# A model of resource partitioning between foraging bees

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## Abstract

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

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

# Introduction

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

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

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

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

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

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

# METHODS

### *Model overview*

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

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

### ***Environment***

*Simulations with one foragers*

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

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

*Simulations with two foragers*

We explored conditions leading to resource partitioning by running model simulations with two foragers. Here we simulated environments containing 10 flowers (each bee had to visit five rewarding flowers to fill its crop to capacity). To test whether model predictions were robust to variations in resource spatial distribution, we simulated three types of environments characterized by different levels of resource patchiness: (*i*) a patch of 10 flowers, (*ii*) two patches of five flowers each, and (*iii*) three patches of five, three and two flowers respectively (see examples in Fig. S2). We generated flower patches into a spatial range comparable to the one used in both experimental setups (Lihoreau *et al.* 2012b; Woodgate *et al.* 2017): about 500 $m^2$ with a minimum distance of 160 m between each patch center. Within a patch, flowers were randomly distributed according to two constraints: (i) flowers were at least 20 m apart from each other, (ii) the maximum distance of each flower from the center of the patch was 40 m. This ensured that each patch had a maximum diameter of 80 m and inter-flower distances were smaller between all flowers of the same patch than between all flowers of different patches.

***Movements***

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

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

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

***Learning***

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

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

### *Competitive interactions*

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

### *Statistical Analyses*

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

*Simulations with one forager*

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

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

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

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

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

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

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

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

*Simulations with two foragers*

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

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

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

*iii*) the degree of resource partitioning among bees, based on network modularity $Q$ (Pasquaretta and Jeanson 2018; Pasquaretta *et al.* 2019). $Q$ is calculated using the *computeModules* function implemented in the R package 'bipartite' (Dormann *et al.* 2008) using the DIRTLPAwb+ algorithm recently developed by Beckett (2016). Although $Q$ ranges between 0 (the two bees visit the same flowers) and 1 (the two bees do not visit any flower in common), the comparison of modularity between networks requires normalization because the magnitude of modularity depends on network configuration (e.g., total number of flower visits) (Dormann and Strauss 2014; Beckett 2016). For each network, we computed :

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

where $Q_{max}$ is the modularity in a rearranged network that maximizes the number of modules (Pasquaretta and Jeanson 2018).

*iv*) an index of collective foraging efficiency, $QL_{group}$, computed for each foraging bout *i*, to estimate the cumulated efficiency of all foraging bees, as:

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

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

To assess whether the trends across foraging bouts obtained from simulations with two bees differed between models (Fig. 1) and type of environments (Fig. S2), we applied GLMMs for each of the following response variables: (*i*) frequency of competition types (Poisson error distribution), (*ii*) $SI_{ab}$

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

# RESULTS

## *Simulations with one forager*

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

## *Simulations with two foragers*

*Exploitation and interference competition*

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

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

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

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

*Route similarity*

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

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

*Resource partitioning*

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

*Collective foraging efficiency*

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

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

## Discussion

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

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

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

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

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

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

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

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## Figure legends

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

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

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

# Supplementary materials

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

We ran a sensitivity analyses for the two main parameters: the positive and negative reinforcement. As we had no a priori understanding of how the model behaved with different values of the two main parameters of the model (positive and negative reinforcement), we explored the spectrum of potential outcomes with different sets of parameters. We ran simulations on ranges of positive (1, 1.2, 1.4, 1.6, 1.8, 2) and negative (0, 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 environment type explored (one, two and three patches, Fig. S2). We simulated 10 environments for each environment type and computed 100 simulations of 50 foraging bouts per iteration (i.e. 1000 simulations per environment type and set of parameters).

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

We also looked at how this same index evolved over successive foraging bouts, for each pair of bees. Fig. S4 shows the dynamics of mean $Q_{norm}$ index across 50 foraging bouts for each combination of 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, 0.7, 0.8, 0.9, 1) parameters, and each environment type (one patch, two patches, three patches). Higher values of both positive and negative reinforcement factors most often lead to faster resource partitioning (with some uncertainty due to the probabilistic nature of the model). Combinations of values in which the negative reinforcement factor is missing (violet gradient curves) led to a decrease in partitioning.

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

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

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

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

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

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

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

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

**Figure S3** Heatmap showing the mean $Q_{norm}$ Index value after 50 foraging bouts (mean over 1000 simulations on 10 arrays of the same environment type), for each combination of 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, 0.7, 0.8, 0.9, 1) parameters, and for each environment type (one patch, two patches, three patches). For simplicity we inverted the values of negative reinforcement here. 0 being models without negative reinforcement.

