, three patches). For simplicity we inverted the values of
715 negative reinforcement here. 0 being models without negative reinforcement.

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719 **Figure S5.** Qualitative comparisons of route qualities (A) and similarities (B) between simulations and
720 experimental data (negative array of flowers as in Woodgate *et al.* 2017) for one forager. Light blue:
721 simulations with positive reinforcement only (model 1). Dark blue: simulations with positive and negative
722 reinforcement (model 2). For each dataset, we show the estimated average trends across foraging bouts
723 (colored curves), along with their 95% CI (gray areas). For simplicity, in the simulation plot we only
724 represent a subsample of three random bees with their estimated 95% CI. Average trends were estimated
725 using GLMM Binomial model with bee identity as random effect (bee identity nested in simulation identity
726 for simulated data).

727

728 **Figure S6.** Boxplot representing the distribution of the initial probabilities of visiting each flower in different
729 environments (one patch with uniformly distributed flowers; two patches with five uniformly distributed
730 flowers per patch; three patches of five, three and two uniformly distributed flowers; see examples Fig. S1).
731 Median (solid horizontal line), first and third quartiles (box) and maximum and minimum values are
732 represented.

733

734 **Figure S7.** Evolution of the mean final Q_{norm} index (after 100 foraging bouts) as a function of increase
735 resources availability. The model run has the positive reinforcement factor set at 1.5, and the negative rein-
736 forcement factor set at 0.75 with 5 bees in environments of one patch.

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738 **Video S1.** Example of simulation of five bees foraging in an environment with one patch of 50 flowers. Both
739 positive and negative reinforcement rules are implemented (model 2). Bees performed 100 foraging bouts.

