1 When should bees be flower constant? An agent-based model

2 highlights the importance of social information and foraging

3 conditions

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10 **Abstract**

11 1. Many bee species show flower constancy, *i.e.* a tendency to visit flowers of one type

12   during a foraging trip. Flower constancy is important for plant reproduction, but whether

13   bees also benefit from flower constancy remains unclear. Social bees, which often use

14   communication about food sources, show particularly strong flower constancy.

15 2. We hypothesised that the sharing of social information increases the benefits of flower

16   constancy because foragers share information selectively about high-quality food

17   sources, thereby reducing the need to sample alternatives. We also asked if foraging

18   landscapes affect flower constancy. We developed an agent-based model that allowed

19   us to simulate bee colonies with and without communication and flower constancy in

20   different foraging environments.

21 3. Flower constancy alone performed poorly in all environments, while indiscriminate

22   flower choice was often the most successful strategy. However, communication

23   improved the performance of flower constant colonies in nearly all tested environments.

24   This combination was particularly successful when high-quality food sources were

25   abundant and competition was weak.

26   4. Our findings help explain why social bees tend to be more flower constant than solitary

27   bees and suggest that flower constancy can be an adaptive strategy in social bees.

28   Simulations suggest that anthropogenic changes of foraging landscapes will have

29   different effects on the foraging performance of bees that vary in flower constancy.

30

31   **Introduction**

32   Most flowering plant species are animal pollinated and bees, in particular, are important

33   pollinators of wild and agricultural plants (Bawa, 1990; Klein et al., 2007; Ollerton et al., 2011).

34   Several biological features explain why bees are helpful agents of reproduction for plants,

35   including their abundance and their often broad (*i.e.* polylectic) diet in combination with a

36   tendency to specialise on a particular flower type during an individual foraging bout. The latter

37   behaviour, called flower constancy (Bateman, 1951; Chittka et al., 1999; Darwin, 1876; Grüter

38   & Ratnieks, 2011; Waser, 1986), reduces conspecific pollen loss and heterospecific pollen

39   deposition, both of which can reduce plant fitness (Ashman & Arceo-Gómez, 2013; Campbell

40   & Motten, 1985; Chittka et al., 1999; Morales & Traveset, 2008; Waser, 1986). Flower

41   constancy is also thought to enhance the coexistence of different plant species and, thus, shapes

42   plant community structure (Morales & Traveset, 2008; Song & Feldman, 2014).

43   From a pollinator perspective, however, the benefits of flower constancy are less

44   obvious. Ignoring potentially superior flower species appears to contradict optimal foraging

45   theory (King & Marshall, 2022; Latty & Trueblood, 2020; Waser, 1986; Wells & Wells, 1983,

46   1986). Why then are pollinators flower constant? The most widely accepted view is that flower

47   constancy is driven by cognitive limitations, which can include (*i*) slow learning to forage

48   efficiently on a new flower species, (*ii*) an inability to memorise more than one or a few flower

49   types, (*iii*) unstable short-term memories which are prone to being erased by competing

50   information or (*iv*) an inability to retrieve long-term memory about different flower species fast

51   enough to be an efficient generalist (Darwin, 1876; Heinrich, 1979; Lewis, 1986; Menzel, 1999;

52   Raine & Chittka, 2007; Waser, 1986; for reviews see Chittka et al., 1999; Grüter & Ratnieks,

53   2011). These cognitive limitations are likely to cause time delays as a bee tries to extract nectar

54   from a flower after switching from a different species and they may increase switching times

55   (Chittka et al., 1999; Goulson et al., 1997; Lewis, 1986; Raine & Chittka, 2007).

56   The "cognitive limitations hypothesis" as an explanation for flower constancy is not

57   without challenges. Given that efficient foraging is likely to be under strong natural selection

58   due to its effects on reproductive success (Heinrich, 1979), why does natural selection not lead

59   to the evolution of lower flower constancy in all bees? How can we explain the finding that

60   individual bees often show plasticity in their flower constancy, e.g. by being more flower

61   constant after finding good rewards (Chittka et al., 1997; Grüter et al., 2011; Wells & Rathore,

62   1994; but see Hill et al., 1997) or the distances between food sources are shorter (Gegear &

63   Thomson, 2004; Kunin, 1993; Mardern & Waddington, 1981)? Why do bee species vary in

64   their degree of flower constancy? Social bees, in particular, are often highly flower constant

65   (Cholis et al., 2020; Free, 1963; Heinrich, 1976, 1979; Hill et al., 1997; Kozuharova, 2018;

66   Pangestika et al., 2017; Rossi et al., 2015; Slaa et al., 2003; White et al., 2001; but see Martínez-

67   Bauer et al., 2021), while flower constancy seems to be less pronounced in solitary bees

68   (Bateman, 1951; Campbell & Motten, 1985; Eckhardt et al., 2014; Jakobsson et al., 2008; Pohl

69   et al., 2011; Smith et al., 2019; Waser, 1986; Williams & Tepedino, 2003). Smith et al. (2019),

70   for example, studied pollen composition of 56 bee species and found that individual social bees

71   showed a higher degree of specialisation during a foraging bout than solitary species. Different

72   ecological needs could explain this difference. Solitary bees need to collect all required

73   nutrients by themselves, potentially favouring a strategy of mixing resources during a foraging

74   trip even if this has energetic costs (e.g. Eckhardt et al., 2014; Williams & Tepedino, 2003). In

75   social species, on the other hand, different bees from the same colony can specialise on different

76   types of resources and flower species to cover their nutritional needs.

77   Foragers of many social bees share information about profitable food sources, and this

78   could affect the value of flower constancy. Honeybees use the waggle dance to indicate the

79   odour (type) and location of profitable food sources (von Frisch, 1967) and some stingless bees

80   lay pheromone trails (Grüter, 2020; Jarau, 2009; Lindauer & Kerr, 1960; Nieh, 2004). Stingless

81   bees and bumblebees inform nestmates about the availability and odour of a good food source

82   by means of excitatory or jostling runs inside their nest (Dornhaus & Chittka, 2004; Hrncir,

83   2009). Trophallaxis – food transfer between bees – is performed by honey bees and stingless

84   bees (Farina et al., 2012; Farina & Grüter, 2009; Hart & Ratnieks, 2002; Hrncir et al., 2006;

85   Krausa et al., 2017; von Frisch, 1967) and is another behaviour that allows nestmates to learn

86   the odour of available food sources (Aguilar et al., 2005; Farina et al., 2005; Lindauer & Kerr,

87   1960; von Frisch, 1967). These different communication behaviours share two common

88   features. First, they depend on food quality. Dances, pheromone trails, jostling runs and

89   trophallaxes occur at higher frequencies if the exploited food sources are of higher quality

90   (Farina et al., 2012; Hrncir, 2009; Krausa et al., 2017; Lindauer & Kerr, 1960; von Frisch,

91   1967). Second, during these social interactions, nestmates can learn the odour of the exploited

92   flower species and acquire a preference for this flower species in the field.

93   Heinrich (1976) was probably the first to propose a link between recruitment

94   communication and flower constancy. Since recruiting bees share information selectively about

95   high-quality food sources, recruits can discover profitable flower types without the costs of

96   sampling different, lower-quality plant species. This does not require that foragers are able to

97   direct nestmates to a specific location, as in honeybees and some stingless bees, but depends

98   more generally on foragers biasing the food search towards flower types that are more

99   profitable. Among the social bees, bumble bees seem to be less flower constant that honey bees

100   (Bateman, 1951; Grant, 1950; Martínez-Bauer et al., 2021; Smith et al., 2019), possibly because

101   their communication system is less sophisticated than that of honey bees (Heinrich, 1976).

102   Experimental studies of the benefits of flower constancy and how they depend on social

103   and ecological traits are logistically challenging for several reasons. For example, it is often not

104   possible to manipulate the degree of flower constancy while keeping other factors constant.

105   Agent-based simulation models can be a useful complementary tool to evaluate how biological

106   and ecological factors affect the benefits of a behavioural strategy. We developed an agent-

107   based simulation model to test the hypothesis that flower constancy is more beneficial in bees

108   that communicate about profitable food sources than in bees without communication. Colonies

109   consisting of virtual bees (agents) were either flower constant or they chose food sources

110   randomly (indiscriminately) in environments that varied in the number and quality of food

111   sources. Some studies have found that bees adjust the degree of flower constancy depending on

112   the foraging conditions, being more flower constant if the rewards on offer are better (Chittka

113   et al., 1997; Grüter et al., 2011; Wells & Rathore, 1994; but see Hill et al., 1997) and the

114   distances between food sources (or density) are shorter (Gegear & Thomson, 2004; Kunin,

115   1993; Marden & Waddington, 1981). We, therefore, expected flower constancy to be more

116   beneficial in environments with more flowers and larger reward sizes. Exploitation competition,

117   on the other hand, is expected to favour a indiscriminate choice because greater competition

118   increases the costs of rejecting a reward (Pulliam, 1974).