**Figure S4.** Dynamic of the mean $Q_{norm}$ Index across foraging bouts for each combination of positive (1.0, 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

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

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

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

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

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

**Figure 1**

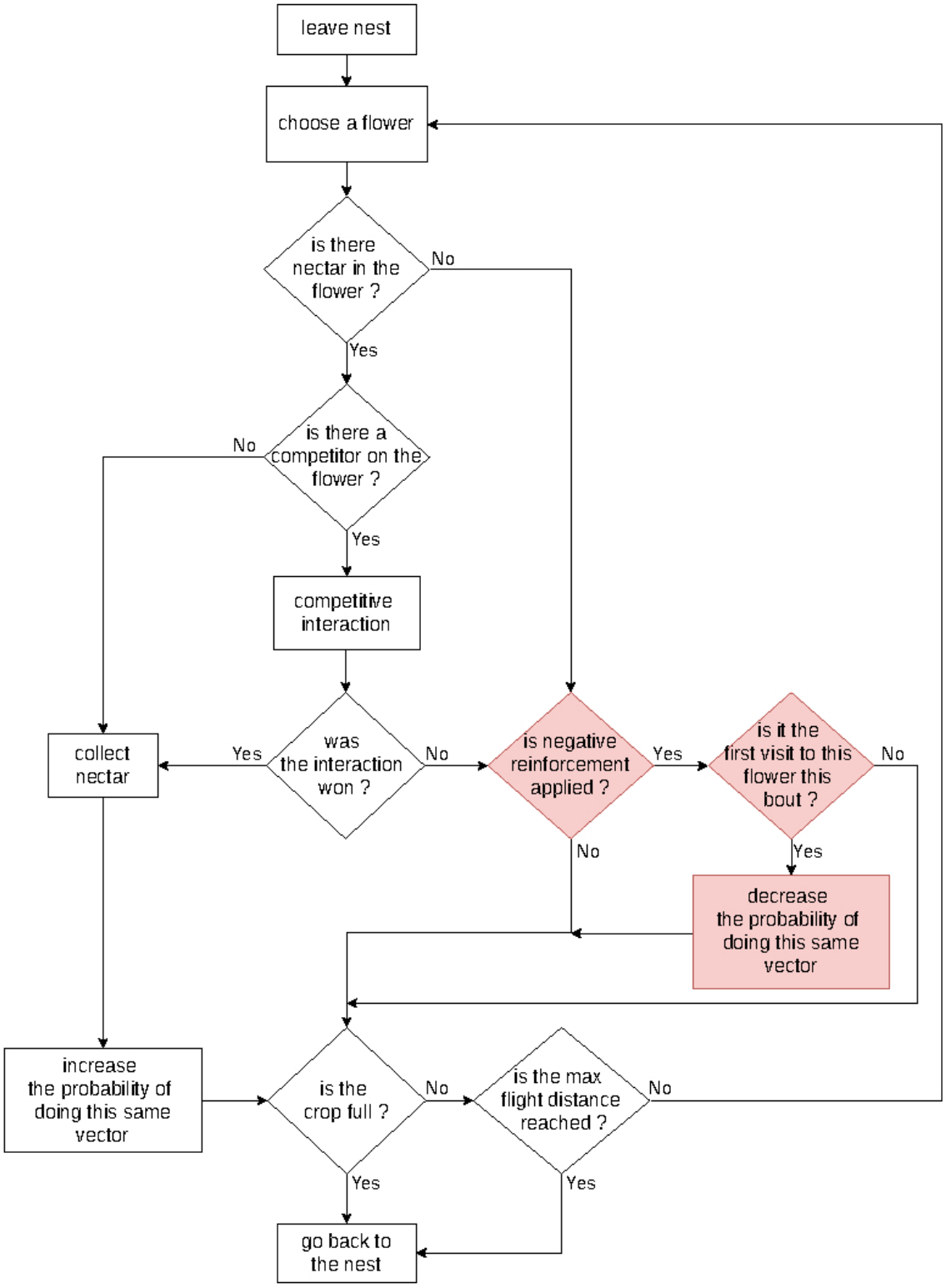

leave nest
choose a flower
is there nectar in the flower ?
No
Yes
is there a competitor on the flower ?
No
Yes
competitive interaction
collect nectar
Yes
was the interaction won ?
No
is negative reinforcement applied ?
Yes
is it the first visit to this flower this bout ?
No
Yes
No
decrease the probability of doing this same vector
increase the probability of doing this same vector
is the crop full ?
No
is the max flight distance reached ?
No
Yes
Yes
go back to the nest