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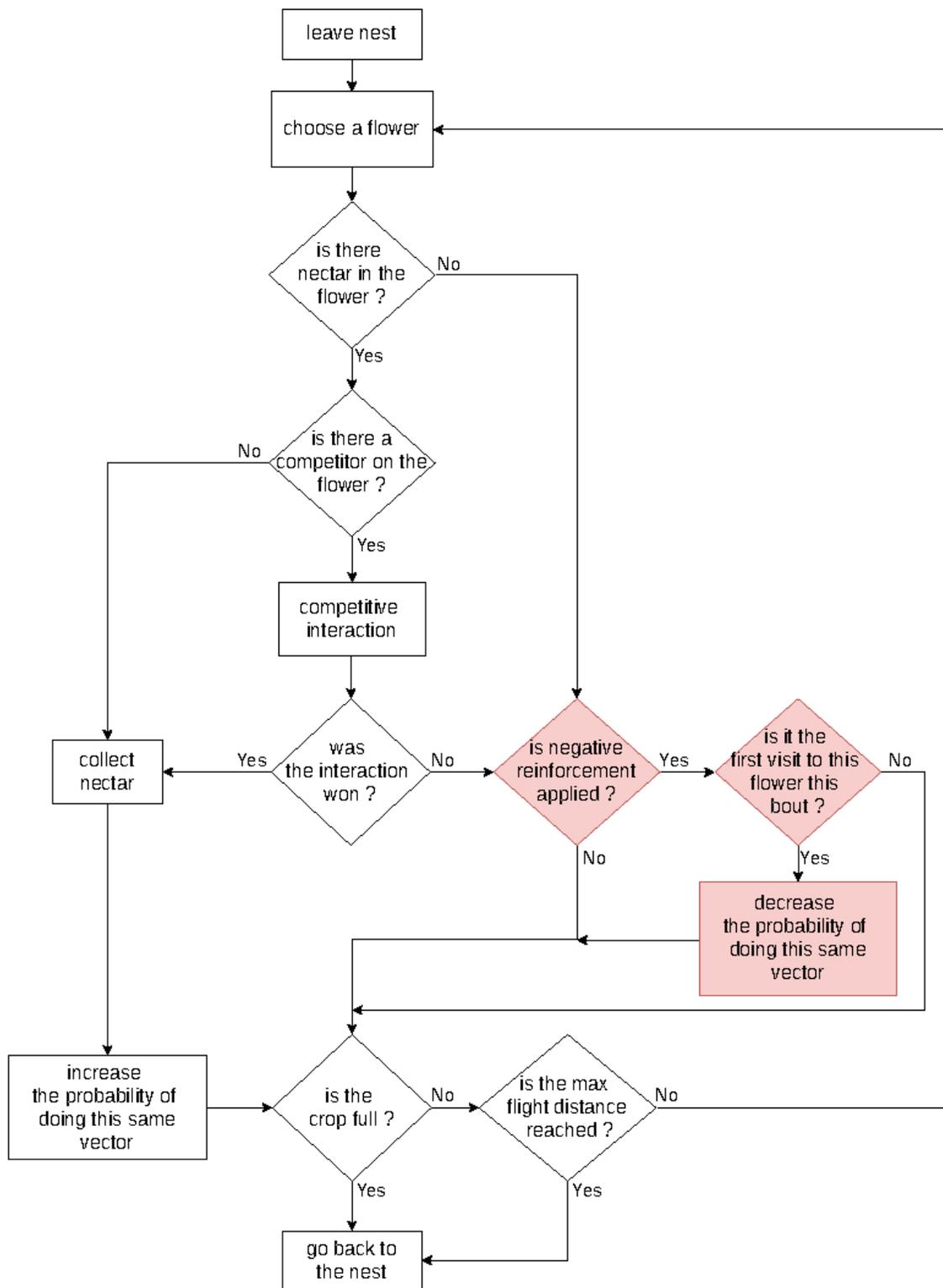
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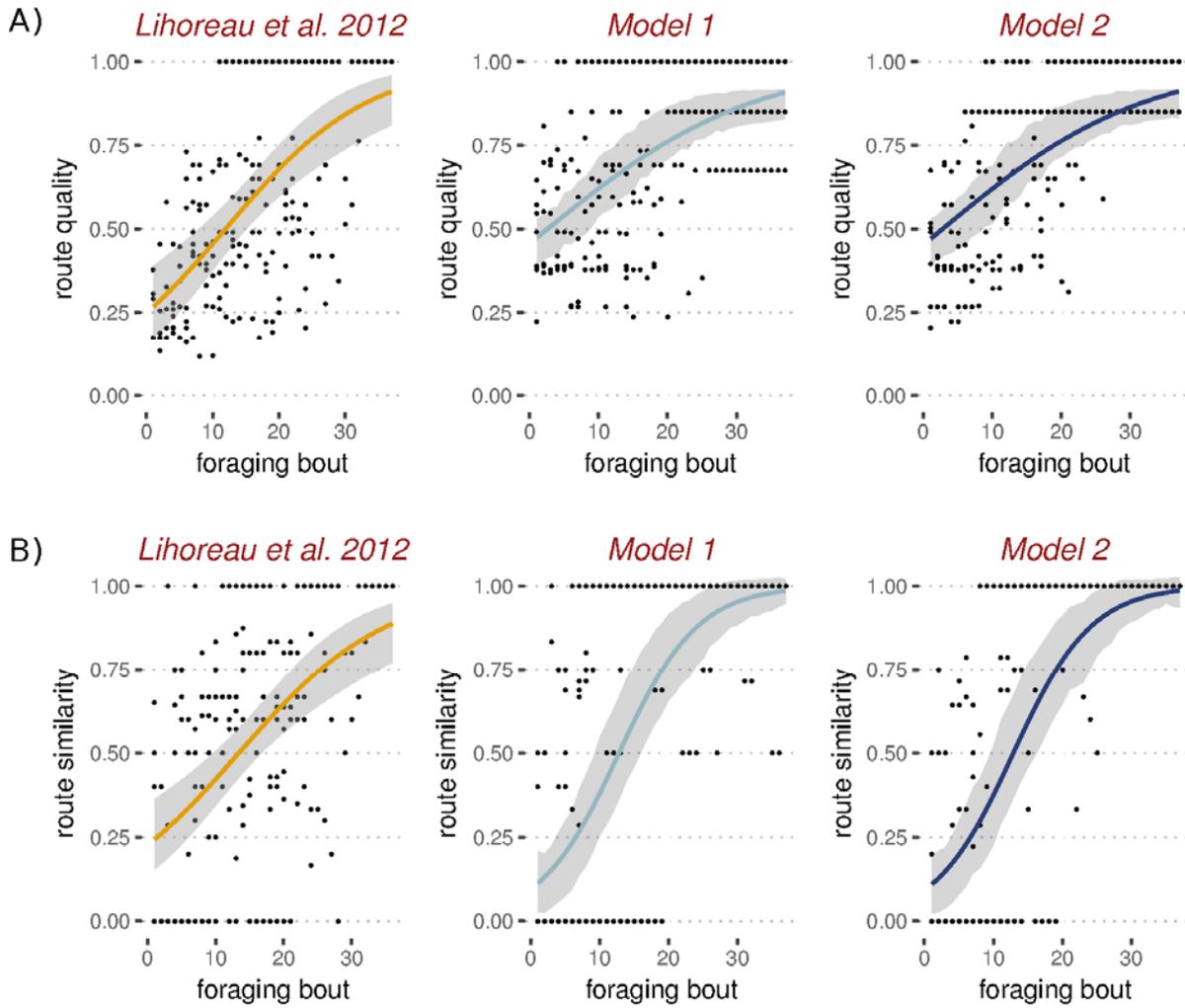
760 **Figure 1**