119

120   **The model**

121   We built an agent-based model (ABM) using the programming software NetLogo 6.1

122   (Wilensky, 1999) (see supplementary material for NetLogo file). It is an extension and further

123   analysis of the model developed in Grüter & Hayes (in preparation), which analysed foraging

124   distances. The model simulates an environment with a colony surrounded by food sources. The

125   agents ("bees") operate on a two-dimensional square grid with 400 x 400 patches. A single

126   patch length corresponds to 5 meters and 1 tick corresponds to 1 second. Thus, the size of the

127   virtual world corresponds to 2 x 2 km. The nest of the colony is positioned in the centre of the

128   grid (x=0, y=0). In the default situation, environments contained two different flower types that

129   differed in the rewards they offered.

130   The model allows simulating a wide range of parameter values, but for the purpose of

131   this study we based our default parameters, such as the nest stay time (t_{nest}), flight speed (v_{flight}),

132   metabolic costs of flying (M_{cost}), and crop capacity (*Crop*) on the Western honeybee *Apis*

133   *mellifera* because we have accurate information about these relevant biological parameters in

134   *Apis mellifera*. Other values were tested (see Table 1 and section *Sensitivity analysis and model*

135   *exploration*).

136   Foragers in social bees use different behavioural mechanisms to transmit social

137   information and, thereby, influence the food source preferences of their nestmates (see

138   introduction). The model does not simulate a particular behaviour, but a generic process that

139   biases the food preferences of nestmates, which could correspond to jostling runs, trophallaxis

140   or the waggle dance.

141

142   *Entities and state variables*

143   <u>Bees</u>

144   The default colony size was 100 agents (forager bees), which corresponds to the size of the

145   forager pool in many species of bumble bees (Westphal et al., 2006) and stingless bees (Grüter,

146   2020). Agents could assume any of the following states: (1) *generalists*, (2) *feeding forager*,

147   (3) *searching forager*, (4) *returning forager*, (5) *inside-nest-worker* and (6) *influencer* (see Fig.

148   1).

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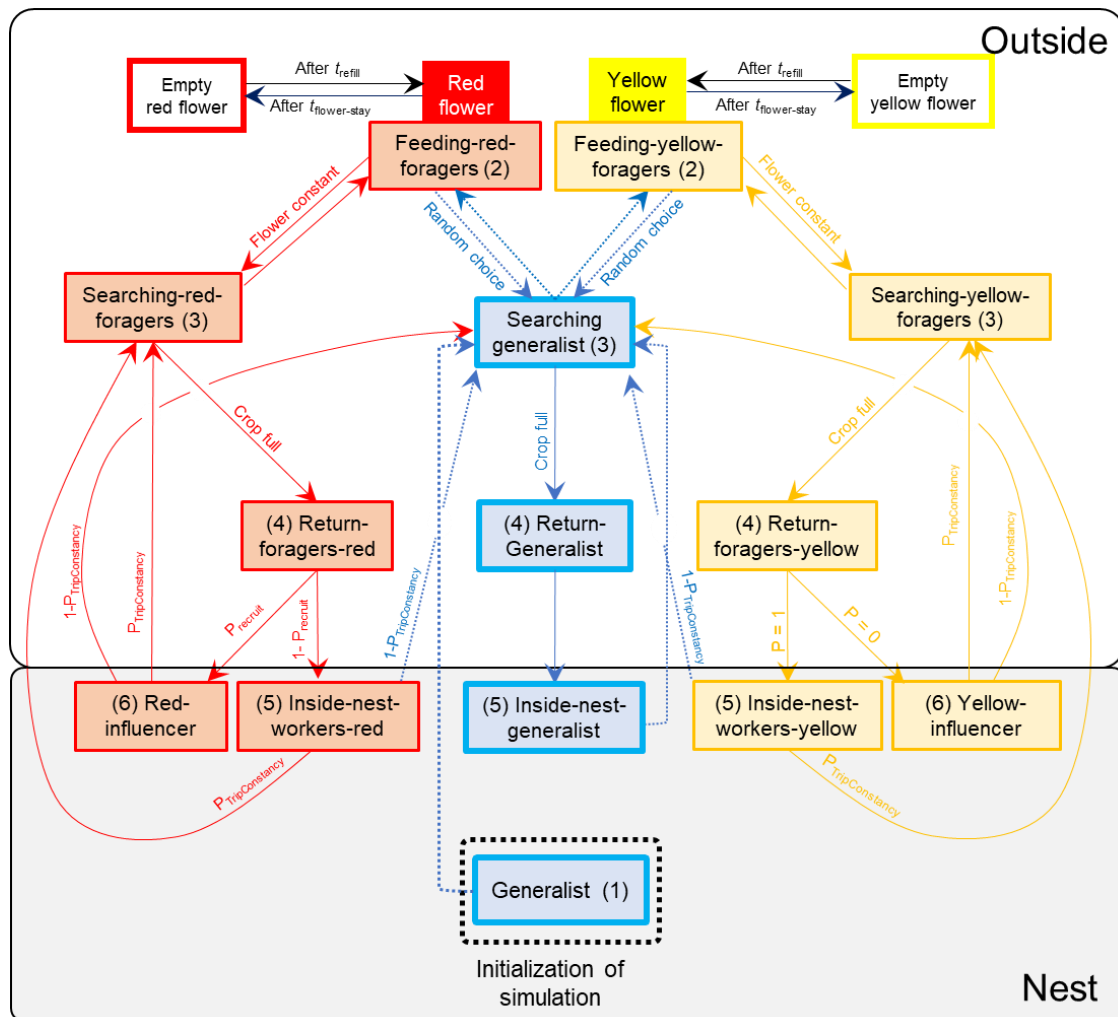
Fig. 1. State diagram showing the different states of the agents and the possible transitions between states. Here, yellow flowers were arbitrarily chosen to represent a lower-quality food source, therefore, the default probability that foragers visiting yellow flowers would become influencers after their return to the nest was 0.

Agents begin the simulation in the centre of the nest with energy = 0 as *generalists*. They then move at a flying speed of 1.4 patch/tick (v_{flight}), corresponding to a flight speed of *Apis mellifera* (7 m/sec, von Frisch 1967). Their random search behaviour follows a Lévy-flight pattern (with $\mu = 2.4$ as default) (Reynolds, 2009; Reynolds et al., 2007). A Lévy-flight consists of a random sequence of flight segments whose lengths, l, come from a probability distribution function having a power-law tail, $P(l) \sim l^{-\mu}$, with $1 < \mu < 3$ (Reynolds et al., 2007). The speed of agents moving inside the nest (v_{nest}) was arbitrarily chosen to be 0.1 (patch/tick). Flying has a

162   metabolic cost (M_{cost}) of 0.032 Joule (J) per tick in the default condition (Heinrich, 1975;

163   Willmer, 2011). Once an agent encounters a food source, they remain on the food source for 60

164   ticks ($t_{flower-stay}$) under default conditions (*feeding foragers*), irrespective of whether they were

165   choosing indiscriminately or are flower constant. Thus, we assume that the time spent handling

166   a flower or flowers in a patch and extracting the reward is the same for flower constant and

167   indiscriminate foragers. This was chosen as the default condition to explore whether flower

168   constancy can be an adaptive strategy in the absence of cognitive constraints.

169   The agent then continues to forage (*searching foragers*) until its crop is full, after which

170   it returns to the nest (*returning foragers*) to unload its energy and stay in the nest for 300 ticks

171   ($t_{nest-stay}$) (Farina, 2000; Seeley, 1986; von Frisch, 1967). In the default condition, only foragers

172   visiting the high-quality food source could become *influencers* (*i.e.* bees that bias the food

173   choice of other bees) upon return to the nest. *Influencers* target *inside-nest-workers* that are not

174   yet flower-constant to the high-quality food type by changing the latter's preference if they

175   encountered each other on same patch inside the nest. Following such an encounter, *inside-*

176   *nest-workers* become flower constancy for the high-quality type.

177   Since recruitment behaviours often depend on the food source distance (with greater

178   foraging distances lowering the probability of recruitment), we simulated recruitment curves

179   where the probability of becoming an *influencer* decreased with increasing distance of the last

180   visited food patch (Fig. S1).

181

182   *Food sources*

183   In the default condition, two different types of food sources can be found in the environment,

184   mimicking the typical situation in experimental flower constancy studies (e.g. Chittka et al.,

185   1997; Goulson & Wright, 1998; Grüter et al., 2011; Ishii & Masuda, 2014; Wells & Wells,

186   1983). The food source types differ in the rewards they offer per visit. Natural bee-visited

187   flowers offer between 0.1 and 10 µL of nectar per flower (Willmer, 2011, p. 203). For the

188 default condition, we chose 5μL (29.07 J) for the high-quality type and 2.5μL (14.535 J) for the

189 low-quality type. This reward could represent an individual flower that offers a large reward or

190 a small patch of several flowers, each offering smaller quantities, or it could represent a larger

191 patch of flowers that is shared by several bees.