**Figure 2**

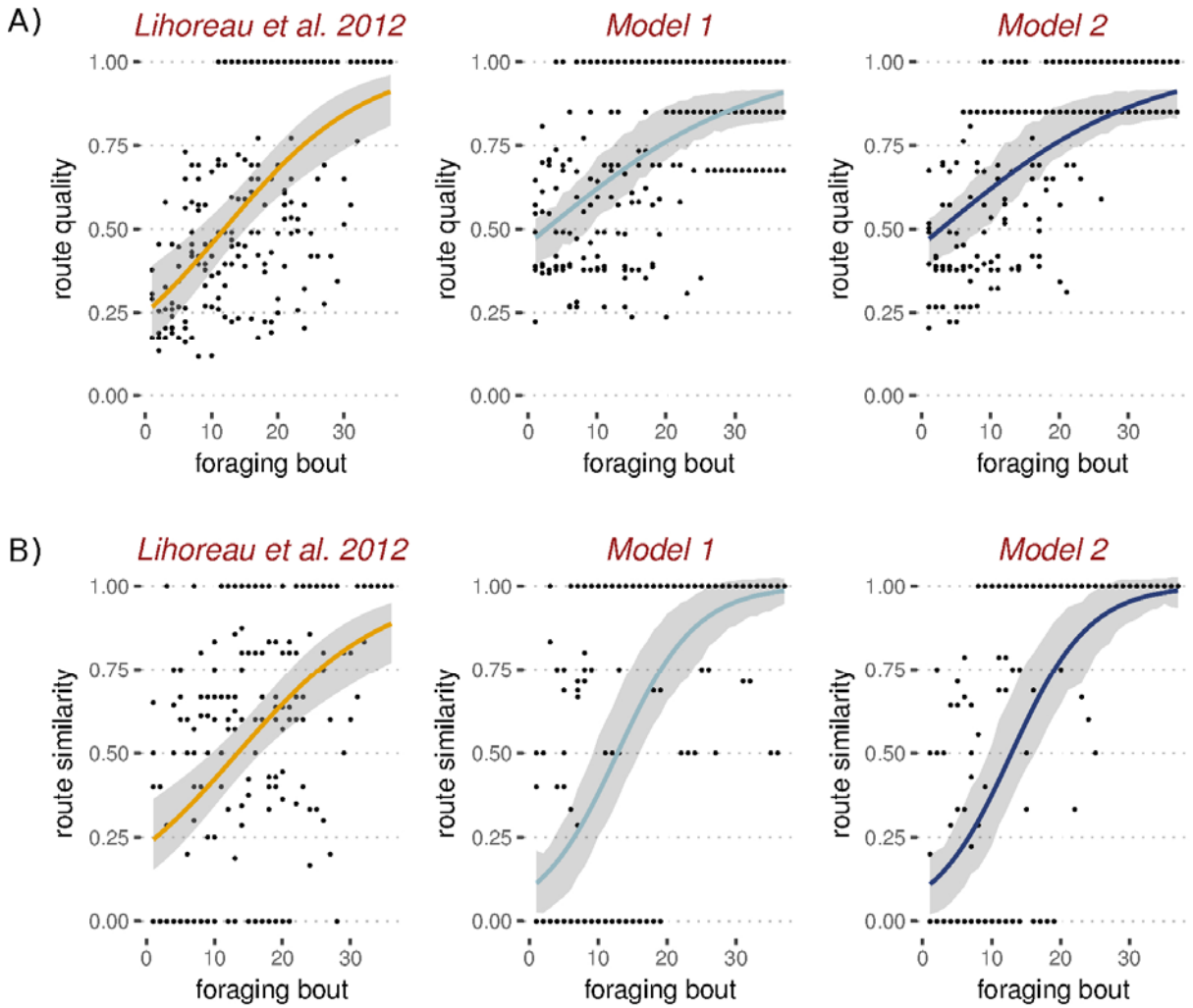

A)
Lihoreau et al. 2012
Model 1
Model 2
route quality
1.00
0.75
0.50
0.25
0.00
0
10
20
30
foraging bout
B)
Lihoreau et al. 2012
Model 1
Model 2
route similarity
1.00
0.75
0.50
0.25
0.00
0
10
20
30
foraging bout