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762 **Figure 2**

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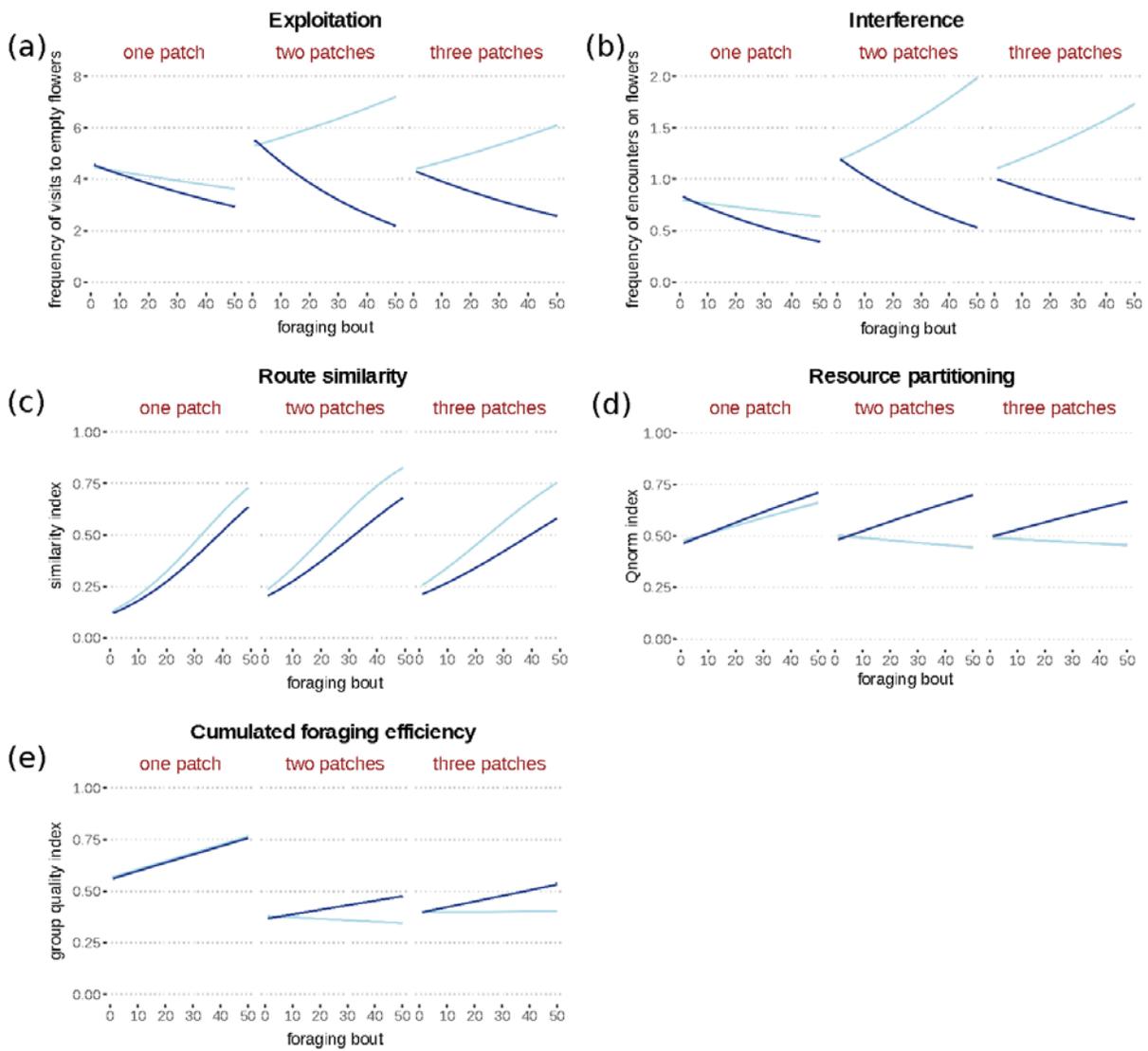
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773 **Figure 3**