192   We tested different refill times (t_{refill}) for food sources: 0, 1200 and 3600 ticks (Stout &

193 Goulson, 2002). When $t_{refill} = 0$, food sources became rewarding again immediately after the

194 visit of a bee. This simulates conditions under which bees have a high probability of finding a

195 reward after landing on food source, which might occasionally occur at food patches. With

196 $t_{refill} = 3600$, a food source (flower or patch) was empty for the equivalent of an hour after it had

197 been visited by a bee, leading to intense exploitation competition among bees. The number of

198 food sources per type in the simulated environment varied between 1500 (low abundance) and

199 4500 (high abundance). Default conditions simulated even numbers of food sources for both

200 food source types, but we also explored uneven food source abundances (Table 1). We

201 measured the average foraging distance of bees during a simulation run to confirm that the

202 simulated conditions led to naturally realistic average foraging distances for many social bees

203 (271 ± 130 m; range 63-581 m; N = 1800 simulations in default conditions) (Kohl et al., 2020;

204 Van Nieuwstadt & Iraheta, 1996; Walther-Hellwig & Frankl, 2000).

205   The energy collected by agents with a full crop was estimated in the following way:

206 *Apis mellifera* can carry up to ~70 μL of nectar in their crop, but they usually carry less (I'Anson

207 Price et al., 2019; Núñez, 1966). The crop load has been shown to depend on the quality of the

208 visited food source, with lower quality food sources leading to smaller crop loads (Núñez, 1966,

209 1970). Agents visiting the low-quality flower type foraged until their crop contained 25μL,

210 whereas agents visiting the high-quality food type collected 50μL per foraging trip. Generalist

211 bees that choose indiscriminately have an intermediate crop load, reflecting the relative number

212 of high- and low-quality food sources in the environment. For example, in an environment with

213 an even number of high- and low-quality food sources, they collect 37.5μL per foraging trip.

214   Sugar concentration of collected nectar varies considerably from c. 10-70% (I'Anson Price,

215   2018; Seeley, 1986; Willmer, 2011). We chose an average sugar concentration of 35%,

216   providing 5.814 J/μL.

217   Each simulation lasted 36,000 ticks (i.e. 10 hours), simulating a day with good foraging

218   conditions. We measured the total energy collected by a colony during this period divided by

219   the number of agents (Energy/bee). Our main questions were if the energy/bee depended on

220   flower constancy (vs. indiscriminate choice), communication (vs. no communication), refill

221   time, the number of food sources and reward size. We also tested situations when flower

222   constancy was lower after visiting a low-quality food source ($Constancy_{LQ}$) (Grüter et al.,

223   2011), when there were 4 food source types and when indiscriminate flower choice increased

224   the time to extract a reward from a food source (*i.e.* to simulate cognitive constraints) (Chittka

225   et al., 1999).

226

227   *Sensitivity analysis and model exploration*

228   We varied a range of other factors to explore how they affected our results. These included

229   colony size, crop load size, flower stay time, metabolic costs, nest stay time, Lévy flight μ,

230   selectivity of communication (*i.e.* bees foraging on low-quality food source become *influencers*

231   with the same probability as those foraging on the high-quality type) and the shape of the

232   recruitment curve (see Fig. S1).

233   We performed 30 runs per parameter combination. We do not provide *p*-values due to

234   the arbitrariness of the simulation number but indicate 95%-confidence intervals to facilitate

235   interpretation of effect sizes.

236

237   **Table 1:** Overview of the model variables and the used values.

Variables	Description	Default values	Other values tested	Information source

|				
Colony size	Number of foragers in a colony	100	5-300	Westphal et al. 2006; Grüter 2020
FS_{number}	Number of food sources per type	3000	1500, 4500	arbitrary
FS_{size}	Size of food sources	1 patch		arbitrary
FS types	Number of food source types	2	4	arbitrary
$Reward_{HQ}$	Nectar amount per food source	5μl	2.5μl, 10μl	Willmer 2011
$Reward_{LQ}$	Nectar amount per food source	2.5μl	1.25μl, 5μl	Willmer 2011
v_{flight}	Flight speed	1.4 patch/tick		von Frisch 1967
M_{cost}	Metabolic costs of flight, J/tick	0.032	0.016, 0.064	Heinrich 1975; Willmer 2011
$t_{flower-stay}$	Time spent at food source	60 ticks	20, 180	arbitrary
v_{nest}	Movement speed inside nest	0.1 patch/tick		arbitrary
$t_{nest-stay}$	Time in nest between trips	300 ticks	150, 450	Farina 2000
$Crop_{HQ}$	Crop load when flower constant to HQ food sources	50μl	25 μl, 100 μl	Núñez 1966
$Crop_{LQ}$	Crop load when flower constant to LQ food sources	25μl	12.5 μl, 50μl	Núñez 1966
$Crop_{Random}$	Crop load without flower constancy	37.5μl	50μl	Núñez 1966
t_{refill}	Time until food sources offer food again	0 ticks	1200, 3600	Stout & Goulson, 2002
Lévy μ	Lévy flight parameter	2.4	1.8, 3.0	Reynolds et al. 2009
$Constancy_{HQ}$	Probability to remain constant to a type after leaving a high-quality food source during flower constant simulations	100%		Grüter et al. 2011
$Constancy_{LQ}$	Probability to remain constant to a type after leaving a low-quality food source during flower constant simulations	100%	90%, 95%	Grüter et al. 2011

238

239

Results

Food source abundance and refill speed

We found that communication about the high-quality flower type did not affect the collected

energy if bees chose food sources indiscriminately (Fig. 2). However, if colonies were flower

constant, communication increased the energy collected by bees in all situations when the two

flower types were equally abundant (Fig. 2, see also Figs. 4-8), showing an interaction between

246   flower constancy and communication. The combination of communication and flower

247   constancy was relatively more beneficial when high-quality food sources were easy to find,

248   either because they were highly abundant (Fig. 2c,f,i) or because visited food sources

249   replenished quickly (Fig. 2a,b,c).

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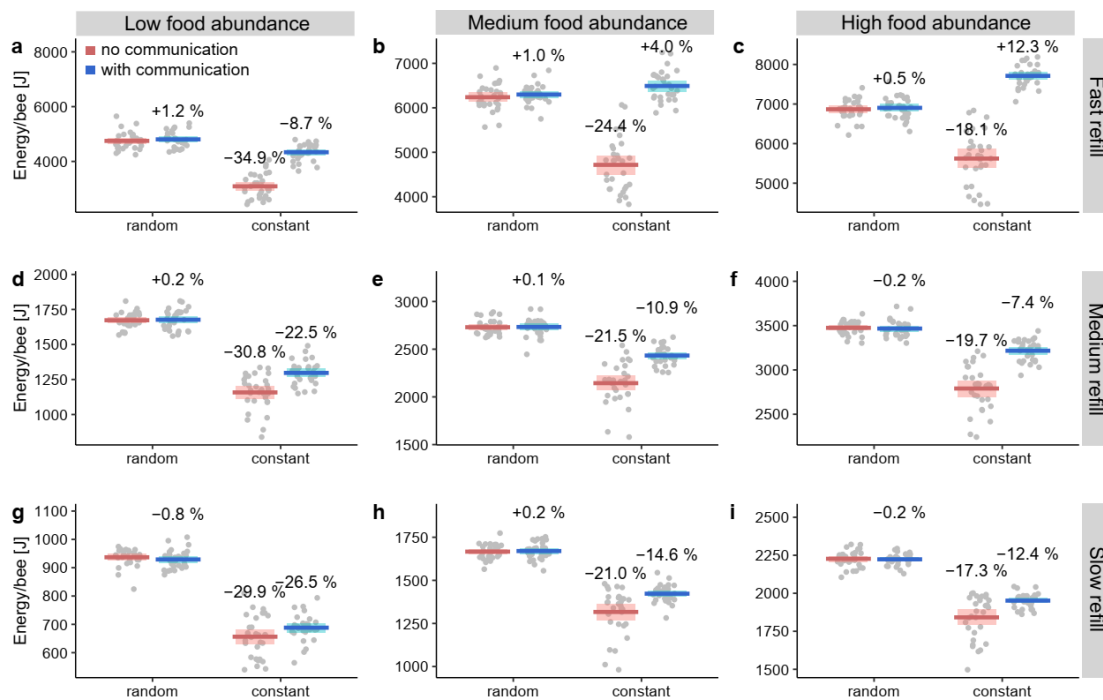
Fig. 2. Energy collected per bee (Joule) under varying food abundances (1500, 3000 and 4500 food sources per type) and refill times (0, 1200 and 3600 ticks). Colonies either showed flower constancy (constant) or they chose food source indiscriminately (random). Plots show the mean and the 95%-confidence based on 30 simulations (grey dots). Numbers show % of change compared to random choice without communication.