**Figure 3**

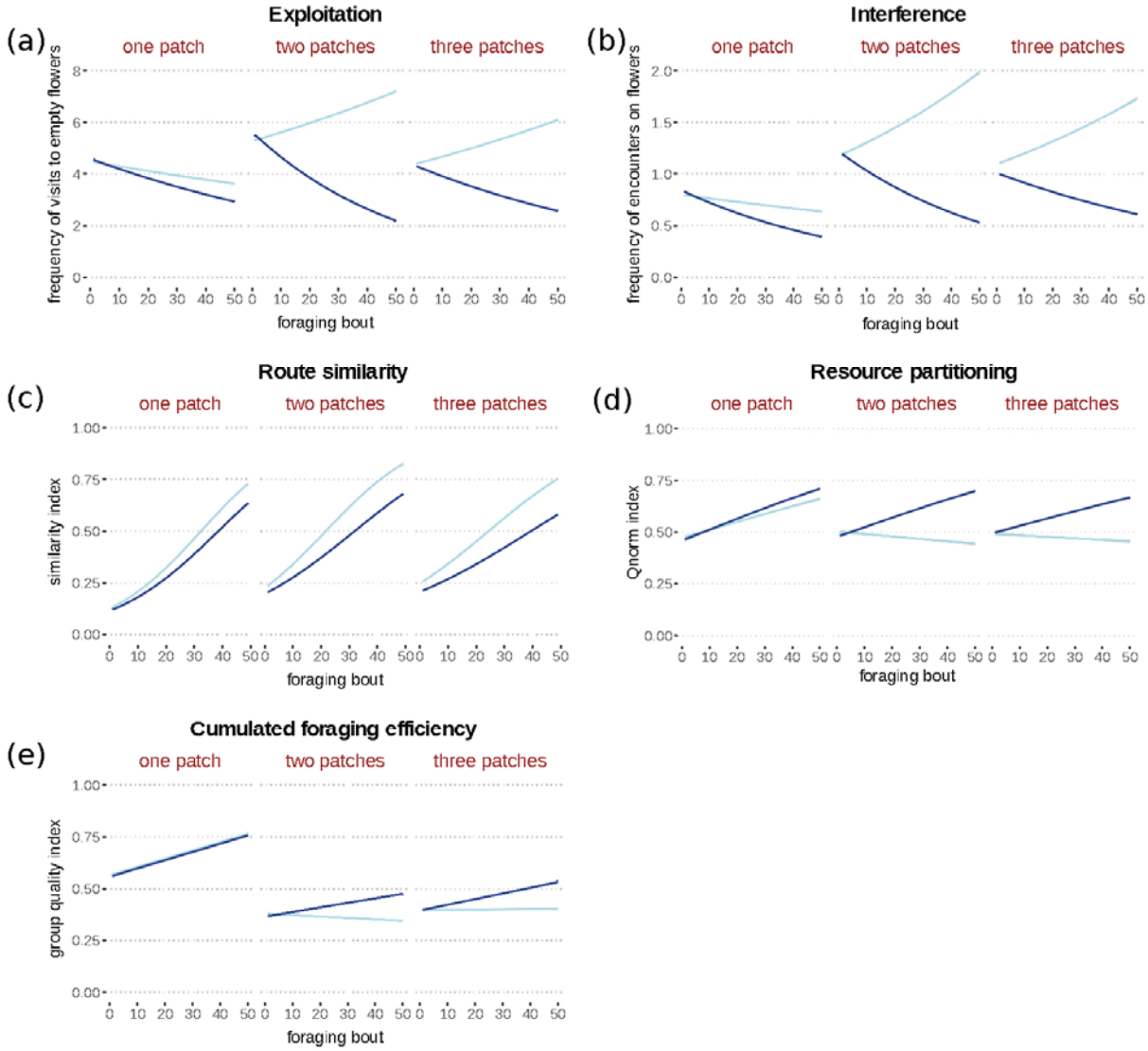
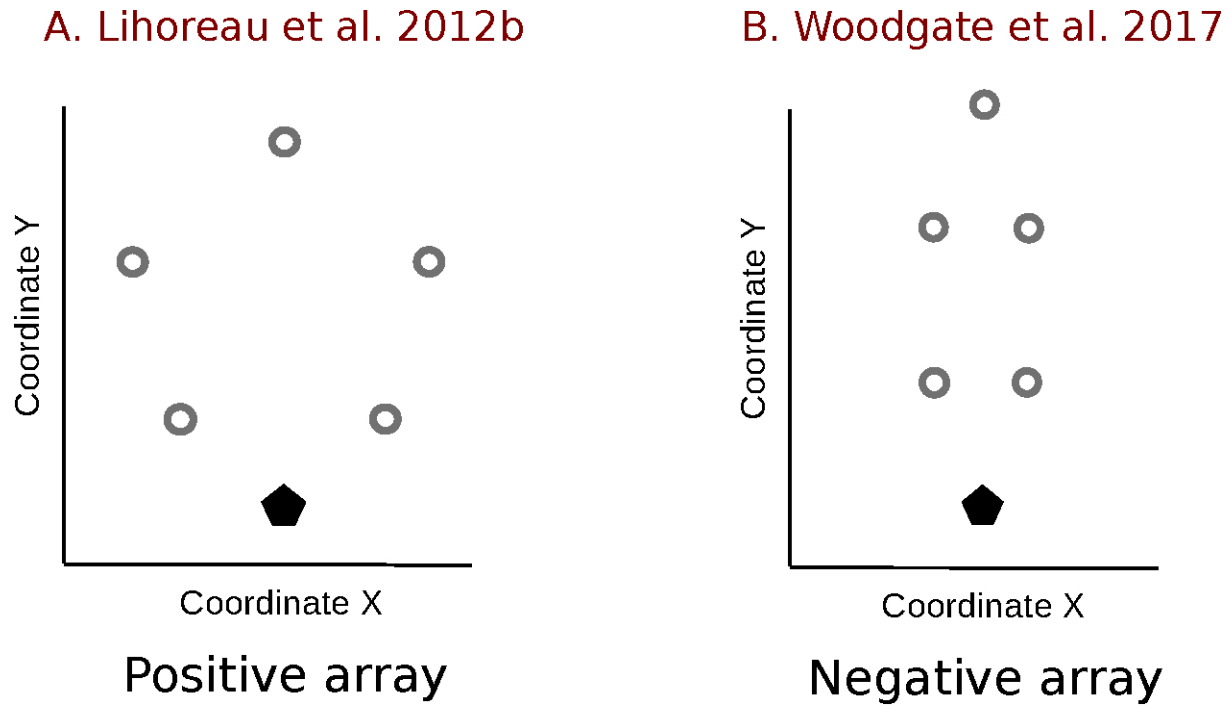

(a)
Exploitation
one patch
two patches
three patches
frequency of visits to empty flowers
foraging bout
(b)
Interference
one patch
two patches
three patches
frequency of encounters on flowers
foraging bout
(c)
Route similarity
one patch
two patches
three patches
similarity index
foraging bout
(d)
Resource partitioning
one patch
two patches
three patches
Qnorm index
foraging bout
(e)
Cumulated foraging efficiency
one patch
two patches
three patches
group quality index
foraging bout

**Figure S1**


A. Lihoreau et al. 2012b
Coordinate Y
Coordinate X
Positive array
B. Woodgate et al. 2017
Coordinate Y
Coordinate X
Negative array