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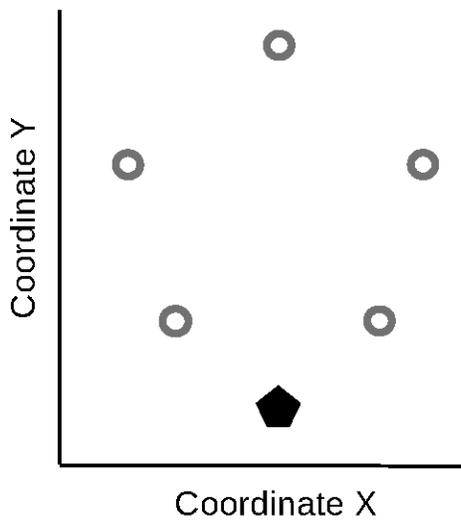
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782 **Figure S1**

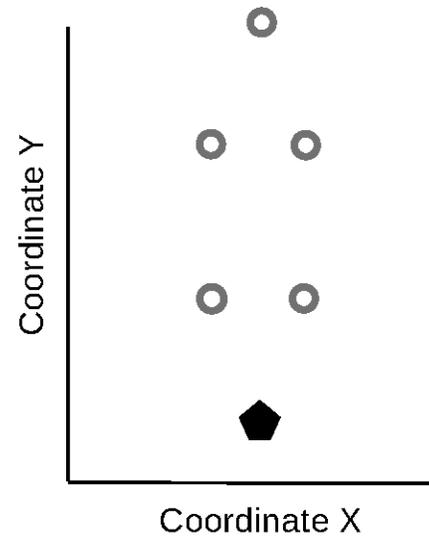
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A. Lihoreau et al. 2012b