In the most favourable conditions, flower constancy in combination with communication was

the most successful combination (Fig. 2b, c). In all other conditions, indiscriminate choice was

the most successful strategy.

261   The relative abundance of the two food source types also played an important role.

262   Flower constancy combined with communication was relatively more successful when high-

263   quality food sources were more common than the low-quality flower type compared to when

264   they were rarer than the lower-quality flower type (Fig. 3). When high-quality food sources

265   represented the common flower type, colonies with flower constancy and communication were

266   either more successful (Fig. 3b) or not much less successful than colonies with indiscriminate

267   choice (Fig. 3d).

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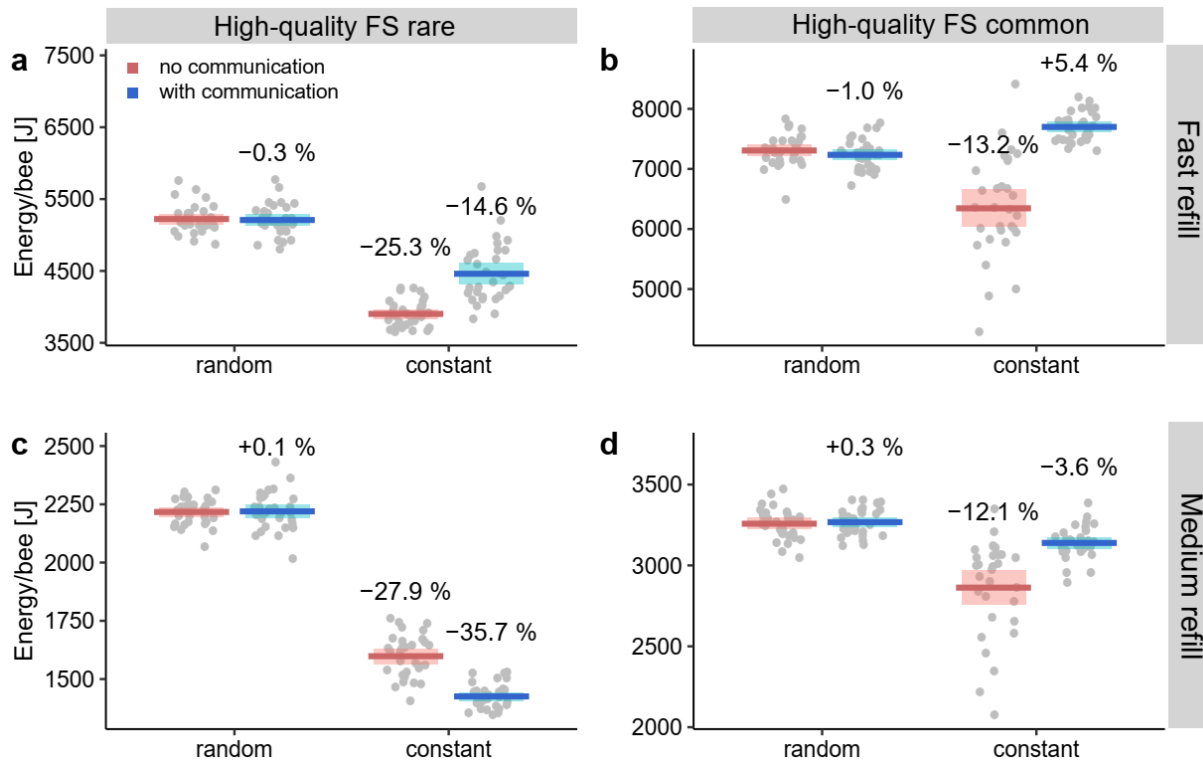
Fig. 3. Energy collected per bee (Joule) when high-quality food sources were either rare (1500) or
common (4500) compared to the low-quality food sources (3000). Default values were used for the
other parameters (Table 1).

272

273   However, indiscriminate choice was considerably more successful when high-quality food

274   sources were in the minority (Fig. 3a,c). When high-quality food sources were particularly

275   difficult to find, communication lowered the foraging success of flower constant colonies (Fig.

276   3c). Under these circumstances, communication directs the foragers of a colony towards a rare

277   food source, leading to long search times.

278

279   *Reward sizes*

280   Reward quantities are known to affect flower constancy, with bees becoming more flower

281   constant with increasing reward quantities (Chittka et al., 1997; Grüter et al., 2011; Wells &

282   Rathore, 1994). In accordance with this observation, we found that flower constancy became

283   relatively more successful (energy/bee) as reward sizes of both high- and low-quality food

284   sources increased (Fig. 4). However, indiscriminate choice was the most successful strategy in

285   many tested environments.
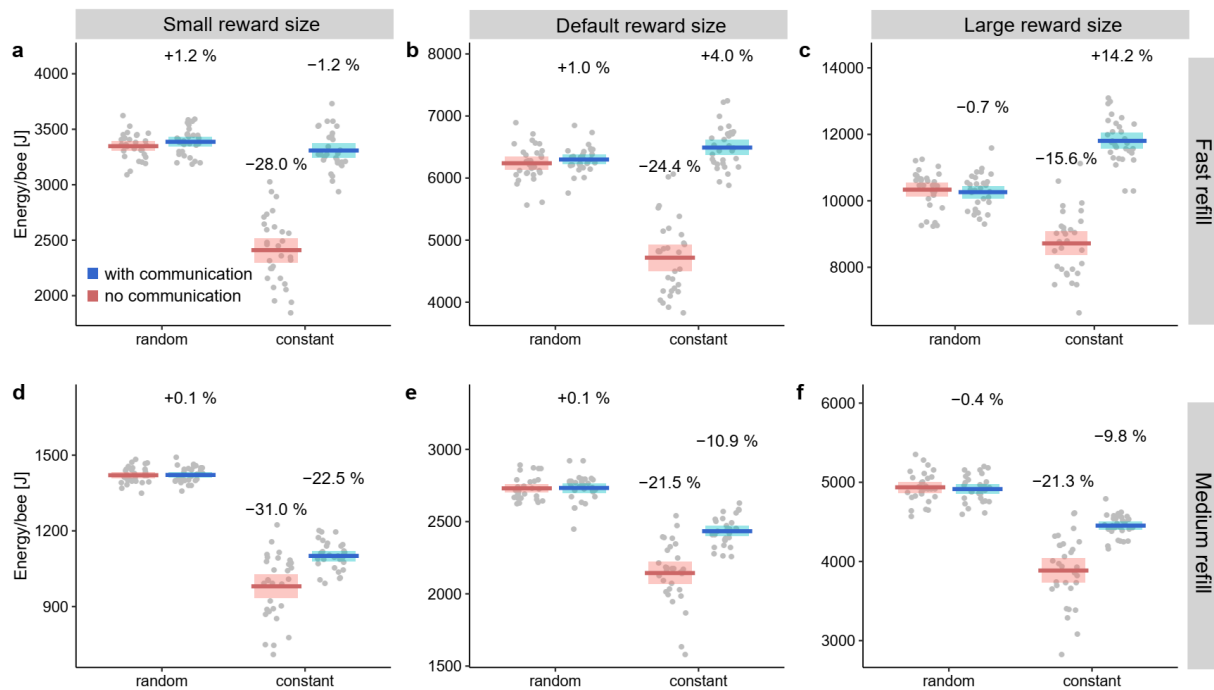
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287   **Fig. 4.** Energy collected per bee (Joule) when rewards were (a) smaller (2.5μl and 1.25μl) or (c) larger
288   (10μl and 5μl) than in the (b) default situation (5μl and 2.5μl). Medium food source abundance was
289   simulated; default values were used for the other parameters (Table 1). Blue shows means and 95%-
290   CI for colonies using communication, red shows data for colonies choosing indiscriminately.