*

**Figure S2**

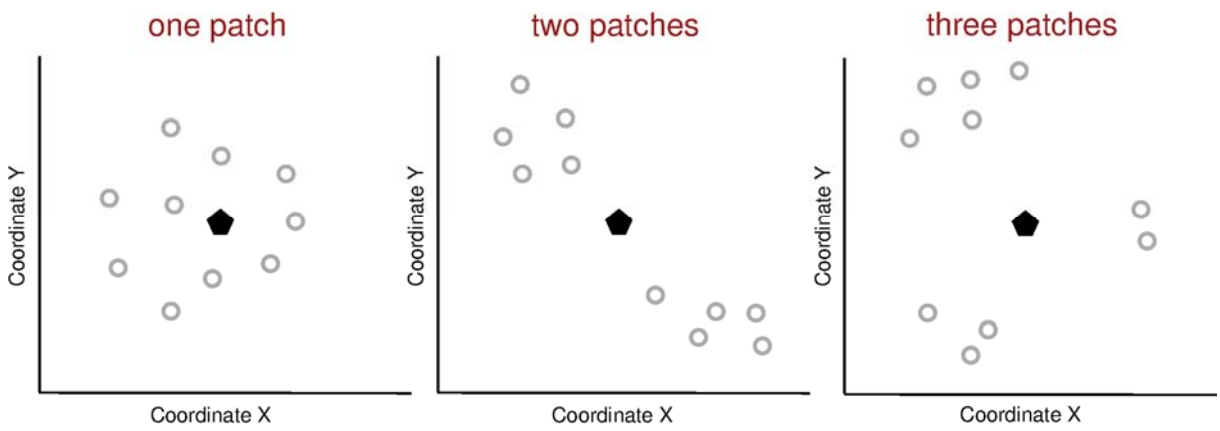



**Figure S3**

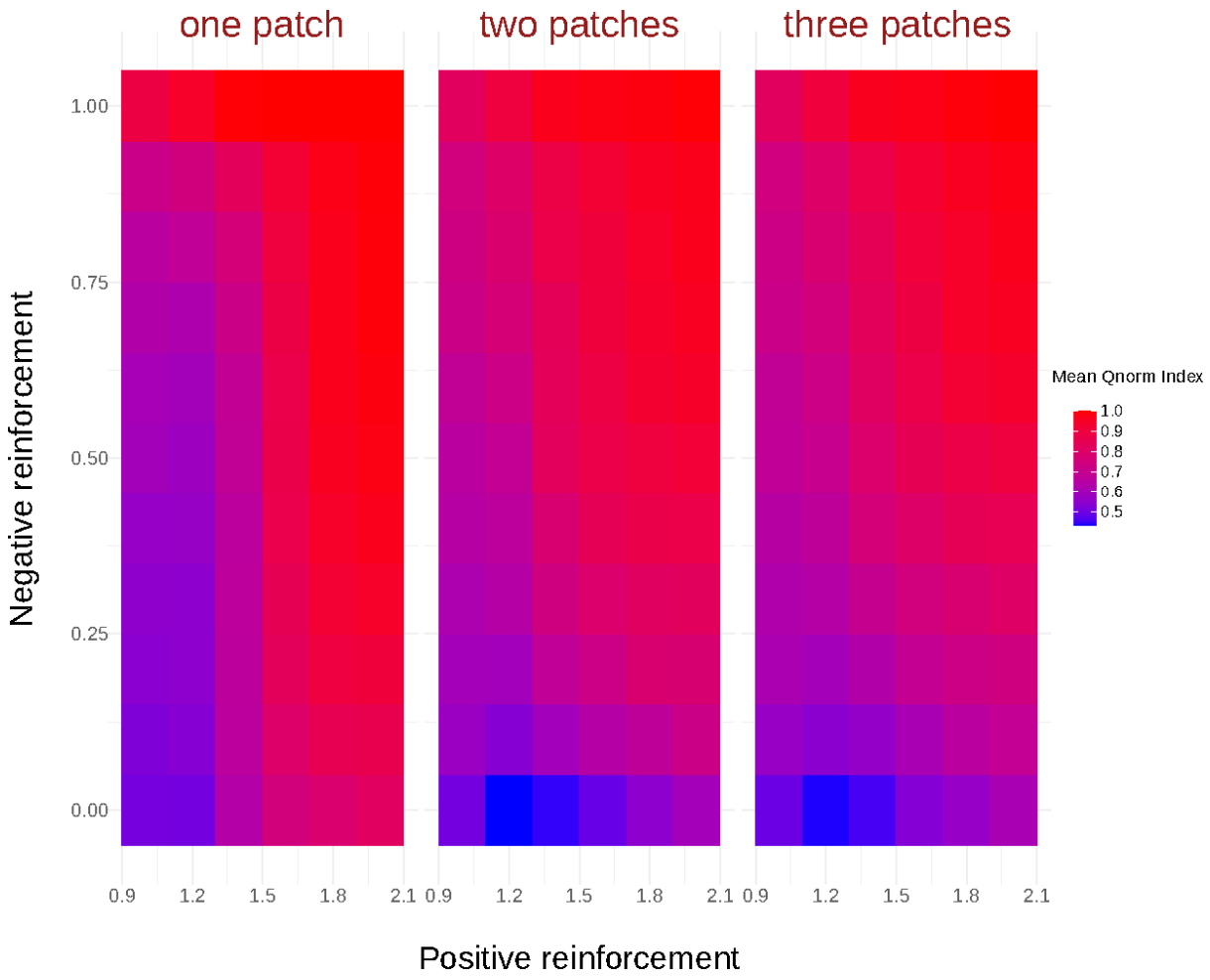



**Figure S4**

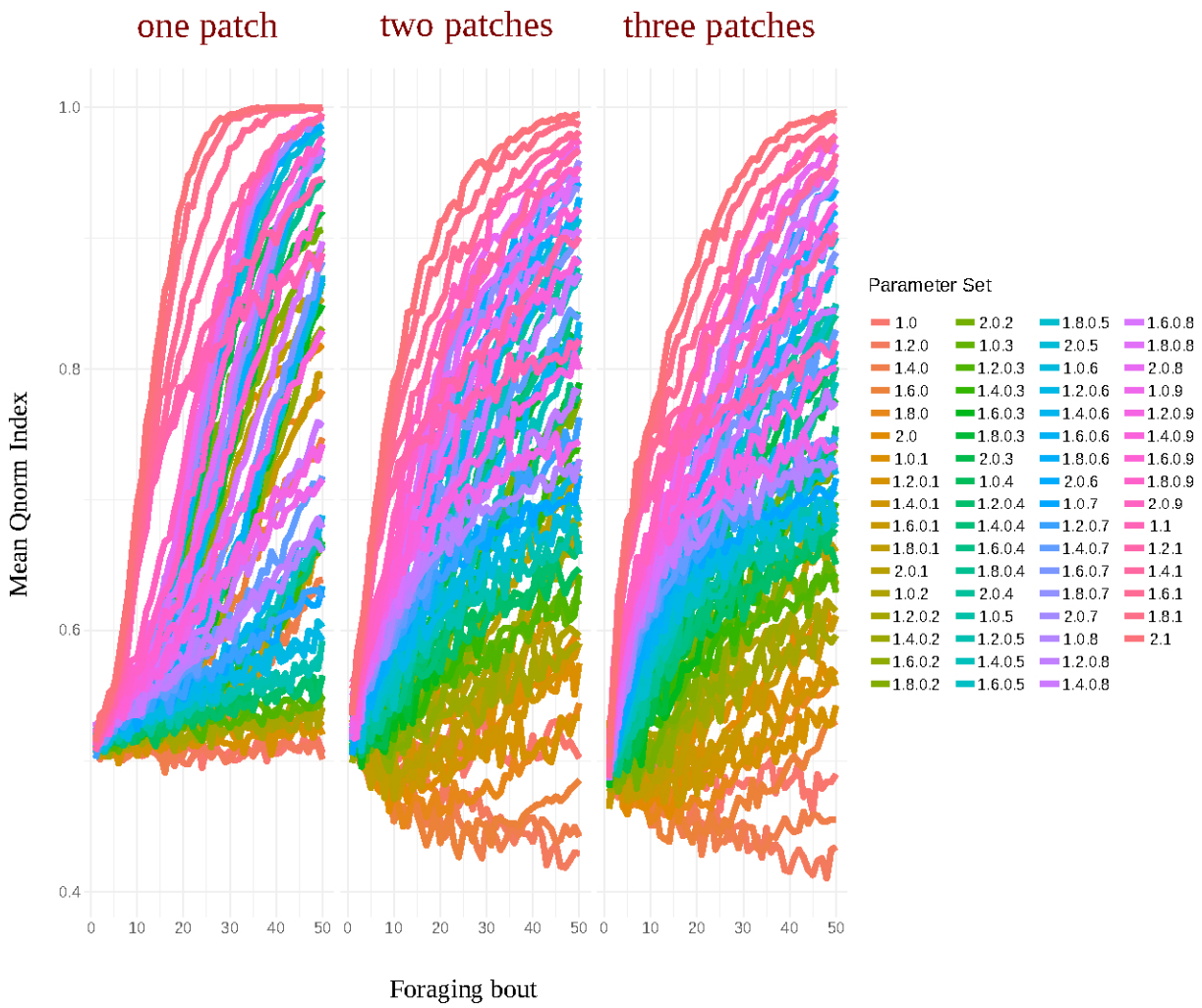

one patch
two patches
three patches
Mean Qnorm Index
1.0
0.8
0.6
0.4
0
10
20
30
40
50
Foraging bout
Parameter Set
1.0
1.2.0
1.4.0
1.6.0
1.8.0
2.0
1.0.1
1.2.0.1
1.4.0.1
1.6.0.1
1.8.0.1
2.0.1
1.0.2
1.2.0.2
1.4.0.2
1.6.0.2
1.8.0.2
2.0.2
1.0.3
1.2.0.3
1.4.0.3
1.6.0.3
1.8.0.3
2.0.3
1.0.4
1.2.0.4
1.4.0.4
1.6.0.4
1.8.0.4
2.0.4
1.0.5
1.2.0.5
1.4.0.5
1.6.0.5
1.8.0.5
2.0.5
1.0.6
1.2.0.6
1.4.0.6
1.6.0.6
1.8.0.6
2.0.6
1.0.7
1.2.0.7
1.4.0.7
1.6.0.7
1.8.0.7
2.0.7
1.0.8
1.2.0.8
1.4.0.8
1.6.0.8
1.8.0.8
2.0.8
1.0.9
1.2.0.9
1.4.0.9
1.6.0.9
1.8.0.9
2.0.9
1.1
1.2.1
1.4.1
1.6.1
1.8.1
2.1