Positive array

B. Woodgate et al. 2017



Negative array

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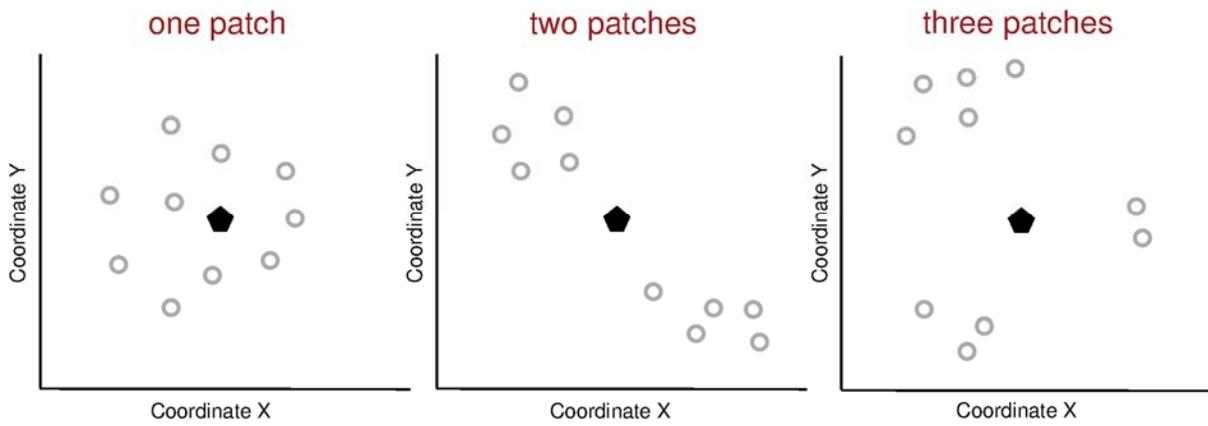
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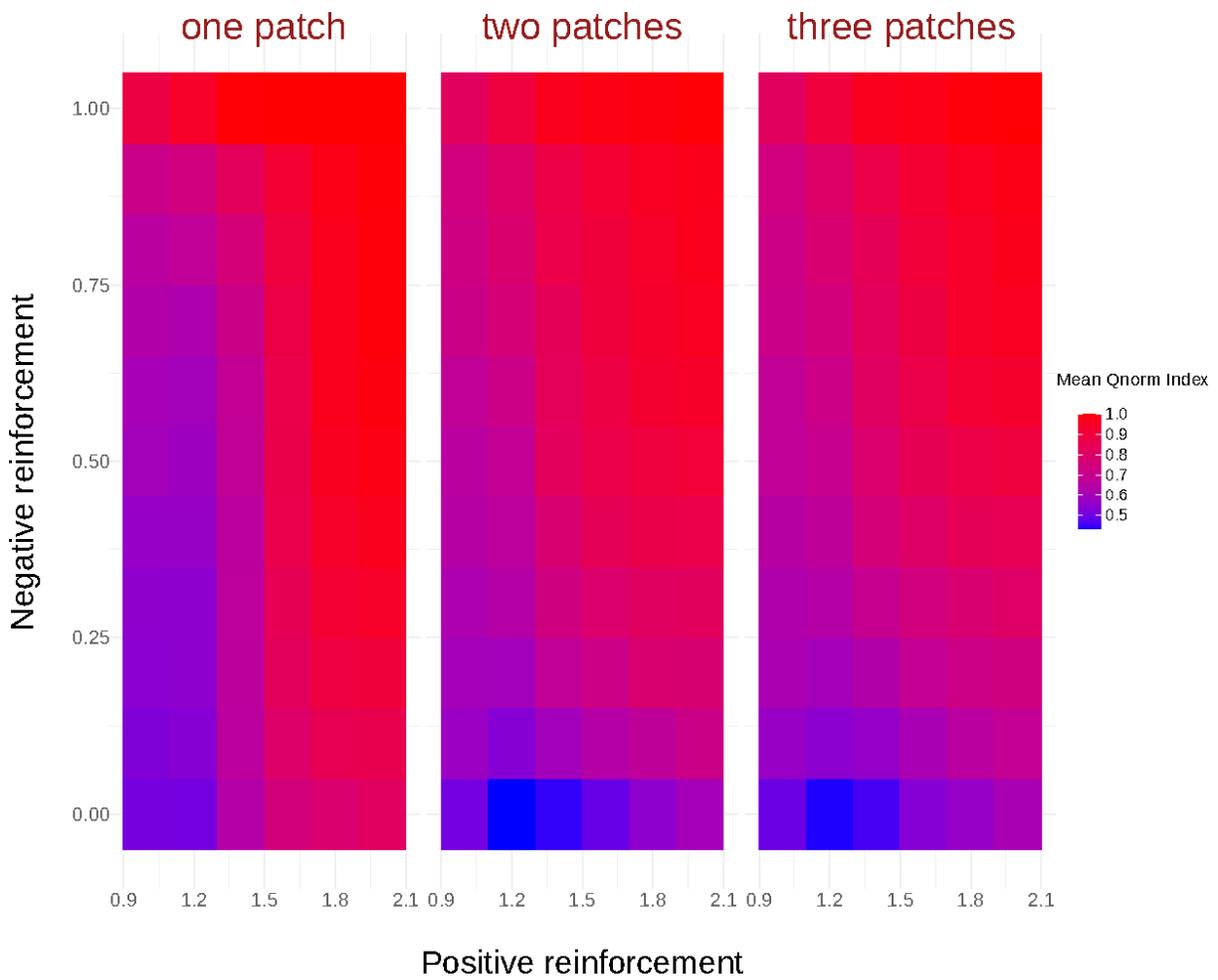
798 **Figure S2**