291

292   *Time needed to collect a reward*

293   The time bees need to extract a reward from a flower will affect the time costs of foraging

294   decisions and, if the refill time is >0, it will affect the number of depleted food sources in the

295   environment. Under default conditions, bees needed 60 ticks (1 minute) to obtain the reward

296   from a flower/food patch. We explored how different values for $t_{Flower-stay}$ affected the benefits

297   of flower constancy and communication. Increasing the time needed to obtain a reward

298   increased the relative benefits of combined flower constancy and communication compared to

299   short reward collection times (Fig. 5).
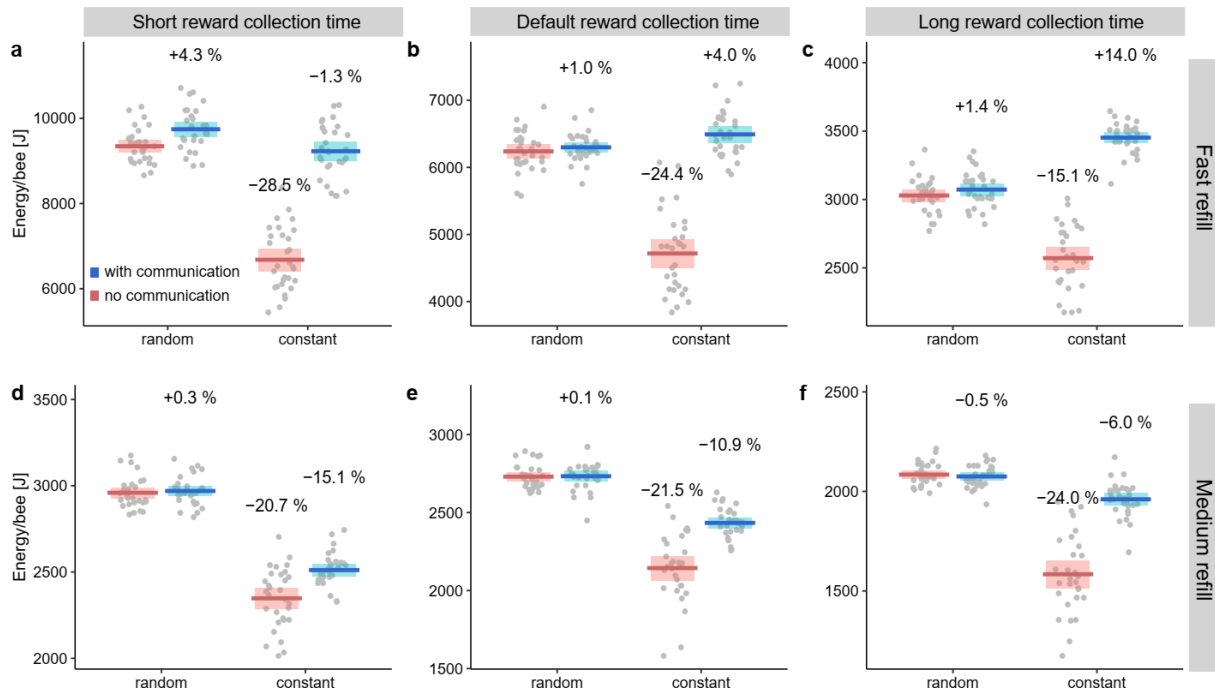
Fig. 5. Energy collected per bee (Joule) when the time required to obtain a reward from a food source was (a,d) shorter (20 ticks) or (c,f) longer (180 ticks) than in the (b,e) default situation (60 ticks). Default values and a medium food source abundance were simulated (Table 1).

Quality dependent flower constancy

Under default conditions, flower constancy did not depend on the quality of the food source ("spontaneous flower constancy", Hill et al., 1997). We simulated situations when bees visiting a low-quality food source were slightly less flower constant (they had a 90% or a 95% chance to remain flower constant on the subsequent visit, as in Grüter et al., 2011). Our results show that this quality-dependent flower constancy considerably improves the energy collected by colonies following this strategy of quality-dependent flower constancy (Fig. 6).
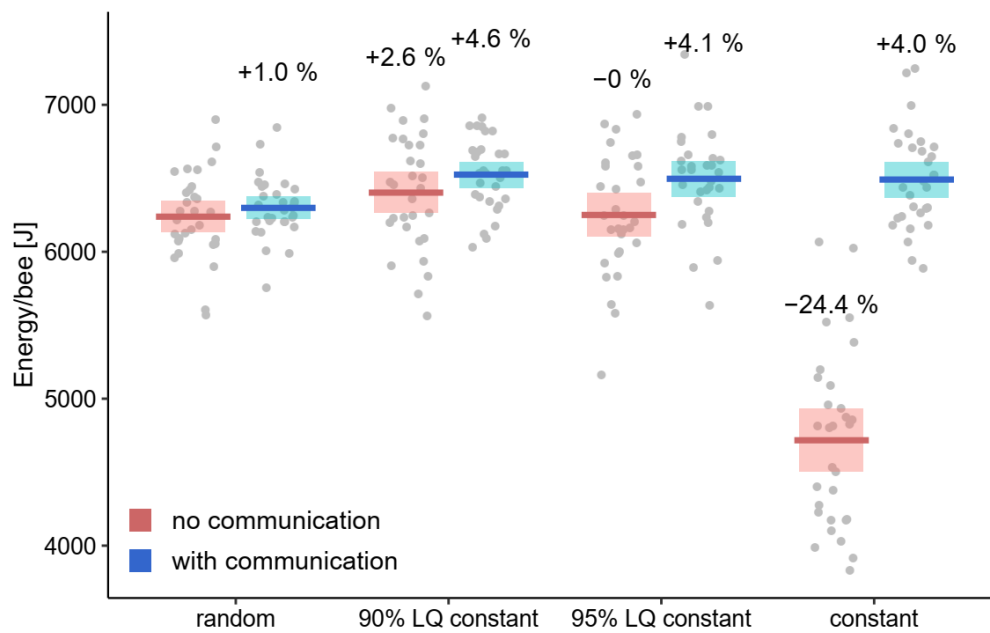
Fig. 6. Energy collected per bee (Joule) when bees foraged indiscriminately, when they showed reduced flower constancy after visiting a low-quality food source (90% LQ constant or 95% LQ constant) and when they were strictly flower constant. Refill time was 0, default values were used for the other parameters (Table 1).

Exploring environments with 4 food types

When environments provide four different types of food sources rather than two, flower constancy is less favourable overall (Fig. 7). In other words, indiscriminate flower choice is highly beneficial in an environment where flower constancy would limit the options a forager has to a small subset (25% of all food sources) of all available food sources than with two food source types (Fig. 7).

We tested situations where one, two or three of the four plant types were of high quality, while the remaining food sources were of low quality. While it was always beneficial to use communication when colonies were also flower constant, the relative benefits of communication diminished as the number of high-quality food types and the refilling time increased. Unsurprisingly, therefore, foraging in an environment that consists mainly of high-quality food sources belonging to different plant species somewhat diminishes the value of using communication to direct foragers towards higher-quality food sources.

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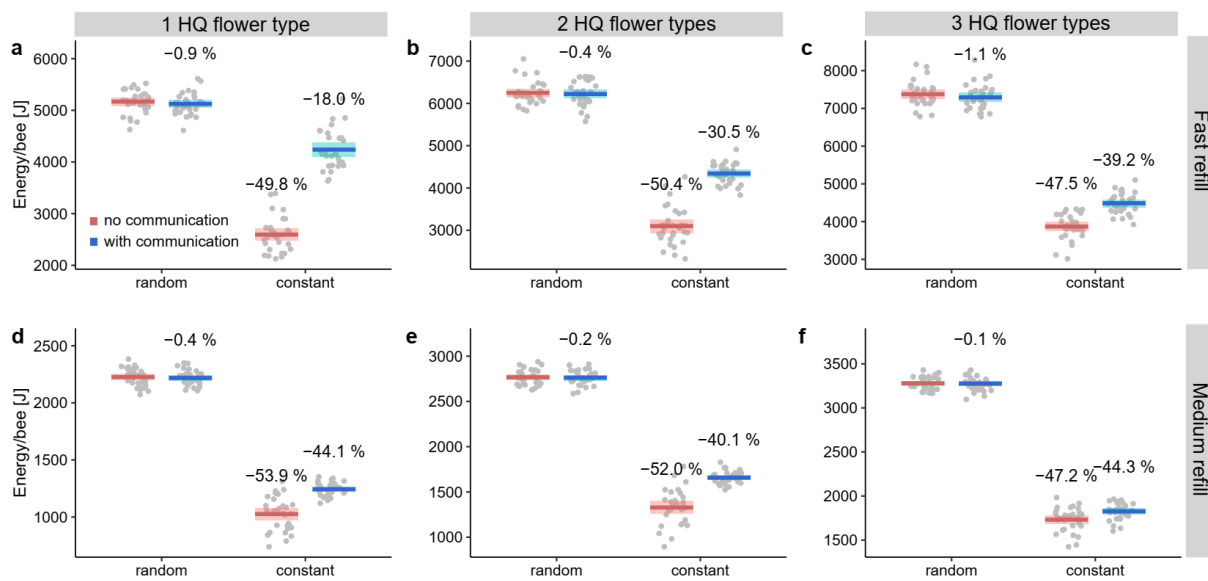
Fig. 7. Energy collected per bee (Joule) when bees foraged in an environment of four flower species. In (a) & (d), one of the four plant types was of high quality, while the remaining three types were of low quality. In (b) & (e), two of four types were of high quality and in (c) & (f), three of flower types were of high quality. Food sources were refilling either at a fast or a medium rate.