**Figure S5**

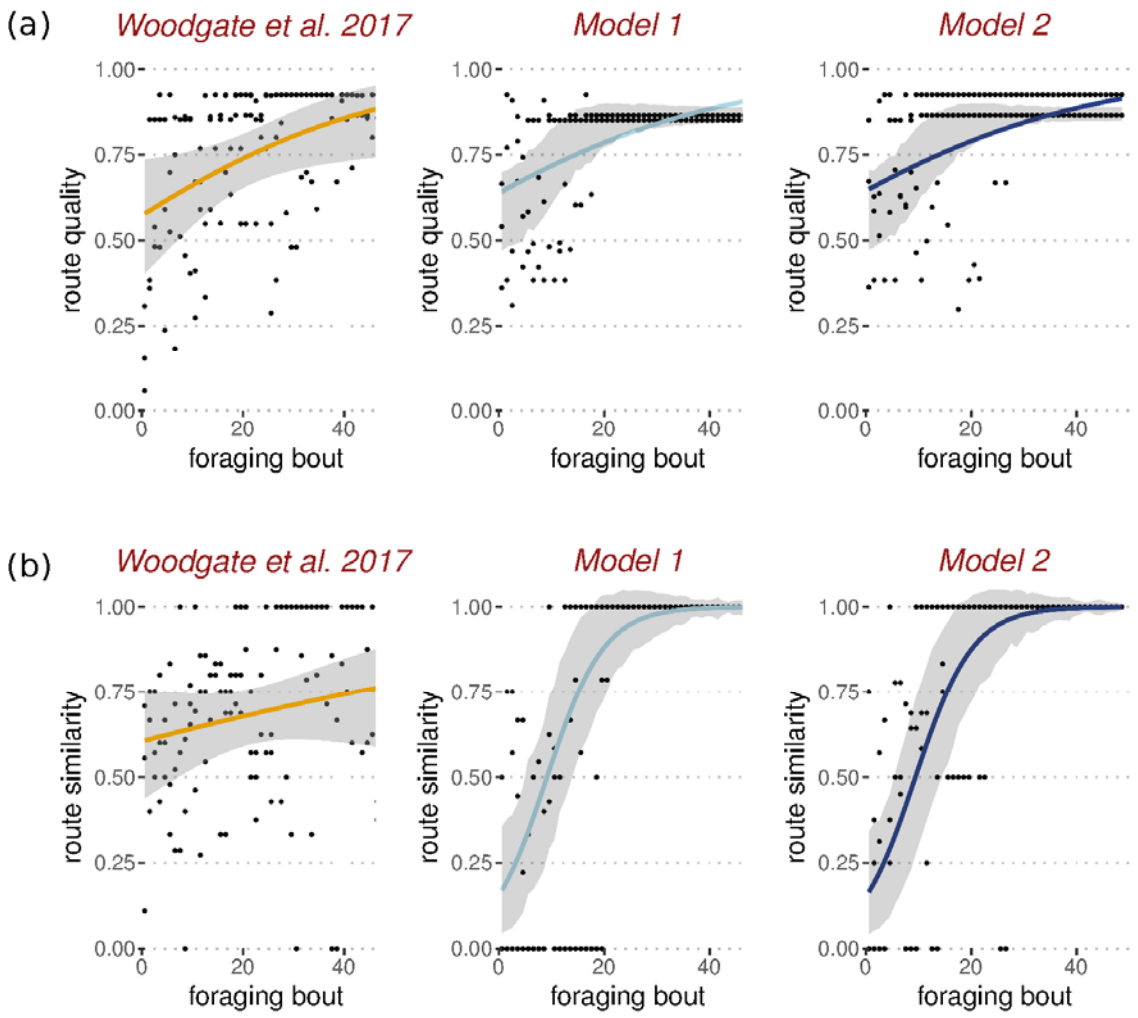

(a)
Woodgate et al. 2017
Model 1
Model 2
route quality
1.00
0.75
0.50
0.25
0.00
0
20
40
foraging bout
(b)
Woodgate et al. 2017
Model 1
Model 2
route similarity
1.00
0.75
0.50
0.25
0.00
0
20
40
foraging bout