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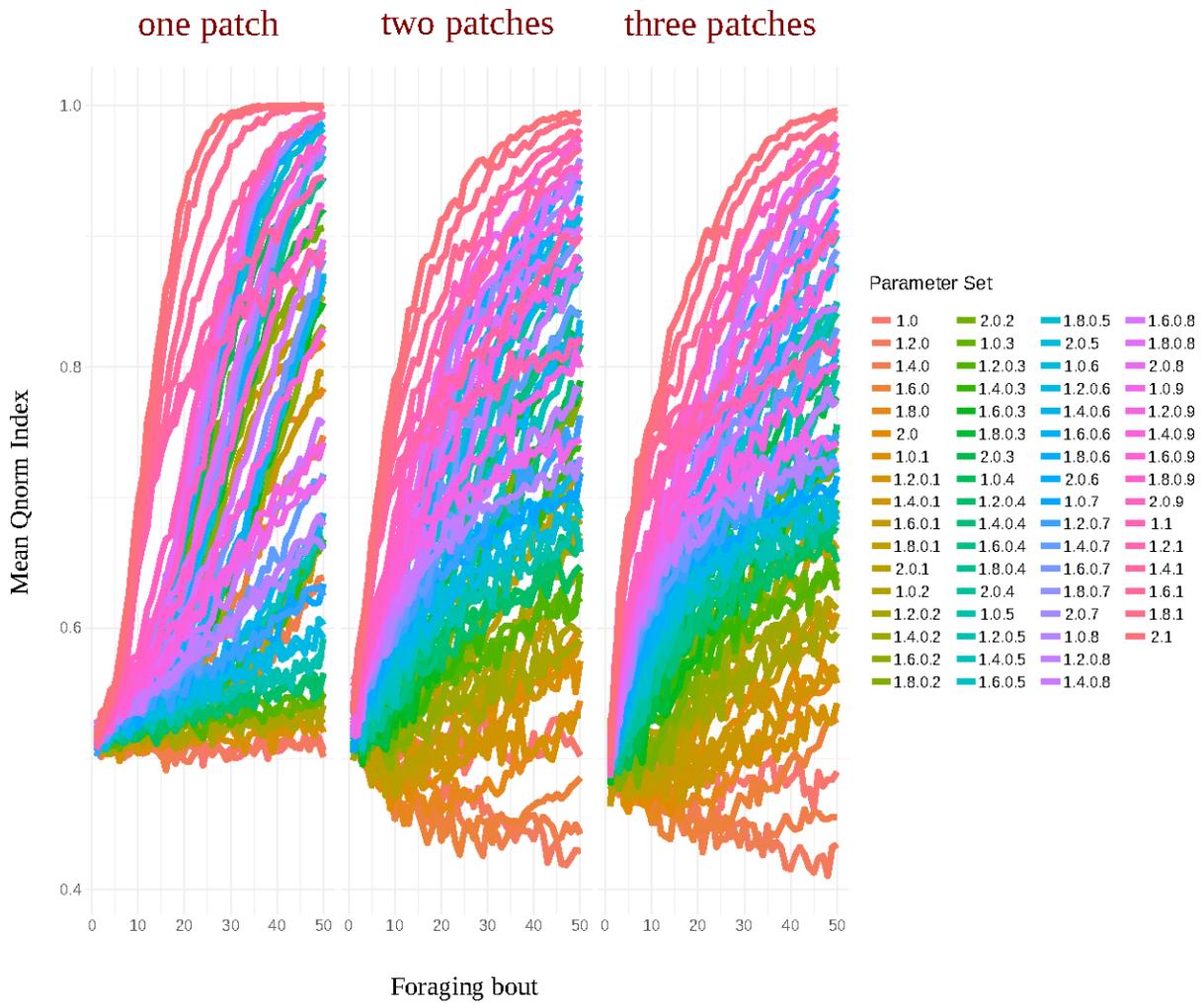
801 **Figure S3**