338

Time penalty for non-specialists

340   So far, we have assumed that there are no additional time costs (e.g. as a result of cognitive

341   limitations) for bees that do not specialise on a particular type of food source. To explore the

342   consequences of cognitive limitations, we simulated situations when indiscriminate bees

343   require more time to extract a reward from a food source compared to flower constant bees. A

344   time penalty for indiscriminate bees favours flower constant colonies, especially those that also

345   communicate the high-quality flower type to nestmates (Fig. 8).

346
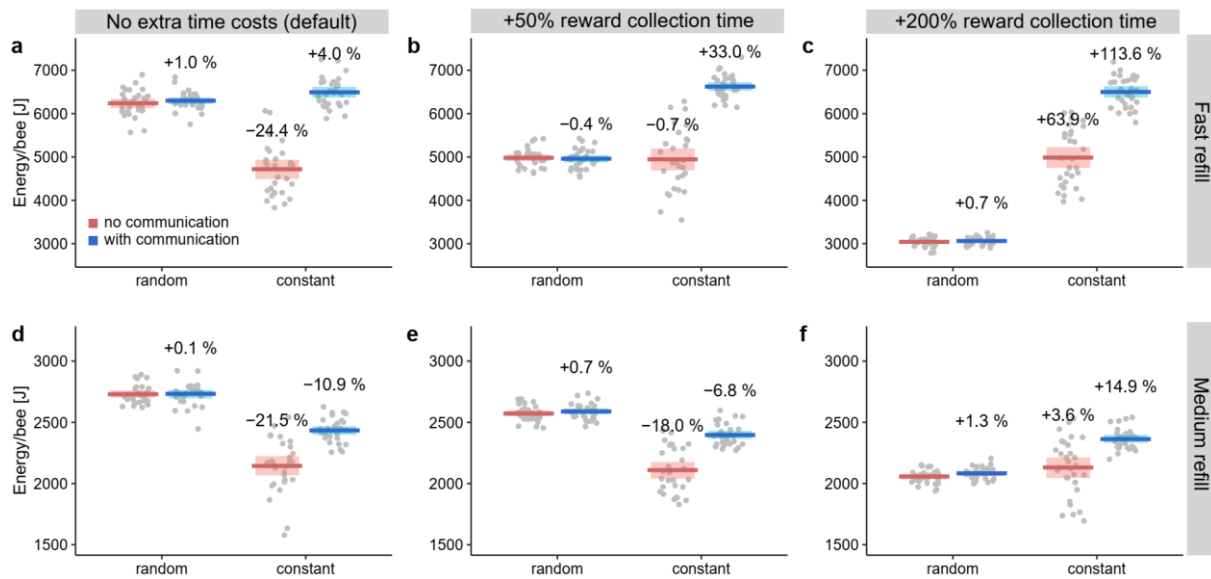
Fig. 8. Energy collected per bee (Joule) when non-specialists needed 50% (b, e) or 200% (c, f) more time than flower constant bees to obtain a reward from a food source. Food sources were refilling either at a fast (t_{refill} =0) or a medium rate (t_{refill} = 1200). Default values were used for the other parameters (Table 1).

Sensitivity analysis and model exploration

Varying colony size from 5 to 300 (Fig. S2) does not greatly affect the general pattern observed for the default colony size of 100 (see Fig. 2). When food sources refill at a fast rate (Fig. S2a), bees do not experience exploitation competition and colony size does not affect the energy collected by individual bees. Increasing the refill time while also increasing the number of agents searching for food, on the other hand, increases exploitation competition and, therefore, lowers the energy collected by individual bees (Fig. S2b,c).

Using different recruitment curves (Fig. S1) had no noticeable effect on the energy collected by bees, but non-selective recruitment (recruitment to both high- and low-quality food sources) lowers the collected energy to levels similar to those of flower constant colonies without communication (Fig. S3). Changing the metabolic costs of flying or the Lévy-flight μ has little effect on the overall pattern (Fig. S4, S5), whereas increasing the time spent inside the nest in-between foraging trips reduces the energy collected by bees, but less so in colonies with

366   flower constancy (Fig. S6). Thus, longer nest stay times favour flower constancy. Flower

367   constancy was also favoured when bees had smaller crop sizes (Fig. S7).

368

369   **Discussion**

370   Results from our simulations suggest that flower constancy without communication is less

371   successful than indiscriminate choice under all tested conditions. Flower constancy imposes

372   significant costs because it (*i*) limits the available options to a subset of all available flowers,

373   thereby increasing time and energy costs during foraging, and (*ii*) causes many foragers to

374   specialise on a sub-optimal flower type. Communication about the high-quality flower type

375   positively interacted with flower constancy (Fig. 2) and considerably improved the foraging

376   success of flower constant colonies by. Communication allows a colony to focus on high-

377   quality flowers, thereby reducing the second type of cost (*ii*). Many species of social bees have

378   evolved mechanisms of reward-quality dependent recruitment communication, which allow

379   *influencers* to affect the foraging decisions of their nestmates towards a particular flower type,

380   mainly via olfactory learning (Dornhaus & Chittka, 1999; Farina et al., 2012; Jarau & Hrncir,

381   2009; Lindauer & Kerr, 1960; von Frisch, 1967). This, in turn, lowers the benefits of sampling

382   alternative flower species and highlights the importance of social information use as a process

383   of information-filtering (Grüter et al., 2010; Rendell et al., 2010). Our findings can help explain

384   why social bees tend to be more flower constant than solitary bees (e.g. Smith et al., 2019;

385   Waser, 1986).

386   The general foraging conditions had a strong effect on the value of flower constancy

387   and the strength of its interaction with communication. Flower constancy in combination with

388   communication was the most successful strategy when foraging conditions were very

389   favourable, while indiscriminate choice was the better strategy when foraging options were

390   more limited. For instance, flower constancy in combination with communication was

391   beneficial when foragers did not encounter empty food sources (refill time of 0) and food

392   sources were abundant (Fig. 2b,c), when most food sources were of high-quality (Fig. 3b) and

393   when rewards were large (Fig. 4c). These findings are consistent with empirical studies showing

394   that bees are more flower constant when flower density is higher (Chittka et al., 1997; Kunin,

395   1993; Marden & Waddington, 1981) and rewards are larger (Chittka et al., 1997; Greggers &

396   Menzel, 1993; Grüter et al., 2011). Similarly, predator-prey models show that the abundance of

397   a prey item has a positive effect on diet specialisation of the predator (Pulliam, 1974). If food

398   sources took time to replenish, resulting in many empty food sources due to exploitation

399   competition, indiscriminate choice was more successful (Fig. 2d-i), suggesting that rejecting

400   flowers due to flower constancy is more costly in environments that offer fewer options.

401   Changes in the temporal dynamics of foraging trips affected the performance of the

402   different strategy by changing the relative costs of ignoring flowers (*i*) and choosing suboptimal

403   food sources (*ii*). Flower constancy in combination with communication performed relatively

404   better if bees required more time to extract a reward from a food source (Fig. 5). One

405   explanation for this is that visiting low-quality food sources, which is common with

406   indiscriminate choice, becomes relatively more costly as the time costs of a flower visit

407   increase. Thus, longer flower handling times, e.g. due to a complex flower morphology, favour

408   flower constancy from both an adaptive and a constraints-based perspective (see Chittka et al.,

409   1999 for arguments based on cognitive constraints). Flower constancy in combination with

410   communication performed relatively better when bees stayed in their nest longer (Fig. S6) and

411   had smaller crops (Fig. S7). These findings are somewhat puzzling, but one explanation could

412   be that longer nest stay times provide *influencers* with more opportunities to communicate their

413   findings to other bees. When food sources need time to replenish, longer nest stay times will

414   reduce the number of depleted food sources a bee encounters, which favours flower constancy

415   in combination with communication (Fig. 2b,c). Similarly, when bees have smaller crop loads,

416   they visit fewer food sources per trip and spend a larger proportion of their time in the nest,

417   reducing exploitation competition and the number of depleted food sources. Crop size will

418 depend on body size and one might, therefore, predict that smaller bees are more flower

419 constant, which is consistent with comparative data (Smith et al. 2019). However, it is unlikely

420 that there is straight forward relationship between crop size, body size and flower constancy in

421 nature because body size covaries with numerous other extrinsic and intrinsic factors, including

422 foraging conditions, metabolic costs, flying speed or sensory acuity (Gervais et al., 2020; Grab

423 et al., 2019; Spaethe et al., 2007), all of which might affect flower constancy.