**Figure S6**

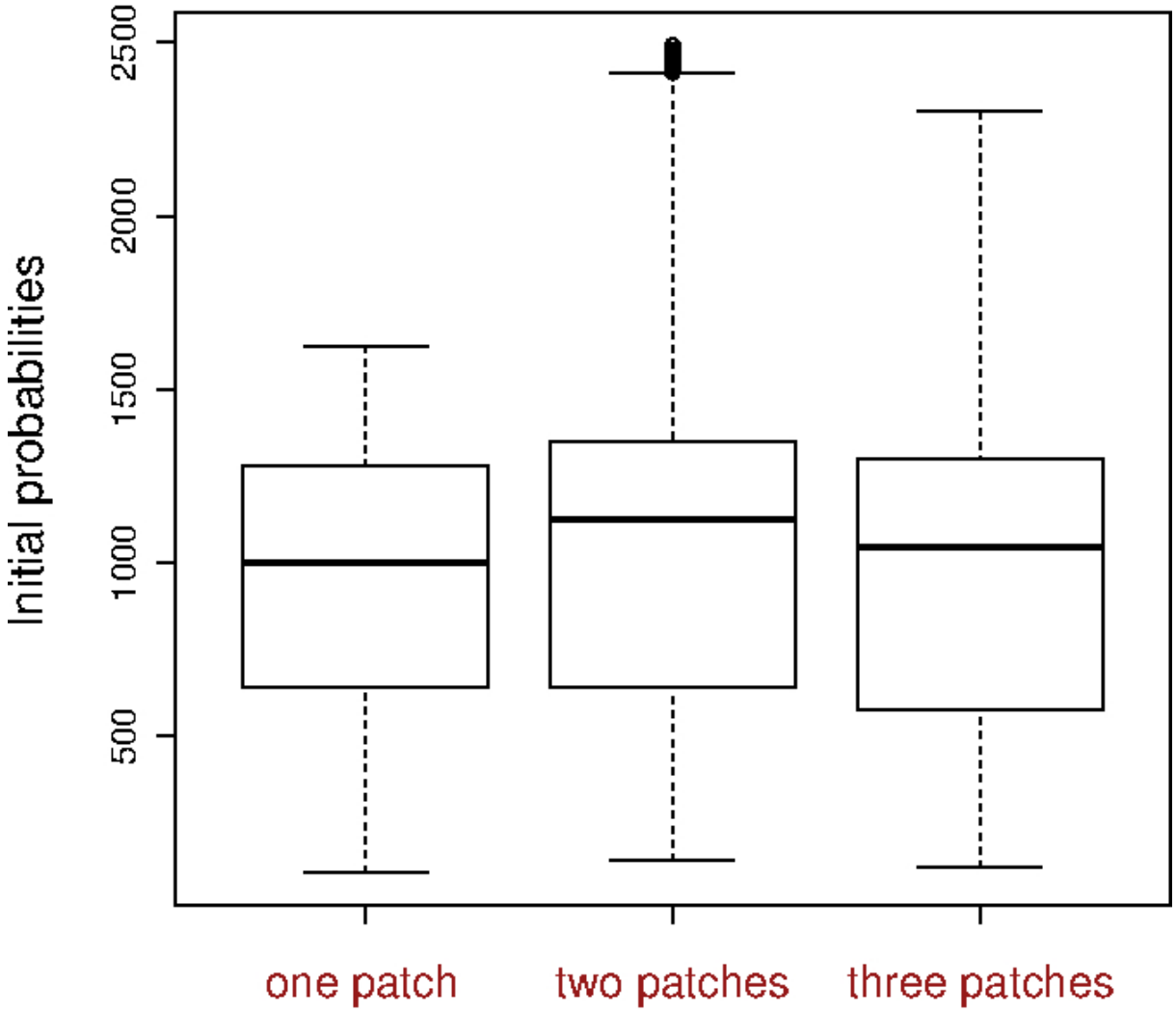
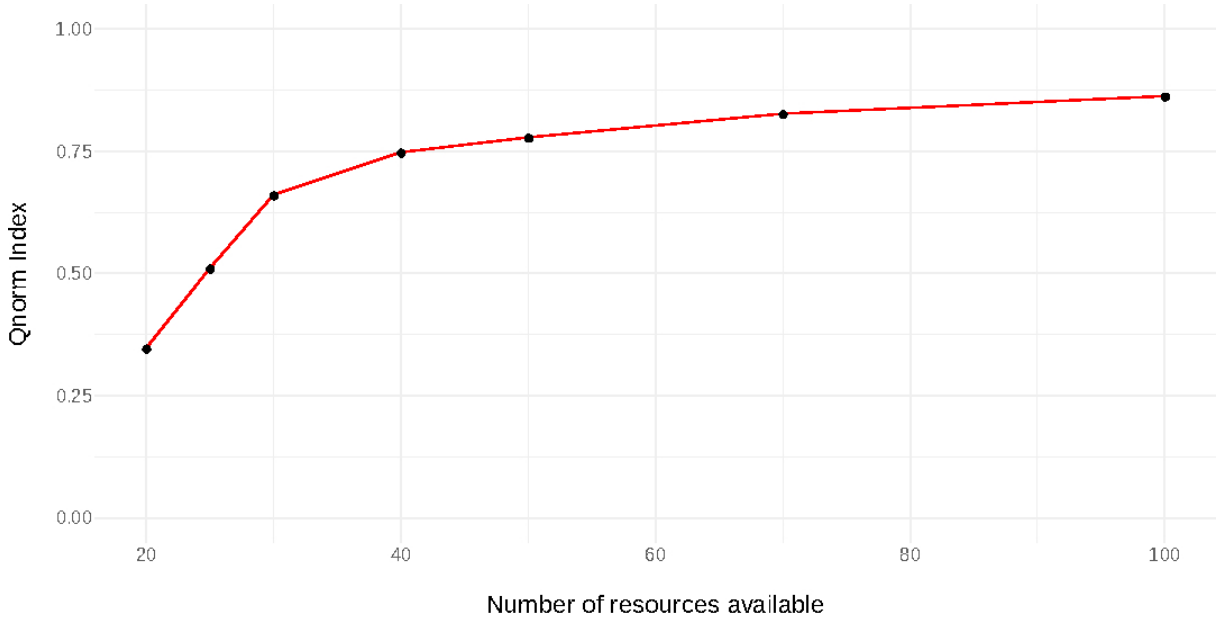

Initial probabilities
500
1000
1500
2000
2500
one patch
two patches
three patches

**Figure S7**


1.00
0.75
0.50
0.25
0.00
Qnorm Index
20
40
60
80
100
Number of resources available