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803 **Figure S4**

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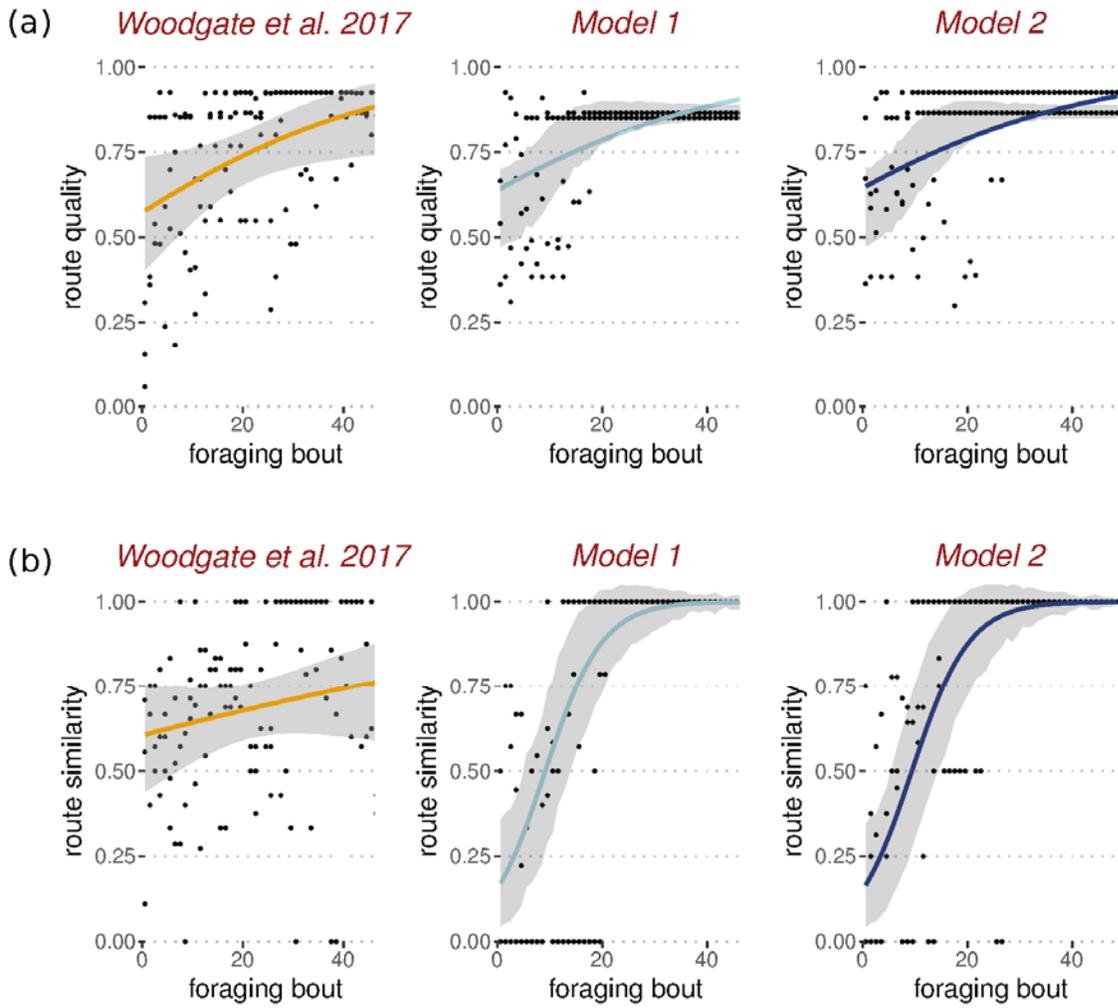
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814 **Figure S5**

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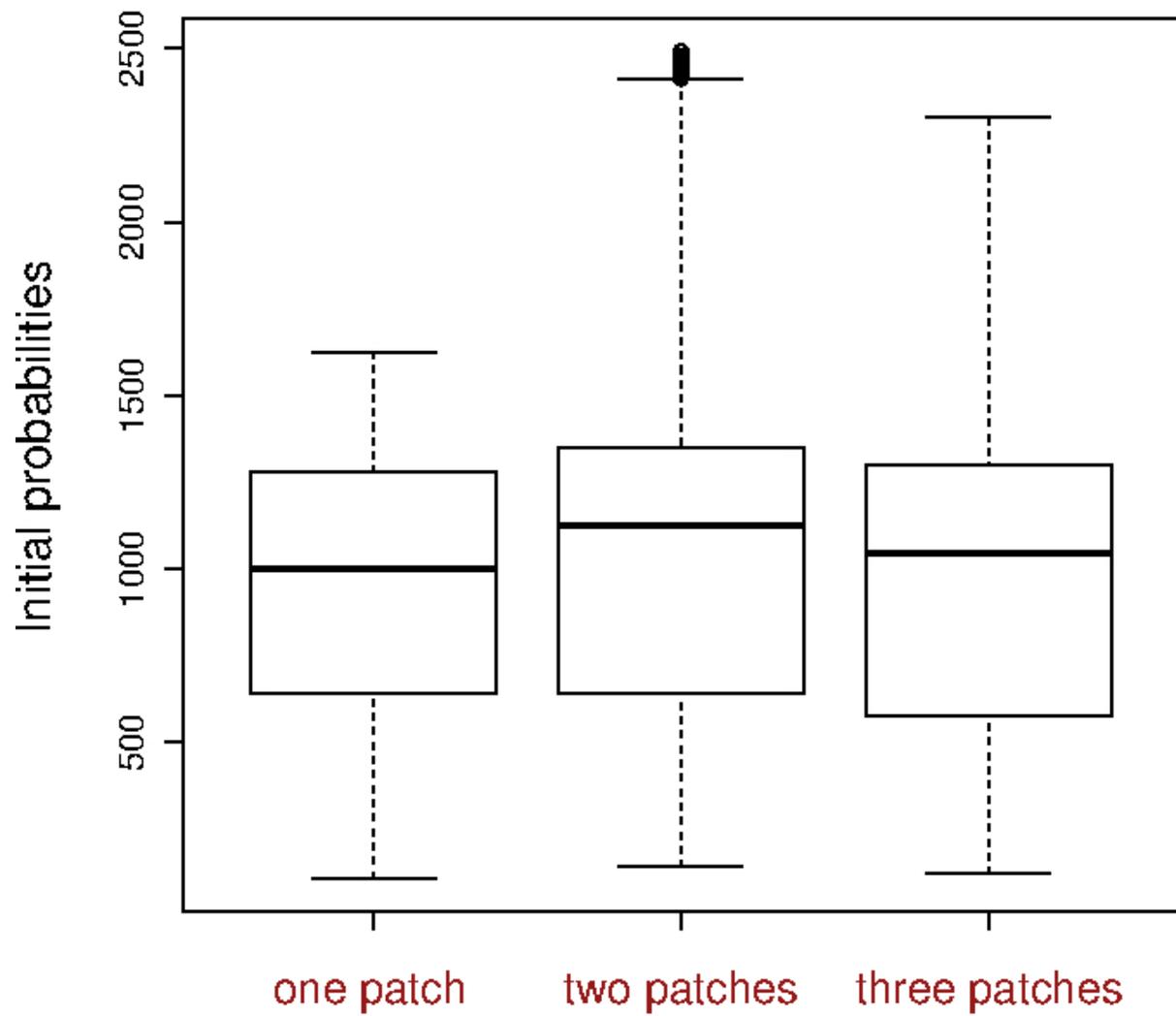
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825 **Figure S6**