424   The Western honey bee *Apis mellifera* is strongly flower constant, but there is

425 disagreement about whether and when flower constancy depends on the profitability of visited

426 flowers. Some studies have suggested that flower constancy is often "spontaneous", *i.e.*

427 unrelated to reward size (Wells & Wells 1983; Hill et al. 1996, 2001; Sanderson et al. 2006),

428 whereas others have found that honey bees adjust flower constancy according to the

429 profitability of rewards (Greggers & Menzel 1993; Chittka et al. 1997; bumble bees: Heinrich

430 1976, 1979b; reviewed in Grüter & Ratnieks 2011). Our simulations show that context-

431 dependent flower constancy is more successful than strict ("spontaneous") flower constancy

432 (Fig. 6). When bees visiting the less profitable food type were only 90-95% flower constant,

433 colonies collected about 25% more energy than colonies with strict flower constancy. As is the

434 case with communication, context-dependent flower constancy allows bees to switch from the

435 low-quality to the high-quality flower species over time (type (*ii*) costs).

436   Human impacts have significantly affected the diversity of plant species found in some

437 environments, especially in intensively farmed habitats (e.g. Potts et al., 2010; Tew et al., 2021),

438 which is likely to affect the costs and benefits of flower constancy. In our simulations, flower

439 constancy performed considerably worse when there were four rather than two flower types

440 (Fig. 7). With more plant species present, flower constant bees will ignore most of the available

441 options and focus on a small subset of all food sources, thereby dramatically increasing

442 opportunity costs (type (*i*) costs). Thus, bees should be less flower constant in more diverse

443 foraging environments. Flower constant bees, in turn, might suffer a reduction in foraging

444 success in more biodiverse habitats. These findings challenge the reasoning behind the "costly

445 information hypothesis", which argues that flower constancy is an adaptive foraging strategy

446 because acquiring information about suitable alternatives would cost too much time and energy

447 if there are several plant species available (Chittka et al., 1999; Grüter & Ratnieks, 2011). In

448 flower diverse environments, bees should accept even low-quality food source if it means they

449 can cut time and energy costs imposed by flower constancy. Empirical studies on the links

450 between floral diversity and flower constancy provide contrasting results. While Gervais et al.

451 (2020) and Martínez-Bauer et al. (2021) found that increasing plant diversity was associated

452 with lower flower constancy in *Bombus impatiens* and *B. terrestris*, Austin et al. (2019) found

453 that bumble bees became more flower constant when there are more options available. The

454 latter finding is more consistent with a "cognitive limitations" perspective, since deciding

455 among more options would be cognitively more challenging and flower constancy, therefore, a

456 possible solution to avoid switching costs (see also Chittka et al. 1997; Gegear & Thomson

457 2004). Decision making is often impaired as the number of choices increases (Latty &

458 Trueblood, 2020). The different studies differ in that the first two were performed under natural

459 conditions, whereas Austin et al. (2019) was experimental. Non-experimental surveys can be

460 confounded by numerous factors, such as differences in rewards, clustering of flowers or

461 management, whereas experimental studies might fail to capture crucial features of natural

462 environments that affect decision-making (Fawcett et al., 2014).

463   Agent-based models have important limitations. Simulation outcomes depend on the

464 underlying assumptions and the parameters chosen when building the model, some of which

465 are arbitrary or simplistic. As a result, ABMs potentially miss important natural features that

466 shape decision-making (Fawcett et al., 2014). For example, we assumed that food sources are

467 randomly distributed, whereas natural foraging environments are often spatially heterogenous

468 and patchy, which is likely to affect the value of flower constancy. Patchiness can lead to flower

469 constancy "by accident" if bees forage in large patches, even if they choose flowers

470   indiscriminately. We might, therefore, expect increasing patchiness to lead to more similar

471   outcomes for flower constant and indiscriminate foragers. Pulliam's (1974) predator-prey

472   model found that an increasingly clumped prey distribution favours a more specialised diet in

473   predators and we might expect a similar finding in plant pollinator interactions. Agent-based

474   models also have important strengths because they allow us to systematically vary factors that

475   cannot be manipulated experimentally, such as tuning flower constancy or recruitment

476   communication while keeping all other factors constant. ABMs should be seen as a useful tool

477   to complement empirical studies.

478   One of the aims of our model was to test whether flower constancy could be an adaptive

479   strategy *per se* under some foraging conditions, *i.e.* in the absence of cognitive constraints. If,

480   however, switching between flower species leads to increased time costs or reduced reward

481   sizes (Chittka et al., 1999; Darwin, 1876; Grüter & Ratnieks, 2011; Lewis, 1986; Raine &

482   Chittka, 2007), flower constancy, with or without communication, becomes a much more

483   beneficial strategy under a wide range of conditions (Fig. 8c,f). The reasons for flower

484   constancy in pollinators are likely to be complex and depend on both constraints and adaptive

485   processes, to varying degrees in different species. However, our results suggest that a more

486   pronounced flower constancy in social bees is more likely due to increased performance of

487   flower constancy in social species due to social traits, rather than the result of poorer cognitive

488   abilities in social bees compared to solitary bees (Amaya-Márquez & Wells, 2008; Dukas &

489   Real, 1991).

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714   **Fig. S1**
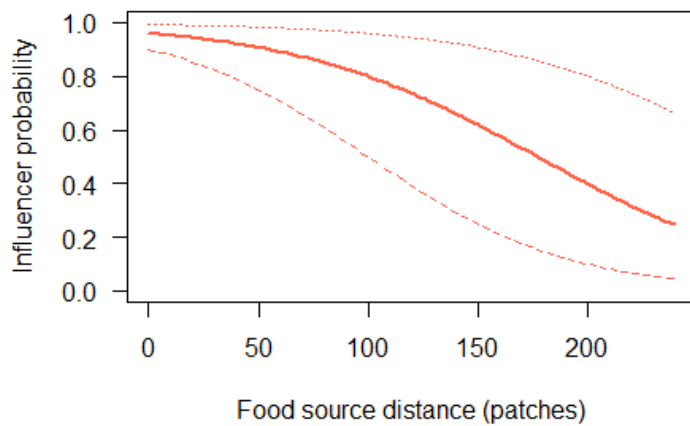
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716   **Fig. S1**. Probability that a returning bee that visited the high-quality food type (red) becomes an

717   influencer inside the nest. Bees visiting the low-quality food type did not become influencers under

718   default conditions. Thick red line shows the default probability. The other two lines show other tested

719   probability curves. 1 patch ~ 5 m.
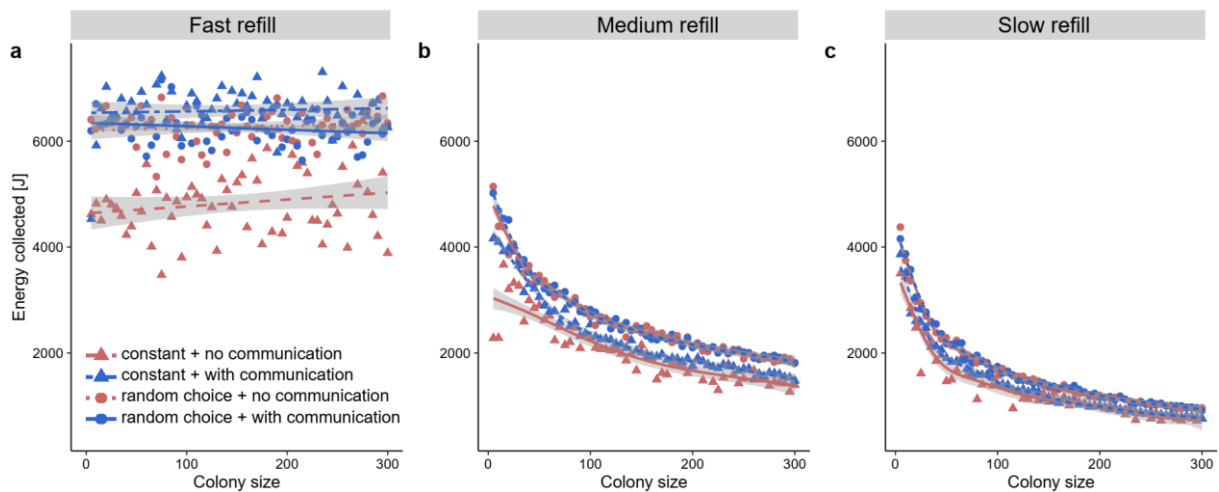
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735 **Fig. S2**

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737 **Fig. S2**. Energy collected per bee for different colony sizes and different refill speeds (fast refill, $t_{refill} = 0$;

738 medium refill, $t_{refill} = 1200$; slow refill, $t_{refill} = 3600$). Lines in (a) show best fit lines based on linear

739 regression. In (b) and (c), generalised additive models (GAM) were used to fit curves. Grey bands show

740 95% confidence intervals. Default values were used for other parameters.