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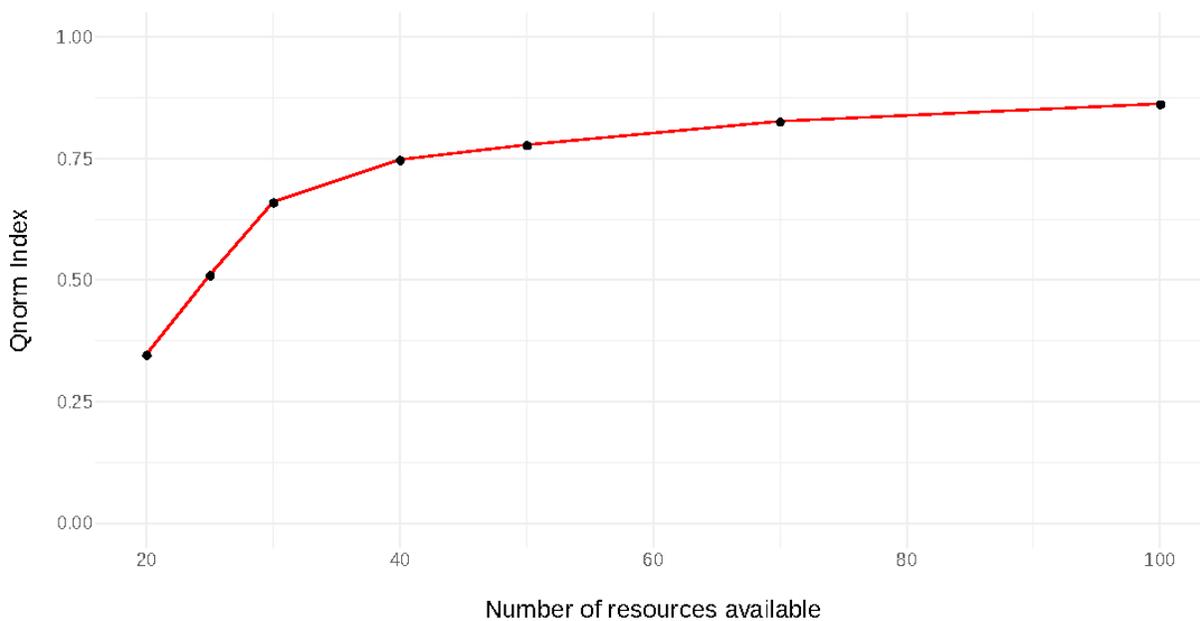
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835 **Figure S7**



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