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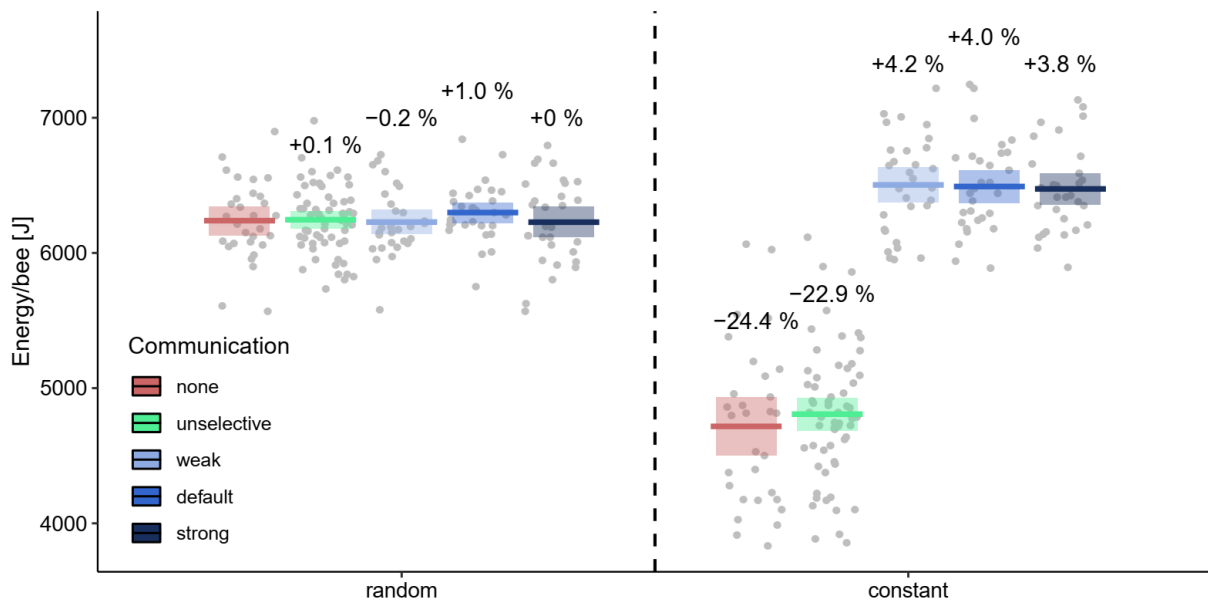
Fig. S3

Fig. S3. Energy collected per bee for different types of communication, with or without flower constancy. The different recruitment strengths (weak, default and strong) correspond to the three different curves shown in S1. Unselective refers to a situation where bees communicate equally about high- and low-quality food sources (assuming the default curve shown in Fig. S1). Means and 95%-confidence intervals are shown.
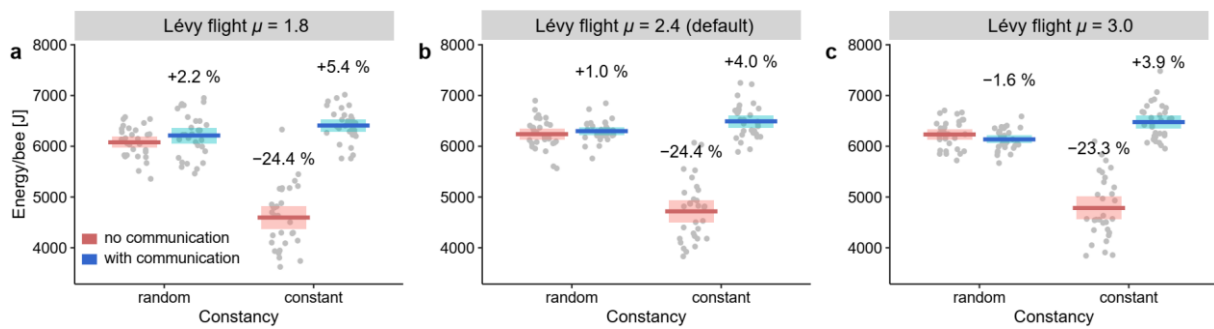
774 **Fig. S4**

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776 **Fig. S4**. Energy per bee (Joule) collected using different Lévy-flight μ values, which determines the

777 distribution of the segment lengths l that constitute a Lévy-flight, with $P(l) \sim l^{\mu}$. Food sources that refill

778 immediately were simulated. Default values were used for the other parameters (Table 1).

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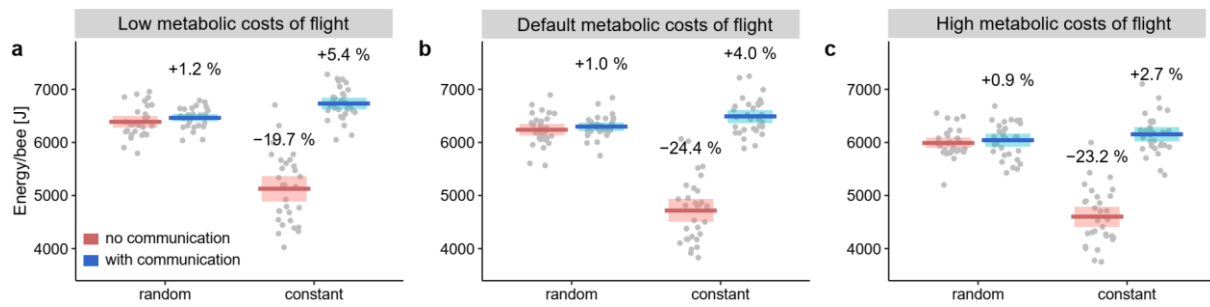785

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800 **Fig. S5**

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802 **Fig. S5**. Energy per bee (Joule) collected using different flight energy costs (low = 0.016 J/tick; default

803 = 0.032 J/tick; high = 0.064 J/tick). Food sources refilled immediately. Default values were used for the

804 other parameters (Table 1).

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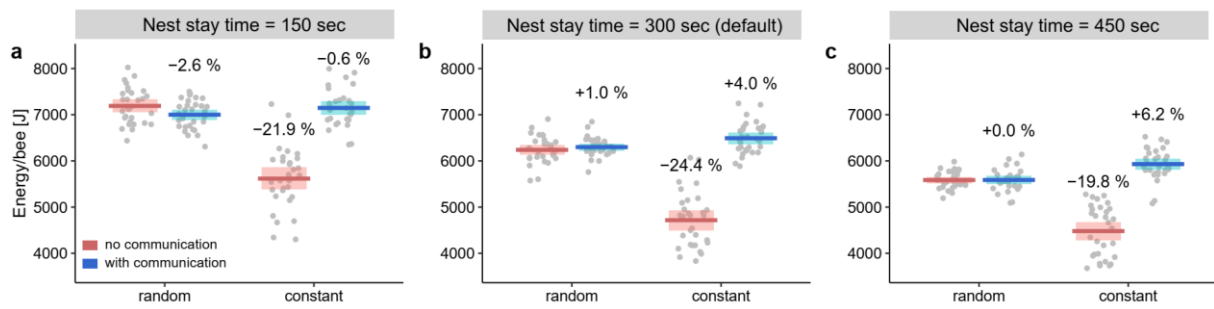
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824 **Fig. S6**

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826 **Fig. S6**. Energy per bee (Joule) collected using different nest stay times. Food sources refilled

827 immediately. Default values were used for the other parameters (Table 1).

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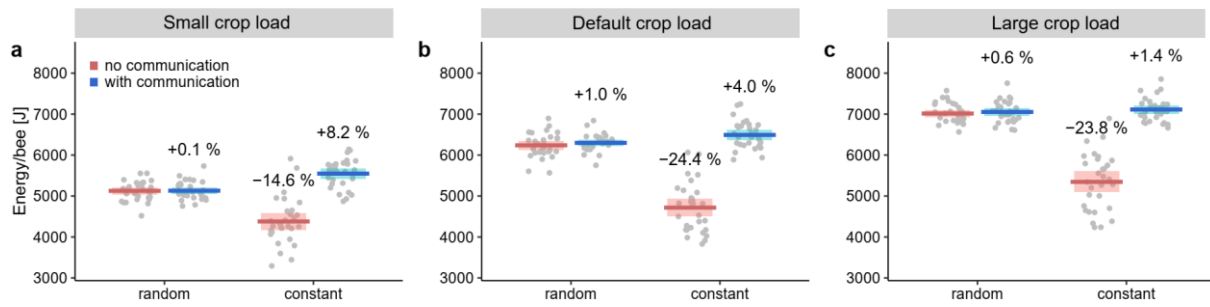
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Fig. S7

Fig. S7. Energy per bee (Joule) collected with different crop loads. (a) Small crop loads mean that bees constant to high-quality food sources filled their crop to 25µl, whereas bees constant to low-quality food sources returned to their nest if their crop load was 12.5µl. Bees choosing food sources randomly had intermediate crop loads (18.75µl). (c) Bees with large crop loads foraged until they had 100µl (constant to high-quality food sources), 50µl (constant to low-quality food sources or 75µl (randomly choosing bees). Food sources refilled immediately. Default values were used for the other parameters (Table 1).